

Close encounters of three kinds: impacts of leg, wing, and body collisions on flight performance in carpenter bees

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Abstract

Flying insects often forage among cluttered vegetation that forms a series of obstacles in their flight path. Recent studies have focused on behaviors needed to navigate clutter while avoiding all physical contact, and as a result, we know little about flight behaviors that do involve encounters with obstacles. Here, we challenged carpenter bees (*Xylocopa varipuncta*) to fly through narrow gaps in an obstacle course to determine the kinds of obstacle encounters they experience, as well as the consequences for flight performance. We observed three kinds of encounters: leg, body, and wing collisions. Wing collisions occurred most frequently (in about 40% of flights, up to 25 times per flight) but these had little effect on flight speed or body orientation. In contrast, body and leg collisions, which each occurred in about 20% of flights (1-2 times per flight), resulted in decreased flight speeds and increased rates of body rotation (yaw). Wing and body collisions, but not leg collisions, were more likely to occur in wind versus still air. Thus, physical encounters with obstacles may be a frequent occurrence for insects flying in some environments, and the immediate effects of these encounters on flight performance depends on the body part involved.

Keywords: Obstacles; Biomechanics; Hymenoptera; Wind; Maneuverability

Introduction

Flying animals frequently interact with cluttered vegetation in their habitats. Many birds, for instance, nest and perch in trees and pursue prey through dense foliage [1,2], and many insects forage for nectar and pollen among dense patches of flowers [3,4]. In each case, animals navigate around a series of vegetative structures that functionally serve as obstacles and constrain navigable paths [5,6]. Traversing obstacles while in flight requires coordinated detection of obstacles (e.g., visually) and rapid alteration of the flight path, for example by decelerating, accelerating, or changing body orientation [7–11]. However, most studies of obstacle traversal in flight focus on behaviors required to completely avoid obstacles, with little consideration of what happens when animals do make contact with obstacles (e.g., collisions). This contrasts with studies of terrestrial locomotion that consider obstacle encounters as an integral part of traversing terrestrial landscapes [12–14]. Thus, we know relatively little about the effects of physical encounters with obstacles on the performance of flying animals.

37 Encounters with obstacles can alter locomotory performance at the time of the collision and
38 also lead to performance-altering injuries that may be immediate or cumulative. Intuitively, the
39 effect of obstacle encounters seems likely to involve some ballistic component – i.e., an animal’s
40 motion is redirected or slowed. However, the observed effect may deviate from intuition based
41 on the animal’s mechanics and behavior, as well as details of the obstacle encounter, such as the
42 initial motion of the animal and which body structures contact the obstacle [13]. Tolerance for
43 collisions may vary between taxa – for instance, birds of prey can suffer bone fractures that
44 eventually heal, whereas wing damage in insects is permanent [1,15]. Because wing damage can
45 increase mortality in insects, the avoidance and consequences of wing collisions has been
46 emphasized in many insect flight studies [9,10,16–18]. Furthermore, numerous insect species
47 have wing morphologies that minimize damage by flexibly deforming during obstacle
48 encounters, and these features have become the focus of studies aimed at extracting wing designs
49 for bio-inspired flying vehicles [19–21]. As a result, our knowledge about obstacle encounters in
50 flying insects is heavily focused on a specific anatomical structure, the wing, even though
51 obstacle encounters and injuries can occur to other parts of the body [1]. We therefore know
52 little about the full range and consequences of obstacle encounters that occur during insect flight.

53 Here, we use the Valley Carpenter Bee, *Xylocopa varipuncta*, to determine the types of
54 obstacle encounters that can occur in flying insects and their consequences for performance.
55 Among bees (family Apidae), carpenter bees in the genus *Xylocopa* are exceptionally large (wing
56 span > 4 cm) and are important pollinators of crops and wild plants [22]. Thus, they commonly
57 face the challenge of maneuvering a large body through dense foliage. *Xylocopa* spp. are also
58 models for physiological and neurobiological studies due to their large flight muscles and visual
59 acuity [22,23]. We used high-speed video cameras to film *X. varipuncta* flying through narrow
60 gaps in an obstacle course with varying environmental conditions, including moving vs.
61 stationary obstacles and wind vs. still air, in a laboratory flight tunnel. Using these data, we
62 answered the following questions: (1) How frequent are different kinds of obstacle encounters?,
63 (2) What environmental factors affect the likelihood of encounters?, and (3) What are the
64 performance consequences of each kind of encounter?

65

66 **Methods**

67 Female carpenter bees (*Xylocopa varipuncta*, $n = 15$) were collected from the University of
68 California, Davis campus and used immediately in flight experiments. Individual bees were
69 placed in a flight tunnel (20 x 19 x 115 cm; width x height x length) [10,24], which included a
70 series of vertical obstacles that spanned the middle of the tunnel (obstacle diameter = 7 mm,
71 space between obstacles = 34.44 ± 2.80 mm; mean \pm SD). The bees’ wing spans (45.19 ± 2.11
72 mm, tip to tip) were larger than between obstacles; thus, bees needed to rotate their body (e.g.,
73 yaw) to pass between obstacles. Obstacles were attached to a mechanical arm that oscillated
74 laterally (amplitude = 21 mm, frequency = 2 Hz) or remained stationary. Fans at each end of the
75 tunnel could be turned on to produce a gentle breeze (mean velocity = 0.54 m/s) or off for still
76 air. Wind direction was constant: bees flying in one direction experienced headwinds and in the
77 other direction tailwinds. Up to 12 flights through the obstacles were elicited per bee, using full

78 spectrum lights at each end of the tunnel [10,24]. Obstacle motion (stationary versus moving)
79 was fixed for a given bee, but all bees experienced wind and still air, with wind condition
80 switched after approximately six flights and the order of wind conditions alternated between
81 bees. Thus, test conditions were still air with stationary obstacles ($n = 40$ flights) or moving
82 obstacles ($n = 34$), and wind with stationary obstacles ($n = 42$) or moving obstacles ($n = 29$).

83 Flights were filmed at 1500 frames/s with two synchronized Phantom v611 cameras
84 (Vision Research, Inc., Wayne, NJ, USA) positioned 30° from the vertical on opposite sides of
85 the obstacles. Cameras were calibrated using a standard checkerboard calibration method and
86 MATLAB functions [25,26]. In each video, the positions of the bee's head (midpoint between
87 antennae), thorax (approximating the body centroid), and wing tips were tracked with the
88 machine-learning software DeepLabCut [27]. Tracked points were checked and manually
89 corrected, and obstacle positions labeled using DLTdv6 in MATLAB [28]. Labeled positions
90 were converted from two-dimensional coordinates in each camera view into three-dimensional
91 space using MATLAB functions.

92 We classified and counted each obstacle encounter. The most common encounters were
93 body collisions (head, thorax, or abdomen contacted obstacles), leg collisions (one or more
94 forelegs contacted obstacles), and wing collisions (the distal half of one or more forewings
95 contacted obstacles) (Fig. 1).

96 To test which experimental conditions contributed to the occurrence of encounters, we
97 used a generalized linear mixed-effects model (GLMM). Models were implemented as logistic
98 regression models with the 'glmer' function in the R package *lme4* [29], with variables for wind
99 (yes versus no), flight direction (upstream versus downstream), and obstacle motion (moving
100 versus stationary). Bee identity was included as a random effect to account for multiple
101 observations per individual. We allowed for statistical interactions between all experimental
102 variables and generated alternative models by removing terms in a stepwise selection process.
103 Models were compared by their Akaike's Information Criterion (AIC) via the 'AIC' function in
104 the R package *stats* [30]. Models with the lowest AIC were evaluated with the 'Anova' function
105 from the R package *car* [30].

106 Among flights with obstacle encounters, there was wider variation in the number of wing
107 collisions per flight (range = 1-25) compared to body collisions (range = 1-2) or leg collisions
108 (maximum = 1). We tested which experimental variables best predicted the number of wing
109 collisions per flight by using a GLMM with a Poisson distribution on flights with at least one
110 wing collision. Model selection and evaluation were carried out as described above. Post-hoc
111 comparisons of model terms were conducted with Tukey HSD tests using the 'lsmeans' function
112 in the R package *emmeans* [33].

113 We assessed how obstacle encounters affected flight performance. In every video, we
114 identified the first occurrence of each encounter type and defined a 20-ms period before and after
115 each event. This temporal window allowed us to quantify performance immediately before and
116 after encounters, as in [20]. Occasionally, pre- and post-encounter periods contained additional
117 collisions, a common outcome when flying near clutter, but the narrow analysis window allowed

118 us to examine changes in flight performance primarily occurring around the focal obstacle
119 encounter. Videos yielded either one, two, or three encounter types ($n = 42, 26,$ and 9 flights,
120 respectively).

121 For each encounter, we measured the change in horizontal ground speed and yaw angle
122 between the pre- and post-encounter periods, as well as the post-encounter yaw rate, where yaw
123 angle was the body angle about the vertical axis. To calculate kinematics, we smoothed three-
124 dimensional position data with cubic smoothing spline curves via the ‘smooth.spline’ function in
125 *stats*. Horizontal ground speed was calculated as the change in x-y position (lateral and
126 longitudinal movements, omitting vertical motion) per time. Yaw was calculated by converting
127 the Cartesian coordinates of the head and thorax to spherical coordinates via the ‘cart2sph’
128 function in the R package *pracma* [31] and finding the horizontal angle between the body points
129 and the tunnel’s long axis. Yaw rate was calculated as change in yaw per time.

130 We used a linear mixed-effects model to test whether the change in flight metrics
131 depended on encounter type, wind condition, and/or obstacle motion. Models were implemented
132 with the ‘lme’ function in the R package *nlme* [32]. Model selection, evaluation, and post-hoc
133 comparisons were carried out as described above. Assumptions of normality and homogeneity
134 of variances were checked with Shapiro’s Tests and Levene’s Tests, respectively. When
135 necessary, variance structures of model terms were modified using the ‘varIdent’ function in
136 *nlme*.

137

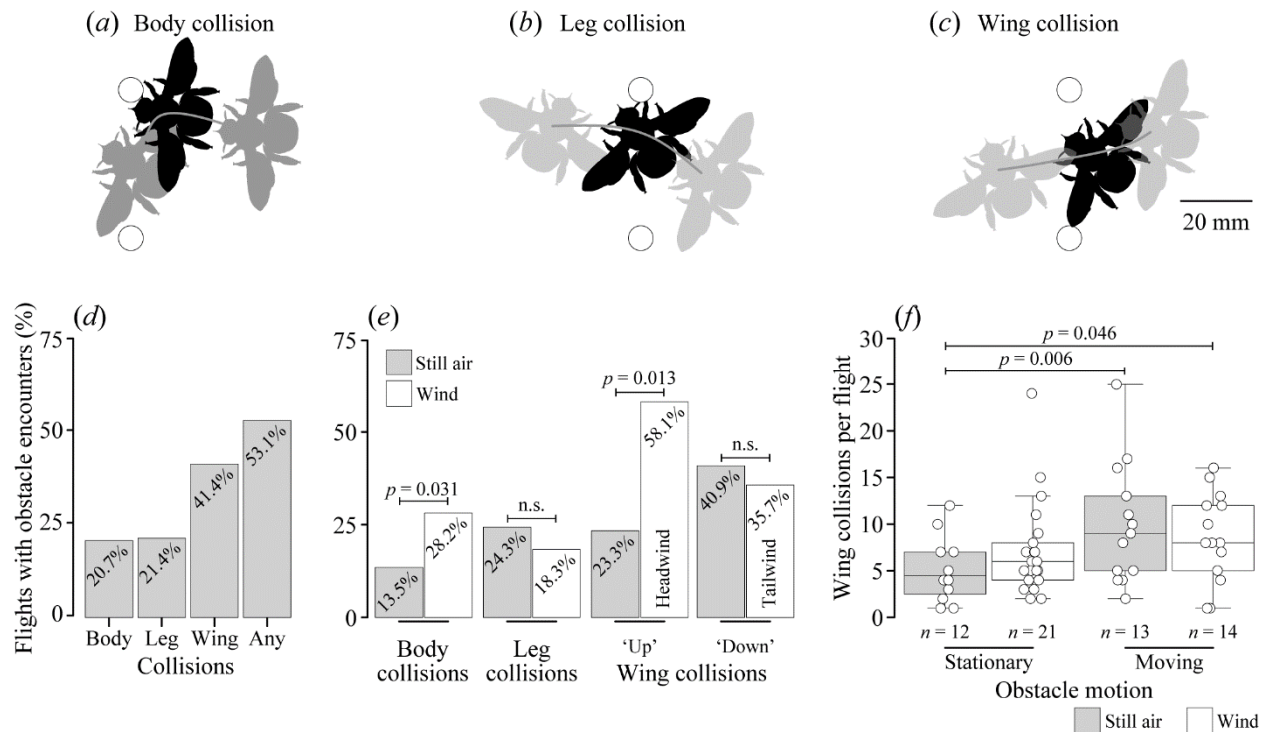
138 **Results**

139 Of the 145 recorded flights from *Xylocopa varipuncta*, 20.7% ($n = 30$) included a body
140 collision, 21.4% ($n = 31$) included a leg collision, and 41.4% ($n = 60$) included a wing collision;
141 overall, more than half of flights (53.1%, $n = 68$) included some type of obstacle encounter (Fig.
142 1d). Body collisions were more likely to occur in wind (frequency = 28.2%, $n = 20/71$ flights)
143 versus still air (13.5%, $n = 10/74$ flights) (GLMM: $\chi^2 = 4.673$, $df = 1$, $p = 0.031$), whereas leg
144 collisions showed similar frequencies between wind (18.3%, $n = 13/71$ flights) and still air
145 (24.3%, $n = 18/74$ flights; Fig. 2e) ($\chi^2 = 1.426$, $df = 1$, $p = 0.232$). Wing collision frequency
146 depended on wind and flight direction ($\chi^2 = 6.341$, $df = 1$, $p = 0.012$), such that flights in
147 headwinds (but not in tailwinds) were more likely to contain wing collisions (58.1%, $n = 25/43$
148 flights) than flights in the same direction with still air (23.3%, $n = 7/30$ flights; Fig. 2e) (Tukey
149 HSD tests: $p = 0.013$). Notably, our AIC-based model selection process indicated that obstacle
150 motion was not a strong predictor of the likelihood of any encounter type occurring.

151 Among flights with wing collisions, the number of wing collisions per flight depended on
152 wind and obstacle motion ($\chi^2 = 7.011$, $df = 1$, $p = 0.008$; Fig. 1f). Flights in still air with
153 stationary obstacles had fewer wing collisions (5.3 ± 3.5 wing collisions; mean \pm SD) than
154 flights in still air with moving obstacles (9.9 ± 6.5 wing collisions) (Tukey HSD test: $p = 0.006$)
155 or flights in wind with moving obstacles (8.6 ± 4.8 wing collisions) ($p = 0.046$).

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158

159 **Figure 1.** Types of obstacle encounters observed in carpenter bees. Top row: real examples of
 160 (a) body, (b) leg, and (c) wing collisions in bees flying past obstacles from right to left (see
 161 supplementary movies). Black outlines show the moment of each encounter. Gray outlines
 162 show body positions 20 ms before and after encounters. White circles show obstacle positions.
 163 Bottom row: (d) frequencies of encounter types, and (e) frequencies grouped by wind condition
 164 and, for wing collisions, by flight direction. 'Up' and 'Down' refer to separate directions in the
 165 flight tunnel. (f) Number of wing collisions per flight (excluding flights without wing
 166 collisions), grouped by wind condition and obstacle motion. Brackets show statistical
 167 comparisons ($p < 0.05$ for significance; 'n.s.' = not significant). Only environmental factors (i.e.,
 168 wind, flight direction, obstacle motion) retained by the models are shown.

169

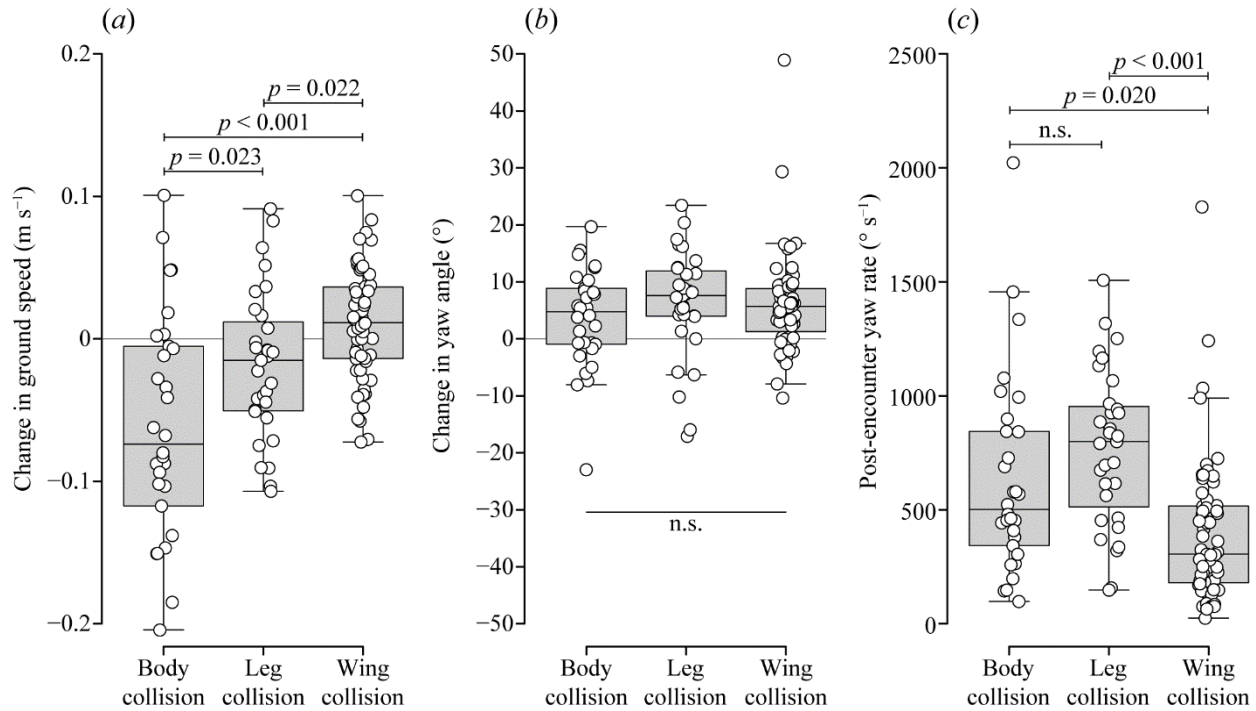
170 Body, leg, and wing collisions (Fig. 1a-c) each had distinctive effects on ground speed,
 171 with large decreases in speed after body collisions (-0.07 ± 0.08 m/s), small decreases after leg
 172 collisions (-0.02 ± 0.05 m/s), and small increases after wing collisions (0.01 ± 0.04 m/s) (Fig. 2a)
 173 ($\chi^2 = 25.896$, $df = 2$, $p < 0.005$; Tukey HSD tests: $p < 0.05$).

174

175 Changes in bees' yaw angle resulting from collisions were not affected by encounter type
 176 ($\chi^2 = 0.574$, $df = 2$, $p = 0.751$) (Fig. 2b) but were affected by wind, with larger changes in yaw
 177 angle for bees flying in still air ($7.29 \pm 6.12^\circ$) versus wind ($3.96 \pm 10.33^\circ$) ($\chi^2 = 7.378$, $df = 1$, $p =$
 178 0.007). Post-encounter yaw rate depended on encounter type ($\chi^2 = 21.284$, $df = 2$, $p < 0.005$)

179 (Fig. 2c), with slower rates after wing collisions (305.6 [333.6] %/s; median [interquartile range])
180 versus body collisions (501.5 [491.4] %/s) (Tukey HSD test: $p = 0.020$) and leg collisions (799.2
181 [440.3] %/s) ($p < 0.005$) (Fig. 2c).

182



183

184 **Figure 2.** Effects of obstacle encounters on flight. Changes in (a) horizontal ground speed and
185 (b) yaw angle between the pre- and post-encounter periods, and (c) post-encounter yaw rate ($n =$
186 30 body collisions, 31 leg collisions, 60 wing collisions). Increases in yaw (b) indicate rotations
187 away from the tunnel's centerline. Brackets show statistical comparisons ($p < 0.05$ for
188 significance; 'n.s.' = not significant).

189

190 Discussion

191 We found that carpenter bees experienced three distinct types of obstacle encounters
192 when traversing challenging flight environments. Wing collisions were the most frequent
193 encounter (occurring in about 40% of flights), but body and leg collisions each occurred in
194 approximately 20% of flights as well. These results suggest that collisions with obstacles may be
195 common for insects flying through natural, complex environments, such as cluttered vegetation,
196 and that these encounters are diverse – both in terms of the environmental conditions that
197 increase their likelihood and in their effects on flight performance.

198 Wind increased the likelihood of some encounters, but this effect was not uniform. Body
199 collisions occurred more frequently in wind, but leg collisions were not affected – and wing
200 collisions occurred more frequently only for bees flying into a headwind. Obstacle motion did

201 not affect the likelihood of any type of encounter, but obstacle motion (in still air or in wind) did
202 lead to a greater number of wing collisions for flights in which wing collisions occurred. Given
203 that our experiment tested only one obstacle arrangement, one type of obstacle motion, and one
204 mild wind speed, it is clear that additional studies would greatly improve our understanding of
205 how environmental variables affect the likelihood and consequences of obstacle encounters.

206 Most insect flight studies focus on collision-free flight, yet in our study more than half of
207 the flights recorded (53.1%) contained at least one type of collision, suggesting that additional
208 research is needed on flights involving obstacle encounters. In addition, most previous studies
209 addressing collisions have focused only on wing collisions, in part because wing collisions lead
210 to cumulative damage that can impair flight performance over time. However, our work
211 suggests that other types of obstacle encounters, such as body and leg collisions, may have more
212 important immediate effects on flight performance, leading to larger reductions in flight speed
213 and larger changes in body rotation rates than wing collisions. Overall, our work suggests that
214 the incidence, diversity, and potential effects of obstacle encounters experienced by flying
215 insects remains vastly underexplored in the scientific literature.

216

217 **Data accessibility**

218 Data are available from the Dryad Digital Repository <https://doi.org/10.25338/B8M939>.

219 **Conflict of interest declaration**

220 We declare we have no competing interests.

221 **Authors' contributions**

222 **Nicholas P. Burnett:** Conceptualization, Methodology, Investigation, Formal analysis, Data
223 curation, Writing – original draft, Visualization, Funding acquisition. **Stacey A. Combes:**
224 Conceptualization, Methodology, Supervision, Project administration, Writing – review &
225 editing.

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