Pigeons trade efficiency for stability in response to level of challenge during confined flight

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Individuals traversing challenging obstacles are faced with a decision: they can adopt traversal strategies that minimally disrupt their normal locomotion patterns or they can adopt strategies that substantially alter their gait, conferring new advantages and disadvantages. We flew pigeons (Columba livia) through an array of vertical obstacles in a flight arena, presenting them with this choice. The pigeons selected either a strategy involving only a slight pause in the normal wing beat cycle, or a wings-folded posture granting reduced efficiency but greater stability should a misjudgment lead to collision. The more stable but less efficient flight strategy was not used to traverse easy obstacles with wide gaps for passage but came to dominate the postures used as obstacle challenge increased with narrower gaps and there was a greater chance of a collision. These results indicate that birds weigh potential obstacle negotiation strategies and estimate task difficulty during locomotor pattern selection.

Results

Two Distinct Postures Used—Wing Pausing and Wing Folding. Although a variety of navigation methods were expected, two distinct and stereotyped postures (with some overlap in posture metrics, depicted in Fig. 1 A–C and Fig. S1) were used by pigeons when traversing vertically spaced obstacles. The wings-paused posture was achieved by holding the wings static at the top of upstroke, resuming the wing beat cycle once past the obstacles. The wings-flexed or -folded posture was used in traversal by interrupting the wing stroke at any point, and retracting the wings closely to the body. Wings held in the paused posture are elevated higher and at a steeper pitch than those in the folded posture (Fig. 1 B and C). The wings-folded posture is similar to that adopted by many passerines during intermittent bounding flight, although pigeons do not exhibit such flight behavior when flying in open spaces (11). Distinct from wing position during bounding flight, however, in the wing-folded posture the pigeon’s shoulder remained elevated, whereas the elbow was flexed and the hand wing retracted (adducted) across the body to narrow wing profile breadth.

A Shift from Wing Pausing to Folding as Gaps Shrink. The distribution of traversal methods used by the individual pigeons changed with the gap size between the obstacles they were navigating. In general, ignoring the effect of gap size, the paused posture was used more often than the folded posture. When gaps were wide (~0.4 wingspans), the paused posture was used in almost all trials, but when gaps became narrower and more challenging, the folded posture became the more common strategy (Fig. 2). This shift to the folded posture in narrower spacings continued.

Significance

The real world is a cluttered environment and animals traversing it are faced with innumerable obstacles in their normal locomotion. During normal flight, birds have to avoid hitting trees, lampposts, and other members of flocks. To investigate flight strategies used in these circumstances, we presented pigeons with a simplified challenge, a series of vertical gaps with variable spacings. The pigeons used two discrete postures. One posture granted them greater flight efficiency but was more disrupted when they collided with obstacles, and was used for traversing larger gaps. An alternate flight posture was less efficient but more stable when slight collisions occurred, and was used for traversing smaller gaps. To our knowledge, this is the first time we have seen flight strategies tuned during use in cluttered environments.

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gradually until, at the most challenging spacing that the pigeons would traverse, the folded posture was used in over 60% of trials.

**Paused Posture Disrupts Flight Less—Shorter Duration and Less Height Lost.** That the paused posture is preferentially used when traversing wider, less challenging gaps suggests that it confers benefits over the folded posture; several flight metrics support this (Fig. 3 and Table 1). To assess this, we constructed models that looked at the effects on flight metrics of the traversal method used and gap size, in addition to which pigeon was completing each trial. Trial flight metrics included the following: (i) the time it takes to complete a maneuver, (ii) the height lost during and immediately after the maneuver, (iii) the speed at which the obstacles were approached, (iv) the velocity of the wingtip on the first downstroke after passing through the gap, and (v) the projected position of the wings within a stroke on pass through, had no interruption occurred.

Traversal method had a significant ($P_{\text{effect}} = 0.039$) effect on the time for which a posture is held, with the wings-paused method taking less time than the wings-folded method (Fig. 3A and Table 1). Gap size had no significant effect on maneuver duration ($P_{\text{effect}} = 0.197$).

A longer interruption of the wing beat cycle may be expected to result in more height lost during the traversal. This expectation was borne out; trials in which the folded posture was used lost a mean of 17 cm more height than in trials in which the paused posture was used ($P = 0.019$; Fig. 3B; with some disagreement between analysis methods discussed in Table 1). Both maneuver duration and height lost could be expected to vary with the speed of the individual passing through the gap: faster speeds making for faster transits requiring shorter interruption of the wing beat cycle and consequentially less interruption of lift generation. This would suggest that the advantages of the wings-paused posture seen in maneuver duration and height lost were actually due to differences in preobstacle flight speed, rather than due to a direct effect of the traversal method on the listed metrics. In practice, preobstacle flight speed was not significantly affected by traversal method ($P_{\text{effect}} = 0.440$; Fig. 3C and Table 1), failing to contradict the demonstrated dependence of the prior flight metrics on traversal method and instead supporting the idea that the wings-paused posture is itself less disruptive of flight.

Interestingly, preobstacle flight speed depended upon gap size ($P_{\text{effect}} < 0.001$; Fig. 3C and Table 1). This suggests an element of caution or apprehension is present in flight control, with more challenging trials being approached and traversed more slowly than those with a wider margin for error before a collision occurs.

In addition to the shorter interruption of the wing beat cycle, the wings-paused posture may allow the initial downstroke after passing although the obstacle to be stronger, as the wings are prepositioned for downstroke initiation. This effect was not seen, however, with only gap size having a significant effect on the downstroke velocity following the passage through the obstacle array (Fig. 3D and Table 1). This, too, fails to contradict the idea

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**Fig. 1.** Two traversal postures: wings paused in upstroke and wings folded. Two stereotyped groups of postures were adopted in traversing the gaps between obstacles: (A) the “wings-paused” case in which the wings were held at the top of upstroke, with downstroke resuming on the far side of the obstacle array, and (B) the “wings-folded” case in which the wing stroke was interrupted and the wings tucked along the body and unfolded after passing between obstacles. These postures were quantitatively classified into paused and folded clusters (C) by applying a normal mixtures model to wrist elevation and wing pitch. Each posture class exhibits a stereotyped or typical posture near the centroid of their respective clusters, within a distribution of similar poses. In D, wrist elevation, the height difference between the mean of the torso-mounted markers shown in Fig. 5S4A and the wrist marker, is directly compared between postures. Similarly, in E, wing pitch, the pitch angle between wrist-wingtip line and upper-lower torso markers line, is directly compared between postures. In both cases, one-way ANOVA tests show significant differences between each posture’s mean pitch and elevation. Additionally, standard least-squares linear models of pitch and elevation as they depend on individual pigeon, traversal method (pause or fold), gap size, and the interaction between traversal method and gap size show traversal method as having a significant effect ($P_{\text{effect}} < 0.001$ in both cases).

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**Fig. 2.** Fraction of trials using each posture as gap size changes. As the openings narrow, the strategy used shifts from predominantly pausing the wings to folding the wings in a majority of trials. A least-squares linear fit to the fraction folded or fraction paused, means across individuals, shows a significant dependence on gap size ($P = 0.035$ in both cases, as each is the inverse of the other).
Effects of traversal method and gap size on flight metrics. Flight metrics are affected by individual pigeon used, traversal method, and gap size. The interactions between traversal method, gap size, and flight metrics are shown here as quantile plots (with outlier whiskers), whereas their significance is judged by ANOVA. Traversing the obstacles with the paused posture (A) takes less time than doing so with the folded posture and (B) loses less height than doing so with the folded posture. These advantages of the paused postures are not a result of either (C) faster traversal of the obstacle array when the paused posture is used nor of (D) faster downstroke speed when the paused posture is used; neither of these flight metrics are significantly affected by traversal method. Likewise, maneuver duration and height lost are not correlated with gap size. This rules out preference for the wings-paused posture itself is less disruptive of flight and lift generation.

**No Significant Effect of Projected Wing Stroke Position.** A further alternate hypothesis to explain the posture choice would be that selection is governed by an individual’s position in the wing beat cycle during obstacle approach. Plausibly, the paused posture may be used in cases where the wing beat cycle would have been at or near the top of upstroke during obstacle traversal and the folded posture preferentially selected where the wings would be near the bottom of downstroke or transitioning into upstroke. However, the predicted position within the wing beat cycle (as a fraction of the complete upstroke-peak to upstroke-peak wing beat remaining) is not significantly different between the traversal methods ($P_{\text{effect}} = 0.338$; Fig. 3E and Table 1). This supports that decision factors other than location within the wing stroke are responsible for the posture used.

**Folded Posture Is More Stable in the Face of Collisions.** At the narrow spacing at which the wings-paused posture was used, occasional contact between the wings and the poles was observed as a result of turn-induced roll from the maneuvering required to center the bird in the gap (11% of trials, predominantly at the smallest two gap sizes, insufficient to block traversal in all but 1.8% of trials). This contact suggests that the wings-folded posture used to navigate narrower spacings provides some collision-related fitness benefits predicted by the flight metrics either by reducing collisions with obstacles in challenging cases, or by mitigating the consequences of collisions when they do occur. Measurements of the distance between wingtip markers indicate that the average stereotyped wings-paused posture actually has a narrower profile than that of the folded posture: 16 cm in the paused case compared with 18 cm in the folded case. Although stereotyped profiles do not account for the narrowest achievable width under either posture, this does not support use of the wings-folded posture as a means to reduce the frequency of collisions through a reduced forward profile.

However, modeled collision responses suggest that the folded posture is less susceptible to perturbation than is the paused posture. To analyze this, responses to collisions were quantified with rigid-body models of the two postures (Fig. 4A and B) using digitized marker locations and previously described mass distributions ($9$). All observed collisions occurred along the leading edge of the distal section of the hand wing; no head, body, or proximal wing collisions were observed. In colliding areas of the hand wing, a perturbing force induced a rotational acceleration -20% higher in the paused posture than in the folded posture (Fig. 4C). The reduced response to a perturbation by the folded-wing posture suggests its use when narrower gaps are present may serve to reduce the consequences of unintended collisions with obstacles and increase flight stability.

**Discussion**

When faced with an obstacle, an animal may alter its gait as it attempts to traverse it. Here, pigeons traversing challenging vertical obstacles choose between a traversal strategy of greater efficiency and a strategy that grants greater stability when a misjudgment leads to collision. Sensibly, the efficient flight strategy is not significantly different between the traversal methods ($P_{\text{effect}} = 0.338$; Fig. 3E and Table 1). This supports that decision factors other than location within the wing stroke are responsible for the posture used.
Table 1. Parameter effect significance

<table>
<thead>
<tr>
<th>Model effect</th>
<th>Manuever duration, s F ratio</th>
<th>Height lost, m F ratio</th>
<th>Preobstacle speed, m/s F ratio</th>
<th>Downstroke speed, m/s F ratio</th>
<th>Stroke fraction at maneuver F ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pigeon</td>
<td>1.15 0.327</td>
<td>7.02 &lt;0.001*</td>
<td>9.85 &lt;0.001*</td>
<td>1.14 0.334</td>
<td>0.18 0.907</td>
</tr>
<tr>
<td>Traversal method</td>
<td>4.55 0.039*</td>
<td>2.22 0.142</td>
<td>0.61 0.440</td>
<td>0.73 0.340</td>
<td>0.93 0.338</td>
</tr>
<tr>
<td>Gap size</td>
<td>1.63 0.197</td>
<td>8.09 &lt;0.001*</td>
<td>13.04 &lt;0.001*</td>
<td>3.78 0.035*</td>
<td>1.64 0.192</td>
</tr>
<tr>
<td>Traversal method × gap size</td>
<td>0.78 0.514</td>
<td>0.66 0.581</td>
<td>0.62 0.602</td>
<td>1.75 0.192</td>
<td>1.30 0.284</td>
</tr>
</tbody>
</table>

*F ratios and effect significance probabilities for parameters in standard least-squares linear models of flight metrics as they depend on individual pigeon, traversal method (pause or fold), gap size, and the interaction of traversal method and gap size. All models that show at least one significant effect, denoted by *, have fits significantly better than random. The individual pigeon used in a given trial affects both the height lost during obstacle traversal and preobstacle speed. The traversal method used has an effect on the time it takes to complete the maneuver, compared with a direct ANOVA comparison in Fig. 3, which indicates an interaction between height lost and traversal method. Gap size affects height lost, preobstacle speed, and the speed of the first downstroke following obstacle traversal, whereas the cross of traversal method and gap size has no significant effects.

chosen where gaps are wider and there is less chance of a collision occurring, whereas the more stable strategy is used only as the probability of a misjudged traversal increases.

That the folded posture is the less efficient of the two used is suggested both directly by the increased maneuver duration and height lost in paused traversals, and indirectly by the aerodynamic measurements made of pigeons and other birds in intermittent flight experiments in wind tunnels where flapping was momentarily ceased (11, 12). Pigeons do not engage in intermittent bounding flight with a wings-folded phase in free flight, either in the wild or in wind tunnels (11). This is likely due to the decline in bounding flight’s efficiency advantage as body size increases: by the time a bird reaches the size of a pigeon, there is little or no energy savings from bounding flight (13). This adverse scaling of bounding energetics is attributed to the mass-specific power needed in bounding flight; larger fliers lack sufficient reserve capacity to generate the larger lift needed to effect and realize an energetic savings from periods of ballistic flight. That pigeons lack the lift reserves needed to benefit from bounding flight is further supported by the lack of difference in wingtip downstroke speed between traversal methods. As a proxy for pectoralis force, this suggests that there is no reserve power to generate more lift and halt the height loss associated with the longer maneuver that results from the interruption of lift generation seen in the wings-folded posture (14). Thus, the folded posture is the energetically unfavorable approach to obstacle traversals.

However, although the folded posture lacks the efficiency of the paused posture, the primary advantage of the folded posture appears to lie in its increased resistance to perturbation when obstacles being traversed collide with distal wing sections. This increased resistance to perturbation or stability, as shown in our rigid-body model, is likely due to the folded posture’s combination of (i) a decreased lever arm upon which a collision force can act, and (ii) a shallower angle of the collision relative to the surface of the wing allowing more of the force to be shed. These stability advantages explain the selection of a flight maneuver whose opportunity cost is decreased efficiency, and suggests an element of risk assessment where the known decrease in efficiency is balanced against the estimated likelihood of collision.

The choice between these two postures seems mediated by an element of caution or uncertainty. We interpret the approach speed as a proxy indicator of caution or uncertainty, as decreased flight speed permits more time to plan passage through the obstacles but requires increasing amounts of energy as speed decreases. This energy increase is particularly sharp in the sub-5-m/s speed regime used across all obstacle approaches (10). It is likely that the significant decrease in approach speed as trial challenge increases indicates an increased level of caution on the part of the birds, caution that informs the choice of traversal posture.

In these obstacle traversal flights, pigeons demonstrated that, when faced by a challenge, an individual selects more minimal or more substantial interruption of their locomotion pattern and that the level of challenge may mediate the decision. Uncertainty, likelihood of collision, and negative consequences of failed traversals are all factors that drive locomotion strategies toward more

Fig. 4. Stability comparison between postures. Positions of the body, the head, and along the wings (as in Fig. S3A) determine the locations of point masses in a mass distribution model (9). Spheres whose volume is proportional to their relative mass depict both posture models, with black and eye markings for orientation. In the normalized paused posture (A), the mass of the wings is extended above and outward from the body. In the wings-folded posture (B), the wings are tucked lower and closer to the body. The posture models are used to calculate (C) the response to a perturbing torque generated by a simulated forward flight collision between the environment and the hand wing (where all observed obstacle collisions were observed to impact). This response is given as the angular acceleration (dω/dt) resulting from a perturbing torque, normalized to the maximal acceleration, providing a measurement of destabilizing rotation to be countered following wing strikes. The folded posture suffers less rotational perturbation across 90% of the wingspan, reflecting a more stable posture.
cautious choices, whereas the decreased efficiency or speed of cautious choices push toward unaltered locomotion.

Methods

Pigeon Care. Four wild-caught pigeons were housed in a communal coop at the Concord Field Station (Bedford, MA) in accordance with protocols approved by Harvard University’s Institutional Animal Care and Use Committee. When used in flight trials, birds were transported to experimental facilities in individual carriers and provided food and water ad libitum.

Flight Corridor and Obstacles. A 24-m-long by 2.3-m-wide by 2.3-m-tall flight corridor was used for these trials (Fig. S2). The flight corridor’s walls were hung plastic sheeting with which the birds avoided contact or collisions. The ceiling was constructed of stretched 2-cm netting to permit illumination and high-speed filming of flight from above without allowing birds to pass above obstacles in the flight corridor.

An obstacle array was placed in the center of the flight corridor, consisting of a line of evenly spaced vertical PVC poles. These obstacle poles reached from the floor to the ceiling of the corridor and were 4.2 cm in diameter. The poles were fixed to an extruded aluminum rail (80/20, Inc.) at floor level, allowing the space between adjacent poles to be increased or decreased between trials. Thus, the birds were obliged to traverse obstacle arrays containing gaps between 13 and 26 cm, ~0.2–0.4 wingspans for the mean 64-cm wingspan of birds used in this study. Random permutations of gap sizes were used from trial to trial, minimizing anticipation and learning.

Birds were trained to fly on cue between 1.2-m-tall perches placed at either end of the corridor. Flight obstacles were located a minimum of 8.5 m from either perch, causing the birds to consistently approach the obstacles in level flight. No significant difference in flight path height or angle was observed across trials for individual pigeons. In all gap sizes used, pigeons voluntarily traversed the obstacle array in more than 95% of the attempted trials. Trials in which the bird refused to traverse the obstacle array were discarded. Use of gap sizes below 0.2 wingspans resulted in sharply increased refusal rates.

Filming and Markers. Throughout all trials (n = 78), birds were recorded with three FastCam SA3 and two FastCam 1024PCI cameras (Photron). Synchronized movie was recorded at 500 Hz with a shutter speed of 1/1,000 s. Movies were saved and evaluated as uncompressed AVIs. Excerpts from these movies are shown in Fig. S1.

Custom active markers (eight sub-0.1-g surface-mount infrared light-emitting diodes) were mounted to key anatomical locations to speed movie processing (Fig. S3A). These active markers appeared to the infrared sensitive cameras as bright point sources but did not attract the attention of the pigeons to which they were mounted. A backpack-mounted lithium battery system powered these markers. The combined backpack and marker system never exceeded 9% of an individual’s mass. Active markers were placed at the center of the head, 2 cm from the left and right wingtips, and in a plane on the bird’s back surrounding the powering battery. Marker locations were reconstructed using DLTdv5 (15) and analyzed using custom MATLAB (Mathworks) and Python scripts. Raw point clouds from this digitization are shown segregated by posture in Fig. S3B. When tracking markers over multiple frames, marker location was filtered by a fourth-order Butterworth filter with a low-pass cutoff frequency of 100 Hz, more than twice the wing beat frequency.

Trial Evaluation and Modeling of Effects. On viewing flights at reduced playback speed, two distinct postures were used to traverse the obstacle array: (i) a paused posture where the wings were held at the top of the wing stroke, and (ii) a folded posture where the hand wing was hinged back, adducting at the wrist to reduce the wingspan.

Each trial’s posture was first visually coded as paused or folded after examining multiple views (by one observer: C.D.W.). Following this, sufficient points were visible for digitization during the execution of a posture to quantitatively classify 88% of trials by two posture metrics: (i) wing pitch relative to the torso’s backpack markers and (ii) elevation of the wrist markers above the torso’s backpack markers (Fig. 1C). These two metrics were segregated into groups using a Gaussian or normal mixtures model in statistical analysis software JMP (SAS Institute). Treating the trials’ locations in pitch-elevation space as a mixture of normal distributions permits the small intersection of the folded and paused populations seen in Fig. 1C. We treat a >50% affinity for a given group as assignment into that group. This assignment method, when applied to the 88% of trials that we quantitatively scored, agreed with visual coding in all but 12% of cases. Further analysis use the normal mixture posture classification for the 59 trials where it is available and the (validated as largely agreeing) visual classification for the remaining trials in which markers were partially occluded.

Referenced metrics of flights are calculated from tracked marker data in the following fashion. Flight speed was taken from differentiation over time of the location of the head-mounted active markers. Wing stroke interruption was determined by marking the times at which the wingtip markers were observed to first cease and then resume the stereotyped pattern of the wing beat cycle. The point at which the birds passed the obstacles was taken to be when the head marker location passed through the plane defined by the obstacle poles. Downstroke wing speed was taken from the maximum velocity of the wingtip marker on the first downstroke after resumption of flapping, although this method was only taken from the subset of trials (80% of all) in which the view of the wingtip markers was not obstructed by obstacles. The wing beat cycle was determined by selecting the points at which the wings were at the peak of upstroke and the bottom of downstroke. The cycle duration was found by taking the mean of the resulting upstroke and downstroke durations. The position in this cycle at which a pigeon would be during obstacle traversal, had it not interrupted its wing beat cycle, was found by projecting the mean cycle forward from the last upstroke or downstroke completion before obstacle traversal.

For flight metrics, effects were screened for significance using standard least-squares linear models in JMP. Models were treated as three-way ANOVAs with interaction subject to the fixed factors: individual pigeon, gap size, maneuver method, and the interaction between gap size and maneuver method. Model effects were deemed to have significantly affected a flight metric based upon F ratio and corresponding P values (~0.05 taken to be a statistically significant effect size). Model results are summarized in Table 1 and Fig. 3.

Stability estimations shown in Fig. 4 were calculated as the instantaneous angular acceleration resulting from a force applied to a point along a rigid-body model of the pigeon:

$$\mathbf{\ddot{\omega}} = \mathbf{\frac{\partial}{\partial t}} \mathbf{\omega} + (\mathbf{\mathbf{l}} - 1)^{-1} \mathbf{\omega} \times (\mathbf{\mathbf{I}}(\mathbf{F}))$$

The mass locations in the rigid-body model were calculated from marker positions (Fig. S3A) and the mass magnitudes were taken as fractions of the individual’s body mass measured directly preceding flight trials, both as in Ros et al. (9).

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