

VARIATION IN KINEMATICS AND DYNAMICS OF THE LANDING FLIGHTS OF PIGEONS ON A NOVEL PERCH

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Summary

Pigeons made 10 flights to a novel perch. Kinematic measurements of these flights were obtained from video recordings, and the forces exerted on the perch on each landing were measured. There was wide variation (20-fold range) in the kinetic energy of the pigeons just before landing, arising almost entirely from variation in horizontal velocity. The maximum force exerted on the perch varied in magnitude from approximately twice to eight times the pigeons' body weight, and in direction from 40 to 90° below the horizontal. In landings with high final kinetic energy, the maximum force exerted on the perch was larger and was applied at a shallower angle than in those with low final kinetic energy. Landing flights with

high final kinetic energy showed straighter trajectories and a larger peak deceleration during the last 300 ms of approach flight than those with low final kinetic energy, which had downward-curving trajectories and a more prolonged and steady pattern of deceleration. Mean final kinetic energy was lower in the first two landings made on the perch than in subsequent landings, indicating that pigeons are more likely to adopt a slow, downward-curving approach to a novel perch and a fast, straight approach to a familiar one.

Key words: pigeon, *Columba livia*, landing, flight, kinematics, kinetic energy, force.

Introduction

Birds are able to land from flight on many kinds of surface, including flat expanses of ground or water, vertical tree trunks and perches such as ledges or branches. Landings may be performed in turbulent air, and some kinds of perch may sway in the wind or flex as the bird touches down. The control systems that allow birds to land under all these conditions are of interest both as examples of general mechanisms of fast and accurate visual control of movement and also for their importance in the evolution of avian flight.

One possible means of landing is by making a slow, hovering descent onto a perch. By descending slowly, a bird can gain time in which to adjust its trajectory and so reduce the risk of errors in placing its feet. Such errors could cause torsional forces that may damage the feet or legs (Caple *et al.* 1983). This 'hovering' form of landing is predicted to be energetically expensive and, owing to the adverse scaling of mass-specific power (Pennycuick, 1975; Rayner, 1979), is only possible for small birds.

Alternatively, a bird could land by following a shallow descent trajectory, either gliding or in powered flight. Once close enough to the ground, it could increase the angle of attack to slow its forward speed and stall the flow of air over its wings, as a pilot does when landing by flaring. This form of landing will be possible for a bird of any size and will be energetically

cheaper than a hovering landing. A shallow descent onto a suitable ground surface will require relatively simple control of speed and trajectory, but will pose greater problems for a bird attempting to land on a discrete perch. Since the approach is faster than in a hovering landing, there will be less time for adjusting the trajectory close to the perch and a greater risk of a damaging error on contact with it.

Hovering and shallow descent both require aerodynamic adjustments to brake a bird's flight, but differ in the relative timing and strength of braking of horizontal and vertical motion. It is therefore possible that they represent the ends of a continuum of forms of landing flight. Different species will operate in different parts of this range, and it is likely that any particular species will be able to adjust its mode of landing according to circumstances such as the speed and direction of the landing approach, the type of landing surface and the motion of the surrounding air. The landing methods used by birds can therefore be investigated not only by comparing different species but also by analysing variation in landing behaviour within a species. Here, we will adopt the latter approach. We will examine variation in the form of landing flight in domestic pigeons (*Columba livia*), because they are medium-sized birds capable of hovering briefly and, hence, are likely to exhibit a range of forms of landing.

In the experiments described here, a perch that was novel to the birds was used to achieve the required variation between flights. This method contrasts with previous work (e.g. Lee *et al.* 1993), which has typically taken mean measurements across samples of flights. The present methods are also novel in a second respect, as they involve simultaneous measurement of both kinematic and dynamic variables. By using an instrumented perch to measure the forces exerted by pigeons on landing, as Bonser and Rayner (1996) did for landings by starlings (*Sturnus vulgaris*), and combining these results with kinematic data from video recordings of the same landings, we can more completely describe each landing.

Materials and methods

Experiment 1

Twenty-three homing pigeons (*Columba livia* L.), of both sexes and at least 1 year old, were used. Experiments were carried out in a flight cage 5.47 m long \times 0.87 m wide \times 2.04 m high, with a brick rear wall and a wire mesh roof and front wall. A cylindrical wooden perch 750 mm long and 20 mm in diameter was placed across the cage, 3.3 m from the entrance hatch to the pigeon loft and at approximately the same height (0.9 m) above the ground.

Eleven pigeons were given free access to the flight cage and the perch for several months. Each one was then allowed to enter the cage individually and was video-recorded while making one landing flight onto the perch. The other twelve birds were also allowed several months to become familiar with the flight cage, but the perch was never present in it until testing began. Birds were tested individually by encouraging them to fly towards the novel perch, and the first 10 landings made on it by each bird were video-recorded. Video recordings were made at 50 fields s^{-1} , under natural light, using a Panasonic MV7 camera with a 1 ms electronic shutter. Recordings were made during the 3 h period either side of noon, under weather conditions ranging from clear sky to full cloud cover.

The field of view of the camera covered the last 0.9 m of the approach flight, and between 8 and 18 frames at 40 ms intervals were obtained from each flight, depending upon the approach speed. Single video frames of the first five flights and of the tenth flight of each bird were photographed from a monitor screen, and an SAC Graf/Bar digitizer was used to obtain from each frame the x and y coordinates of the centre of the eye. The coordinates of markers on the front and back walls of the cage were used to calculate a calibration factor for converting pixels to actual distances, assuming that the bird's head lay in a plane half-way between the two walls. The maximum possible range of variation in actual position will give an error in this calibration of $\pm 2.5\%$.

Approach speed during landing was calculated from the distance between eye positions in the frame in which the feet contacted the perch and in the frame 360 ms earlier. In flights during which the eye was obscured by the wing in either of these frames, the position in the previous frame was used and the time interval was adjusted accordingly. The overall trajectory of

landing flight was measured as the angle relative to the horizontal of a line joining the first available eye coordinates with those in the frame where the feet were first in contact with the perch.

Experiment 2

Eleven pigeons (mass 0.49 ± 0.07 kg, mean \pm s.d.) were given several months to become familiar with the flight cage and then made 10 landings each on a novel perch. The procedure described above for experiment 1 was followed, apart from two differences. First, video recordings of landing flights were analysed by grabbing single video fields (taken at 50 fields s^{-1}); coordinates of the eye and of the calibration markers were measured directly from the stored images. This procedure allowed measurements to be obtained at 20 ms intervals.

Second, birds landed on a perch designed to measure the horizontal and vertical components of the force acting on the perch during landing. The perch was cylindrical, 650 mm long and 22 mm in diameter, attached to mountings allowing free and independent movement in the horizontal and vertical directions. The masses of the horizontal and vertical components of the mountings were, respectively, 1.25 kg and 2.9 kg. The two pairs of leaf springs supporting the mounts had spring coefficients of 1.28 N mm^{-1} and 1.21 N mm^{-1} , respectively. There were two pairs of dashpots on each mounting, with damping coefficients of $35 \text{ N m}^{-1} \text{ s} \pm 30\%$ (horizontal) and $45 \text{ N m}^{-1} \text{ s} \pm 25\%$ (vertical). The displacement of the perch was measured by two potentiometers mounted vertically and horizontally at one end of the perch assembly. The outputs of the potentiometers were digitized at 100 Hz and input to a microcomputer. On each flight, a manual signal just before the bird landed started a program which stored on disc 1000 successive pairs of digitized x and y displacements. Each data set therefore began with a variable number of baseline values for perch position, followed by values sampling the trajectory of the perch, at 10 ms intervals, for up to 10 s after initial impact.

Dynamic variables

The perch was calibrated by measuring the potentiometer outputs when static weights were applied horizontally and vertically to the centre of the perch, and scaling factors in the two axes were calculated from the regressions of output on weight. Horizontal and vertical potentiometer outputs were measured when vertical and horizontal forces were applied, and these measurements were used to estimate cross-talk at 5% and 1% in the two cases, respectively.

Because the potentiometers were mounted at one end of the perch, further calibrations were carried out to determine the relationship between horizontal and vertical scaling factors and the distance from the centre of the perch at which force was applied. The range of distances over which the force of pigeons' landings was applied was estimated from the values for vertical potentiometer output once the perch had come to rest. Since a bird's weight is constant over a series of flights, any variation in resting vertical output is due to variation in lateral position on the perch. For individual birds, the range of resting outputs over their 10 flights was between $\pm 3\%$ and

$\pm 9\%$. Taking the latter value as the worst case, this implied that landing position varied by only ± 30 mm on either side of the centre of the perch, confirming observations that the narrow flight cage forced the birds to fly close to its centre. Over this range, the effect of distance on either scaling factor introduced an error of approximately $\pm 10\%$. However, the error involved in using the ratio of horizontal and vertical displacements to calculate the direction of the force applied to the perch is rather smaller, because variation in the ratio of horizontal to vertical scaling factors is only $\pm 6\%$ in this worst case.

The calibration data were used to calculate the forces acting on the springs at 10 ms intervals following a bird's contact with the perch, within the limits of accuracy described above. Since the perch moves, there are also forces acting to accelerate it and its mountings horizontally and vertically. These were calculated at each 10 ms interval as the product of (i) the masses of the components of the perch assembly moving in each axis, and (ii) the accelerations of the perch in each axis. These accelerations were obtained by first converting potentiometer outputs to displacements, using the calibration factors for the potentiometers, and then using the time series of displacements to calculate accelerations by numerical differentiation. Finally, the forces exerted by the dashpots on the perch were calculated at 10 ms intervals as the product of perch velocity and damping coefficient in each axis. The total horizontal and vertical forces on the perch were obtained by adding the three component forces, and the maximum resultant force and its direction relative to the horizontal were identified in each landing.

Kinematic variables

The x and y coordinates of the centre of the bird's eye were obtained from each video field (i.e. at 20 ms intervals), from the first field in which the eye was visible to that in which the feet contacted the perch. In fields where the eye was obscured by the wing, its position was interpolated from adjacent fields. The eye was chosen as the point on the body that could be located with maximum accuracy, but this procedure required smoothing of the data to eliminate variation in velocity arising from head-bobbing. During landing flight, pigeons bob their heads in synchrony with the wingbeat cycle (Davies and Green, 1988; Green *et al.* 1994). To determine the correct smoothing procedure, the mean period of the wingbeat cycle was measured in each landing flight. Over all flights, the mean period was 128 ms (corresponding to a wingbeat frequency of 7.8 Hz), with a range of 117–145 ms (or 6.9–8.5 Hz, $N=55$).

Since the nearest multiple of the 20 ms sampling interval to the mean period is 6, the horizontal and vertical velocities of the birds were estimated by taking distances travelled by the eye in a 120 ms window advanced 20 ms between estimates. Horizontal and vertical accelerations were then estimated by taking changes in velocity measurements in a 120 ms window, advanced 20 ms between estimates. Following smoothing, the maximum errors in velocity and acceleration estimates arising from digitisation error were $\pm 0.06 \text{ m s}^{-1}$ and $\pm 1 \text{ m s}^{-2}$, respectively. The final kinematic variable obtained was the local trajectory of the path of the eye, relative to the horizontal. This was estimated by

taking sets of six successive eye coordinates and calculating the arctangent of the slope of the reduced major axis regression.

Since the frequency of head bobbing in each individual landing may differ somewhat from the frequency assumed for smoothing purposes, any difference will cause a small error in the smoothed values. By simulating head bobbing as a sinusoidal wave form and comparing different frequencies within the observed range with the chosen frequency, it was found that the worst case error was no greater than 30% of the amplitude of the wave. As the amplitude of bobbing of a pigeon's head during landing flight is approximately 20 mm, and the period of the window is 120 ms, the maximum error in the calculated velocity values will be no more than 0.05 m s^{-1} (i.e. $0.02 \times 0.3 / 0.12 \text{ m s}^{-1}$).

Results

Experiment 1

Of the twelve pigeons for which the perch was novel, eight landed on it within seven flights, a ninth landed after 29 flights, and the remaining three could not be induced to land and were excluded from the following analysis. Fig. 1 shows the mean and coefficient of variation (standard deviation/mean) of approach speed, across these nine birds, in the first five landing flights and in the tenth landing flight. The increase in speed over trials was significant (Friedman test, $\chi_r^2=13.9$, d.f.=5, $P=0.016$), but no differences between speeds on successive pairs of trials were significant. Mean flight speeds for individual birds, across landings, ranged from 1.27 to 1.69 m s^{-1} , with standard deviations of between 0.1 and 0.4 m s^{-1} .

Fig. 1 also shows the mean and coefficient of variation of approach speed of the 11 pigeons for which the perch was familiar. Together, the data show that flight speed increases and the variability of speed tends to decrease over the first four landings on a novel perch, after which values are similar to those recorded with a familiar perch.

Mean landing trajectory (Fig. 2) does not change significantly over the first 10 landing flights (Friedman test,

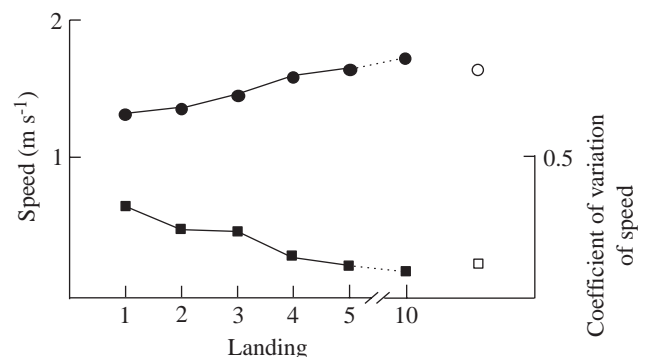


Fig. 1. Mean (circles) and coefficient of variation (squares) of approach speed across birds ($N=9$) in landing flights 1–5 and 10 (filled symbols). The open symbols show the mean and coefficient of variation of speed for birds for which the perch was highly familiar ($N=11$).

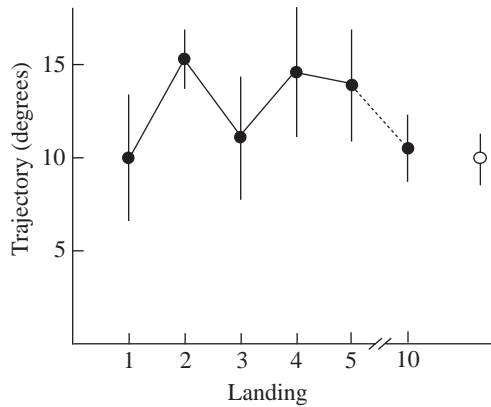


Fig. 2. Mean trajectory relative to the horizontal across birds ($N=9$) in landing flights 1–5 and 10 (filled circles). The open circle indicates the mean trajectory for birds for which the perch was highly familiar ($N=11$). Vertical bars indicate ± 1 S.E.M.

$\chi^2=5.3$, d.f.=5, $P=0.39$). The variability of the landing trajectory tends to decrease over the 10 trials to a value typical of landings on a familiar perch, apart from an anomalously low value on the second trial.

Experiment 2

Variation in landing flight variables

To examine variation in the kinematic and dynamic variables measured, and the relationships between them, a set of landing flights was selected in which all variables were available. Of the 110 flights, 12 were excluded because equipment failures caused either video or perch data to be lost. A further 39 were excluded because the bird's eye was obscured by the frame supporting the perch for more than two fields before contact, limiting the accuracy of kinematic measurements at the end of the flights. Finally, four flights in which the overall trajectory was upwards were excluded, leaving a total of 55 flights from 10 birds.

The first step in data analysis was to estimate the kinetic energy that birds still possessed after braking during the approach to the perch. Values of final horizontal and vertical velocity for each landing were used to calculate the final path velocity, and kinetic energy was estimated as the product of

the square of this velocity and half the bird's mass. The smoothing algorithm described above means that this value is from a 120 ms window centred 50 ms before contact (or in some cases, where the eye was obscured in one or two fields, 70 or 90 ms before contact).

Values of kinetic energy varied considerably, from 0.04 to 0.86 J. Comparing absolute values of velocity, horizontal components are greater than vertical components (means 0.94 and 0.41 m s^{-1} , respectively), implying that most of the birds' kinetic energy arises from horizontal velocity. The horizontal component is also more variable than the vertical component (standard deviations 0.29 and 0.17 m s^{-1} , respectively). Fig. 3 shows final kinetic energy plotted against each component of final velocity. Kinetic energy is strongly correlated with horizontal velocity ($r=0.928$, d.f.=53, $P<0.01$), as expected, but is not correlated with vertical velocity ($r=-0.022$, d.f.=53, $P>0.05$).

The second step is to compare final kinetic energy with measurements of forces acting on the perch as pigeons landed. The maximum force exerted on the perch varied between 7.5 and 31.2 N. In terms of a typical pigeon weighing 0.4 kg, this range is from approximately two to eight times body weight. In Fig. 4, final kinetic energy is plotted against the magnitude and direction of the maximum force on the perch. Kinetic energy is positively correlated with maximum force ($r=0.503$, d.f.=53, $P<0.001$) and negatively correlated with its direction ($r=-0.486$, d.f.=53, $P<0.001$). When the magnitudes and directions of maximum force were recalculated using values of damping coefficients at the extremes of their range of error (see Materials and methods), these correlations remained significant at $P<0.01$ (for magnitude) and at $P<0.05$ (for direction). Pigeons landing with high final kinetic energy apply a greater force on the perch and at a shallower angle than do birds landing with low kinetic energy.

Possible relationships between final kinetic energy and the kinematic properties of flights over the whole approach path recorded were examined in plots of velocity, acceleration and trajectory. Two examples, for landings with low and high final kinetic energy, are shown in Fig. 5. Landings with low final kinetic energy tended to show a steadily increasing trajectory, implying that the flight path curved downwards, whereas those with high final kinetic energy tended to have a relatively straight path. A simple index of flight path curvature was obtained by subtracting the first trajectory value from the last; Fig. 6A shows

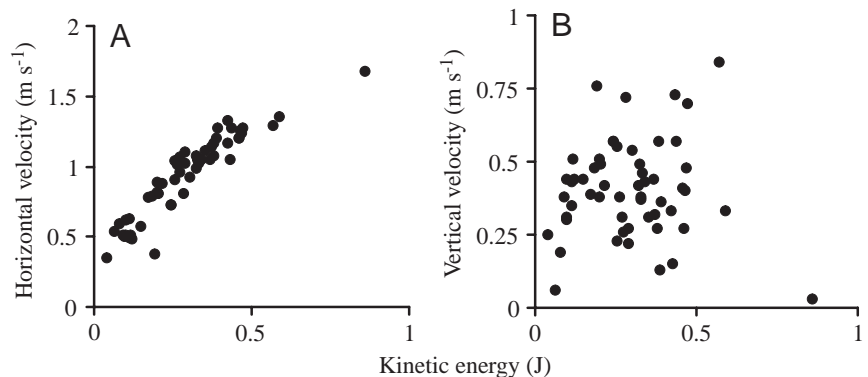


Fig. 3. Relationship between final kinetic energy and (A) final horizontal velocity or (B) final vertical velocity of 10 pigeons in 55 flights approaching a novel perch. Absolute values of velocity are shown.

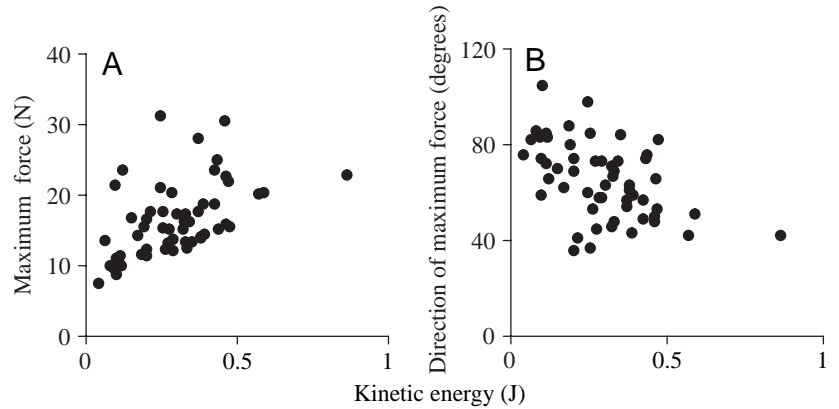


Fig. 4. Relationships between final kinetic energy and (A) maximum force exerted on the perch or (B) the direction of the maximum force relative to the horizontal (increasing angle denotes a more vertical force) for 10 pigeons in 55 landing flights.

this index plotted against final kinetic energy. The two variables are negatively correlated ($r=-0.538$, $d.f.=53$, $P<0.001$), confirming that flights with low final kinetic energy are more strongly curved than are those with high final kinetic energy.

Landings with high final kinetic energy often showed a large peak in horizontal deceleration close to landing, while those with low energy showed either an earlier peak or no clear peak (see Fig. 5). The maximum horizontal deceleration in the last 180 ms of acceleration measurements, and therefore in the last 300–340 ms of flight, was used as an index of the size and timing of deceleration (a 180 ms cut-off was chosen because it was the length of the recording of the fastest flight made). Fig. 6B shows this index plotted against final kinetic energy. The two variables are positively correlated ($r=0.503$, $d.f.=53$, $P<0.001$), confirming that flights with high final kinetic energy have a larger peak in horizontal deceleration late in approach flight.

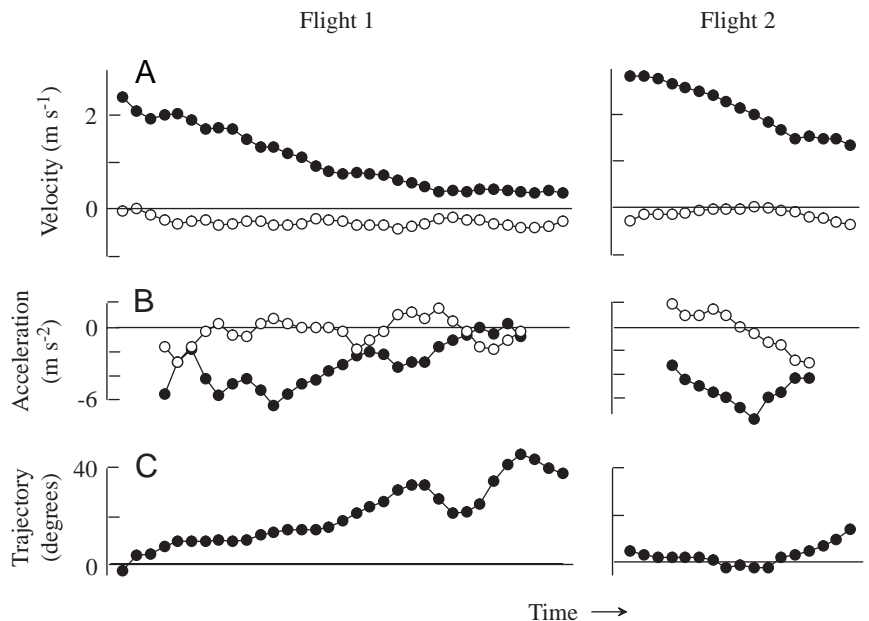
Effects of perch novelty

Since the eye was obscured in more than two video fields before landing in a number of flights, changes in final kinetic

energy as the perch became familiar could not be tested systematically. To provide an indication of changes in final kinetic energy, values from the 55 flights used in the above analysis were averaged over successive pairs of flights. These mean values (Fig. 7) appear to increase over the first four flights, and then decrease slightly after the sixth flight. A statistical comparison was made between the first two flights and flights 5–10. Mean values for final kinetic energy were calculated for each bird from all values available in each of these categories. Eight birds provided sufficient data to calculate both means. For these birds, mean final kinetic energy was 0.25 ± 0.12 J in flights 1–2 and 0.36 ± 0.14 J (means \pm S.D.) in flights 5–10. This difference was significant (Wilcoxon test, $t=1$, $N=8$, $P=0.017$).

Changes in dynamic variables as the perch became familiar were examined using data from the 10 birds for which perch displacements were successfully recorded from all landings. Fig. 8 shows the mean maximum force exerted on the perch by these birds, and its mean direction, over the 10 successive landings. The maximum force appears to increase over the first four landings, but there is no

Fig. 5. Velocity (A), acceleration (B) and trajectory (C) over the course of two landing flights. Flight 1 has low final kinetic energy (0.04 J), flight 2 has high final kinetic energy (0.59 J). (A) Velocity: filled circles represent the horizontal component (positive values are perchwards); open circles represent the vertical component (positive values are downwards). (B) Acceleration: filled circles show the horizontal component (positive values denote increases in perchward velocity); open circles show the vertical component (positive values denote increases in downward velocity). In all three plots, points are plotted at 20 ms intervals.



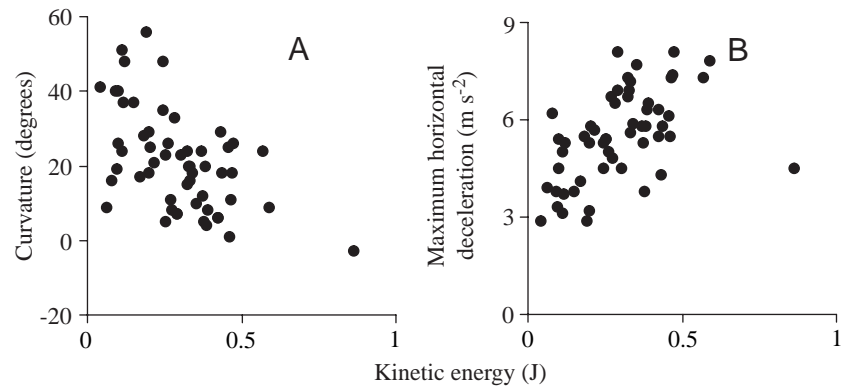


Fig. 6. Relationship between final kinetic energy and (A) curvature of the flight path or (B) maximum horizontal deceleration during the last 300–340 ms of flight for 10 pigeons in 55 landing flights.

significant change over the full 10 landings (Friedman test, $\chi^2=13$, d.f.=9, $P=0.17$). There is also no significant change in the direction of the maximum force over the 10 landings (Friedman test, $\chi^2=10.2$, d.f.=9, $P=0.35$).

Discussion

Variability in landing flight

During the periods of landing flight recorded in experiment 2, pigeons braked and lost kinetic energy. The amount of energy remaining just before contact with the perch varied over an approximately 20-fold range; this variation had no apparent effect on the success or smoothness of landing. Variation in final kinetic energy was due almost entirely to variation in final horizontal velocity, with final vertical velocity making little or no contribution. In particular, there were no landings with high kinetic energy in which birds descended nearly vertically onto the perch.

The data-smoothing algorithm used means that the final kinetic energy is estimated 50–90 ms before contact with the perch, but the further deceleration that can occur in this time (equivalent to approximately half a wingbeat cycle) is small. The correlation between final kinetic energy and the maximum force exerted on the perch implies that little kinetic energy is dissipated by aerodynamic means during this period and that

this energy must therefore be dissipated on landing by the perch and in the bird's legs and lower body.

Heppner and Anderson (1985) found that pigeon take-off flight requires a large downward thrust exerted by the legs in order to gain height before the first downstroke of the wings. These jumps at take-off reach heights of up to 0.03 m, implying that the potential energy gained by a bird of typical mass 0.4 kg is approximately 0.12 J. Our estimated mean kinetic energy on contact with the perch is 0.29 J; given that some of this energy is absorbed by the perch, the mechanical energy gained on take-off is comparable with the energy absorbed by the legs on landing. The functional anatomy of pigeons' legs is therefore critical for both take-off and landing, and this is likely to be the case in other birds with relatively large mass.

Comparable data from another species have been reported by Bonser and Rayner (1996), who measured the forces exerted on a perch as starlings (*Sturnus vulgaris*) landed and took off. The peak resultant force on landing ranged from 0.5 to 2 N, with a mean of 1.2 N, an order of magnitude lower than the forces exerted by pigeons in the present study (Fig. 4A). As a multiple of mean starling body weight, this range is from just below 1 to approximately 3, which is still somewhat lower than the comparable values for pigeons obtained here (2–8 times body weight). This difference implies that pigeons are able to perform landings in which proportionately more kinetic energy is dissipated on landing than are starlings. The direction of the peak force when starlings landed ranged from 50 to 90°, which is similar to the range observed here for pigeons (Fig. 4B).

Our results also identified two approach flight variables which are correlated with final kinetic energy. A relatively straight trajectory and a large peak in deceleration late in approach are associated with high kinetic energy, while a downward-curving trajectory and a more even pattern of deceleration across the approach are associated with low kinetic energy.

To summarise, a number of kinematic and dynamic variables of pigeon landing flight vary together. The extremes of the range of variation can be characterised as low- and high-kinetic-energy landings. In a low-kinetic-energy landing, a pigeon brakes steadily over the last metre of approach flight and follows a downward-curving trajectory. Its horizontal and vertical velocity just before landing are low, and therefore its kinetic energy is

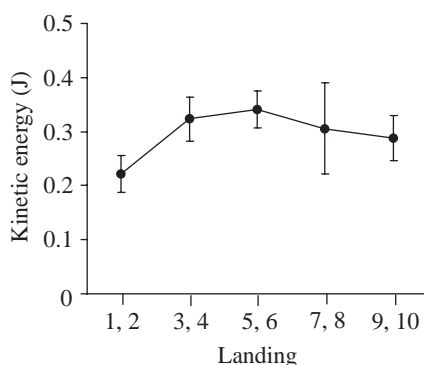


Fig. 7. Final kinetic energy for all landing flights for which complete data were available ($N=55$). Means are calculated over adjacent pairs of landings ($N=12, 10, 12, 9, 12$, respectively). Vertical bars indicate ± 1 S.E.M.

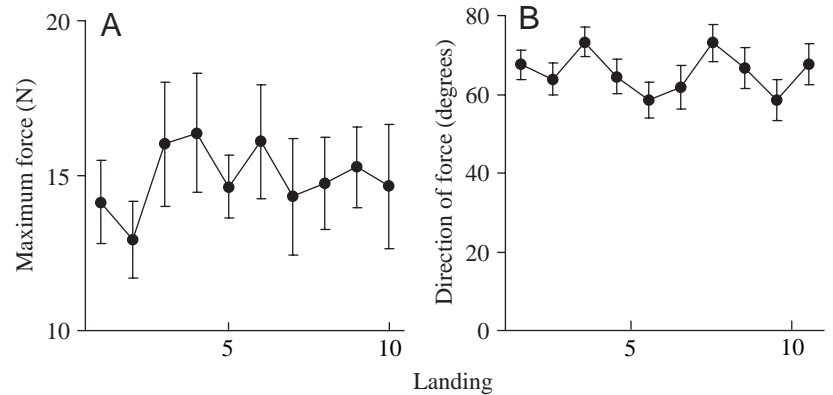


Fig. 8. Mean maximum force exerted on the perch (A) and its direction (B) over the first 10 landings by 10 birds. Values are means \pm S.E.M.

low (<0.1 J). It strikes the perch with a maximum force of approximately twice its body weight, at a direction approximately 80° below the horizontal. In a high-kinetic-energy landing, a large braking force is applied late in the approach, which has a relatively straight trajectory. Horizontal velocity just before landing is high, as is kinetic energy (>0.5 J). The bird strikes the perch with a maximum force of up to eight times its body weight, at an angle of approximately 50° .

Changes in landing flight with perch familiarity

The results of experiments 1 and 2 together provide evidence that pigeons are more likely to perform low-kinetic-energy landings on a novel perch, while high-kinetic energy landings occur more frequently as a perch becomes familiar. In experiment 1, the mean speed of approach increased over the first four landing flights to a novel perch from approximately 1.3 to 1.7 m s^{-1} , while the variability of approach speed tended to decrease. Over the same flights, there was no change in approach trajectory but a tendency for variability in trajectory to decrease. The increase in speed as the perch becomes familiar suggests that there may be a preference for fast rather than slow landing flights, possibly to reduce the power demands imposed by slow flight.

Experiment 2 showed a consistent trend in final kinetic energy, which tended to increase over the first four landings and was significantly greater in flights 5–10 than in the first two flights. The force exerted on the perch also tended to increase over the first four landings, as would be expected if the extra kinetic energy on landing was not all dissipated in the pigeons' legs.

The results of experiment 2 are consistent with the findings of Lee *et al.* (1993) that deceleration increases over the course of a pigeon's approach to a perch and that contact is at a substantial forward velocity. Their analysis used kinematic variables averaged over a sample of flights to a highly familiar perch, and so their conclusions will have described only high-kinetic-energy landings, in which there is a marked peak in deceleration close to the perch and a high final horizontal velocity. The present results demonstrate variability in the kinematics of landing flight that was not apparent in that earlier analysis.

Implications for aerodynamics and control

In the Introduction, two possible forms of landing flight were considered. Hovering landings will assist precise control of foot

placement on a perch, but cannot be performed by large birds lacking sufficient mass-specific power. Conversely, shallow descents require less expenditure of metabolic energy, but appear to present problems of control when landing on a perch. Although we did not observe pigeons hovering during any landing flights, the low horizontal velocities measured in some flights indicate that low-kinetic-energy landings closely approach a hypothetical 'hovering' pattern. In the high-kinetic-energy landings seen more often in our sample, the approach trajectory is relatively straight and final horizontal velocity is high, as would be expected in a shallow descent. It is striking that pigeons are able to make accurate contact with a perch from a fast, straight approach of this kind and do not require a slow, hovering descent to make final adjustments. The implication is that sufficiently accurate visual control of flight speed and direction can be achieved at some distance from the perch.

The variation that we have described in landing flight will have consequences for a pigeon's expenditure of metabolic energy and its risk of injury on landing. In a low-kinetic-energy landing, most of the kinetic energy of flight is lost through braking while airborne and little is dissipated on contact with the perch, in the leg muscles and by other elastic mechanisms. There is more time available in which to adjust the final approach and to place the feet accurately, and less risk of injury to the feet and legs. However, metabolic energy must be expended to maintain slow flapping flight. In a high-kinetic-energy landing, less kinetic energy is lost through braking and more is dissipated on contact. Such a landing flight is metabolically cheaper, as it requires slow flapping flight to be maintained for only one or two wingbeats, but it will also incur a greater risk of injury if the feet are misplaced in some way on contact.

The smaller forces relative to body weight exerted on a landing perch by starlings (Bonser and Rayner, 1996) suggest that their landings may be organised in a 'hovering' mode and that they may not use the high-kinetic-energy form of landing preferred by pigeons. This would be consistent with the difference between the two species in weight and therefore in the metabolic demands of slow flapping flight. Further measurements of kinematic variables during starling landing flights would be required to test for such differences between the two species.

The relative costs and benefits to pigeons of low- and high-kinetic-energy landings are consistent with the changes that we

have observed in their frequencies as a perch becomes familiar. By performing a low-kinetic-energy landing on a novel perch, a bird can reduce the risk of injury if the perch breaks or if it has surface features that could damage the feet. When the perch is familiar and these risks are no longer present, the metabolic work required for slow flapping flight can be conserved by performing a high-kinetic-energy landing, allowing more energy to be dissipated in the perch and legs.

The finding that pigeons make adaptive changes in landing flight behaviour as a perch becomes familiar prompts a number of hypotheses about other properties of perches that they might be able to detect or learn. Are pigeons more likely to perform a low-kinetic-energy landing on a perch with visual features indicating that it is fragile or has an uneven surface? Do pigeons 'search' for the optimum final kinetic energy for a particular perch, as the downward trend in kinetic energy in later flights (see Fig. 7) suggests? Are pigeons able to adjust their landing flight to take account of the mechanical properties of perches capable of dissipating very high kinetic energy or of storing kinetic energy as elastic energy in the way that many tree branches do? The methods that we have used, extended to a range of different perches, could be used to answer these questions and so to define the scope of the capacities of pigeons for adaptive modification of landing flight.

The variation in pigeon landing flight that we have described also provides a potentially useful tool for the analysis of sensory and motor components of flight control. The existing literature on this subject suggests several questions for future research. During landing flight, the activity of forelimb and tail muscles changes, causing adjustments in wing and tail shape that are responsible for braking (Dial, 1992a,b; Gatesy and Dial, 1993). The detailed timing of these changes over the course of landing has not yet been described, and it will be important to determine how the timing of various motor components differs between low- and high-kinetic-energy landing flights, and how this variation affects patterns of deceleration and flight curvature. Variation in landing flight also provides a means of analysing the visual information used to time actions in relation to the approaching perch. This approach has been applied to foot extension (Davies and Green, 1990) and could be extended to other motor components of braking and landing. The orientation of the head during flight plays a role in the control of the landing trajectory (Green *et al.* 1994), and more detailed analyses of changes in head posture during high- and low-kinetic-energy landing flights could shed light on the links between the head-neck and flight control systems of pigeons.

Does the variation that we have observed arise from continuous variation in one or more control parameters or does it represent two or more distinct modes of flight control? If there are distinct modes, what are the factors that pigeons use to select the appropriate one during the approach to landing? The execution of each mode could be largely automatic once it is selected, but the selection mechanism is an added complexity. In contrast, a continuum requires no selection between modes, but presents a more complex ongoing control problem during approach to find the best position on the continuum.

Finally, we should note that there are implications of these findings for theories of the evolution of flight (e.g. Bock, 1986; Caple *et al.* 1983; Gatesy and Dial, 1996; Ostrom, 1986). A pigeon-sized animal capable of gliding could land on the ground from a shallow descent. To land accurately on a perch, however, the capacity for powered flight would be essential either to hover slowly downwards or to achieve sufficiently precise control of the speed and direction of a shallow descent. Any complete account of the evolution of flight must consider not only how animals become airborne but also how they can land safely.

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