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2 **Main Manuscript for**

3 Bumblebees perceive their environment in relation to their body size 4 and form to minimize inflight collisions

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24 Main Text
25 Figures 1 to 3

Abstract

Animals that move through complex habitats must frequently contend with obstacles in their path. Humans and other highly cognitive vertebrates avoid collisions by perceiving the relationship between the layout of their surroundings and the properties of their own body profile and action capacity (1, 2). It is unknown whether insects, which have much smaller brains, possess such abilities. We used bumblebees, which vary widely in body size and regularly forage in dense vegetation, to investigate whether flying insects consider their own size and form when interacting with their surroundings. Bumblebees trained to fly in a tunnel were sporadically presented with an obstructing wall containing a gap that varied in width. Bees successfully flew through narrow gaps, even those that were much smaller than their wingspans, by first performing lateral scanning (side-to-side flights) to visually assess the aperture. Bees then reoriented their in-flight posture (i.e. yaw, or heading angle) while passing through, minimizing their projected frontal width and mitigating collisions; in extreme cases, bees flew entirely sideways through the gap. Both the time that bees spent scanning during their approach and the extent to which they reoriented themselves to pass through the gap were determined not by the absolute size of the gap, but by the size of the gap relative to each bee's own wingspan. Our findings suggest that, similar to humans and other vertebrates, flying bumblebees perceive the affordance of their surroundings relative their own body size and form to navigate safely through complex environments.

Significance Statement

Like many other animals, including humans, insects frequently move through densely cluttered environments to perform activities critical for their survival, such as foraging. Vertebrates avoid collisions by perceiving their surroundings in relation to their body size and form, but it is unknown whether insects, with much smaller brains, possess such skills. We discovered that flying bumblebees judge the gap between obstacles relative to their wingspan and form and reorient themselves to fly sideways through tight spaces. Our findings suggest that bees too evaluate the affordance of their surroundings and account for their own size and form to safely navigate through complex environments. This novel facet of insect flight poses questions about the neural requisites for perception of self-size in animals.

Main Text

Avoiding collisions with obstacles is a requirement for successful locomotion through most natural habitats, where the physical environment is often cluttered and complex. At the most elemental level, animals moving through their environments need to identify gaps between obstacles and assess their passability. In this context, whether a gap between obstacles "affords" passing is determined by the fit between the spatial layout of the environment and the properties of the organism's form and action system, as described in classical theses on affordances (2–4). In humans and other highly cognitive vertebrates, the perception of affordances for performing visually guided actions such as grasping, passing through apertures, and climbing is actively shaped throughout ontogeny, as body size, configuration, and experience change (1, 2, 5–7). However, the strategies used by animals with much smaller brains, such as insects, to contend with the challenges of navigating environmental clutter and heterogeneity are unclear.

We used bumblebees to investigate whether flying insects take into account their own size during interactions with their surroundings. Bumblebees and other volant insects that travel long distances (8) and frequently encounter regions of dense clutter can be expected to exhibit strategies to avoid collisions, because damage to sensitive structures such as the wings is irreparable and adversely impacts flight performance and lifespan (9, 10). For an animal attempting to navigate through tight spaces, perceiving the relationship between the layout of the environment and its own size can help inform the animal of its potential for collision-free passage. Bumblebee workers naturally

display large variation in body size within a given colony (11, 12), and thus are particularly suitable models for testing the effects of insect body size on aerial navigation, and for determining whether insects perceive the external environment in relation to their own spatial dimensions.

To elicit repeatable flight behavior, we trained foraging bumblebees to fly within a $1.6 \times 0.3 \times 0.3$m ($l \times w \times h$) flight tunnel that separated the hive from a foraging arena (see Materials and Methods, Fig. S1 and SV1). After bees were habituated to the setup and began foraging normally, we placed an unexpected obstacle within the tunnel, consisting of a thin vertical wall (5mm thickness) spanning the tunnel's width and height. The obstructing wall contained a rectangular gap starting midway up and extending to the top of the wall (see Materials and Methods, Fig. S1 and SV1). The width of the gap was varied between 20-60 mm over different trials, with the presenting order of gap sizes chosen randomly. A high-speed camera placed above the tunnel was used to record bees' instantaneous positions, heading/yaw orientations (Fig. 1a) and trajectories as they approached the obstructing wall and passed through the gap. To prevent bees from becoming familiar with the experimental paradigm, the obstructing wall was removed after each flight recording. In total, we recorded and analyzed over 400 flights of bees of varying body sizes flying through seven different gap sizes (Table ST1). For the population of bees recorded, wingspan was the longest dimension of the body and it varied linearly by a factor of 2.1 compared to their longitudinal body length while in-flight (Fig. S2a).

Results and Discussion

Upon entering the tunnel, all bees flew steadily towards the obstructing wall and began performing lateral scanning maneuvers (flying from side to side), while maintaining a steady gaze directed towards the gap (Fig. 1, S3, SV2). Bees scanned the region between the edges of the gap, and mean scanning amplitude was equal to or smaller than gap width in all cases (Fig. 2a). To determine how bee size affected the strategies used by bees to fly through gaps of various sizes, we binned bees into three groups based on their wingspan (see Materials and Methods). Bees of all sizes performed scanning movements of similar amplitude ahead of each gap, and the amplitude of these maneuvers relative to the gap size consistently increased with decreasing gap size (Fig. 2a).

What could the purpose of these scanning maneuvers be? Bees are known to use the signals provided by their compound eyes to extract optic flow information, which is influenced by their aerial trajectory and gaze strategy, for spatial perception and flight-control in their environment (13, 14). The maneuvers performed ahead of the gap (Fig. 1, S3 & SV2-4) were similar to peering flights displayed by wasps, honeybees and bumblebees while memorizing landmarks (15–19), or for depth estimation and spatial localization tasks (20–25). Lateral peering is an active vision strategy in which insects vary the roll angle of their body to redirect a component of the aerodynamic force, creating steady, laterally oscillating flight trajectories (20, 22, 25, 26). Bees scanning in the vicinity of the gap presented all of the characteristics of lateral peering, including maintaining the gap in their frontal visual field (Fig. S4), where visual acuity is highest (27), and maneuvering sideways by modulating their lateral acceleration (Fig. S5). By peering between the edges of the gap, bees could combine the time-course of their body roll angle, a proxy for lateral acceleration (28), and the angular velocity of the edges of the gap on their retina to discern the spatial dimensions of the gap (see SI and Fig. S6 for elaboration). This mechanistic explanation could also account for the body-size insensitivity and consistent magnitude of scanning by bees ahead of each gap (Fig. 2a, ST4-7).

All bees performed more peering passes and engaged in these maneuvers for longer durations when approaching narrower gaps (Fig. 2b, c). In addition, larger bees spent more time in the vicinity of the gap before attempting to pass through. Repeated peering passes may help improve bees' estimation of the gap's spatial properties, by comparing repeated measurements performed during

each pass. This would be particularly important for traversing narrower gaps, where the required maneuver is larger, and the margin of error is lower during gap traversal. Improving confidence through repeated measurements would also be beneficial if bees do indeed derive estimates of gap size via our proposed mechanism of integrating rate-based metrics of optic flow and flight trajectory (body roll-induced lateral accelerations, see SI), which may be noisy and imprecise.

After performing lateral peering maneuvers, all bees were able to successfully fly through the gap, even when traversing the narrowest gap, which was smaller than the wingspan of most of the bees (Fig. 1&3a). To accomplish this, bees tended to reorient themselves (i.e. fly sideways, increasing their yaw/heading angle) as they passed through gaps (Fig. 1, S1&3 & SV2&5). Bees displayed higher yaw angles (more body reorientation) when passing through smaller gaps, and this trend was consistent across all body sizes (Fig. 3a, compare subfigures in S1, S3, SV2-4). By increasing their yaw angle with respect to the flight direction, bees effectively reduced their projected frontal width (i.e., the dimension that they needed to fit between the edges of the gap), because their longitudinal body length was significantly shorter than their wingspan (Fig. S2b). All bees reoriented themselves maximally (flying completely sideways) when passing through the narrowest gaps (<30 mm), whereas only the larger bees tended to reorient when traversing the widest gap (60 mm; Fig. 3a). We found the largest differences in traversal behavior across bees of different sizes for flights through intermediate-sized gaps, where larger bees consistently reoriented more compared to smaller bees (Fig. 3a, compare subfigures in S1, S3). The deliberate modulation of their body orientation while crossing gaps of different sizes provides an indication that bees do indeed factor in their own body size and form in determining how to maneuver through cluttered environments.

When we examined the reorienting response of individual bees with respect to the normalized gap size (gap size divided by each individual's wingspan), we found a sigmoidal relationship that was consistent across the entire body-size range (Fig. 3b). This suggests that bees' reactions to the upcoming flight challenge (i.e., the degree to which they reoriented their bodies) was based not on the absolute size of the gap, but rather on the size of the gap relative to their own wingspan. This systematic modulation of body orientation in response to relative gap size bears remarkable similarity to the shoulder rotation response displayed by humans when passing through apertures (1). Adult humans and children initiate a body rotation when walking through apertures that are <1.5x their shoulder width and maximally rotate their shoulders when apertures are equivalent to their shoulder width (1, 29).

The gap traversal behavior we observed in bees suggests that their strategy for navigating in complex environments includes not only the putative optomotor framework for flight control, but also incorporates properties of the insect's own form. Although this behavioral performance of bees is similar to that of humans, this finding does not necessarily imply that bees maintain internal embodiments of themselves as has been claimed for humans, apes, dogs and other vertebrates (5–7), that they are cognitively aware of their own body dimensions. Nevertheless, at the behavioral level, bees appear to take account of their body size and form in relation the environment to modulate their flight strategy. The perception of environmental properties in relation to body size to maneuver through narrow gaps presents the hallmarks of affordance analysis (1, 2).

How could bees relate visual information about the environment to their own body form? Experiments on walking locusts and fruit flies suggest that experience specific to the locomotion task facilitates the calibration of visual inputs to body features and such calibrations are maintained in the insect's memory (31, 32). These studies reported that the insects calibrate optic flow to stride length during development, resulting in body-scaled information about their environment relative to their leg length. Such body-scaling between visual information and body features is likely to depend on the environmental challenge, and to differ for insects when walking vs. flying, due to differences in sensory input and motor action. Furthermore, the potential cost of collisions is higher during flight (wing damage, crash landing, etc.) than when walking, and this could influence the fidelity of such internal calibrations.

Nevertheless, the processes that facilitate the calibration of visual information to body size, including the role of learning and experience, (31, 32) could be similar across locomotion modes and quite general across species. In walking humans, the visual angle subtended by the edges of an aperture provides body-scaled information about aperture width as a ratio of eye height, and is calibrated to body width to perceive passability (1). Experiments performed by Fath et. al (30) also found that lateral head movements, or heady-swaying, in humans during walking facilitates aperture perception and traversal performance. Previous studies on flying birds have revealed that birds modulate their wing beat or tuck in their wings to negotiate gaps, and have suggested that birds may calibrate the rate of expansion of the angle subtended by the edges of the gap to gauge its size (33). The scanning maneuvers we observed in bees as they approached a gap would generate optic flow that specifies gap size in the same length unit as the bee's lateral velocity (see SI, Fig. S6). If the latter is calibrated by experience during development in wingspans per second, then the gap size estimated from peering would be scaled to bees' own body width.

Learning through trial and error from previous flights through cluttered environments, without any intrinsic knowledge, might be another potential mechanism that may contribute to the calibration of visual information, enabling bees to learn body-scaled information for the affordances of gaps. However, the identification of relevant visual variables and their relations with other sensorimotor cues needed to develop the behavioral strategies displayed by bees suggests a relatively complex learning process. Note that bees not only judge gaps based on their wingspan, but also reorient to an angle that takes advantage of their body shape and allows them to pass through narrow gaps. Furthermore, collisions with obstacles in cluttered environments lead to irreparable wing damage, and thus acquiring information about their own body size solely through trial and error learning may be an option with limited feasibility. However, many studies have demonstrated bumblebees' ability to rapidly learn complex relations and abstract concepts across sensory modalities (34). Since the bees in our study were experienced flyers, the scaling of visual information to body form either solely through trial and error or in combination with alternative mechanisms is likely to have been well developed.

Although bees were able to successfully fly through gaps under all conditions, they more frequently made contact with the edges of the gap (touching the edges with extended legs or the head/antennae, SV6) or experienced wing collisions with the edges as gap size decreased, suggesting that learning could involve such feedback from these body parts. Contact with the edges of the gap occurred in a small portion of flights when gap size was approximately twice the bees' wingspan, and the frequency of flights in which contact occurred increased sharply with decreasing relative gap size (Fig. 3c&d). Wing collisions did not occur until gap size was reduced to approximately 1.5 times the wingspan, and the proportion of flights where wing collisions occurred also increased with decreasing relative gap size (Fig. 3c). In some extreme cases, bees "head-butted" the obstructing wall as they flew sideways through the gap (SV7). Such apparently deliberate contacts made between the bee's head or limbs and the obstacle were likely aimed at protecting the more delicate wings from collisions. The fact that bees did experience frequent wing collisions when flying through smaller gaps (e.g., during ~40% of flights when flying through gaps equal to the wing span; Fig. 3b), despite consistently reorienting themselves, highlights the challenge of navigating safely through dense clutter, and points to the importance of morphological adaptations in wings that allow them to tolerate collisions (35).

Our observations reveal a novel facet of insect behavior and highlights the relatively limited neural infrastructure needed to take account of self-form when performing visually guided tasks. This suggests that the capacity to perceive affordances during locomotion through complex environments, a capacity only reported so far for vertebrate animals, could be widespread among insects. The comparison of bees' performance with that of other animals highlights the various behavioral strategies employed for perceiving the affordances of the environment across different animal taxa (Fig. S7). From an ecological perspective, the robustness and consistency with which

bumblebees in our study were able to navigate through such a challenging environment is likely a key trait that allows these important pollinators to efficiently collect resources in complex, cluttered environments, and one which contributes to their survival.

Materials and Methods

Experiment setup

Experiments were performed on individual workers from *Bombus terrestris* (Linnaeus 1758) colonies that were maintained within the lab. Hives were sourced from a commercial breeder (Koppert Biological Systems) and placed within a 0.4×0.4×0.3 m mesh enclosure that was covered with dark cloth to simulate the natural underground habitat of the bees. The hive enclosure was connected to a flight tunnel (0.3×0.3x1.5 m) that led to a 2x1.5x2m foraging chamber, which in turn provided access to the outdoor environment. Apart from outdoor foraging resources, the bees were also provided ad libitum access gravity feeders containing 30% sucrose solution placed within the foraging chamber Connections between the hive enclosure, flight tunnel and foraging chamber were made using 30 mm i.d. and 150 mm long flexible silicon tubing. Consistent foraging flights by numerous worker bees were observed within 1 day of moving a new hive to the enclosure. Experiments were performed once steady and consistent foraging traffic was noted within the flight tunnel, defined as when >15 flights per minute were observed. The temperature within the hive enclosure, flight tunnel and foraging chamber was maintained at 23°C. Ample natural lighting from the windows was available for within the foraging chamber and flight tunnel. The bees were given 1 week to habituate to the environment before experiments began.

Bumblebee individuals within a hive display natural variation in body size, and our goal was to collect sufficient data from bees covering this entire range of sizes. However, preliminary tests revealed that the majority of bees flying within the flight tunnel were of intermediate size (i.e., smaller and larger bees constituted a smaller portion of individuals that flew within the tunnel). In order to collect a large sample containing bees of widely ranging body sizes flying through gaps of different sizes, we performed experiments on four hives. A total of 400 flights performed by bees from these four hives were recorded and analyzed. The number of flights collected for bees of different body sizes is shown in Fig. S2.

Testing procedure

During experiments, manually controlled gates on either side of the flight tunnel were used to regulate traffic. Only one bee at a time was permitted to enter the flight tunnel, and only bees returning to the hive were considered for analysis as they displayed high motivation to fly through the gap. The sidewalls and floor of the tunnel were lined with a random cloud pattern with spatial frequencies varying by 1/f, similar to that used in (36). An obstacle was created within the flight tunnel by adding a vertical wall containing a rectangular hole (aperture) starting from the middle and extending to the top of the tunnel (see Fig. 1A) that bees were required to fly through to return to the hive. Seven different experimental conditions were tested, with the width of the rectangular gap set to 20, 25, 30, 35, 40, 50, or 60 mm. Gaps <20mm were not tested as the bees did not display flight traversal and instead tended to land on of the edge of the gap and crawl through. For all conditions, the wall containing the gap was placed 0.75 m from the entrance of the tunnel (Fig. 1A). During experimental sessions, the gap size was varied randomly between each recording, while the bees to be subsequently tested were in the foraging chamber. Once a bee passed through the gap and entered the nest, the obstructing wall was removed to inhibit learning or familiarization with the experimental conditions by bees departing from the hive to forage.

To examine the response of naive bees that had never (or rarely) encountered the obstructing wall and flown through the gap, experimental bouts lasted no longer than 30mins. (37) found that foragers perform on average 4-15 foraging trips over the entire day. Thus, it is unlikely that many bees would have performed multiple trips within an experimental bout. experiment bout. Bees were

not individually marked in this study; although this increased the possibility of collecting unequal numbers of flight recordings among different individuals for each condition, the likelihood was greatly reduced by recording consecutive flights from different bees only when bees were returning to the hive. Additionally, because we filmed numerous foragers from different hives and recorded a large number of flight trajectories (n = 400), our dataset is likely to be representative of the population. Finally, because this study was focused on analyzing the flight behavior of bees when passing through gaps (rather than examining individual changes in performance with experience), individual-level monitoring to track learning was not necessary.

Digitization and analysis

Flight trajectory, orientation and morphology

An Optronis CR6 high-speed camera was placed 1.7 m above the midline of the flight tunnel, aimed directly downward over the gap. Flights were recorded at 200 Hz with a 1/500 s shutter, and a region covering 350 mm of length along the tunnel leading to the gap was kept within the field of view. The ceiling of the flight tunnel consisted of 5 mm UV-transmitting transparent acrylic panels that spanned the width of the tunnel. The majority of bees never collided with the roof while on foraging bouts and flights containing roof collisions were omitted from the analysis. Only flights of individuals that appeared to be returning from foraging trips (i.e., bees that made a steady and direct flight towards the obstructing wall) were used for analysis; at least one such flight was observed every minute. Bees carrying pollen were also excluded from this study.

During post-processing, lens distortion was corrected using standard MATLAB Image Processing Toolbox routines. An object of known dimensions was placed within the field of view at mid-height of the tunnel and related to the pixels in the rectified image for 2D spatial calibration. Custom MATLAB script was written to process each image frame and isolate the bee from the background. An ellipse was fitted to the body of the bee in each frame, and the centroid location, body length and width, and heading (yaw angle) were measured over the entire flight. In order to attenuate digitizing errors, the flight trajectories were passed through a 30 Hz second-order Butterworth filter. Yaw/heading orientation was calculated with respect to the flight tunnel using the right-hand rule. As the flights were recorded from a single perspective, body pitch and roll could not be estimated. No systematic bias was noted among recorded flights in the direction to which bees reoriented (i.e., clockwise vs. counterclockwise yaw) while passing through the gap. The body length (estimated as the length of the major axis of the ellipse) varied by <8% over the entire flight sequence, indicating that bees maintained nominally similar altitude as they approached and crossed the gap. In addition, for 10 frames each at the start and finish of the recorded video segment and during gap crossing, the location of the bee's head, wing roots and wing tips were digitized manually. These images also contained shadows indicating the range of wing motion during the flap that were used to estimate the wingspan. A similar method has been used by (38) to measure wing span and estimate wing beat amplitude in bumblebees. We compared measurements from the three sets of manually digitized frames to evaluate consistency in morphological estimates and found <4% variation in the morphological metrics, which was considered acceptable.

The choice of the bins used to separate bees of different wingspans was determined by dividing the entire range of wingspans into three equal segments. For our case the range represented 18 – 33mm therefore the bees were segmented as either small (18 - 23mm), medium (23 – 28mm) or larger (28 – 33mm).

Body Contacts and Wing Collisions

Flights during which bees contacted the edges of the gap with their head, body and/or legs ("body contacts") were visually noted during digitization. Identifying the wing tip path during the stroke for all instances was challenging due to the high wing beat frequency of bees. Wing collisions were therefore estimated during post-processing as follows: a circular wedge with radius equal to the

wing length for each individual bee and angle equivalent to the mean stroke amplitude (derived from the manually digitized frames) was placed at the base of each wing, for all frames as the bees approached and passed through the obstacle. The angular position of the wedge with respect to the body was maintained as the bees varied their heading during flight. Wing collisions were considered to have occurred if the arc intersected the edges of the gap during traversal. We tested this method on several recordings made at 3000 fps (where the wings were clearly visible) and found that wing collisions were reliably identified by the post-processing method.

Peering

Peering was defined as lateral flight maneuvers performed by the bees while maintaining nominally constant gaze in the direction of the gap. These trajectories were identified during post-processing using custom routines written in MATLAB; these routines isolated flight segments during which the bees' dominant velocity was oriented laterally with respect to their body axis and the gap was within 60 Deg of their frontal visual field. In general, the gap remained with 60 Deg of bees' frontal visual field for nearly the entire time when bees were flying near the gap (Fig. S4). In the near vicinity of the gap, the number of lateral peering passes were determined by counting segments of the trajectories where the lateral velocity was reversed before the bees initiated a gap crossing maneuver. Regions very close to the gap (<5mm) were not considered in peering estimation because traversal maneuvers were initiated here. Only trajectory segments >7 mm were considered to represent genuine peering behavior – but this limit on segment length did not significantly influence overall trends in the results (as compared to including segments of all lengths). Total peering time was estimated by summing the time spent by the bees engaging in the lateral maneuvers.

Statistical analysis

Before performing statistical tests, data sets were tested for normality using a Shapiro-Wilk test for the combination of 3 groups (body-size bins) and 7 experimental conditions (gap sizes). We used a two way ANOVA to test for statistical significance of the variation in quantities between bees of different bodysize, followed by post hoc tests to determine which groups differed significantly (for example: we used this test to reject the null hypothesis that the reorientation behaviour of the bees, across the different gaps presented, was insensitive to the bees' wing span (categorized into 3 bins), Fig. 3 & ST11). To compare quantities across bees of different wingspans for a particular gap-size, t-tests were used to assess statistical significance, with an adjusted p-value (Bonferroni multiple testing method, pvalue < 0.01). For example, for each gap size we used this test to verify that the peering amplitude of bees was consistent across the different wingspan bins, Fig. 2 & ST3. Statistical analyses were performed in R (version 3.5.3), using the tidyverse, ggpubr and rstatix libraries.

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Data and materials availability: All data processing code and datasets will be made available on University of Bielefeld's open source repository

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Figures and Tables

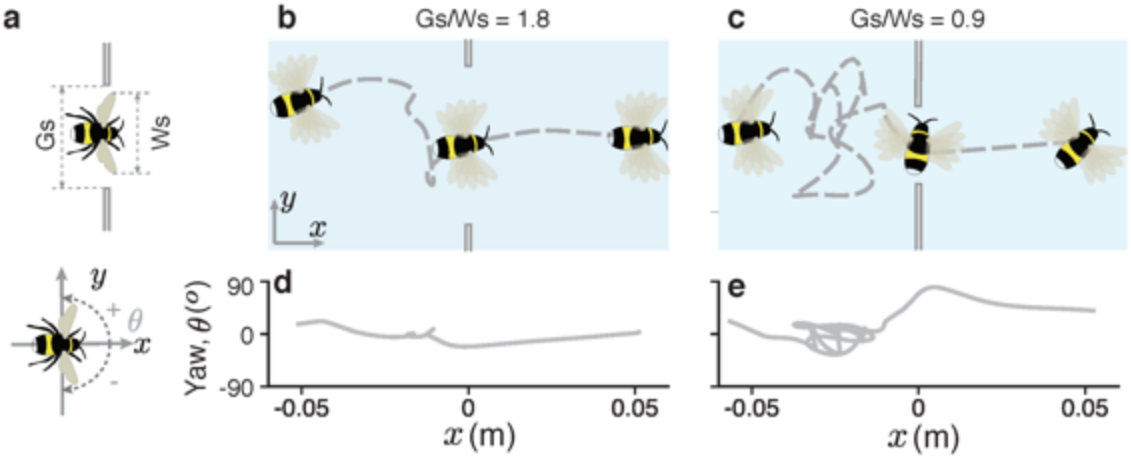

Figure. 1. Bumblebees can safely fly through gaps that are even smaller than their wingspan (a) Illustrations indicating the wingspan of bees (Ws), the size of the gap (Gs) and the positive and negative yaw (heading) angles for bees flying in the tunnel. (b) & (c) are schematic illustrations of the flights of two bees of similar size flying through a gap that is larger (b) and a smaller (c) than their wingspan respectively. Flights consisted of approach, lateral peering, and – for the smaller gap size (c) – body reorientation (an increase in yaw angle) while passing through the gap. (d & e) The instantaneous yaw angle of bees shown in the schematics presented in (b & c). The differences in reorientation behavior can be noted at x = 0 (location of the gap) where in (e) the bee displays a large increase in yaw angle that reorients its body to pass through the small gap, whereas body reorientation in (d) is minimal. For the trial shown in (b) and (d), Ws = 27.5 mm and Gs = 50 mm, while for the trial shown in (c) and (e), Ws = 27 mm and Gs = 25 mm.

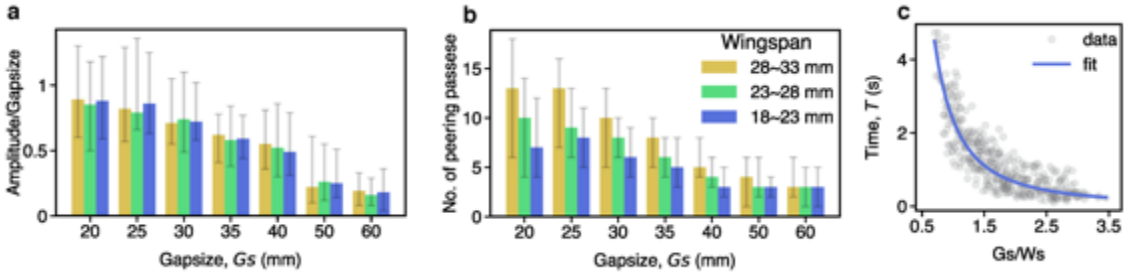

Figure 2. Bumblebees spend more time performing repeated peering ahead of relatively narrow gaps. (a) Mean amplitude of lateral peering movements performed by bees of different wing spans approaching gaps of increasing width (see ST2-4 for statistics). (b) Total number of lateral peering passes performed by bees of different wing spans approaching gaps of increasing width (see ST5-7 for statistics). For (a) and (b), bees were binned by wingspan as follows: Ws =18-23 mm (blue), 23-28 mm (green) and 28–33 (yellow). (c) Scatter plot (n = 400 flights) showing the time individual bees spent performing peering motions relative to the normalized gap size (gap size divided by wingspan; Peering time = $2.344x(Gs/Ws)^{-1.842}$, R^2 = 0.84). The number of flights for different gap sizes and bees of different wingspans are given in ST1.

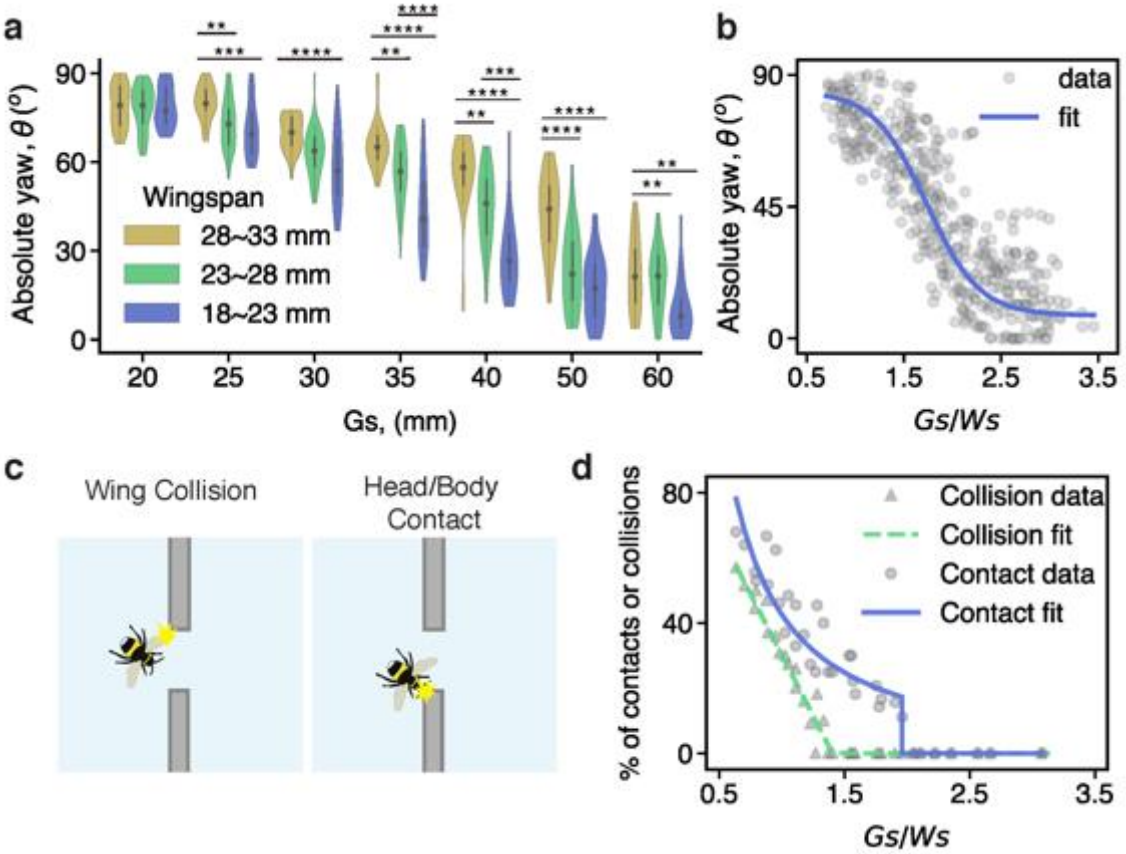

Figure 3. Bumblebees reorient themselves to pass through narrow gaps. (a) Absolute yaw angle of bees at the midpoint of the gap, observed in bees of different wing spans passing through gaps of increasing width (refer ST8-11 for statistics summary) (b) Scatter plot (n=400 flights) showing the absolute yaw angle of bees at the midpoint of the gap relative to normalized gap size (gap size divided by wing span; sigmoidal fit: Yaw = 85.22+(-4.88/(1+$10^{1.7-(Gs/Ws)}$)x1.6), R^2 = 0.82). (c) Schematic illustrations of a bee whose wing is colliding with the edge (left) or who is making contact with the edge (right) while passing through the gap. Contact was considered to have occurred when any part of the bee's body (including limbs, head or antennae, but excluding the wings) touched the edge of the gap. (d) Proportion of flights during which bees' wings collided with the edges, and during which bees' bodies made contact with the edges of the gap, as a function of normalized gap size (gap size divided by wingspan). Bees of different wing spans were first segmented into bins of 3 mm between 18-33mm, and the proportion of collisions or contacts were calculated with respect to the number of flights within each wing-span bin and normalized gap size. Power relation between % of flights with contacts $CO=42.61x(Ws/Gs)^{-1.336}$, $R^2 = 0.86$, linear relation between % of flights of with collisions $CL=-74.76x(Ws/Gs)+105$, $R^2 = 0.93$). See ST1 for dimensional representation of collisions and contacts. The number of flights recorded, contacts and collisions for different gap sizes for bees with different wingspans are given in ST1.