RESEARCH ARTICLE

Bumblebee flight performance in cluttered environments: effects of obstacle orientation, body size and acceleration

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ABSTRACT

Locomotion through structurally complex environments is fundamental to the life history of most flying animals, and the costs associated with movement through clutter have important consequences for the ecology and evolution of volant taxa. However, few studies have directly investigated how flying animals navigate through cluttered environments, or examined which aspects of flight performance are most critical for this challenging task. Here, we examined how body size, acceleration and obstacle orientation affect the flight of bumblebees in an artificial, cluttered environment. Non-steady flight performance is often predicted to decrease with body size, as a result of a presumed reduction in acceleration capacity, but few empirical tests of this hypothesis have been performed in flying animals. We found that increased body size is associated with impaired flight performance (specifically transit time) in cluttered environments, but not with decreased peak accelerations. In addition, previous studies have shown that flying insects can produce higher accelerations along the lateral body axis, suggesting that if maneuvering is constrained by acceleration capacity, insects should perform better when maneuvering around objects laterally rather than vertically. Our data show that bumblebees do generate higher accelerations in the lateral direction, but we found no difference in their ability to pass through obstacle courses requiring lateral versus vertical maneuvering. In sum, our results suggest that acceleration capacity is not a primary determinant of flight performance in clutter, as is often assumed. Rather than being driven by the scaling of acceleration, we show that the reduced flight performance of larger bees in cluttered environments is driven by the allometry of both path sinuosity and mean flight speed. Specifically, differences in collision-avoidance behavior underlie much of the variation in flight performance across body size, with larger bees negotiating obstacles more cautiously. Thus, our results show that cluttered environments challenge the flight capacity of insects, but in surprising ways that emphasize the importance of behavioral and ecological context for understanding flight performance in complex environments.

KEY WORDS: Insect flight, Collision avoidance, *Bombus impatiens*, Clutter, Environmental complexity, Locomotion

INTRODUCTION

Natural environments are highly variable over space and time, and this complexity has important consequences for animal locomotion (Combes and Dudley, 2009; Dickinson et al., 2000). The variable costs and constraints associated with locomotion in complex habitats affect broad ecological patterns of animal movement and habitat use (Combes and Dudley, 2009; Dickinson et al., 2000; Hadley and Betts, 2009; Shepard et al., 2013), as well as biotic interactions (Morice et al., 2013). Determining how environmental complexity affects and limits locomotion is thus key to understanding the ecology and evolution of animals whose fitness is tied to movement through natural environments.

Flying insects must negotiate three-dimensional clutter consisting of biological features such as grass, shrubs and trees, as well as man-made structures such as buildings and cars. Successful navigation through cluttered environments results from a remarkable integration of sensory perception, control strategies, and physiological and morphological adaptations for producing aerodynamic forces and torques (Dudley, 2002b; Lin et al., 2014). The costs associated with moving through structurally complex environments may be particularly acute for flying animals, given the high metabolic costs of flight, particularly at low speeds (Dudley, 2002b).

Historically, the ability to navigate through cluttered environments has been attributed to 'maneuverability', but the definition of this term is problematic. Interpretations can generally be divided into two broad categories: (1) narrower, physiological or mechanical definitions [e.g. minimum radius of curvature (Norberg and Rayner, 1987) or acceleration capacity (i.e. axial agility) (Buchwald and Dudley, 2010; Dillon and Dudley, 2004; Dudley, 2002a)] and (2) broader, integrative definitions [e.g. the ability to avoid collisions in cluttered environments (Stockwell, 2001; Swaddle and Witter, 1998) or the ability to evade a predator (Combes et al., 2012; Domenici, 2001)] that focus on successful performance of a complex task requiring turns and accelerations.

Much of the previous quantitative work on maneuverability has focused on the narrower, physiological and mechanical concepts because these are easier to measure in the laboratory, and because integrative definitions of maneuverability are likely to be context specific (Dudley, 2002a); however, the connections between isolated maneuvers performed in the lab and complex tasks performed in natural environments are not always clear. For example, while both higher acceleration capacity and the ability to fly through cluttered environments are intuitively associated with maneuverability, it is not clear whether the former directly determines the latter.

Despite a wealth of biomechanical and ecomorphological hypotheses, few studies exist that directly link biomechanical flight performance to navigation through clutter. For example, one common prediction is that higher maximum acceleration capacity (including both changes in velocity along a linear path and turning or radial accelerations) should allow for sharper turns and a lower minimum turning radius (Aldridge and Brigham, 1988; Andersson and Norberg, 1981; Thomas, 1996), thus improving biomechanical flight performance in cluttered environments (Norberg and Rayner,

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1987; Thomas and Balmford, 1995). This simple prediction assumes that animals flying through clutter regularly operate near the limits of their acceleration capacity, an assumption that remains almost entirely untested for most taxa. One goal of the current study was therefore to provide direct, empirical data on flying bumblebees that reveal which aspects of biomechanical flight performance are most relevant to the task of successfully navigating through complex environments. We used the length of time required to traverse a cluttered environment (i.e. transit time) as our metric of flight performance. Because energy consumption is largely independent of flight speed in bumblebees (Dudley and Ellington, 1990; Ellington et al., 1990), time spent in flight is closely correlated with total energy consumption, which is at the heart of nearly all foraging decisions in bumblebees (Heinrich, 2004); thus, transit time is likely to be an ecologically relevant feature of flight performance in natural environments.

One salient component of environmental clutter is obstacle orientation. Whereas obstacles in the natural world can occur in any orientation, flying insects are unlikely to have equivalent capacities for maneuvering in all directions. Rotational moments of inertia differ among the three body axes, and flapping wings play a larger role in resisting rotations around some axes (e.g. flapping counter-torque; Hedrick et al., 2009). These differences are likely to affect an insect's ability to generate changes in body position or orientation along various axes, as well as to resist changes imposed by external perturbations. Recent work has shown that bumblebees flying in unsteady flow experience the greatest rotational instabilities around the roll axis and the greatest translational instabilities in the lateral direction, regardless of whether the oncoming flow disturbances are oriented vertically or horizontally (Ravi et al., 2013). This directional instability may arise from the body having a lower rotational moment of inertia around the roll axis than around the pitch or yaw axes. At the same time, decreased inertia around the roll axis could make it easier for bees to initiate voluntary rotations around the roll axis and to move laterally, suggesting that vertically oriented obstacles (which require lateral maneuvers in order to avoid them) may be easier for bees to negotiate than horizontal ones. Despite this potential anisotropy in maneuvering performance, previous studies have focused almost exclusively on lateral maneuvering, in the context of both flight performance (Stockwell, 2001; Swaddle and Witter, 1998) and visual responses to obstacles (Kern et al., 2012).

Body size is also hypothesized to affect flight performance in clutter, and this assertion is supported by at least one previous study, which showed that larger bats experience more collisions when flying through an obstacle course (Stockwell, 2001). Mechanistic explanations for the hypothesis that larger animals perform more poorly in cluttered environments often invoke the predicted decrease in mass-specific force production (and thus acceleration) with increased body size (Vogel, 1994). Maximum mass-specific force production does decrease with body size in bees (Buchwald and Dudley, 2010; Dillon and Dudley, 2004) (although perhaps not across insects more broadly; see Marden, 1987), and there is some evidence that accelerations during free flight decrease with body size in midges (Crompton et al., 2003). Limits to acceleration capacity may reduce an animal's ability to rapidly change its speed and/or direction to avoid collisions, and may also impose limits on flight speed through cluttered environments, as increased speed along a curved path requires higher radial acceleration. Therefore, if bees do rely on maximum acceleration to maneuver through cluttered environments, the predicted negative allometry of acceleration capacity should restrict larger bees to moving more slowly through these environments.

To examine the influence of body size and obstacle orientation on flight performance in cluttered environments, and to determine which aspects of performance are most critical for traversing these environments, we filmed bumblebees (*Bombus impatiens* Cresson 1863) flying through obstacle courses requiring either lateral or vertical maneuvers and reconstructed their three-dimensional flight paths. We analyzed these flight paths to investigate (a) whether flight performance through clutter is impaired in larger bees, (b) whether this effect is due to limitations on maximum acceleration, and (c) whether obstacle orientation affects flight performance in complex environments.

RESULTS
Maximum flight speed in a wind tunnel
To investigate the relationship between body size and maximum flight speed in the absence of obstacles, we tested the maximum flight speed of 19 bumblebee (*B. impatiens*) foragers (ranging from 72 to 260 mg in mass) from a single hive in a wind tunnel. Top flight speed increased significantly with body mass [maximum velocity (m s^{-1}) versus body mass (g), $y=10.48+5.59\times\log_{10}(x)$, $P=0.0007$, $R^2=0.468$; supplementary material Fig. S1].
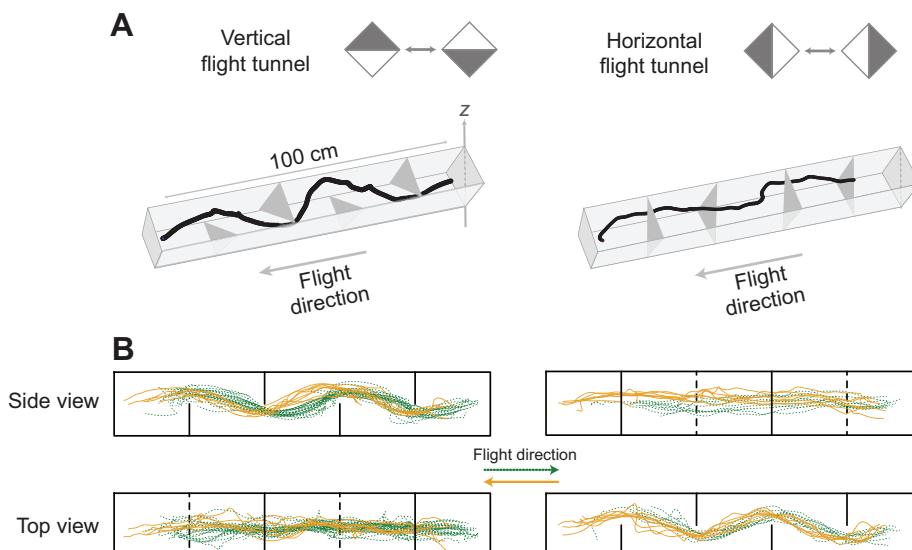

Fig. 1. Flight tunnels with obstacles for testing flight performance in cluttered environments. (A) Schematic diagram of vertical and horizontal flight tunnels. Tunnels had a diamond-shaped cross-section with obstacles alternately occluding either the top and bottom halves of the tunnel to induce vertical maneuvering (vertical flight tunnel, left) or the left and right halves to induce lateral maneuvering (horizontal flight tunnel, right). Sample three-dimensional flight paths through each tunnel are shown below. (B) Flight paths of all bees flying to the right (green dashed line, entering the hive) or to the left (solid yellow line, exiting the hive), through the vertical and horizontal flight tunnels.
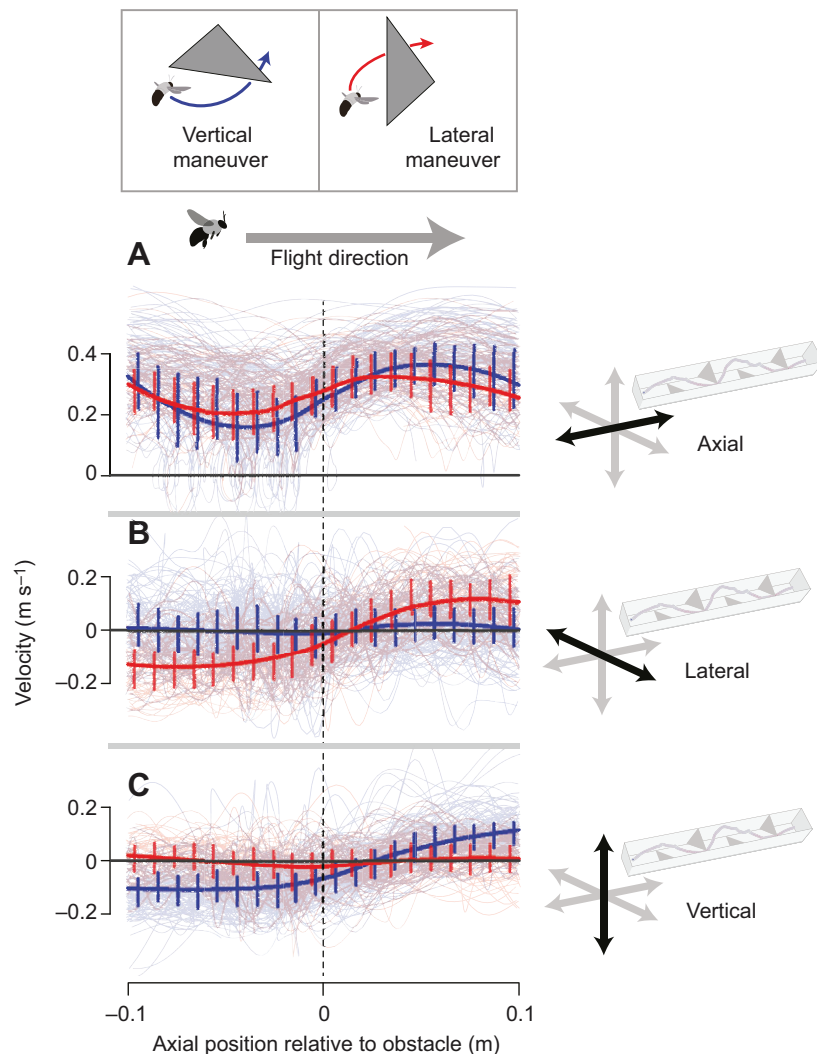
Fig. 2. Flight velocity versus position relative to the obstacle for vertical and lateral maneuvers. (A) Axial, (B) lateral and (C) vertical flight velocity. Thin, transparent traces show raw data for all maneuvers (blue, vertical; red, lateral) in all bees. Solid lines show local regression-smoothed average traces for each type of maneuver, and vertical bars represent interquartile range for spatially binned data at 1 cm intervals.
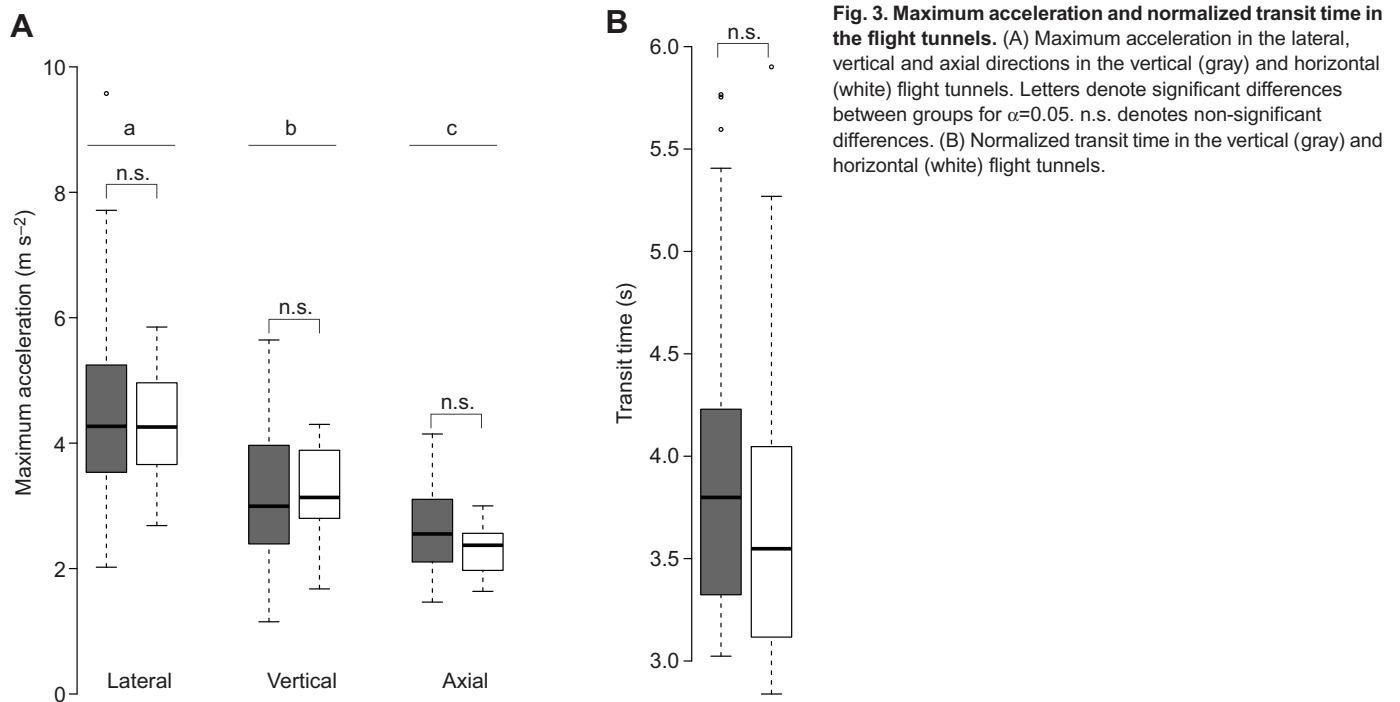
Flight performance in clutter

To investigate flight performance of bumblebees in cluttered environments, we recorded voluntary flight trajectories (N=56) of individual bumblebees either leaving or returning to the hive through one of two flight tunnels. One flight tunnel required the bees to maneuver vertically to avoid obstacles (referred to as the 'vertical' flight tunnel, N=37), while the other required the bees to maneuver laterally (the 'horizontal' flight tunnel, N=19; Fig. 1A). Bees followed a roughly sinusoidal path in the direction of obstacle avoidance (i.e. maneuvering up/down in the vertical flight tunnel and left/right in the horizontal flight tunnel) while maintaining a relatively straight flight path along the other axis (Fig. 1B). Flight paths for bees entering and exiting the hive were qualitatively similar. Median axial velocity (i.e. flight speed along the major axis of the flight tunnel) across trials was 0.28± 0.06 m s^{-1}, in close agreement with (and not significantly different from, t=−1.75, d.f.= 55, P=0.09) previously reported bumblebee flight speeds of 0.29±0.05 m s^{-1} in an obstacle-free flight tunnel with similar dimensions and strong optic flow (Baird et al., 2010).

In both obstacle courses, bees reduced axial velocity before passing obstacles and increased velocity afterwards (Fig. 2A). Lateral and vertical velocity profiles of flights in the two obstacle courses closely mirrored each other. Bees executing vertical maneuvers showed a distinct sign change in vertical velocity before and after passing obstacles (i.e. flying up/down to avoid obstacles and then in the opposite direction to return to their original height), while showing no clear changes in lateral velocity as they passed obstacles; bees executing lateral maneuvers showed the opposite trend, with distinct sign changes in lateral velocity as they maneuvered left/right before and after passing obstacles, with no change in vertical velocity (Fig. 2B,C).

Maximum acceleration differed significantly with direction (i.e. between the axial, vertical and horizontal axes) but not between the two obstacle courses. Overall, maximum lateral acceleration (i.e. acceleration in the horizontal plane, perpendicular to the long axis of the tunnel; Fig. 3A) was higher than maximum vertical acceleration (Fig. 3A; a_{lat}−a_{vert}: t=9.82, d.f.=55, P≪0.01), and both lateral and vertical acceleration were higher than axial acceleration (i.e. acceleration along the long axis of the flight tunnel; Fig. 3A; a_{lat}−a_{ax}: t=10.29, d.f.=55, P≪0.01; a_{vert}−a_{ax}: t=4.08, d.f.=55, P≪0.01). Despite this difference in acceleration across axes, there was no difference in transit time between the vertical and horizontal flight tunnel (Fig. 3B; t=0.94, d.f.=32.5, P=0.35).

Body size had a strong effect on many aspects of flight performance in clutter (Fig. 4). Transit time through the obstacle course increased significantly with body size (Fig. 4A, Table 1). Maximum total acceleration (i.e. three-dimensional acceleration) showed no significant relationship with body size, and had a slightly positive trend towards increasing rather than decreasing with body

Fig. 3. Maximum acceleration and normalized transit time in the flight tunnels. (A) Maximum acceleration in the lateral, vertical and axial directions in the vertical (gray) and horizontal (white) flight tunnels. Letters denote significant differences between groups for $\alpha=0.05$. n.s. denotes non-significant differences. (B) Normalized transit time in the vertical (gray) and horizontal (white) flight tunnels.

size (Fig. 4B, Table 1). Path sinuosity increased significantly with body size (Fig. 4C, Table 1) while median flight speed decreased with body size (Fig. 4D, Table 1).

Maximum acceleration had little direct effect on any aspect of flight performance measured. Acceleration had a significant but weak effect on sinuosity (Fig. 5C, $y=1.106+0.022x$, $t=2.53$, d.f.=54, $P=0.01$, $R^2=0.09$), but no significant effect on either median flight speed (Fig. 5B, $y=0.30+0.0050x$, $t=1.16$, d.f.=54, $P=0.25$) or transit time through the course (Fig. 5A, $y=3.78+0.020x$, $t=0.281$, d.f.=54, $P=0.78$).

Impaired performance at larger body sizes was driven in part by an increase in corrective maneuvering in large bees. The number of corrective maneuvers (quantified as the total number of times bees reversed axial direction to avoid an obstacle) increased significantly with body length (Fig. 6A; $y=e^{-2.19+129.7x}$, $z=3.3$, d.f.=53, $P\ll0.01$), and had a significant, positive relationship with both path sinuosity (Fig. 6B; $y=1.17+0.070x$, $t=7.2$, d.f.=53, $P\ll0.01$, $R^2=0.48$) and flight speed (Fig. 6C; $y=0.346-0.019x$, $t=-3.3$, d.f.=53, $P\ll0.01$, $R^2=0.15$), both of which in turn directly affected transit time through the obstacle course (Fig. 4C,D).

DISCUSSION
The role of acceleration in flight performance through clutter
Our results show that larger bumblebees move more slowly through structural clutter (Fig. 4A), despite being capable of faster top flight speeds in a wind tunnel. While such impaired maneuverability at large body size is often attributed to the scaling of maximum acceleration capacity, we found no evidence to support this hypothesis for bumblebees.

First, we found a statistically insignificant positive trend in the relationship between maximum observed acceleration and body size in bumblebees (Fig. 4B; supplementary material Fig. S2), whereas a negative relationship is expected from both theoretical and empirical results for bees (Buchwald and Dudley, 2010; Dillon and Dudley, 2004). While this could potentially be due to

methodological differences (e.g. measuring accelerations in free-flight versus load-lifting experiments), we believe a more parsimonious explanation is that the behavioral context presented here (voluntarily maneuvering around obstacles) does not elicit or require maximum acceleration from bumblebees. However, data on maximum acceleration in free flight are rare, and further experiments directly comparing maximum free-flight acceleration across behavioral contexts would be valuable for interpreting different assays of maximum flight performance.

A second, more direct line of evidence supporting the conclusion that scaling of maximum acceleration is not responsible for the flight performance trends we observed is that maximum acceleration had no direct effect on median flight speed (Fig. 5B), and only a weak effect on path sinuosity (Fig. 5A). Median flight speed and path sinuosity explain nearly all (~96%) of the variance in transit time (data not shown), and thus our results provide no evidence that maximum acceleration contributes directly to transit time through an obstacle course (Fig. 5C).

Finally, bumblebees in our flight trials exhibited anisotropy in maximum acceleration along different axes, with lateral accelerations being significantly higher than vertical accelerations (Fig. 3A). If maximum acceleration capacity limited transit time through an obstacle course, we would predict that transit time in the vertical obstacle course (which requires vertical movements to traverse) would be longer than in the horizontal obstacle course; however, there was in fact no difference in transit time between the two obstacle courses (Fig. 3C).

Alternative mechanisms for the effects of body size on flight performance
Although we found no evidence that maximum acceleration limits flight performance in cluttered environments, we did find that body size has a significant effect on both sinuosity and flight speed, the two fundamental components of transit time, suggesting that these variables may be more important in understanding limitations to flight in clutter than maximum acceleration capacity.
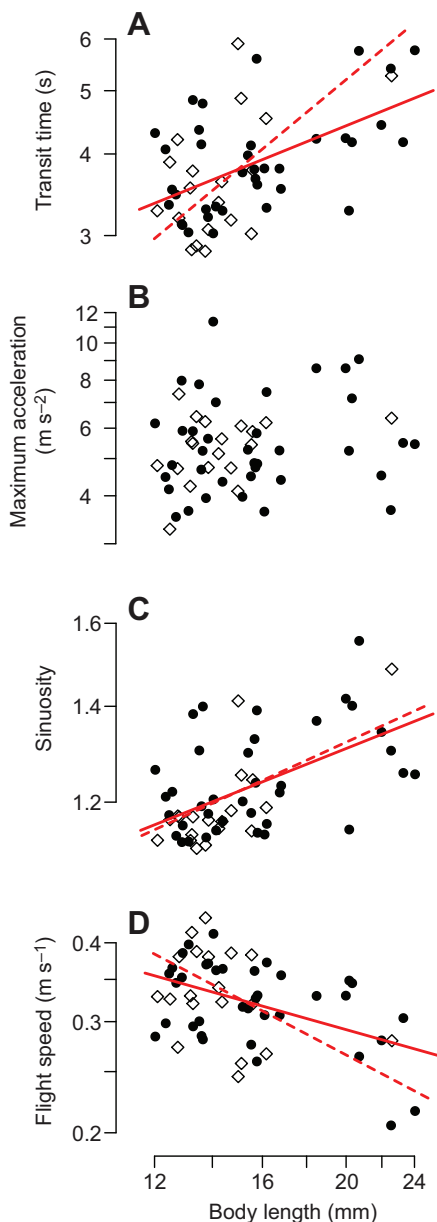
Fig. 4. Effect of body size on flight performance across trials in the flight tunnels. Log-transformed (A) transit time, (B) maximum acceleration, (C) sinuosity and (D) flight speed data versus body length for the vertical flight tunnel (filled circles) and horizontal flight tunnel (open diamonds). Red lines show results of ordinary least squares (solid) and major axis (dashed) regression for variables where body length has a significant effect at the $\alpha=0.05$ level (Table 1).

Fig. 5. Effect of maximum acceleration on flight performance across trials in the flight tunnels. (A) Transit time, (B) flight speed and (C) sinuosity data are shown versus maximum acceleration for the vertical flight tunnel (filled circles) and horizontal flight tunnel (open diamonds). Red lines show results of ordinary least squares regression for variables where maximum acceleration has a significant effect at the $\alpha=0.05$ level.

Corrective maneuvers and flight performance in clutter

One important proximate factor in determining both path sinuosity and median flight speed was the number of corrective maneuvers performed by bees during flight trials. We found that performing more corrective maneuvers significantly increased path sinuosity and decreased median flight speed (Fig. 6B,C), and that the number of corrective maneuvers increased significantly with body size (Fig. 6A). These corrective maneuvers appear to be distinct from saccades or intermittent turns characteristic of flight in flies (Tammero and Dickinson, 2002) and bees (Boeddeker et al., 2010), as they were not distributed continuously throughout flights; corrective maneuvers were instead concentrated at times just before
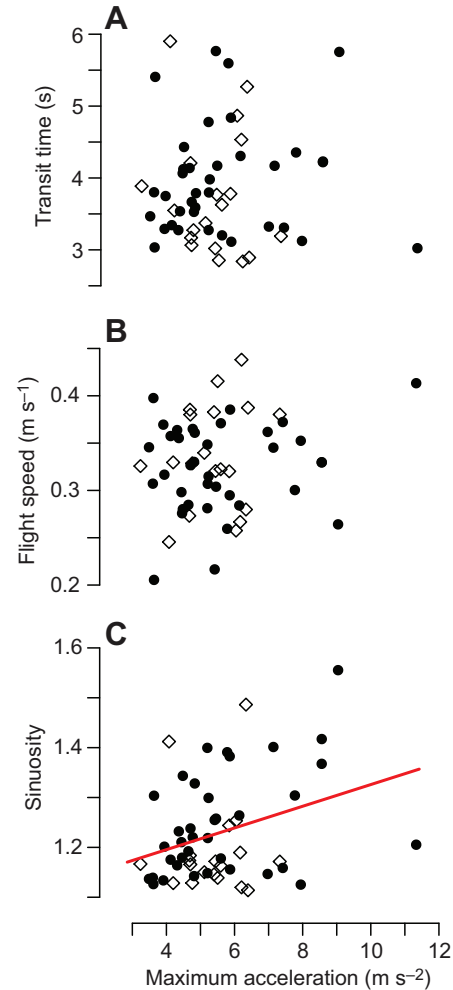
the bees passed obstacles (visible as traces that drop below the x-axis in Fig. 2A), and thus appear to be a form of collision avoidance behavior. The reason that corrective maneuvers affect path sinuosity seems clear, as such maneuvers necessarily increase the path length of flights. The relationship between corrective maneuvers and median speed is somewhat less clear, but is most likely driven by the reduction in velocity associated with the direction reversals that were performed as bees approached obstacles (Fig. 2).

Why do larger bees reverse direction to avoid obstacles more often than smaller bees? Potential explanations include allometric scaling of the visual system among bumblebees (see below), as well as the possibility that the extended body dimensions of larger bees increase the risk of collision. If collisions are more likely to occur in large bees as a result of their body dimensions and bees respond to impending collisions with corrective maneuvers (which appears to be true; Fig. 2A), then this could explain the greater number of corrective maneuvers in larger bees. This hypothesis raises intriguing questions about how individual-level flight characteristics are tuned in bees. For example, do large and small bees have innate differences in collision avoidance behavior, or are these differences learned? Future studies addressing the role of learning and other factors

Table 1. Results from ordinary least squares and major axis regression of four flight metrics against body size

Variable (y)	P	R^2	OLS		MA	
			Slope	Intercept	Slope	Intercept
Transit time (s)	≪0.01	0.26	0.53	1.55	1.10	2.58
Max. acceleration (m s^{-2})	0.10	0.03	0.24	1.17	4.22	8.4
Sinuosity	≪0.01	0.30	0.24	0.52	0.28	0.59
Median flight speed (m s^{-1})	≪0.01	0.20	−0.38	−1.19	−0.72	−1.80

OLS, ordinary least squares; MA, major axis.
All equations are of the form $\log_{10}(y)=$intercept$+$slope$\times\log_{10}$(body length), where body length is in m.

contributing to the flight path characteristics of individual bees flying through complex environments will be of particular interest in parsing these intriguing hypotheses.

Additional drivers of sinuosity and flight speed
Corrective maneuvers explain some, but not all, of the effect of body size on flight performance; the number of corrective maneuvers can account for approximately 67% of the variation in sinuosity and 45% of the variation in flight speed (see Materials and methods, 'Are corrective maneuvers sufficient to explain variation in speed

Fig. 6. Body length, sinuosity and flight speed versus number of corrective maneuvers. (A) Number of corrective maneuvers versus body length across all trials for the vertical flight tunnel (filled circles) and horizontal flight tunnel (open diamonds). Solid red line shows the predicted values ±1 s.d. (dashed lines) from a generalized model. (B) Sinuosity and (C) flight speed versus the number of corrective maneuvers across trials. Solid red lines represent the results of ordinary least squares regression for variables where the number of corrective maneuvers has a significant effect at the α=0.05 level.

and sinuosity?'). Some of the additional variation in path sinuosity with body size could result from simple geometry: larger bees have to leave more space between their body centroid and nearby obstacles to avoid collisions, and this necessarily results in longer, more sinuous flight paths. Assuming geometric similarity in flight paths, minimum path length through the obstacle course should be approximately 12% higher in a 24 mm bee versus a 12 mm one (assuming a clearance radius equal to half body length), perhaps helping to explain some of the residual variation in sinuosity.

The variation in flight speed across bees is somewhat less well explained by the number of course corrections, implying that other important factors contribute to the relationship between body size and flight speed. One known driver of free-flight speed in insects is cage size; in hawkmoths (*Manduca sexta*), smaller cages result in lower flight speeds, particularly near walls (Stevenson et al., 1995). If bumblebees react similarly to cages, and if the effects of cage size are relative to body length rather than being a function of absolute distance, then the same obstacle course may induce slower flight in larger bees than in smaller ones.

The mechanism that would drive such a body size-specific response to similar obstacle spacing is not clear, but it could be related to the processing of optic flow (i.e. the pattern of image motion across the eye), which many insects use to regulate flight speed. When enclosure size decreases, the rate of optic flow increases as a result of the increased proximity of enclosure surfaces and edges. Hawkmoths likely decrease flight speed in small enclosures in response to the increased optic flow rate near surfaces. Honeybees (Srinivasan et al., 1996) and bumblebees (Baird et al., 2010) similarly reduce flight speed in narrower tunnels in response to increased optic flow rate. The allometric scaling of the visual system in bumblebees could also contribute to this effect. Visual acuity (measured as the inverse of ommatidial acceptance angle) and the number of ommatidia per eye both increase with body size in bumblebees (Spaethe, 2003), and these factors could potentially affect the sensing of optic flow rate.

Regardless of the mechanisms involved, one of the ultimate reasons for reducing flight speed with body size in cluttered environments could be the scaling of material stresses (and the associated structural damage) during collisions with obstacles. In particular, material stress (τ) is defined as $\tau=\mathbf{F}/A$, where $\mathbf{F}$ is force and A is area. Assuming constant velocity and impact time, the force during a collision with an immovable object will be proportional to mass, and area will be proportional to surface area. As the ratio of volume (i.e. mass) to surface area increases with body size, this implies that material stresses (and thus potential damage) increase with body size. The scaling of material stress plays an important role in the allometry of body design and posture in mammals (Biewener, 1990), and may play an important role in the allometry of collisions during terrestrial locomotion in insects (Jayaram and Full, 2015). Thus, reducing flight velocity could be a strategy for reducing momentum and the potential damage that would result from
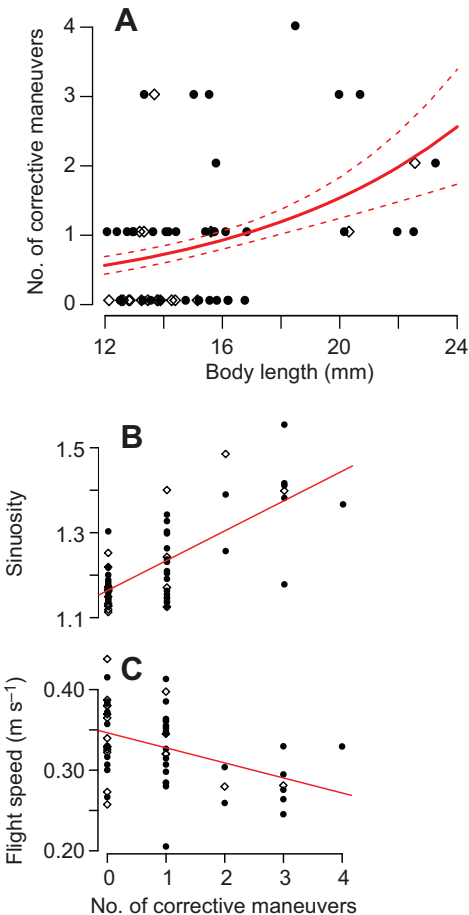
collisions in larger bees. The need to mitigate damage resulting from collisions has clearly played an important role in shaping insect wing morphology (Foster and Cartar, 2011; Mountcastle and Combes, 2014), but few data exist to directly address the hypothesis that collision damage scales allometrically in insects.

Anisotropy of acceleration performance

Our finding that maximum accelerations are larger along the lateral axis is in accordance with previous findings that bumblebees flying through unsteady flow display the greatest accelerations in the lateral direction (Ravi et al., 2013). While in the previous study it was difficult to distinguish the effects of flow perturbations from voluntary flight maneuvers, the accelerations observed in the current study were clearly voluntary. Whether these results reflect a fundamental mechanical limitation on accelerations produced along the vertical and longitudinal axes, or whether there is an alternative explanation (such as behavioral disposition to lateral movements) remains unclear. Roll-based, lateral maneuvers are also dominant in honeybee flight (Boeddeker et al., 2010), so this may be a general feature of hymenopteran flight, or of insect flight more broadly; however, comparative data on movement along various axes during free flight in a wide range of insects is necessary to determine the generality of these results.

Conclusions

Our results show that maximum acceleration capacity is not the most important driver of flight performance in cluttered environments. Rather, flight speed and path length seem to be more critical in determining how quickly bees can negotiate complex environments. Both of these components may be strongly affected by learning, and one important limitation to the current study is that individual experience was not controlled, nor were individuals tracked over repeated trials to determine whether their performance changed with experience. While we do not believe that experience is likely to confound our results concerning body size, as the average size of bumblebee workers typically does not change over time (Couvillon et al., 2010) (so bees of different sizes should not differ systematically in age and experience level), this study cannot directly address the importance of learning for flight performance in cluttered environments. However, previous work clearly shows that on a larger spatial scale, bumblebees optimize flight routes (Lihoreau et al., 2012) and increase flight speed (Ohashi et al., 2008) with experience. Likewise, age may have important effects on flight performance (Vance et al., 2009), either through physiological changes or through the accumulation of morphological damage (Cartar, 1992). Future work addressing the role of behavioral context, learning and path optimization within individuals across time will be particularly important for understanding how flying insects negotiate complex natural environments.

Another limitation of not tracking individual bees is that single bees could be represented multiple times in the dataset, potentially resulting in pseudoreplication of the data. While we do not believe that pseudoreplication plays a significant role in our dataset, because we recorded trials from only a small fraction of the total foraging trips from the hive per day (~20 trials recorded per day out of several hundred foraging trips), our methodology cannot directly address the importance of this effect.

We also performed the current work with a single colony of *B. impatiens*, and social insects can display marked behavioral differences between colonies (LeBoeuf and Grozinger, 2014; Pinter-Wollman, 2012; Maebe et al., 2013). There has been no previous work to our knowledge exploring colony-level variation in

flight performance, and our single-hive experimental design did not allow us to test for colony-level effects. Investigating colony-level differences in flight performance is an important future direction for studies of the biomechanics and behavioral responses of bees flying in complex environments.

Regardless of the mechanisms driving the effect of body size on flight performance, our results support the hypothesis that confined environments reduce flight speed compared with open environments, thereby increasing flight energy cost for bumblebees. This cost appears to be higher for larger bees; our wind tunnel tests demonstrate that larger individuals are capable of faster forward flight (and thus lower cost of transport, or energy required to move a given distance), but they are restricted to operating at flight speeds lower than those of small individuals when flying in clutter (Fig. 4D). This finding suggests an intriguing way in which the relationship between body size and flight speed may be affected by obstacle spacing in natural environments. At high spatial frequency (i.e. with small distances between obstacles), small bees can move through the environment more rapidly than large ones, while at very low spatial frequency (i.e. functionally open environments), large bees likely move faster. This implies that at some intermediate spatial frequency, there should be no effect of body size on flight performance. Future work investigating how the spatial frequency of obstacles affects the relationship between body size and flight performance, and exploring the variation in spatial frequencies found in natural environments would be particularly interesting.

The tradeoff we have demonstrated between flight performance in cluttered versus open environments also has important implications for the evolution of body size in insects, and in bumblebees in particular, as workers from the same hive can vary by up to an order of magnitude in size (Goulson, 2003). Large bumblebee workers outperform small workers in nearly every task measured to date (Cnaani and Hefetz, 1994; Goulson et al., 2002; Kapustjanskij et al., 2007; although see Couvillon and Dornhaus, 2010), but spatially complex environments may provide an important context where small body size is favored (Foster and Cartar, 2011). Future work investigating whether the differences in transit time observed here translate to differential resource acquisition rates in cluttered environments would be of particular interest in understanding the ecological implications of our findings.

MATERIALS AND METHODS
Maximum flight speed in a wind tunnel

A captive, mature colony of *B. impatiens* (BioBest) was given unlimited access to nectar and pollen in a foraging chamber. Individual foragers were removed from the chamber, weighed and introduced into the working section (90×45×45 cm) of a wind tunnel. Wind speed was set at 2 m s^{-1} until bees initiated upwind flight, then raised incrementally after 8 s of sustained flight at each speed until the bee was unable to maintain forward flight. Wind speed was then reduced until bees resumed flight. This procedure was repeated two more times to collect three total estimates of top flight speed, the highest of which was recorded as maximum flight speed.

An important limitation of this wind tunnel assay, which is inherent to most lab-based locomotory studies, is that lab-based assays of flight performance may not always be reflective of performance in natural environments (Combes et al., 2012; Riley et al., 1999). Our wind tunnel differs from natural environments in important ways. First, the arena through which insects fly is greatly reduced. Second, in our arena, bees receive little to no optic flow despite flying at high speeds. While this situation has a potential natural analog (i.e. a bee flying into a strong headwind with a high wind speed but low or zero ground speed; see Riley et al., 1999 for a discussion of bumblebee flight in crosswinds), it is nonetheless important to note that top flight speeds in a wind tunnel may not accurately reflect top

flight speeds in natural environments. While we do not believe this will change the overall direction of the allometry of top flight speed (as larger bees are more likely to be impaired by the size constraints of the tunnel than small bees), laboratory assays of flight performance often underestimate true flight capacity (Combes et al., 2012; Riley et al., 1999); thus, we consider it likely that bumblebees flying in open, natural environments are capable of faster top flight speeds than those reported here.

Flight performance in clutter

Two flight tunnels ($13 \times 13 \times 100$ cm) were connected at one end to a foraging chamber containing a single mature, captive colony of *B. impatiens* and at the other end to openings allowing access to the outdoor environment. The colony was provided with nectar but not pollen in the hive, motivating foragers to exit and enter the hive through the flight tunnels to gather pollen. Each flight tunnel was diamond-shaped in cross-section and contained four triangular obstacles; the obstacles blocked half the cross-sectional area of the tunnel and were evenly spaced 20 cm apart in alternating orientations (Fig. 1), forcing bees to maneuver around the obstacles. In the 'vertical' flight tunnel, alternating triangles blocked the upper and lower halves of the tunnel, forcing bees to maneuver up and down. In the 'horizontal' tunnel, triangles blocked the left and right sides of the tunnel, forcing bees to maneuver side-to-side (Fig. 1).

The bottom two surfaces of the flight tunnels were covered with a black and white textured floral pattern that provided strong optic flow, while the upper two surfaces of the tunnels were left open to allow for filming and digitization. Obstacles were covered in tan paper that allowed them to be distinguished from the background, but did not obstruct visualization and digitization. The hive and flight tunnels were located in a temperature-controlled room maintained at 22°C and were surrounded on three sides by windows that provided natural lighting. The clear tunnel walls allowed bees at least a partial view of objects within the naturalistic arena of the room where experiments were conducted. All trials were collected between 3 and 6 June 2013 between 10:00 h and 18:00 h, a period during which bumblebees typically forage. Any flight sequences where bees did not make clear progress through the flight tunnels or where they collided with the external walls of the tunnel were excluded from the analysis.

Three-dimensional flight paths were recorded at 125 frames s^{-1} using two calibrated and synchronized Photron SA3 video cameras positioned approximately 1.5 m lateral to and 0.5 m above the two tunnels, with an angle of approximately 60 deg between them. Body centroids were digitized using DLTdv5 (Hedrick, 2008) and position traces were filtered (10 Hz low-pass, fifth order Butterworth) in Matlab. Body length was measured from each video sequence by digitizing the position of the head and tip of the abdomen, and measuring the three-dimensional distance between these points. These measurements were performed in three frames from different segments of the same video, to account for any potential effects of posture, and the mean of these three measurements was used as an estimate of body length. Average pair-wise correlations between the three independent measurements of body length for each bee were high (mean $r=0.92$), indicating that this is a reliable estimate of body length. Body length and wet body mass were also found to be highly correlated in a random sample of 20 *B. impatiens* workers from a separate BioBest hive (Pearson correlation coefficient=0.95, supplementary material Fig. S3), as is common in many insects (Rogers et al., 1977).

To investigate characteristic velocity profiles of bees maneuvering around obstacles, we separated each trial into spatially discrete turning maneuvers, each spanning from 10 cm before to 10 cm after one of the four obstacles in the axial direction (Fig. 2). These maneuvers were composed of four different types: two types of lateral maneuvers (maneuvering either to the left or to the right of an obstacle) and two types of vertical maneuvers (maneuvering either over or under an obstacle). Because of qualitative similarity (see supplementary material Fig. S4), maneuvers to the right of an obstacle were reflected across the x–z plane and pooled with maneuvers to the left of an obstacle. Similarly, maneuvers over an obstacle were reflected across the x–y plane and combined with maneuvers under an obstacle. We also pooled maneuvers from different parts of the obstacle courses (i.e. the first versus the last obstacle encountered) because there were no clear qualitative differences between these (see supplementary material Fig. S5).

Through this process, all maneuvers performed by bees traversing the two obstacle courses were condensed down to two basic types: a lateral maneuver or a vertical maneuver. Trends in axial, lateral and vertical velocity during these maneuvers were characterized using local regression smoothing and spatial binning of instantaneous velocity values (Fig. 2).

Transit time was calculated as the total number of digitized frames divided by the frame rate, normalized by the proportion of the obstacle course traversed during the sequence (i.e. linear distance traveled along the long axis of the tunnel divided by total tunnel length). Path sinuosity was calculated as the total path length (i.e. the sum of instantaneous displacements along the entire flight trajectory) divided by linear displacement, or the three-dimensional distance between the start and end points of the flight path. Instantaneous flight speeds were calculated as instantaneous displacement divided by frame length (0.008 s), and median speed along the flight path was determined for each trial.

Instantaneous accelerations were calculated along three axes in a global frame of reference, with the axial axis parallel to the long axis of the flight tunnel, the lateral axis perpendicular to the tunnel axis in the horizontal plane, and the vertical axis oriented in the direction of gravity. Accelerations measured along these global axes are not necessarily correlated with accelerations produced in the bee's frame of reference, as the bee's longitudinal body axis can rotate (e.g. yaw) relative to the longitudinal axis of the flight tunnel. In our experiments, however, bumblebees appeared to maintain a forward-facing body orientation (in line with the longitudinal axis of the tunnel) nearly continuously throughout all flights; this is consistent with the largely roll-based, lateral maneuvering that bumblebees perform when flying towards a target in oncoming flow (Ravi et al., 2013), as well as with landmark-oriented flights in honeybees (Boeddeker and Hemmi, 2010). Under these conditions, global accelerations are highly correlated with accelerations in the bee's frame of reference, and thus we consider global accelerations to be reliable estimates of accelerations produced in the local body frame.

Instantaneous total acceleration was calculated at each time step from acceleration vectors in the three global axes by applying the Pythagorean theorem in three dimensions. The resulting total acceleration encompasses both tangential acceleration (i.e. change in speed along a linear trajectory) and radial acceleration (i.e. acceleration perpendicular to the flight trajectory associated with turning). We estimated maximum acceleration during each trial as the 95th percentile of instantaneous accelerations throughout the sequence. This metric provides a conservative estimate of maximum acceleration, which minimizes the effects of noise introduced by digitizing and differentiation; two less conservative estimates (98th percentile of accelerations and the average of the two highest acceleration peaks) yielded qualitatively similar results (supplementary material Fig. S2).

The number of corrective maneuvers performed was quantified by summing the number of sign changes in axial velocity, then dividing this number by two and rounding up to the nearest integer. If a bee flying forward comes to a stop in front of an obstacle, flies backward briefly, then continues flying forward past the obstacle, this counts as a single corrective maneuver. Sign changes in axial velocity can be caused by either voluntary corrective maneuvers or involuntary collisions with obstacles. In practice, however, apparent collisions were rare (accounting for less than 10% of sign changes in axial velocity), and often occurred as part of a voluntary deceleration (i.e. the bee had begun to decelerate and then lightly clipped the obstacle before completely decelerating). Because of their relative rarity and because video resolution made it nearly impossible to distinguish between near-collisions and maneuvers where the bees made physical contact with the obstacle, all sign changes of axial velocity were included in the count of corrective maneuvers.

Data analysis

All statistical analyses were performed in R (R Development Core Team, 2008) with $\alpha=0.05$. To test for differences in lateral versus vertical acceleration between the two different flight tunnels, we performed a two-way ANOVA with acceleration direction and obstacle course orientation as explanatory factors, and maximum acceleration as a response variable; this was followed by *post hoc* t-tests (paired between acceleration axes, unpaired

between obstacle courses). To test for overall transit time differences between the two flight tunnels, we performed an unpaired *t*-test of normalized transit time versus obstacle orientation.

The relationships between log-transformed body size (preferable for allometric data; Mascaro et al., 2014) and flight metrics were analyzed with linear regression models, including obstacle orientation (vertical versus horizontal) and flight direction (exiting versus entering the hive) as covariates, using the lm( ) function in R. No significant effects of obstacle orientation or flight direction were found for any of the flight metrics, so these variables were removed. Final models (with all trials pooled) analyzed the relationship between flight metrics and body size using major axis regression (generally more appropriate for allometric data than ordinary least squares regression; Warton et al., 2006), using the lmodel2 package in R. Results from both ordinary least squares regression and major axis regression are reported in Table 1 and shown in Fig. 4.

Because accelerations are particularly sensitive to digitizing noise and the effects of filtering frequency, we performed a sensitivity analysis on the linear regression between log-transformed maximum acceleration and body length, comparing the slope and significance of this relationship as filtering frequency changes, and using three different metrics of maximum acceleration (peak acceleration, 98th percentile and 95th percentile). Although acceleration metrics and filter frequency strongly affected both the slope and significance of the relationship, the estimated slope between these variables was always positive (supplementary material Fig. S2).

We used ordinary least squares regression to test the effect of maximum acceleration on path sinuosity, median flight speed and transit time (Fig. 5), and the effect of the number of corrective maneuvers on path sinuosity (Fig. 6B) and median flight velocity (Fig. 6C). To test the effects of body size on the number of corrective maneuvers (Fig. 6A), we created a generalized linear model with a Poisson distribution (more appropriate for count data than simple linear regression) and log link using the glm( ) function in R (R Development Core Team, 2008).

It is important to note that the number of observations differed between the two flight arenas, with the vertical flight tunnel having nearly twice as many (N=37) trials as the horizontal flight tunnel (N=19). The horizontal flight tunnel also had relatively few trials with large bees (i.e. bees over 17 mm in length). To determine whether this affected our findings, we ran the same analyses on data from the vertical and horizontal flight tunnels separately (results not shown). Data from the vertical flight tunnel displayed the same relationships and qualitative patterns of significance as the pooled data in all analyses. Data from the horizontal flight tunnel showed the same relationships as the pooled data in all analyses, and the same levels of significance in most analyses, with two exceptions: the effect of body size on flight speed (Fig. 4D) was only marginally significant for the horizontal tunnel data alone (P=0.06) and the effect of maximum acceleration on path sinuosity (Fig. 5C) was not significant (P=0.42). The lack of statistical significance in these two relationships for the horizontal data alone may be due to the smaller number of data points for large bees in this flight tunnel, which would reduce our power to identify statistical trends.

Are corrective maneuvers sufficient to explain variation in speed and sinuosity?

One way to address this question is to combine the models of (a) effects of body size on the number of corrective maneuvers and (b) effects of corrective maneuvers on sinuosity and flight speed to predict the effect size of observed variation in sinuosity and flight speed. These estimates can then be compared with the observed variation in sinuosity and speed across body size. For example, our model predicts roughly 0.53 corrective maneuvers for a 12 mm bee on average and 2.53 corrective maneuvers for a 24 mm bee (Fig. 6A). In turn, our model of the effect of corrective maneuvers on sinuosity predicts a sinuosity of 1.20 for 0.53 corrective maneuvers and a sinuosity of 1.34 for 2.53 corrective maneuvers (Fig. 6B). In combination, these models thus predict that path sinuosity will change from 1.2 to 1.34, going from a 12 to a 24 mm bee (an effect size of 0.14). Our ordinary least squares model of the effect of body length on sinuosity, however, predicts a shift in path sinuosity from 1.16 to 1.37 over the same size range, with an effect size of 0.21 (Fig. 4C). From this, we conclude that the effect of body length on the number of corrective maneuvers can explain roughly 67% of

the variance in sinuosity across body size. For median flight speed, we predict a shift from 0.336 m s^{-1} to 0.299 m s^{-1} (Fig. 6C) over the same range of body length. The actual shift over this range is from 0.355 m s^{-1} to 0.272 m s^{-1} (Fig. 6C), indicating that the effect of body size on corrective maneuvers can explain around 45% of the observed variation in flight speed across body size. It should also be noted that these estimates are based on ordinary least squares regression, which offers a more conservative prediction of the effect of body size than major axis regression.

Author contributions
J.D.C., S.R., A.M.M. and S.A.C. designed the experiments. J.D.C. and S.R. performed the experimental trials. J.D.C. performed computational and statistical analyses. J.D.C., S.R., A.M.M. and S.A.C. wrote the manuscript.

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