Visual guidance of forward flight in hummingbirds reveals control based on image features instead of pattern velocity

Roslyn Dakin^a, Tyee K. Fellows^a, and Douglas L. Altshuler^{a,1}

^aDepartment of Zoology, University of British Columbia, Vancouver, BC, Canada V6T 1Z4

Edited by John G. Hildebrand, University of Arizona, Tucson, AZ, and approved June 14, 2016 (received for review February 25, 2016)

Information about self-motion and obstacles in the environment is encoded by optic flow, the movement of images on the eye. Decades of research have revealed that flying insects control speed, altitude, and trajectory by a simple strategy of maintaining or balancing the translational velocity of images on the eyes, known as pattern velocity. It has been proposed that birds may use a similar algorithm but this hypothesis has not been tested directly. We examined the influence of pattern velocity on avian flight by manipulating the motion of patterns on the walls of a tunnel traversed by Anna's hummingbirds. Contrary to prediction, we found that lateral course control is not based on regulating nasal-to-temporal pattern velocity. Instead, birds closely monitored feature height in the vertical axis, and steered away from taller features even in the absence of nasal-to-temporal pattern velocity cues. For vertical course control, we observed that birds adjusted their flight altitude in response to upward motion of the horizontal plane, which simulates vertical descent. Collectively, our results suggest that birds avoid collisions using visual cues in the vertical axis. Specifically, we propose that birds monitor the vertical extent of features in the lateral visual field to assess distances to the side, and vertical pattern velocity to avoid collisions with the ground. These distinct strategies may derive from greater need to avoid collisions in birds, compared with small insects.

automated tracking | vision | locomotion | optic flow | optomotor

How are birds able to fly through dense forest and open spaces without colliding or crashing to the ground (1)? The translational motion of images on the eye (hereafter referred to as “pattern velocity”) provides a rich source of information about self-motion and the surrounding environment and has been shown to play a prominent role in the visual guidance strategies of all flying animals studied to date (2–5). Honey bees use pattern velocity for a diverse set of flight controls: they balance pattern velocity on their left and right sides to navigate narrow passageways (6); they regulate pattern velocity to control their flight speed (7) and altitude (8); and they integrate pattern velocity to estimate distances to foraging sites, communicating this information to hive mates (9, 10). Pattern velocity thus represents an elegant solution to insect flight control that is robust to a range of spatial frequencies and contrasts (2, 3, 6, 7).

In the first study to ask whether birds also use a similar strategy, Bhagavatula et al. (11) trained five budgerigars to fly repeatedly down a tunnel. The authors found that like bees (6), the budgerigars steered away from vertically oriented gratings that provided strong nasal-to-temporal (fore-aft) pattern velocity, and toward horizontally oriented gratings and blank walls that provided little to no nasal-to-temporal pattern velocity. However, because Bhagavatula et al. (11) used only stationary gratings and did not manipulate pattern velocity directly, the exact mechanism used by birds remains to be confirmed. More recent experiments demonstrate that pattern velocity does not affect the flight speed of budgerigars (12) in the same manner as it does flying insects (3, 13). Unlike bees and flies, the budgerigars increased their speed only slightly in response to large decreases in nasal-to-temporal pattern velocity, and they were not affected by large increases (12), demonstrating that birds do

not adjust their flight speed to hold nasal-to-temporal pattern velocity constant.

To determine if avian visual control of steering in flight differs from that of insects, we studied hummingbirds, agile fliers that perform rapid cruising flight as well as extended bouts of hover (14, 15). We used an automated tracking system to record more than 3,100 flights of birds in free flight traversing a narrow tunnel where the wall patterns could be experimentally controlled (Fig. 1). We measured the average lateral position of the birds as they crossed the tunnel (Movie S1). Because hummingbirds can be trained to perform many trips to and from a feeder, we were able to explore a broad range of stimulus patterns. The results of our first two experiments indicate that, contrary to what had been previously proposed (11), birds do not steer to balance nasal-to-temporal pattern velocity like insects (Movie S2). We then performed three additional experiments to understand how other visual cues may influence avian flight control. From our collective results, we propose that birds use a different set of strategies based on changes in both vertical feature size and vertical pattern velocity.

Results

We first asked if birds, like insects, steer by balancing pattern velocity. Our first experiment manipulated the motion of vertical grating patterns on the left and right sides of the 59-cm-wide tunnel (Fig. 2A) ($n = 297$ flights by 6 birds). The grating pattern on one wall was moved at a rate of 0.34 m/s either toward or away from the feeder while the pattern on the other wall was held stationary. The control treatment had stationary gratings on both sides. The experimental manipulations would have resulted in a $\pm 17\%$ change in nasal-to-temporal pattern velocity on one side for a bird flying at the average forward flight speed of 2.0 m/s [95% confidence interval (CI) 1.8, 2.2] along the midline of the

Significance

Birds can steer a precise course at high speed, but little is known about how they avoid collisions with surrounding objects and the ground. We manipulated the visual environment of hummingbirds as they flew across a long chamber to evaluate how they use visual information for course control. We found that lateral course control is based on the vertical size of features, rather than the strategy observed in insects of regulating fore-aft image velocity. However, like insects, birds use image velocity in the vertical axis for altitude control. Our results suggest that in natural settings, birds may avoid collisions by monitoring the vertical size, expansion, and relative position of obstacles.

Author contributions: R.D., T.K.F., and D.L.A. designed research; R.D., T.K.F., and D.L.A. performed research; R.D. analyzed data; and R.D. and D.L.A. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Data deposition: The data reported in this paper have been deposited in the Figshare data repository (https://figshare.com/articles/statistical_supplement_flight_course_control_R3382759).

¹To whom correspondence should be addressed. Email: doug@zoology.ubc.ca.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1603221113/-DCSupplemental.

Fig. 4. Lateral course control is based on the size of horizontal features, even in the absence of nasal-to-temporal pattern velocity. Hummingbirds had a strong tendency to steer away from vertical stripe gratings and toward horizontal gratings, but only when the horizontal stripes were relatively small (2.3-cm period size; top two rows of *A*). This steering response was diminished by the presence of large horizontal stripes (18.4-cm period size; bottom two rows of *A*). Additional tests confirmed that birds steered away from horizontal gratings with a larger period size even in the absence of vertical stripes that generate nasal-to-temporal pattern velocity (*B*) (Movie S2). The middle column shows grand means for individual birds and probability densities, as in Fig. 2. Effect sizes are calculated as the average difference between the pink and blue treatments. Stimulus features are not drawn to scale. Statistical significance: *** $P < 0.001$; * $P < 0.05$; ns $P > 0.05$.

pigeon brain, part of the tectofugal pathway (19). This same nucleus also contains cells that respond to expansion scaled by apparent size (equal to $1/\tau$, where τ is the time-to-collision) and expansion scaled by an exponential function of apparent size (known as η) (19). These cues can inform an animal about the nearness in time of an impending collision, triggering an appropriately timed response without knowledge of the true size or distance of the approaching object (27, 28). It was recently discovered that the zebra finch nucleus rotundus also contains cells that respond during simulated flight if an approaching feature is located at the point of expansion, suggesting that the tectofugal pathway may also be involved in flight control (22).

In this study, the birds steered toward positions that would have reduced feature expansion, ρ , in the vertical axis resulting from any additional lateral deviation (Fig. 5C). In treatments with the same pattern on both sides, the birds remained on average centered over the midline (Fig. 5D; see the *SI Appendix* for details). This finding indicates that the birds were not necessarily attracted to the fine horizontal gratings, suggesting instead that they may have been less repelled by them. Additional experiments are needed to test whether lateral course control is indeed based on our proposed mechanism of expansion reduction (because smaller features do not expand as rapidly) (Fig. 5), as opposed to an attraction effect or an effect of feature size independent of expansion. For example, the avian visual system may be tuned to particular feature sizes or spatial frequencies that may be easy to resolve visually and track (5, 18, 29, 30). Additional studies that directly manipulate expansion are needed to test these alternatives. Another question is whether this differs across bird species with diverse visual systems and flight styles.

Our results do not rule out the use of pattern velocity altogether. Indeed, we suggest that birds use vertical pattern velocity to maintain flight altitude, similar to *Drosophila* (16). It is possible that we might have been able to observe an effect of nasal-to-temporal pattern velocity on lateral course control with much larger manipulations, or manipulations in other parts of the visual field [e.g., ventral (8)]. It is important to note that like the hummingbirds in our study, the budgerigars and honey bees in other studies also had extensive experience in the flight chamber (6, 11, 12), and both birds and bees are capable of sophisticated spatial memory and mapping (10, 31–33). Unlike previous studies, our results conclusively demonstrate that birds use the vertical extent (i.e., height) of features in the lateral visual field to guide flight, even in the absence of strong nasal-to-temporal pattern velocity cues (Fig. 4 and Movie S2). This finding has implications for studies across other taxa: a tendency to steer away from vertical gratings does not necessarily imply a response to nasal-to-temporal pattern velocity (e.g., refs. 4, 34, 35).

Collectively, our findings suggest that birds control forward flight by monitoring changes in the vertical axis: specifically, the height of features and vertical pattern velocity. This finding is consistent with other laboratory studies showing that flying birds rapidly stabilize key features in their visual field (36). In nature, collisions may be avoided by monitoring changes in the apparent size of features (22), such as trees and branches, as well as changes in the vertical position of those features. Although our experiments focused on manipulating a limited number of cues, we do not suggest that these represent the only visual guidance strategies used by birds. Indeed, the birds in our study and in previous studies could avoid collisions despite a variety of visual patterns (Movie S2) (11). The birds may also monitor and stabilize features in the frontal optic flow field (1, 22, 26, 36), which in our study would have included features such as the perch, feeder, and edges of the rectangular end walls of the chamber. Natural scenes provide an even richer mosaic of optic flow cues for distance estimation. Expansion may be especially useful in this context (27), because most natural objects are large enough that the expansion rate rises very rapidly even at slow approach velocities (e.g., 0.1 m/s in Fig. 5).

The discovery of a visual guidance algorithm based on the vertical extent of features in the lateral visual field leads to exciting new questions. Although there have been multiple experiments with insects that demonstrate different mechanisms of forward flight control, the manipulations presented here represent a unique set. To our knowledge, an experiment comparing horizontal grating period sizes (Fig. 4) has not been performed with insects. Thus, we do not know if their visual guidance of forward flight is also influenced by the vertical extent of features. A key distinction between fruit flies (~1 mg), honey bees (~100 mg), and especially hummingbirds (~4,000 mg) is that the magnitude of change in momentum during a collision is much greater for birds, because of their larger body mass. This, explains why bumblebees and other insects often collide with vegetation (37, 38), whereas collisions are

Fig. 5. We propose that expansion may govern lateral course control in birds. Vertical expansion, ρ_v , is defined as the change in the angle, θ , subtended by a feature in the vertical axis (A). The rate of expansion increases much more rapidly for features with a greater vertical extent (i.e., height) (B). Expansion may be perceived as the birds move laterally; this is shown by the green and magenta lines in C and D, which indicate ρ_v at the point of expansion ($\pm 90^\circ$ azimuth, 0° elevation) for a bird moving to the left (green) or right (magenta) at 0.1 m/s (which is typical of the maximum lateral flight speeds observed) (SI Appendix, Table S10). The dashed lines in C and D are the grand mean (average) lateral positions observed for birds that were halfway to the feeder. The shaded regions are the grand mean (average) extremes. Note that all flights started and ended on the midline of the flight tunnel, where lateral position = 0. In our experiments, the birds steered toward a position that would have reduced ρ_v relative to their starting position on the midline (C). When the features on both sides of the tunnel had the same vertical extent (height), the birds remained on average centered on the midline (D). See text in SI Appendix and SI Appendix, Table S10 for details.

a major source of mortality in birds (39). These differences in the risk of damage may lead to different visual guidance strategies, in addition to divergent sensory and neurobiological systems.

One of the most intriguing results across visual guidance studies in insects is that different algorithms are used to control different flight modes (e.g., refs. 16 and 18). Because hummingbird flight is very amenable to study in the laboratory, this presents a powerful opportunity to determine if feature size in general and image expansion in particular are used for guiding different flight modes or restricted to only some aspects of forward flight control. We hope that these questions about visual guidance behavior will also stimulate further research in systems neuroscience that can confirm the proposed mechanisms at a cellular level (22).

Materials and Methods

Animals. Eighteen adult male Anna's hummingbirds (*Calypte anna*) were caught in Vancouver, BC, Canada between March 2014 and April 2015 and housed individually (14). All procedures were approved by the University of British Columbia Animal Care Committee.

Experimental Rig. The flight tunnel consisted of an aluminum frame with acrylic side walls (Fig. 1A). The interior acrylic surface was coated in a frosted window covering (14). Stimulus images were back-projected by six ultrashort-throw DLP projectors (NEC US10w; 120-Hz refresh rate) outside the tunnel (Fig. 1B). Two separate video cards (2GB MSI GeForce GT 640) and splitters (360 MHz VGA) were used to link three projectors on each side. These displays were synchronized by Psychtoolbox-3 (40) for Matlab (Mathworks R2013b). The floor of the tunnel was gray linoleum and the ceiling was nylon netting to permit filming from above. The walls at each end were covered in white paper.

We positioned the feeder and a 10-cm-wide perch 15 cm below the ceiling of the tunnel at either end (Fig. 1A) on the midline. Pilot studies indicated that birds would not descend much lower, as hummingbirds prefer to fly and perch several meters above the ground. Stimulus animations were projected over a depth of 37 cm (Fig. 1A). The walls were blank below the stimulus to facilitate tracking by overhead cameras. For a bird at the average cruising altitude of

1.5 m on the midline, the stimulus subtended 57° vertically on each side. Birds never collided with the walls of the chamber during experiments.

Experimental Stimuli. Stimulus animations were controlled using Psychtoolbox-3 (40). We used red because the DLP projectors produce white by sequentially flashing each of the red-green-blue (RGB) primaries at 120-Hz intervals, and at the outset of this study we did not know that the temporal resolution of Anna's hummingbird vision is below 70 Hz (20). Red was chosen to stimulate the long-wavelength and double-cone photoreceptors involved in motion processing (41) and avian flight behavior (42). For stripe gratings (50% red and 50% black), the average luminance of red features was 8.7 cd/m² (95% CI 8.4, 9.0) and the average luminance of black features was 1.5 cd/m² (95% CI 1.46, 1.54) (Minolta LS-110 photometer). A small incandescent lamp (40 W, 120 Hz) was positioned 1.5 m above the perch to provide additional light and encourage perching at that end. To facilitate filming, near-infrared LED strips (850-nm 5050 lights, environmentallights.com) were affixed along the top of each side of the tunnel, facing the midline. This near-infrared light was detected by our cameras but not the birds because the retinal cones of hummingbirds are not stimulated by wavelengths > 700 nm (41).

For stimuli consisting of stationary horizontal stripes, the color of the topmost stripe was matched for the two walls and was determined randomly, so that birds were sometimes exposed to red on top and sometimes to black on top, depending on the treatment. We verified that the color of the top stripe did not significantly affect the birds' lateral position for treatments with 18.4-cm period horizontal gratings (all $P > 0.27$).

Procedure. Birds in the tunnel were fed ad libitum from a syringe containing 7.5 g/100 mL (wt/vol) sucrose solution. Before an experiment, birds were allowed to explore the stimulus-free tunnel with overhead fluorescent lighting, similar to their aviary housing. A training stimulus consisted of stationary red and black vertical stripe gratings on both side walls. At 10-min intervals, the grating period size was changed (using period sizes 0.58, 1.15, 2.3, 4.6, 9.2, and 18.4 cm, in a different randomly selected order for each bird), with the cycle repeating after 60 min to ensure that birds would be familiar with all sizes. Once birds had begun to feed at regular intervals, the fluorescent lights were turned off. The 60-min training period was repeated at

the beginning of each day to ensure motivation. For experiments using dot stimuli, the training stimulus consisted of stationary dot fields with 20 min at each of the three dot densities (0.47, 0.95, and 1.89 dots/cm²).

Data Collection and Analyses. Experimental treatments were applied in blocks, such that the stimulus changed after a bird was observed to have fed five times. We define a feeding event as the bird traversing the tunnel to dock at the feeder before returning to the perch. The order of treatment blocks was randomized for each bird. Eight cameras (Prosilica GE680, Allied Vision Technologies; Computar H220414C-MP lenses) filmed from above at 100 frames per second (Fig. 1A). Flydra image-based tracking software was used to automatically track the birds' flight trajectories and compute the birds' 3D position (x , y , and z coordinates) in each frame (43). We limited our analyses to times when the birds were within positions 1–5 m along the axial (x) length of the tunnel to omit take-off, landing, and feeder docking. We identified trajectories during feeding events that had a consistent axial flight direction (i.e., toward or away from the feeder), and if more than one trajectory occurred as a bird traversed the chamber, we selected the trajectory with the longest axial (x) distance for analysis. If a bird was tracked for fewer than 2.5 m, that flight was discarded as having insufficient data. In total, 75 of 3,270 flights were discarded (2%) and these were not biased toward any particular treatment.

Because the hummingbirds varied their flight speeds, the times when they flew slowly are represented with more data points in the output of the tracking system. We therefore grouped position and velocity data into 1-cm bins along the axial (x) axis, taking the mean for each bin, and then taking the mean of the bins for each flight to represent the average value while traversing the tunnel. [Movie S1](#) illustrates how average lateral position was calculated from sample flight trajectories. All statistical analyses were performed on these flight averages using R 3.2.1 (44). We analyzed average position using mixed-effects regression models in the nlme package 3.1-120 (45), with a random effect of treatment block nested within individual to account for nonindependence of repeated measures. Hypotheses were evaluated using the glht function in the multcomp package 1.4-0 (46), and P values < 0.05 were considered statistically significant. Data and analyses are provided at https://figshare.com/articles/statistical_supplement_flight_course_control_R/3382759 and in *SI Appendix*.

ACKNOWLEDGMENTS. We thank P. S. Segre, B. Goller, M. V. Srinivasan, D. Lentink, K. Meier, D. Giaschi, D. Schluter, and two anonymous reviewers. The work was supported by a Human Frontier Science Program Grant RGP0003/2013 (to D.L.A.); a Natural Sciences and Engineering Research Council (NSERC) Grant 402677 (to D.L.A.); an NSERC postdoctoral fellowship (to R.D.); and an NSERC graduate fellowship (to T.K.F.).

- Lin H-T, Ros IG, Biewener AA (2014) Through the eyes of a bird: Modelling visually guided obstacle flight. *J R Soc Interface* 11(96):20140239.
- David CT (1982) Compensation for height in the control of ground speed by *Drosophila* in a new, "barber's pole" wind tunnel. *J Comp Physiol* 147(4):485–493.
- Fry SN, Rohrseitz N, Straw AD, Dickinson MH (2009) Visual control of flight speed in *Drosophila melanogaster*. *J Exp Biol* 212(Pt 8):1120–1130.
- Baird E, Kreiss E, Wcislo W, Warrant E, Dacke M (2011) Nocturnal insects use optic flow for flight control. *Biol Lett* 7(4):499–501.
- Dyhr JP, Higgins CM (2010) The spatial frequency tuning of optic-flow-dependent behaviors in the bumblebee *Bombus impatiens*. *J Exp Biol* 213(Pt 10):1643–1650.
- Srinivasan MV, Lehrer M, Kirchner WH, Zhang SW (1991) Range perception through apparent image speed in freely flying honeybees. *Vis Neurosci* 6(5):519–535.
- Baird E, Srinivasan MV, Zhang S, Cowling A (2005) Visual control of flight speed in honeybees. *J Exp Biol* 208(Pt 20):3895–3905.
- Portelli G, Ruffier F, Franceschini N (2010) Honeybees change their height to restore their optic flow. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 196(4):307–313.
- Esch HE, Zhang S, Srinivasan MV, Tautz J (2001) Honeybee dances communicate distances measured by optic flow. *Nature* 411(6837):581–583.
- Srinivasan MV, Zhang S, Altwein M, Tautz J (2000) Honeybee navigation: Nature and calibration of the "odometer". *Science* 287(5454):851–853.
- Bhagavatula PS, Claudianos C, Ibbotson MR, Srinivasan MV (2011) Optic flow cues guide flight in birds. *Curr Biol* 21(21):1794–1799.
- Schiffner I, Srinivasan MV (2015) Direct evidence for vision-based control of flight speed in budgerigars. *Sci Rep* 5:10992.
- Barron A, Srinivasan MV (2006) Visual regulation of ground speed and headwind compensation in freely flying honey bees (*Apis mellifera* L.). *J Exp Biol* 209(Pt 5):978–984.
- Goller B, Altshuler DL (2014) Hummingbirds control hovering flight by stabilizing visual motion. *Proc Natl Acad Sci USA* 111(51):18375–18380.
- Sholtis KM, Shelton RM, Hedrick TL (2015) Field flight dynamics of hummingbirds during territory encroachment and defense. *PLoS One* 10(6):e0125659.
- Straw AD, Lee S, Dickinson MH (2010) Visual control of altitude in flying *Drosophila*. *Curr Biol* 20(17):1550–1556.
- Frost BJ (2010) A taxonomy of different forms of visual motion detection and their underlying neural mechanisms. *Brain Behav Evol* 75(3):218–235.
- Maimon G, Straw AD, Dickinson MH (2008) A simple vision-based algorithm for decision making in flying *Drosophila*. *Curr Biol* 18(6):464–470.
- Sun H, Frost BJ (1998) Computation of different optical variables of looming objects in pigeon nucleus rotundus neurons. *Nat Neurosci* 1(4):296–303.
- Fellows T (2015) Visual resolution of Anna's hummingbirds (*Calypte anna*) in space and time. MSc thesis (University of British Columbia, Vancouver, Canada). Available at <https://open.library.ubc.ca/crlc/collections/ubctheses/24/items/1.0166301>. Accessed June 15, 2015.
- Tammero LF, Dickinson MH (2002) The influence of visual landscape on the free flight behavior of the fruit fly *Drosophila melanogaster*. *J Exp Biol* 205(Pt 3):327–343.
- Eckmeier D, Kern R, Egelhaaf M, Bischof HJ (2013) Encoding of naturalistic optic flow by motion sensitive neurons of nucleus rotundus in the zebra finch (*Taeniopygia guttata*). *Front Integr Neurosci* 7:68.
- Lee DN, Reddish PE, Rand DT (1991) Aerial docking by hummingbirds. *Naturwissenschaften* 78(11):526–527.
- Lee DN, Davies MNO, Green PR, Van der Weel FR (1993) Visual control of velocity of approach by pigeons when landing. *J Exp Biol* 180(1):85–104.
- Lee DN, Reddish PE (1981) Plummeting gannets: A paradigm of ecological optics. *Nature* 293(5830):293–294.
- Kane SA, Fulton AH, Rosenthal LJ (2015) When hawks attack: Animal-borne video studies of goshawk pursuit and prey-evasion strategies. *J Exp Biol* 218(Pt 2):212–222.
- Lee DN (1976) A theory of visual control of braking based on information about time-to-collision. *Perception* 5(4):437–459.
- Gibson JJ (1979) *The Ecological Approach to Visual Perception* (Psychology Press, New York).
- O'Carroll DC, Wiederman SD (2014) Contrast sensitivity and the detection of moving patterns and features. *Philos Trans R Soc Lond B Biol Sci* 369(1636):20130043.
- Reichardt W (1987) Evaluation of optical motion information by movement detectors. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 161(4):533–547.
- Bingman VP, Able KP (2002) Maps in birds: representational mechanisms and neural bases. *Curr Opin Neurobiol* 12(6):745–750.
- Menzel R, et al. (2005) Honey bees navigate according to a map-like spatial memory. *Proc Natl Acad Sci USA* 102(8):3040–3045.
- Krebs JR, Sherry DF, Healy SD, Perry VH, Vaccarino AL (1989) Hippocampal specialization of food-storing birds. *Proc Natl Acad Sci USA* 86(4):1388–1392.
- Scholtyssek C, Dacke M, Kröger R, Baird E (2014) Control of self-motion in dynamic fluids: Fish do it differently from bees. *Biol Lett* 10(5):20140279.
- Ortega-Escobar J, Ruiz MA (2014) Visual odometry in the wolf spider *Lycosa tarantula* (Araneae: Lycosidae). *J Exp Biol* 217(Pt 3):395–401.
- Kress D, van Bokhorst E, Lentink D (2015) How lovebirds maneuver rapidly using super-fast head saccades and image feature stabilization. *PLoS One* 10(6):e0129287.
- Foster DJ, Cartar RV (2011) What causes wing wear in foraging bumble bees? *J Exp Biol* 214(Pt 11):1896–1901.
- Mountcastle AM, Combes SA (2014) Biomechanical strategies for mitigating collision damage in insect wings: Structural design versus embedded elastic materials. *J Exp Biol* 217(Pt 7):1108–1115.
- Loss SR, Will T, Marra PP (2015) Direct mortality of birds from anthropogenic causes. *Annu Rev Ecol Syst* 46:99–120.
- Kleiner M, Brainard D, Pelli D (2007) What's New in Psychtoolbox-3? Version 3. Available at psychtoolbox.org/. Accessed March 3, 2014.
- Herrera G, et al. (2008) Spectral sensitivities of photoreceptors and their role in colour discrimination in the green-backed firecrown hummingbird (*Sephanoides sephaniodes*). *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 194(9):785–794.
- Bhagavatula P, Claudianos C, Ibbotson M, Srinivasan M (2009) Edge detection in landing budgerigars (*Melopsittacus undulatus*). *PLoS One* 4(10):e7301–e7301.
- Straw AD, Branson K, Neumann TR, Dickinson MH (2011) Multi-camera real-time three-dimensional tracking of multiple flying animals. *J R Soc Interface* 8(56):395–409.
- R Core Team (2015) R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, Vienna) Available at: <https://www.R-project.org/>. Accessed June 19, 2015.
- Pinheiro J, Bates D, DebRoy S, Sarkar D; R Core Team (2016) nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-128. Available at <https://cran.r-project.org/web/packages/nlme/index.html>. Accessed July 7, 2016.
- Hothorn T, et al. (2016) multcomp: Simultaneous Inference in General Parametric Models. Version 1.4-5, Available at <https://cran.r-project.org/web/packages/multcomp/index.html>. Accessed June 19, 2015.