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FLIGHT KINEMATICS OF BLACK-BILLED MAGPIES AND PIGEONS OVER A WIDE RANGE OF SPEEDS

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Summary

To investigate how birds that differ in morphology change their wing and body movements while flying at a range of speeds, we analyzed high-speed (60 Hz) video tapes of black-billed magpies (*Pica pica*) flying at speeds of 4–14 m s^{-1} and pigeons (*Columba livia*) flying at 6–20 m s^{-1} in a wind-tunnel. Pigeons had higher wing loading and higher-aspect-ratio wings compared with magpies. Both species alternated phases of steady-speed flight with phases of acceleration and deceleration, particularly at intermediate flight speeds. The birds modulated their wingbeat kinematics among these phases and frequently exhibited non-flapping phases while decelerating. Such modulation in kinematics during forward flight is typical of magpies but not of pigeons in the wild. The behavior of the pigeons may have been a response to the reduced power costs for flight in the closed wind-tunnel relative to those for free flight at similar speeds. During steady-speed flight, wingbeat frequency did not change appreciably with increasing flight speed. Body angle relative to the horizontal, the stroke-plane angles of the wingtip and wrist relative to the horizontal and the angle describing tail spread at mid-downstroke all decreased with increasing flight speed, thereby illustrating a shift in the dominant function of wing flapping from weight support at slow speeds to positive thrust at fast speeds. Using wingbeat kinematics to infer lift production, it appeared that magpies used a vortex-ring gait during steady-speed flight at all speeds whereas pigeons used a vortex-ring gait at 6 and 8 m s^{-1}, a transitional vortex-ring gait at 10 m s^{-1}, and a continuous-vortex gait at faster speeds. Both species used a vortex-ring gait for acceleration and a continuous-vortex gait or a non-flapping phase for deceleration during flight at intermediate wind-tunnel speeds. Pigeons progressively flexed their wings during glides as flight speed increased but never performed bounds. Wingspan during glides in magpies did not vary with flight speed, but the percentage of bounds among non-flapping intervals increased with speed from 10 to 14 m s^{-1}. The use of non-flapping wing postures seemed to be related to the gaits used during flapping and to the aspect ratio of the wings. We develop an 'adverse-scaling' hypothesis in which it is proposed that the ability to reduce metabolic and mechanical power output using flap-bounding flight at fast flight speeds is scaled negatively with body mass. This represents an alternative to the 'fixed-gear' hypothesis previously suggested by other authors to explain the use of intermittent flight in birds. Future comparative studies in the field would be worthwhile, especially if instantaneous flight speeds and within-wingbeat kinematics were documented; new studies in the laboratory should involve simultaneous recording of wing kinematics and aerodynamic forces on the wing.

Key words: black-billed magpie, *Pica pica*, pigeon, *Columba livia*, flight, wingbeat, glide, bound, kinematics, gait, speed.

Introduction

During flapping flight, birds and bats reportedly use two different gaits which can be identified on the basis of the presence or absence of lift production during the upstroke (Kokshaysky, 1979; Spedding *et al*. 1984; Spedding, 1986, 1987*b*, 1992; Pennycuick, 1988; Rayner, 1988, 1991*b*, 1993, 1995). Lift, providing both weight support and thrust, is produced only during the downstroke in the vortex-ring gait, whereas in the continuous-vortex gait, lift is produced during both the downstroke and upstroke (Fig. 1). Many species of birds also use intermittent flight, wherein phases of flapping are interspersed with non-flapping phases during which the wings are extended (flap-gliding) or flexed (flap-bounding; Lighthill, 1977; Rayner, 1977, 1985; Alexander, 1982; DeJong, 1983; Ward-Smith, 1984*a*,*b*; Tobalske and Dial, 1994, Tobalske, 1995, 1996). These intermittent flight styles should possibly be considered to be an integral part of the entire gait of a flying animal. The available evidence suggests that the wings produce lift during glides but not during bounds (Goldspink *et al*. 1978; Spedding, 1987*a;* Thomas *et al*. 1990; Meyers, 1993; Tobalske and Dial, 1994; Tobalske, 1995). At

the least, the use of these intermittent flight styles appears to be related in some way to the use of the different flapping gaits. For example, species that frequently flap-bound also characteristically use a vortex-ring gait during their flapping phases (Rayner, 1991*b*, 1995).

The selection of a flapping gait is dependent upon the speed of flight as well as the morphology of the animal (Rayner, 1988, 1991*b*, 1993, 1995). Regardless of wing shape, most birds and bats use a vortex-ring gait during slow forward flight. However, at faster speeds, species with low-aspect-ratio (short, rounded) wings tend to use a vortex-ring gait whereas animals with high-aspect-ratio (long, pointed) wings tend to use a continuous-vortex gait (Scholey, 1983; Rayner, 1991*b*). The selection of a particular flapping gait also changes with acceleration and deceleration (Rayner, 1991*b*; Tobalske, 1995). Regarding the use of non-flapping phases in birds, some species glide at a wide range of speeds while gradually increasing wing flexion as speed increases [Hankin, 1913; e.g. rock doves (*Columba livia* Gmelin; hereafter referred to as pigeons), Pennycuick, 1968*a*; raptors (Falconiformes), Tucker and Parrott, 1970; Tucker, 1987, 1992; Tucker and Heine, 1990], while other species flap-glide at slow speeds and shift to flap-bounding at faster speeds (e.g. budgerigars *Melopsittacus undulatus* and European starlings *Sturnus vulgaris*; Tobalske and Dial, 1994; Tobalske, 1995).

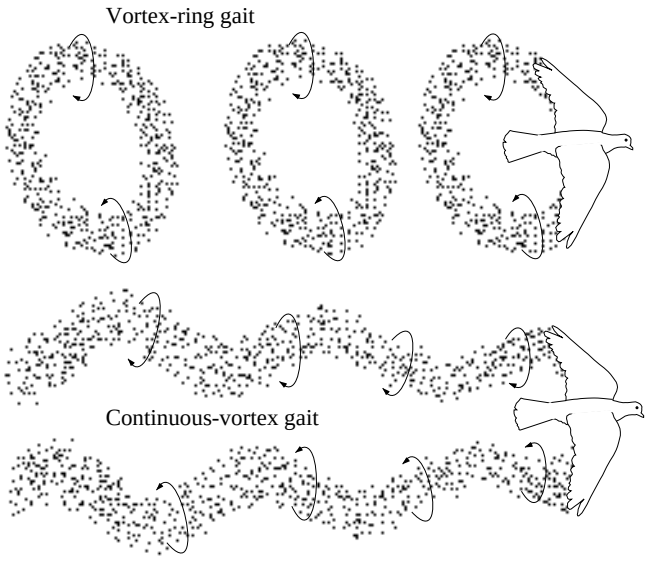

Fig. 1. Gait selection during flapping flight in birds and bats is currently categorized on the basis of the aerodynamic function of the upstroke as revealed through wake-vortex visualization studies during which the animal flies through a cloud of neutrally bouyant particles or soap bubbles (Kokshaysky, 1979; Spedding *et al*. 1984; Spedding, 1986, 1987*b*, 1992; Pennycuick, 1988; Rayner, 1988, 1991*b*; 1993, 1995; Norberg, 1990). In the vortex-ring gait, lift is produced only during downstroke. Kinematic changes in the wing, including flexion and rotation, render the airfoil of the wing ineffective during upstroke. In contrast, lift is produced during both downstroke and upstroke in the continuous-vortex gait. Greater flexion of the wing during upstroke than during downstroke gives rise to an undulating or concertina-shaped wake in the continuous-vortex gait. Figure adapted from Rayner (1988) and Norberg (1990).

Previous researchers have visualized the vortex wakes created by flying animals using stroboscopic photography as the animal flies through a cloud of neutrally buoyant bubbles or small particles (Kokshaysky, 1979; Spedding *et al.* 1984; Rayner *et al*. 1986; Spedding, 1986, 1987*a*,*b*; Rayner, 1991*b*). This technique is useful for estimating aerodynamic function, force production and mechanical power output during flight (Rayner, 1991*b*) but, because the neutrally buoyant bubbles or particles used in vortex visualization studies must be suspended in still air, the animal, rather than the researcher, selects the animal's flight speed. Thus, for most species, it is not clear exactly how gait selection changes over the full range of speeds at which they are capable of flying. The precise role of speed on gait selection during terrestrial locomotion is better understood (Alexander, 1989). Transitions between gaits in terrestrial animals are quite distinct (e.g. the trot/gallop transition) and identify characteristic speeds for scaling locomotor performance (e.g. Fedak *et al.* 1982). Unlike flight studies, however, these studies of terrestrial locomotion are conducted using treadmills that allow the researchers to vary the speed.

For flying animals, a variable-speed wind-tunnel is analogous to a treadmill for animals that walk or run. The animal flies in a clear-walled (i.e. closed-section) or wire-mesh-walled (i.e. open-section) flight chamber through which air is drawn at different speeds, and both lateral and dorsal–ventral views may be obtained directly or with the use of mirrors to observe the animal's flight kinematics (e.g. Pennycuick, 1968*a*,*b*; Torre-Bueno and LaRochelle, 1978; Tobalske and Dial, 1994; Tobalske, 1995; reviewed in Rayner, 1995). Fortunately, the extensive literature on the kinematics of animals in flight (see Scholey, 1983; Norberg, 1990) may be coupled to the vortex visualization data to provide a reasonable interpretation of the aerodynamic consequences of a kinematic event (Rayner, 1991*b*).

Rayner (1993, 1995) provides an equation to predict when gait changes should occur which depends upon the relationship between the aerodynamic conditions at different flight speeds and the efficiency of an active, lift-producing upstroke in a species. Even though the gait used at one speed or across a limited range of speeds has been documented for a number of species (Rayner, 1988, 1991*b*, 1993, 1995), such specific predictions will remain difficult to evaluate in the absence of detailed kinematic or vortex visualization data over a full range of incrementally increasing speeds. For almost all bird species, several important questions remain (Rayner, 1988, 1991*b*). (1) At precisely which speed(s) does a gait transition occur? (2) How do wing and body kinematics change within gaits as speed varies? (3) Which gaits are used for acceleration and deceleration? (4) What is the relationship between the selection of flapping gaits and of non-flapping phases? To begin to answer these questions for birds with different morphologies, we have studied the flight kinematics of black-billed magpies (*Pica pica* L. hereafter referred to as magpies) and pigeons in

a wind-tunnel as we varied airspeed across the range over which they were willing to fly.

Materials and methods

Wind-tunnel and training

The wind-tunnel flight chamber was constructed of clear acrylic (6.3 mm thick) and measured 76 cm×76 cm×91 cm. Air was drawn through the flight chamber by a Buffalo 36-b-vanaxial-asymmetric fan, coupled to a 15 000 W d.c. motor with Edelbrock four-barrel and full racing cam. Airflow was straightened at all airspeeds by a 5 mm honeycomb baffling (10 cm thick) placed upwind from the flight chamber within the funnel intake section. Airflow was laminar in all areas of the flight chamber more than 2.5 cm from the walls, and the velocity of the airflow varied by no more than 4.2 % (Tobalske and Dial, 1994). Wind velocities were monitored with a Dwyer Mark II pitot tube and airspeed indicator calibrated with a Davis TurboMeter electronic airspeed indicator.

The magpies (N=3) and pigeons (N=3) used for the kinematic study were from a larger group of birds used in a variety of flight experiments at the University of Montana, Missoula, MT, USA, and Harvard University, Cambridge, MA, USA. The magpies were trapped from wild populations near Missoula, MT, USA; pigeons were of the Tippler breed, obtained from aviculturalists. Magpies required 4–6 weeks of training before being ready for experimentation; the time required for training the pigeons ranged from 1 to 8 months. Almost all of the magpies trapped from the wild would fly in the tunnel, but the same was true for only 10 % of the pigeons. Training methods were similar to those described by Torre-Bueno and LaRochelle (1978), Tobalske and Dial (1994) and Tobalske (1995). Each bird was trained for approximately 30 min per day to fly, at 2 m s^{-1} speed intervals, across the full range of speeds for which it would sustain flight for at least 30 s (4–14 m s^{-1} for the magpie, 6–20 m s^{-1} for the pigeon). All of the birds were initially trained at the University of Montana (elevation 920 m) before being shipped to Harvard University (elevation <100 m) for subsequent training and experimentation.

Morphometrics

Morphometric variables were collected from each bird after the experiments had been completed. Body mass (g) was measured using a digital balance. Wing measurements, including wing area (cm^2), wingspan (cm), wing length (cm) and length of hand wing (cm), were made with the wings spread as during mid-downstroke (i.e. the emargination on the distal third of each of the primaries was completely separated from adjacent feathers). Wingspan was the distance between the tips of the eighth primaries, length of wing was the distance between the proximal humerus and the tip of the eighth primary, length of hand wing was the distance between the wrist joint and the tip of the eighth primary on the right wing. Wing area was obtained by tracing one wing on millimeter-rule graph paper and counting the number of squares covered by the wing outline; this value did not include any of the area of the body between the wings, as is sometimes the case for measurements of wing area in birds (Pennycuick, 1989*a*; Norberg, 1990). Average wing chord was calculated as single wing area divided by single wing length.

Tail length (cm) was measured from the base of the tail just caudal to the cloaca to the tip of the central retrix; and tail surface area (cm^2) was obtained as for the wing from a tracing on millimeter-rule graph paper of the tail spread to the extent that the acute angle described between the vanes of the outermost retrices was approximately 60 °. Only the area of the tail cranial to the maximum continuous span was included because this is the effective lift-producing region of the avian tail (Thomas, 1993).

Aspect ratio was calculated for a species as the wing span divided by the average wing chord. Wing loading (N m^{-2}) was calculated according to the formula: (9.81 × body mass)/(2 × single wing area). These calculations did not take into account the area of the body between the wings (i.e. unlike Pennycuick, 1989*a*; Norberg, 1990).

Experimentation and analysis

Magpies and pigeons were video-taped at Harvard University while flying at various speeds in the wind tunnel using a Hi-8 video recorder (60 fields s^{-1}, electronic shutter set at 4000 s^{-1}, NTSC standard, Sony model 910). Lateral views were obtained directly through the side of the flight chamber, and dorsal views (not synchronous with the lateral views) were reflected from a mirror mounted at 45 ° on top of the flight chamber. Lateral- and dorsal-view flight sequences, each lasting for at least 10 s, were obtained at each speed for each bird as it flew within the flight chamber. To provide anatomical landmarks for subsequent analysis, 1 cm^2 pieces of red tape were attached to identical landmarks on the body of each bird: the dorsal and ventral tips of the eighth primary, the dorsal and ventral wrist joint, the dorsal center of the head, the lateral center of the head caudal to the eye, the dorsal base of the tail, and the lateral base of the tail.

After the experiments, the Hi-8 video master tapes were transferred to S-VHS with a 60 Hz time code added during transfer (Horita II model TG-50). They were then viewed using a Panasonic AG1960 video player with jog-shuttle advance capability. These video sequences were viewed at normal and slow speeds including single-field advance or reverse using a video monitor and the jog-shuttle advance function. Appropriate fields were then transfered to a Macintosh Quadra 950 computer using Screenplay (Macintosh, Inc.). Viewing and digitizing the anatomical landmarks from the fields of video on the computer were performed using Image (National Institutes of Health) and VideoMotion (supplied by Dr Stephen M. Gatesy) software.

The relatively low fields s^{-1} rate of the video recorder resulted in approximately 10 fields per wingbeat for the average wingbeat in both pigeons or magpies; thus, our maximum measurement error for timing kinematic events was approximately 10 % (Scholey, 1983). This error increased to

20 % for the timing of one half of the wingbeat cycle, approximately the duration of most of the downstrokes. Because of this potential for error, we compared our results from analyses of video images with results from limited samples of high-speed (150–200 Hz) film.

We identified wingbeats and non-flapping phases as being either (1) steady-speed, i.e. matching incurrent airspeed in the flight chamber, (2) accelerative, or (3) decelerative. Flight velocity was calculated from changes in the position of the center of the bird's head during 50 ms (three-field) time intervals. We used the center of the head because it was much steadier during flapping than the body. Acceleration was calculated as the rate of change in flight velocity within the 50 ms intervals. To reduce erratic fluctuations in the data, flight velocity and acceleration values were smoothed as a running average over five points using the formulae in Alexander (1983). Steady flight consisted of no change in velocity in either the anterior–posterior or dorsal–ventral planes for an entire wingbeat during flapping or at least 83 ms (five fields at 60 Hz) of non-flapping flight. Only peak accelerations and decelerations, near $\pm 5\,\mathrm{m\,s^{-2}}$, were used for analysis.

Non-flapping intervals were identified as phases of no wing movement relative to the body lasting at least 50 ms (three fields of video at 60 Hz). Wing postures during these non-flapping phases were classified as being either a glide (wings extended) or a bound (wings flexed against the body, approximately as if perching). We categorized wingspan for 10 non-flapping intervals for each bird and speed. The percentage of non-flapping phases consisting of glides or bounds was then computed for each bird and speed, and a mean value calculated among birds within speeds.

Wingbeat frequency was obtained from a lateral view of a wingbeat during steady-speed flight using movement of the wingtip from the beginning of downstroke to the beginning of the next downstroke. The number of video fields during which the wingbeat occurred was divided by 60 (i.e. fields $\mathrm{s^{-1}}$ of the video camera) to estimate wingbeat frequency. The number of video fields during which downstroke occurred was divided by the total number of fields for the wingbeat and multiplied by 100 to estimate the percentage of the wingbeat consisting of downstroke.

Body and wing profiles and the path of the wrist and the wingtip were traced directly from a video monitor for one magpie and one pigeon. One wingbeat in dorsal view and another in lateral view were traced for a wingbeat of steady-speed flight at each incurrent airspeed. These tracings were scanned into a Macintosh computer and retraced using Canvas (Deneba Software Inc.). Several accelerative and decelerative wingbeats were similarly traced for the magpie and the pigeon flying with the incurrent air in the wind-tunnel set at 10 and $14\,\mathrm{m\,s^{-1}}$, respectively.

Various spans and angles were calculated using digitized points from video fields or directly using a metric ruler and protractor from tracings taken from a video monitor: body angle relative to the horizontal during the beginning of downstroke, stroke-plane angles of the wingtip and wrist relative to the horizontal and relative to the body angle, tail spread as defined by the outermost retrices during mid-downstroke and mid-upstroke, and both wingspan (between the tips of the eighth primaries) and wristspan (between the wrist joints) during mid-downstroke, mid-upstroke, gliding and bounding. A grid on the wall of the flight chamber provided known horizontal and vertical references as well as a scale for transforming all of the measurements to the actual size of the bird.

Values herein are presented as means ± S.E.M. Observed differences between, or among, means are described in general terms rather than with tests of statistical significance.

Results

Morphometrics

There were considerable differences between the morphometrics of magpies and pigeons; in general, pigeons had longer, narrower wings and considerably greater body mass than magpies. Magpies had longer tails and greater tail surface areas (Table 1). Average body mass in pigeons was twice that of magpies. Wing area was slightly greater in magpies than in pigeons, but the pigeons' wingspan and length of hand wing were both greater than those of magpies (Table 1). These differences between species meant that pigeons had higher-aspect-ratio wings and a wing loading twice that of magpies.

Steady-speed flight

Magpies flew at slower speeds in the wind-tunnel than pigeons, although pigeons flew over a greater range of speeds. Magpies could sustain flight for 10 s or more with the wind-tunnel set at speeds from 4 to $14\,\mathrm{m\,s^{-1}}$ and were most willing to fly for extended periods at 8 or $10\,\mathrm{m\,s^{-1}}$. Similarly, the pigeons appeared most comfortable flying at intermediate

Table 1. *Morphometric characteristics of the magpie (*Pica pica*;* N=*5) and the pigeon (*Columba livia*;* N=*3).*

	Magpie		Pigeon	
Variable	Mean	S.E.M.	Mean	S.E.M.
Body mass (g)	158.3	11.6	316.0	2.9
Wing area ($\mathrm{cm^2}$)	320.7	15.3	313.6	4.5
Wingspan (cm)	57.3	1.5	62.2	0.7
Length of wing (cm)	25.1	0.8	27.9	0.2
Length of hand wing (cm)	19.3	0.6	22.4	0.2
Average wing chord (cm)	12.7	0.2	11.2	0.1
Tail length (cm)	24.2	1.6	11.7	1.0
Tail area ($\mathrm{cm^2}$)	137.2	12.0	96.6	1.9
Aspect ratio	4.5	0.1	5.5	0.1
Wing loading ($\mathrm{N\,m^{-2}}$)	2.4	0.1	4.9	0.1

Wing area is for one wing; tail area includes only the effective lift-producing area of the tail, which is cranial to its maximum continuous span (Thomas, 1993). The area of the body between the wings was not included in measurement of wing area and, thus, in calculation of average wing chord, aspect ratio and wing loading (i.e. unlike Pennycuick, 1989*a*; Norberg, 1990).

speeds of 12 or 14 m s^{-1} but sustained flight for at least 10 s at speeds ranging from 6 to 20 m s^{-1}.

Body position within the flight chamber varied according to flight speed in both species, and both species tended to hold their body position within the wind tunnel more constant during flight at the extremes of their speed range. At the slowest speeds, both species flew near the center (halfway between the front and the back) of the flight chamber. At these speeds, magpies tended to maintain their body position in the upper half of the flight chamber (h/H was approximately 0.25, where h is the distance from the center of the bird's body above the altitudinal midline of the flight chamber and H is the vertical height of the flight chamber; Rayner, 1994), whereas pigeons stayed near the altitudinal midline (h/H was approximately 0). At the fastest speeds, both species flew in the rear half of the tunnel, and near the altitudinal midline (h/H was approximately 0). During flight at intermediate speeds within the range of each species, individuals generally moved their body position in the flight chamber forwards and upwards with a series of wingbeats, then backwards and downwards with either wing flapping or a non-flapping phase. These movements were particularly pronounced in the pigeon. Peak altitudes following the ascent generally brought the bird well within the upper quarter of the flight chamber ($h/H \geqslant 0.25$), and minimum altitudes following descent were at or slightly below the altitudinal midline (h/H was 0 to -0.25).

Mean wingbeat frequency during steady-speed flight did not range far from 6 Hz in either species (Fig. 2A). In the magpie, wingbeat frequency was slightly lower between 8 and 12 m s^{-1} than at other speeds, whereas wingbeat frequency in the pigeon was relatively constant at all speeds except for a peak value during flight at 12 m s^{-1}. In both species, the percentage of the wingbeat cycle spent in downstroke decreased with airspeed between the extremes of the speed range but did not change appreciably, or even increased slightly, at intermediate speeds (Fig. 2B). Downstroke made up more than 50 % of the wingbeat cycle for both species, except during wingbeats in the pigeon at 18 and 20 m s^{-1}.

Considerable differences existed between the species with regard to the path of the wingtip and wrist during wingbeats. In the magpie (Fig. 3), the wingtip always described an elliptical path, with the wingtip more anterior during downstroke than during upstroke. In the pigeon (Fig. 4), the wingtips described a 'figure-of-eight' pattern at 6 and 8 m s^{-1}, and an ellipse from 10 to 20 m s^{-1}. At speeds above 10 m s^{-1}, the path of the wingtip moved caudally with increasing speed in the pigeon, but a similar trend was not observed with increasing speed in the magpie. In both species, the wrist described an elliptical or sometimes nearly linear path with the wrist position more caudal during downstroke than during upstroke.

Lateral views revealed that several kinematic variables changed with flight speed in an approximately similar manner for both species (see Figs 3–6): body angle relative to the horizontal decreased, the stroke-plane angles of the wingtip and wrist increased relative to the horizontal, and the legs were progressively flexed. At any given speed, body angle relative

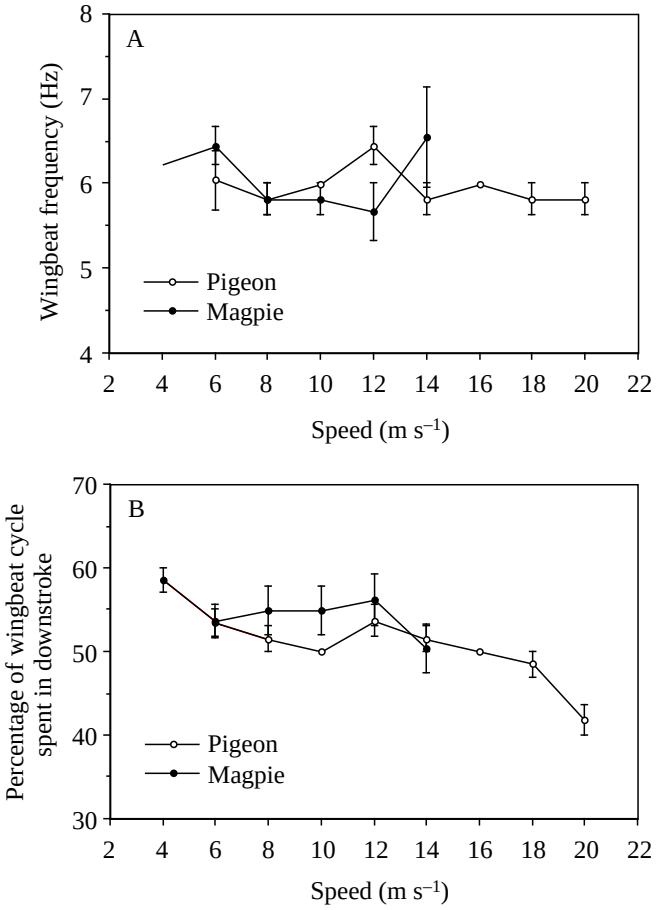

Fig. 2. Wingbeat frequency (A) and the percentage of the wingbeat cycle spent in downstroke (B) in three magpies (*Pica pica*) flying at speeds of 4–14 m s^{-1} and three pigeons (*Columba livia*) flying at speeds of 6–20 m s^{-1} in a variable-speed wind-tunnel. Values are means ± S.E.M.

to the horizontal was always greater for pigeons than for magpies (Fig. 5). In the pigeon, the angle declined sharply between 6 and 10 m s^{-1} and thereafter declined gradually to reach minimum values at 18 and 20 m s^{-1}. Body angle in the magpie decreased progressively with each increase in speed from 4 to 12 m s^{-1} and then it increased slightly at 14 m s^{-1}.

Stroke-plane angles relative to the horizontal for both the wingtip and the wrist were greater at any given speed in the magpie than in the pigeon (Fig. 6A). For both species, however, minimum values were observed at the slowest speed at which the birds flew and reached a plateau near the upper end of their range of speeds. In the magpie, the stroke-plane angle for the wrist was always greater for a given speed than that for the wingtip, primarily because of flexion of the wrist during the first part of downstroke. This was also true for the pigeon during flight at 6 and 8 m s^{-1}, but from 10 to 20 m s^{-1}, with a slight exception at 12 m s^{-1}, the stroke-plane angles for the wrist and wingtip in the pigeon were similar and the wrist was relatively extended at the start of downstroke.

Relative to the midline of the body, the stroke-plane angles for the magpie wrist decreased slightly with speed (Fig. 6B)

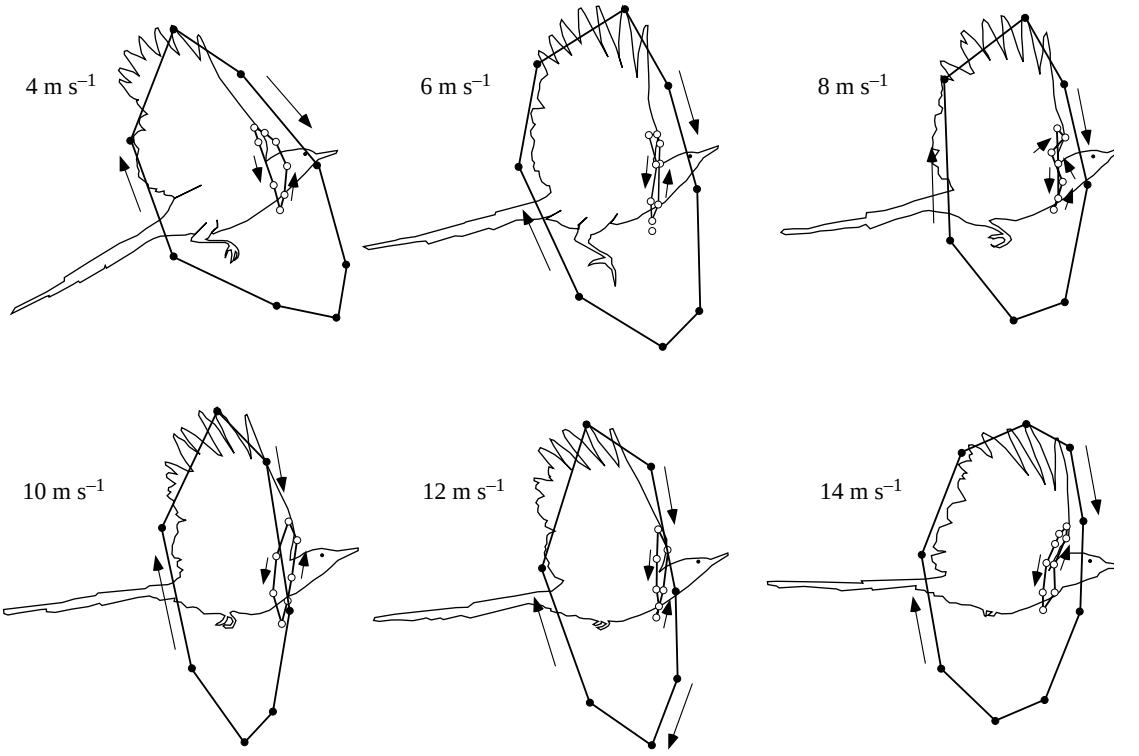

Fig. 3. Lateral views of steady-speed flight illustrating the path of the wingtip (filled circles) and wrist (open circles) of a characteristic wingbeat in a magpie (*Pica pica*) flying at speeds of 4–14 m s^{-1} in a variable-speed wind-tunnel. The bird silhouettes illustrate the body posture at the upstroke/downstroke transition.

from a maximum at 4 m s^{-1} to minimum values at 12 and 14 m s^{-1}. The stroke plane angle for the pigeon wrist was nearly constant across all speeds except for a slight decrease at 10 m s^{-1}. For both species, the stroke-plane angle of the wingtip relative to the body increased with speed up to 8 m s^{-1} in the magpie and 16 m s^{-1} in the pigeon; thereafter, it remained relatively constant (Fig. 6B).

Dorsal views of flight showed that, in both species, wingspan and wristspan were always maximal at mid-downstroke and minimal during mid-upstroke (see Figs 7–9). Although wingspan at mid-downstroke did not change appreciably with airspeed, the tail became progressively less spread in both species as flight speed increased (see Figs 7, 8, 10). In the magpie, the paths of both the wingtips and the wrists were approximately elliptical and changed very little with increasing flight speed (Fig. 7). The wingtips were most caudal at the upstroke/downstroke transition. They were abducted until mid-downstroke, then adducted until mid-upstroke. From mid-upstroke to the upstroke/downstroke transition, they remained relatively close to the midline of the body. The wrists in the magpie followed approximately the same path as the wingtips only over a much smaller area. The wrists were, however, abducted slightly during the last half of upstroke rather than held near the midline of the body as in the wingtips.

In contrast to the relatively constant dorsal-view kinematics of the wingtip and wrist paths in magpies, pigeons showed profound differences between their wing kinematics at 6 and 8 m s^{-1} and those from 12 to 20 m s^{-1} (Figs 8, 9). Kinematics at 10 m s^{-1} shared certain characteristics with those at both slower and faster speeds and thus appeared to be transitional. Particularly at 6 and 8 m s^{-1}, and to a lesser extent at 10 m s^{-1}, the wingtips and wrists described a long path through the air in comparison with the path described at speeds of 12–20 m s^{-1}. At 6 m s^{-1}, the wingtips touched near the midline of the body during the upstroke/downstroke transition. At 6 and 8 m s^{-1}, the wingtips were abducted until mid-downstroke, then followed a path of marked adduction until the downstroke/upstroke transition, abduction until approximately mid-upstroke, and then adduction until the upstroke/downstroke transition. The wrists were held distally during the entire downstroke and were adducted during the first part of upstroke (particularly at 6 m s^{-1}) to reach their minimum span at mid-upstroke. Paths of the wingtips and wrists remained similar at 10 m s^{-1}, except that the wingtips were more sharply adducted at the downstroke/upstroke transition and were not as highly abducted during the upstroke. From 12 to 20 m s^{-1}, dorsal-view wingtip and wrist paths remained relatively constant and considerably different from those at slower speeds. Wingspan and wristspan generally increased from mid-upstroke to mid-downstroke; thereafter, both were usually abducted until mid-upstroke. The wingtip paths were relatively similar during both downstroke and upstroke and crossed at all speeds except at 20 m s^{-1}. The wrists traversed a shorter distance and were generally not as highly adducted at mid-upstroke as during flight at 6–10 m s^{-1}. They followed an elliptical path during wingbeats at 12 m s^{-1} and a more convoluted ‘figure-of-eight’ path from 14 to 20 m s^{-1}.

Flight speed affected the apparent extent of supination of the hand wing during upstroke in pigeons but not in magpies. This supination cannot be observed directly in Figs 3, 4, 7 and 8. Magpies held their wings highly flexed and pronated at mid-

upstroke during flight at all speeds. Pigeons supinated their wings during upstroke at 6 and 8 m s^{-1} but not at 10–20 m s^{-1}.

The average wingspan during mid-downstroke changed less with speed in the magpie than in the pigeon (Fig. 9), while wristspan at mid-downstroke was approximately constant across speeds for both species. Wingspan and wristspan at mid-upstroke showed only minor changes with speed in the magpie relative to the pigeon. In the magpie, wingspan at mid-upstroke decreased particularly from 4 to 10 m s^{-1} and thereafter decreased only slightly to reach a minimum value at 14 m s^{-1}. Wingspan at mid-upstroke in the pigeon was higher from 6 to 10 m s^{-1} than at faster speeds and reached a maximum at 8 m s^{-1}. From 10 to 18 m s^{-1}, wingspan at mid-upstroke decreased; it increased slightly at 20 m s^{-1}. Wristspan in the pigeon at mid-upstroke was smallest at 6 m s^{-1}, increased markedly between 8 and 10 m s^{-1} and thereafter stabilized.

The angle of tail spread at any given speed was generally greater in the pigeon than in the magpie (Fig. 10). Tail spread generally decreased with increasing speed, although it was minimal and relatively constant in the magpie from 10 to 14 m s^{-1} and there was a slight increase in tail spread at mid-downstroke in the pigeon from 18 to 20 m s^{-1}. Tail spread tended to be similar at mid-downstroke and mid-upstroke in both species, except in the magpie from 4 to 8 m s^{-1}, where the degree of tail spread was considerably greater at mid-downstroke than at mid-upstroke. For example, at 6 m s^{-1}, tail spread at mid-downstroke was 57.6±7.6° but it was only 36.9±10.2° at mid-upstroke.

Acceleration and deceleration

Primarily at intermediate flight speeds within their respective ranges, both magpies and pigeons tended to fly within the flight chamber by accelerating with several wingbeats, engaging in steady-speed flight using several

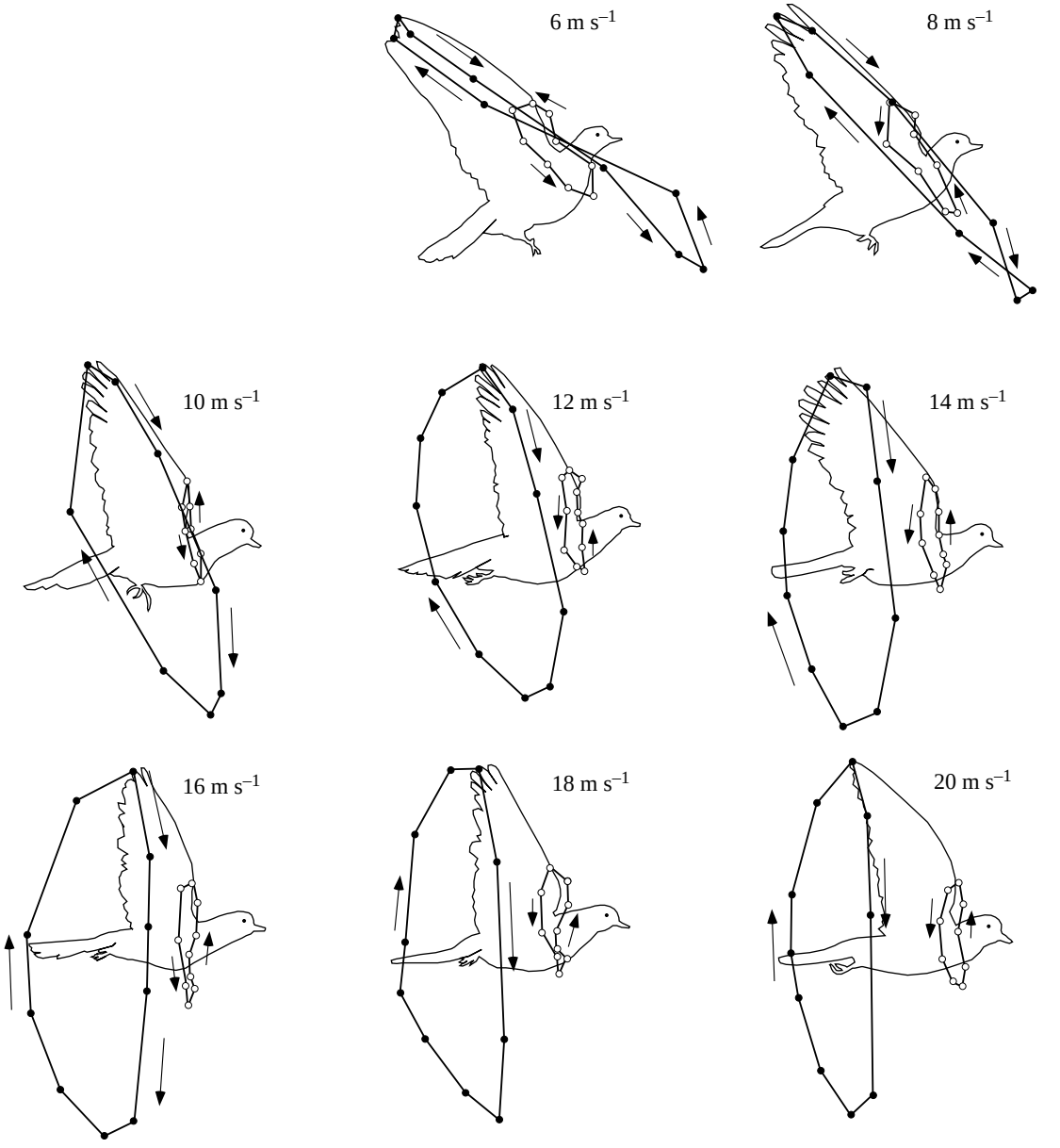

Fig. 4. Lateral views of steady-speed flight illustrating the path of the wingtip (filled circles) and wrist (open circles) of a characteristic wingbeat in a pigeon (*Columba livia*) flying at speeds of 6–20 m s^{-1} in a variable-speed wind-tunnel. The bird silhouettes illustrate the body posture at the upstroke/downstroke transition.

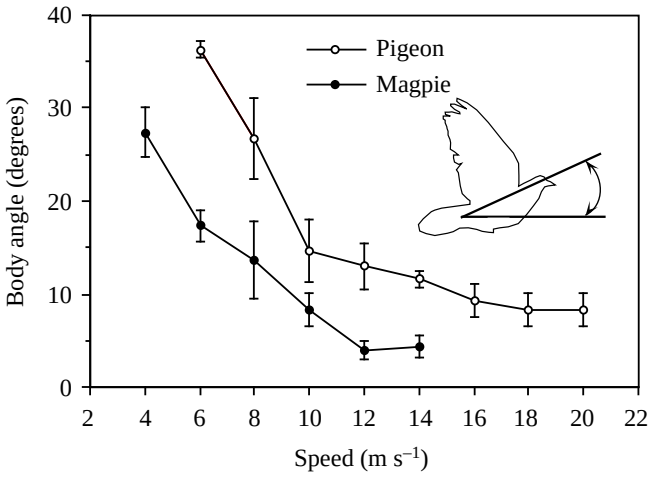

Fig. 5. Body angle relative to the horizontal in three magpies (*Pica pica*) flying at speeds of 4–14 m s^{-1} and three pigeons (*Columba livia*) flying at speeds of 6–20 m s^{-1} in a variable-speed wind-tunnel. Values are means ± S.E.M.

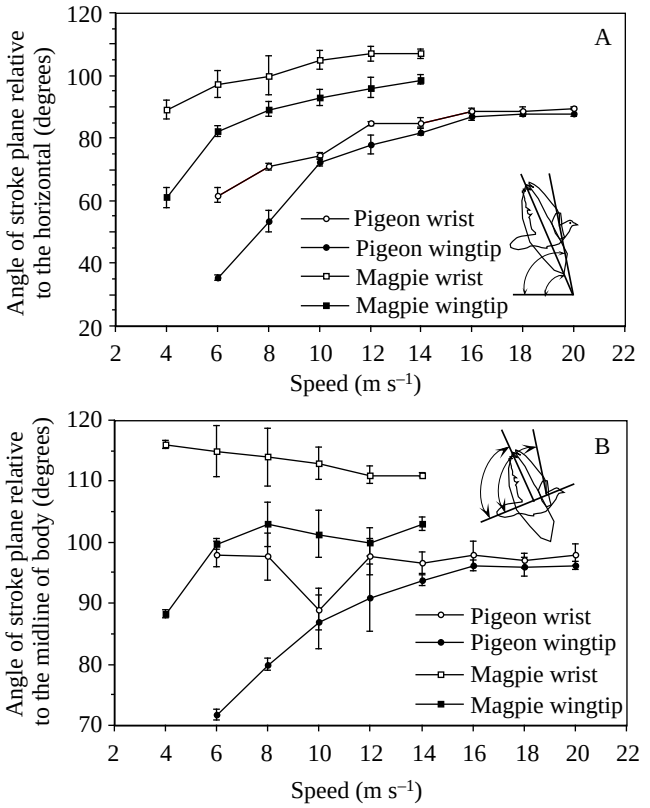

Fig. 6. Stroke-plane angles for the path of the wingtip and wrist relative to the horizontal (A) and relative to the midline of the body (B) in three magpies (*Pica pica*) flying at speeds of 4–14 m s^{-1} and three pigeons (*Columba livia*) flying at speeds of 6–20 m s^{-1} in a variable-speed wind-tunnel. Values are means ± S.E.M.

wingbeats or a non-flapping phase and then decelerating using either wing flapping or a non-flapping phase. The acceleration and deceleration wingbeats we describe were observed in a magpie flying with an incurrent airspeed of 10 m s^{-1} and a pigeon flying with an incurrent airspeed of 14 m s^{-1}, and estimated rates of change in velocity were ±5 m s^{-2}. These birds were the same individuals as those whose results are presented in Figs 3, 4, 7 and 8.

Wingbeat frequency was greater in both species during acceleration than during deceleration. In the examples shown in Fig. 11, wingbeat frequency for the magpie during accleration was 7.5 Hz (lateral view and dorsal view), whereas during deceleration it was 4.3 Hz (lateral view) and 5.5 Hz (dorsal view). Likewise, in the pigeon (Fig. 12), wingbeat frequencies during acceleration were 6.7 Hz (lateral view) and 8.6 Hz (dorsal view), but only 5.5 Hz (lateral view) and 5 Hz (dorsal view) during deceleration.

Both species also shared certain differences in several kinematic patterns between acceleration and deceleration. They both exhibited greater excursion of the wrist during acceleration, as is evident in both lateral and dorsal views (Figs 11, 12). Relative to the horizontal, the stroke-plane angles for the wingtips were similar within species during acceleration and deceleration, but during acceleration stroke-plane angles of the wrist were greater, and body angles relative to the horizontal were smaller, than during deceleration. In the magpie (Fig. 11), the dorsal views revealed that, during acceleration, the wingtips and wrists were drawn close to the midline of the body as during steady-speed flight at all speeds (Figs 3, 7). In contrast, during deceleration, the wingtips and wrists were not adducted during upstroke and thus the wingtips, in particular, described nearly the same path during upstroke and downstroke. In the pigeon, acceleration kinematics resembled steady-speed flight at slower speeds (comparable to flight at 6 and 8 m s^{-1}, Figs 4, 8), with a figure-of-eight wingtip path in lateral perspective (accompanied by wingtip reversal) and, from a dorsal view, the wrists greatly adducted during upstroke. Deceleration in the pigeon was marked by relatively distal placement of the wingtips and wrists during upstroke. During deceleration, the wingtips in particular were more distal during upstroke than during upstroke of steady-speed flight from 12 to 20 m s^{-1} (Fig. 8).

Non-flapping phases

Magpies and pigeons tended to use non-flapping phases while decelerating, although they sometimes maintained wind-tunnel airspeed during the first part of a non-flapping phase by losing altitude. Magpies used non-flapping phases at all flight speeds for which they would fly (4–14 m s^{-1}), but pigeons flapped continuously at 6 m s^{-1} and only used non-flapping phases when flying at 8–20 m s^{-1}. We did not quantify the frequency and duration of non-flapping phases; nonetheless, it was clear that these periods were more frequently exhibited at intermediate speeds for both species (magpie, 6–12 m s^{-1}; pigeon 10–18 m s^{-1}).

Magpies used both glides and bounds during non-flapping phases, but pigeons only used glides. From 4 to 8 m s^{-1}, magpies exhibited glides during all their non-flapping phases, but from 10 to 14 m s^{-1}, the average percentage of bounds

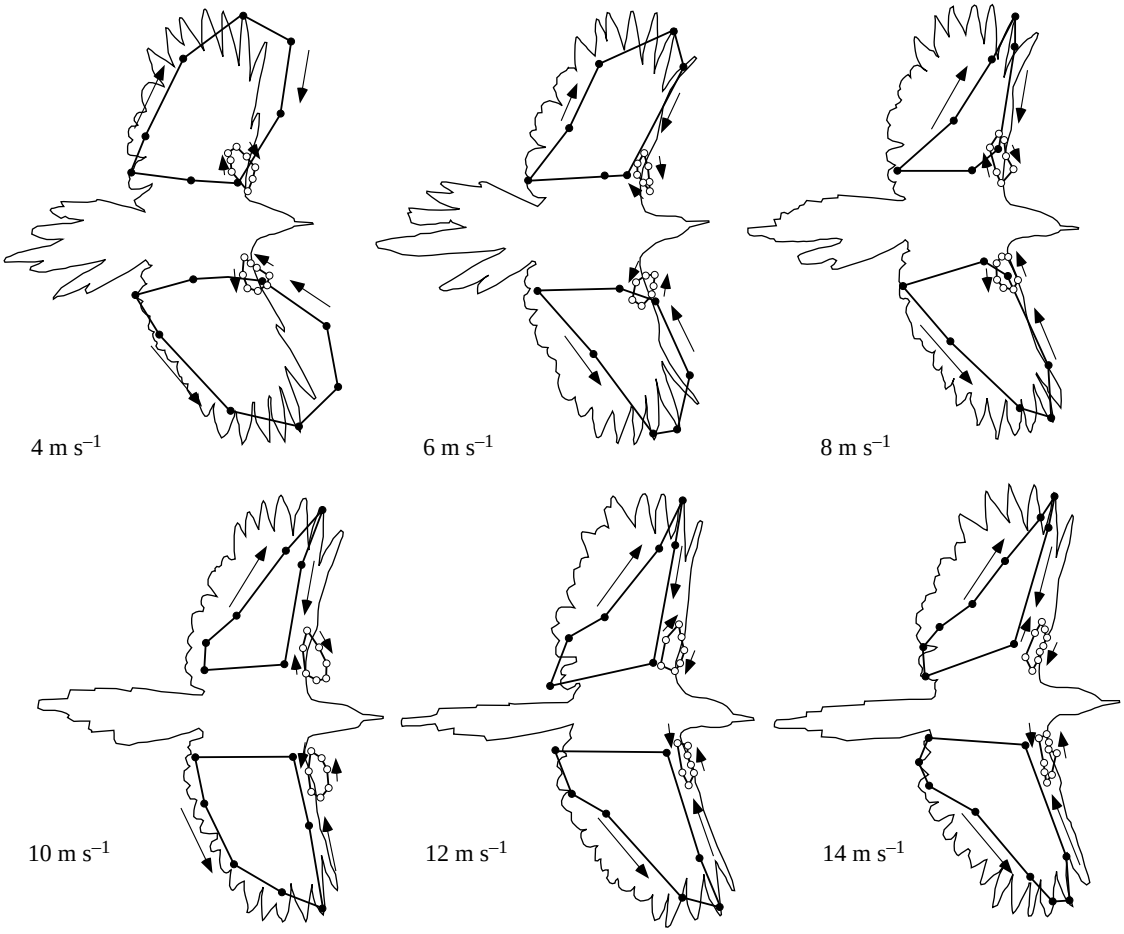

Fig. 7. Dorsal views of steady-speed flight illustrating the path of the wingtip (filled circles) and wrist (open circles) of a characteristic wingbeat in a magpie (*Pica pica*) flying at speeds of 4–14 m s^{-1} in a variable-speed wind-tunnel. The bird silhouettes represent the body posture at the middle of downstroke. During steady-speed flight at all speeds, magpies adducted their wings during upstroke, thereby probably employing a vortex-ring gait.

among all the non-flapping phases observed within a speed increased (Fig. 13). In magpies, wingspan and wristspan during glides decreased only slightly with airspeed (Fig. 14A). Wingspan and wristspan during bounds in magpies were considerably smaller than during glides (Fig. 14A). Both wingspan and wristspan during bounds decreased as airspeed increased from 10 to 14 m s^{-1}.

As speed increased, pigeons reduced wingspan during glides more dramatically than magpies, and wristspan also decreased (Fig. 14B). These values decreased with each increase in speed, except for a slight exception between 14 and 16 m s^{-1}, to reach minimum values at 20 m s^{-1}.

Discussion

The study of wing kinematics in relation to the speed of flight in birds has a rich history (reviews in Scholey, 1983; Rayner, 1988, 1994; Norberg, 1990); the primary contribution we offer from the present investigation rests in detailing kinematic changes in two very different birds over a wide range of incremental speeds. Our results help to define the precise role of airspeed in gait selection during bird flight (Figs 7–9), illustrate a change in the dominant function of wing flapping from weight support at slow speeds to forward thrust at fast speeds (Figs 3–6), show the kinematic events associated with acceleration and deceleration at intermediate flight speeds (Figs 11, 12) and provide evidence for a relationship between the use of flapping and non-flapping gaits within species (Figs 7–9, 13, 14).

We infer the use of specific gaits based upon well-defined relationships between wing kinematics and wake structure in a broad array of bird and bat species (Rayner, 1988, 1991*b*, 1993, 1995; Norberg, 1990). Other gaits may exist in flying vertebrates even though they have not yet been revealed using vortex-visualization techniques (Pennycuick, 1988; Rayner, 1995). When interpreting our results, it is therefore imperative to note that actual wake structures, as revealed through vortex visualization, have never been reported for the magpie. Likewise, for the pigeon, wake structures have only been reported for two speeds: slow, decelerating flight (at 2.4 m s^{-1}; Spedding *et al*. 1984) and qualitatively ‘fast’ flight (speed not reported; Rayner, 1991*b*).

The upstroke kinematics we observed in magpies and pigeons (Figs 7–9, 11, 12) seemed to be consistent with the presence of two different flapping gaits, but several kinematic variables changed with flight speed in a continuous, rather than an apparently discrete, manner; these included body angle, stroke-plane angles for the wingtip and wrist (with the exception of the value for the angle of the wrist path relative to the body at 10 m s^{-1} in the pigeon; Fig. 6B), the angle of

tail spread (Figs 3–8, 10) and the extent of leg flexion (Figs 3, 4). The gradual changes observed in kinematics amounted to within-gait changes in the magpie, but continuous changes across the two gaits in the pigeon. These patterns rather strikingly illustrate the kinematic response of birds to the various sources of drag acting upon them during flapping flight which dictate that weight support is more critical at slower speeds and positive thrust production is more critical at faster

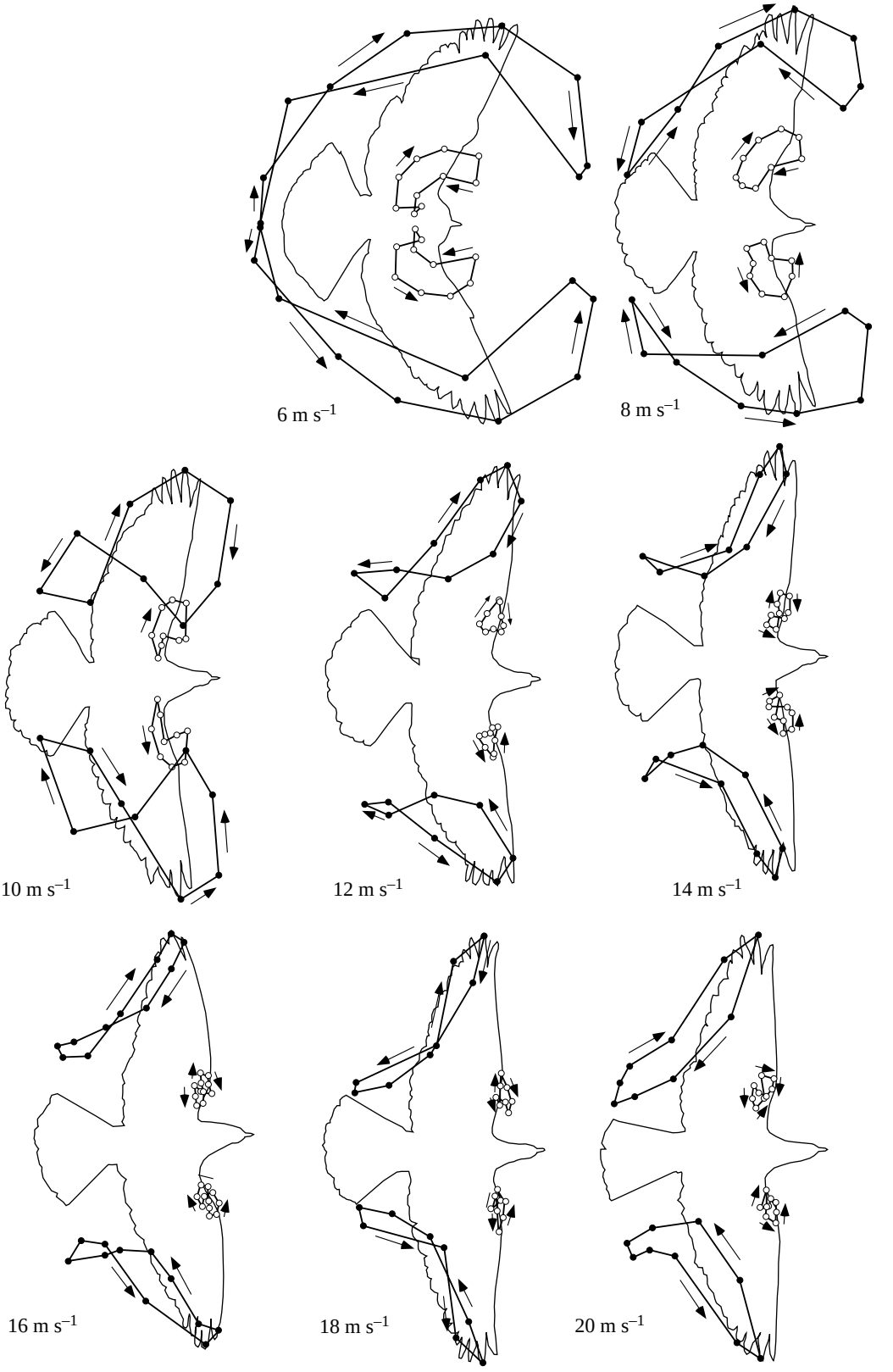

Fig. 8. Dorsal views of steady-speed flight illustrating the path of the wingtip (filled circles) and wrist (open circles) of a characteristic wingbeat in a pigeon (*Columba livia*) flying at speeds of 6–20 m s^{-1} in a variable-speed wind-tunnel. The bird silhouettes represent the body posture at the middle of downstroke. Pigeons adducted their wrists during upstroke while flying at 6 and 8 m s^{-1} (indicating a vortex-ring gait), but left their wrists extended during upstroke at speeds of 12–20 m s^{-1} (indicating a continuous-vortex gait). Wingbeat characteristics at 10 m s^{-1} were transitional between the two gaits.

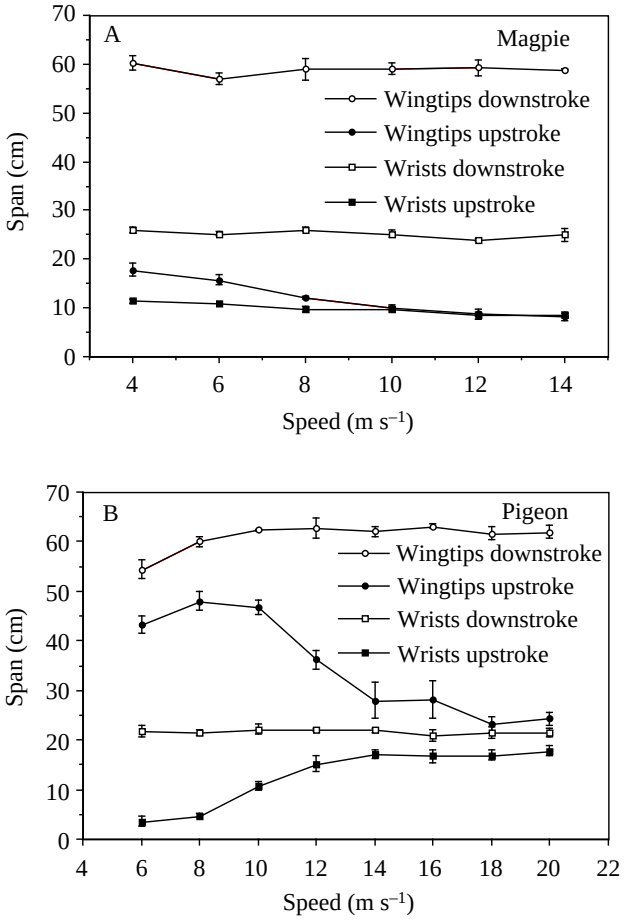

Fig. 9. Wingspan and wristspan during mid-downstroke and mid-upstroke in three magpies (*Pica pica*) flying at speeds of 4–14 m s^{-1} (A) and three pigeons (*Columba livia*) flying at speeds of 6–20 m s^{-1} (B) in a variable-speed wind-tunnel. Values are means ± S.E.M.

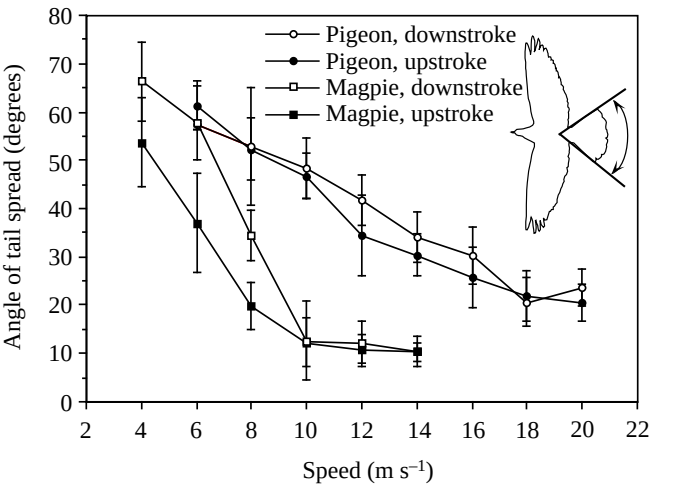

Fig. 10. Angle of tail spread at mid-downstroke and mid-upstroke in three magpie (*Pica pica*) flying at speeds of 4–14 m s^{-1} and three pigeons (*Columba livia*) flying at speeds of 6–20 m s^{-1} in a variable-speed wind-tunnel. Values are means ± S.E.M.

speeds (Scholey, 1983; Aldridge, 1986). When these sources of drag are summed, a smooth, U- or J-shaped curve of the power requirements for flight against speed can be predicted (Pennycuick, 1968*b*, 1975, 1989*a*; Rayner, 1979, 1988; Norberg, 1990; Ellington, 1991).

Vortex-ring gait

The vortex-ring gait is characterized by an upstroke during which the wrists and/or wingtips are markedly adducted, for such kinematics indicate that no aerodynamic forces are being produced by the wing (Rayner, 1988, 1991*b*, 1993, 1995). The vortex is shed at the end of downstroke, and a ring is produced in the wake structure (Fig. 1). On the basis of this criterion, magpies appeared to use a vortex-ring gait during steady-speed flight at all speeds and during acceleration while flying at 10 m s^{-1}, whereas pigeons used a vortex-ring gait during steady-speed flight at speeds from 6 to 10 m s^{-1} and during acceleration at 14 m s^{-1}.

Magpies always greatly adducted both their wrists and wingtips (Figs 7, 9A, 11) and left their handwings pronated while using this gait. These kinematics describe a 'feathered upstroke' (Brown, 1951, 1953, 1963; Bilo, 1971, 1972; Norberg, 1975; Dathe and Oehme, 1978; Scholey, 1983; Aldridge, 1986), and the vortex-ring wake resulting from such a wingbeat has been described for a number of different bird species that have low-aspect-ratio, rounded wings (Kokshaysky, 1979; Spedding, 1986; Rayner, 1988, 1991*b*, 1993, 1995).

The kinematics associated with vortex-wake production differed according to speed in the pigeon. Pigeons left their wingtips extended (but highly supinated) and only adducted their wrists during upstroke of steady-speed flight at 6 and 8 m s^{-1} (Figs 8, 9B), therefore using a 'tip-reversal' upstroke (Brown, 1948, 1951, 1953, 1963; Scholey, 1983; Simpson, 1983) for which Spedding *et al*. (1984) describe the structure of the resulting vortex-ring wake. Tip-reversal upstrokes similar to those we observed at 6 and 8 m s^{-1} are also exhibited during take-off and hovering in the pigeon (Brown, 1948, 1953, 1963; Scholey, 1983; Simpson, 1983). At 10 m s^{-1}, the wing kinematics of the pigeon changed to become more similar to the feathered upstroke of the magpie in that the hand wing was not supinated. One important difference in the feathered upstrokes used in the two species was that pigeons did not adduct their wingtips to the extent observed in the magpie; this is clearly revealed in the wingspan each species exhibited at mid-upstroke (Fig. 9).

The kinematics of the feathered upstroke wingbeat of a pigeon at 10 m s^{-1} was unique in comparison with those at either slower or higher speeds. Wristspan during mid-upstroke was intermediate (Fig. 9B). Although wingspan was relatively large at mid-upstroke, similar to that at 6 and 8 m s^{-1}, the hand wing was pronated and the path of the wingtip from a lateral perspective was elliptical, as during flight at speeds from 12 to 20 m s^{-1} (Fig. 4). Body angle relative to the horizontal was similar to that at higher speeds (Fig. 5). Also, stroke-plane angles were similar for the wingtip and wrist in the pigeon at speeds from 10 to 20 m s^{-1}, while the stroke-plane angles for

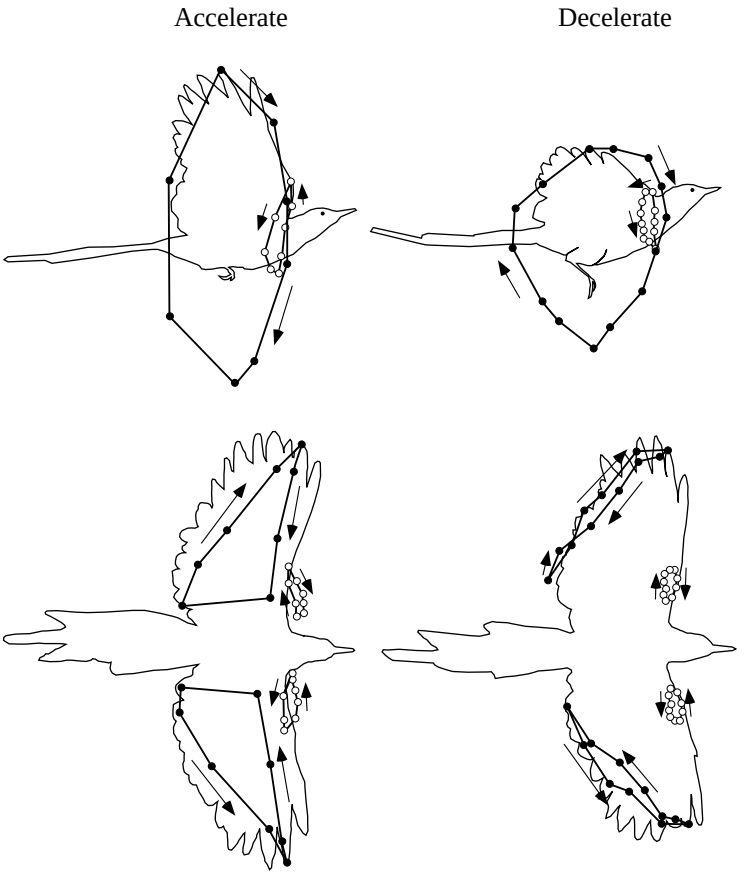

Fig. 11. Lateral and dorsal views illustrating the path of the wingtip (filled circles) and wrist (open circles) of characteristic accelerative and decelerative wingbeats in a magpie (*Pica pica*) with a wind-tunnel airspeed of $10\,\mathrm{m\,s^{-1}}$. The lateral-view bird silhouettes represent the upstroke/downstroke transition, and the dorsal-view bird silhouettes represent mid-downstroke. The number of circles in the wingtip or wrist path indicates the number of video fields (60 Hz) during the wingbeat and is thus inversely proportional to wingbeat frequency.

the wrist were considerably greater than the stroke-plane angles for the wingtip during flight at slower speeds (Fig. 6).

This feathered-upstroke pattern in the pigeon was therefore transitional between the tip-reversed kinematics observed at slower speeds and the kinematics that indicated the use of a continuous-vortex wake at faster speeds. Brown (1951, 1953, 1963) first reported this transitional, feathered-upstroke wingbeat as occurring during moderately slow, forward flight in the pigeon after the bird accelerated from take-off and abandoned the tip-reversal upstroke but before fast (cruise) flight speeds were achieved. Our data add to Brown's observations primarily by providing quantitative estimates of the flight speeds at which pigeons exhibit the different kinematic patterns. Aldridge (1986) reported similar transitions with increasing flight speed in the greater horseshoe bat *Rhinolophus ferruquinum*.

The 'tip-reversal' upstrokes that pigeons used during flight at 6 and $8\,\mathrm{m\,s^{-1}}$ seem to be representative for birds with pointed, high-aspect-ratio wings (Scholey, 1983; Rayner, 1991*b*). Dathe and Oehme (1978), however, found no other anatomical correlates of the use of tip-reversal upstrokes. Similarly, Scholey (1983) showed that wing loading varies substantially among bird species using the same type of upstroke during hovering. The aerodynamic function of the tip-reversal upstroke has been the subject of much speculation (Scholey, 1983). On the basis of kinematic data, some authors have suggested that propulsive forces could result from drag on the tip-reversed wing during upstroke in very slow flight (Brown, 1953, 1963; Aldridge, 1986), but vortex-visualization studies clearly indicate that this type of upstroke is aerodynamically inactive except, perhaps, for the flick phase at the very end of the upstroke, during which circulation may be generated prior to the next downstroke (Rayner, 1991*b*, 1995). Weight support is critical during flight at slower speeds because there is little air circulation from the wings due to forward movement of the bird (induced drag is high; Pennycuick, 1968*b*, 1975; Rayner, 1979, 1991*b*). The disk loading (body mass divided by wingspan) of pigeons was approximately twice that of magpies, and pigeons flew over a greater range of flight speeds. Thus, it is feasible that even the small increase in lift production afforded by early initiation of air circulation during the flick phase of the tip-reversal upstroke could be required for birds with high disk loading to sustain slow flight.

Except for the transitional wingbeats at $10\,\mathrm{m\,s^{-1}}$ in the pigeon, whenever the magpies and pigeons used a vortex-ring gait the stroke-plane angles for the wrist were consistently greater than the stroke-plane angles for the wingtip (Figs 3, 4, 6, 11, 12). This may, therefore, be a characteristic of the vortex-ring gait. It also appears to be a characteristic of wingbeats in birds that have rounded, relatively low-aspect-ratio wings (Scholey, 1983). The increased stroke-plane angle of the wrist was due to greater wrist flexion at the start of downstroke, and Scholey (1983) demonstrates that extension of the wrist during the first part of downstroke significantly increases the velocity

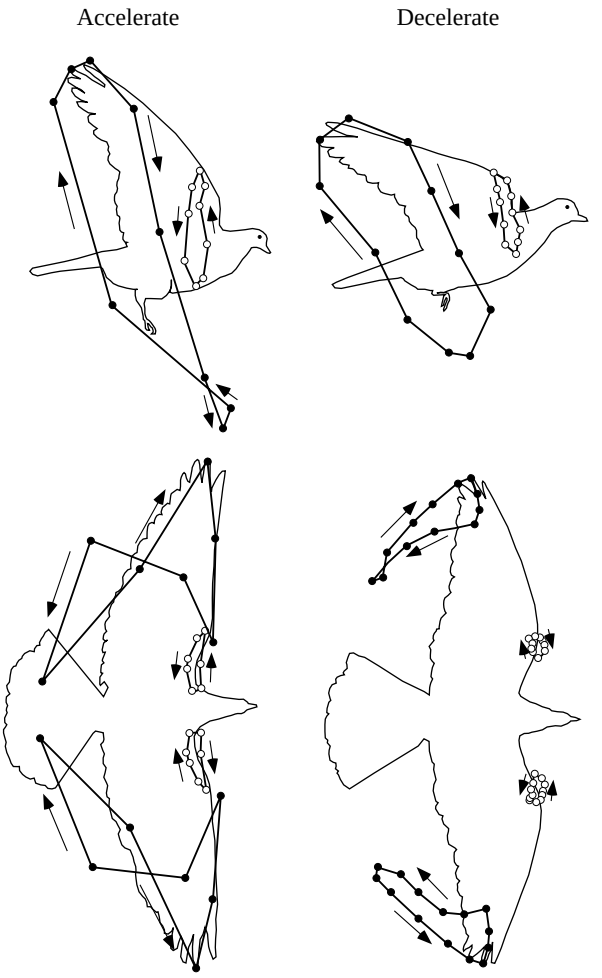

Fig. 12. Lateral and dorsal views illustrating the path of the wingtip (filled circles) and wrist (open circles) of characteristic accelerative and decelerative wingbeats in a pigeon (*Columba livia*) with a wind-tunnel airspeed of $14\,\mathrm{m\,s^{-1}}$. The lateral-view bird silhouettes represent the upstroke/downstroke transition, and the dorsal-view bird silhouettes represent mid-downstroke. The number of circles in the wingtip or wrist path indicates the number of video fields (60 Hz) during the wingbeat and is thus inversely proportional to wingbeat frequency.

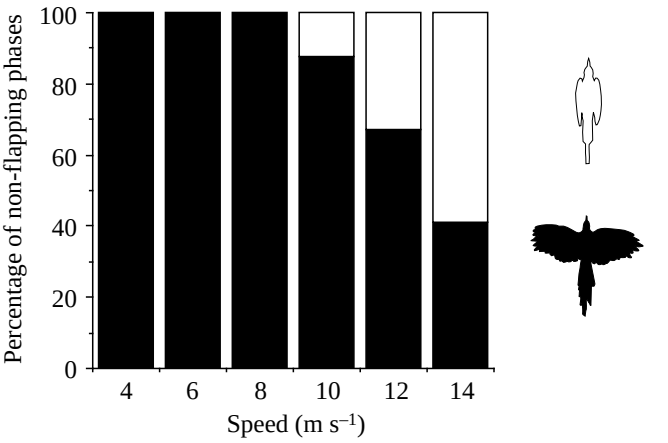

Fig. 13. Average percentage of non-flapping phases within a speed consisting of glides (black areas) or bounds (white areas) in three magpies (*Pica pica*) flying at speeds of 4–$14\,\mathrm{m\,s^{-1}}$ in a variable-speed wind-tunnel. From 4 to $8\,\mathrm{m\,s^{-1}}$, magpies only exhibited glides during non-flapping phases, but from 10 to $14\,\mathrm{m\,s^{-1}}$, the percentage of bounds increased. Pigeons (*Columba livia*) never exhibited bounds during non-flapping phases.

of the distal wing and thereby probably enhances lift production. This would be particularly useful during the vortex-ring gait because all the lift is produced during downstroke (Kokshaysky, 1979; Spedding *et al.* 1984; Spedding 1986, 1987*b*, 1992; Rayner, 1988, 1991*b*, 1993, 1995; Norberg, 1990).

One would also expect an increased duration of downstroke relative to upstroke if all the lift were produced during downstroke (Scholey, 1983; Rayner, 1988). Our results are generally consistent with this prediction (Fig. 2B), because the percentage of the wingbeat spent in downstroke was greatest in both species at their respective slowest speeds, when both species used a vortex-ring gait and weight-support requirements were maximal, and decreased to minimum values at each species' highest speeds, when positive thrust was more critical (Pennycuick, 1968*b*, 1975; Rayner, 1979, 1988, 1991*b*). The greater degree of tail spreading in magpies at mid-downstroke compared with mid-upstroke during flight at slower speeds may have enhanced lift production to assist in weight support (Fig. 10). This behavior is typical of birds that use a feathered upstroke during hovering (Scholey, 1983).

Both species used kinematics during acceleration that indicated a vortex-ring gait (Figs 11, 12), and this behavior is consistent with the production of negative thrust during a lifting upstroke (Spedding, 1987*b*, 1992; Pennycuick, 1988; Rayner, 1988, 1991*b*, 1993, 1995; Norberg, 1990). This negative thrust would be undesirable if a bird wanted to accelerate, but would assist the bird in decelerating. Thus, for acceleration, one would expect a bird either to use a vortex-ring gait or to make kinematic changes to reduce negative thrust during upstroke in the continuous-vortex gait (Rayner, 1988, 1991*b*, 1993, 1995). Consistent with this prediction, during acceleration at $10\,\mathrm{m\,s^{-1}}$ in the magpie, the wingtips and wrists were highly adducted during upstroke, as was typical of the vortex-ring gait used in steady-speed flight. The pigeon, flying at $14\,\mathrm{m\,s^{-1}}$, exhibited a figure-of-eight wingtip path from a lateral perspective with moderate wingtip reversal (supination), and the wrists were also highly adducted during upstroke (Fig. 12). These kinematics suggested a shift towards a vortex-ring gait from the continuous-vortex gait normally used by the pigeon for steady-speed flight at $14\,\mathrm{m\,s^{-1}}$ (Figs 4, 8, 9B).

Note that the accelerative kinematics that we report were taken from flight at $10\,\mathrm{m\,s^{-1}}$ in the magpie and $14\,\mathrm{m\,s^{-1}}$ in the pigeon, and the changes observed during acceleration at these speeds do not necessarily represent the changes that would occur at other speeds. This is because the type of wingbeat kinematics used to change speed should depend on the speed itself (Rayner, 1988, 1991*b*, 1993, 1995). For example, the pigeon shifted towards the use of a vortex-ring gait when

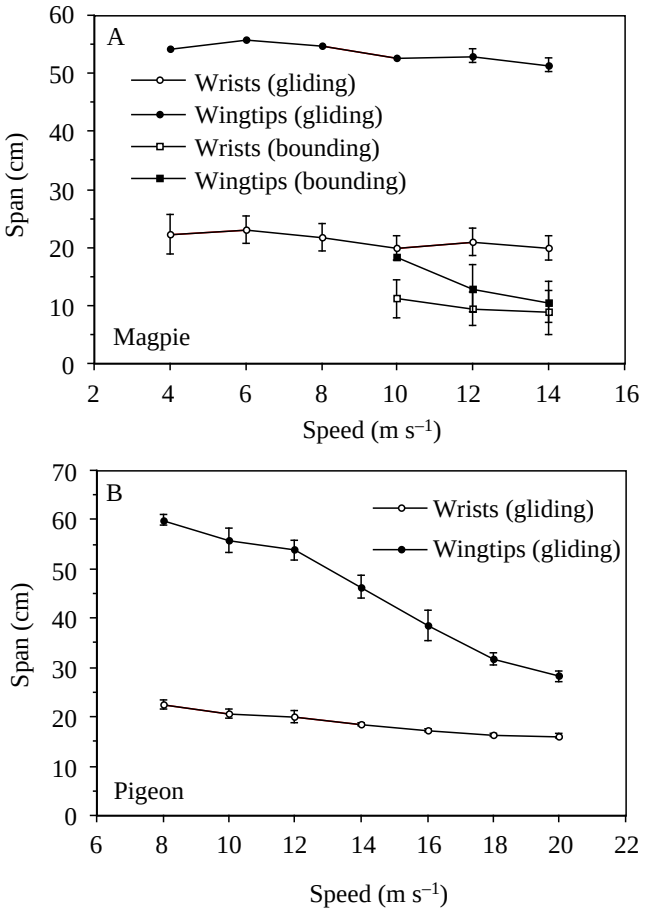

Fig. 14. Wingspan and wristspan during non-flapping phases in three magpies (*Pica pica*) flying at speeds of 4–14 m s^{-1} (A) and three pigeons (*Columba livia*) flying at speeds of 8–20 m s^{-1} (B) in a variable-speed wind-tunnel. Values are means ± S.E.M. The magpies engaged in non-flapping phases at all measured flight speeds, but the pigeons did not use non-flapping phases during flight at 6 m s^{-1}.

accelerating during flight at 14 m s^{-1}, but during flight at 6 m s^{-1} it would already be using a vortex-ring gait, and different kinematic changes would be required for acceleration.

Continuous-vortex gait

Wing kinematics that indicate the use of a continuous-vortex gait include having the wrists and wingtips markedly extended during upstroke so that lift can be produced (Rayner, 1988, 1991*b*, 1993, 1995). The only time we observed the use of a continuous-vortex gait in magpies based on this criterion was during deceleration (Fig. 11), whereas pigeons used a continuous-vortex gait during steady-speed flight from 12 to 20 m s^{-1} and during deceleration at 14 m s^{-1} (Figs 8, 9, 12). These patterns are consistent with data from flow-visualization studies on various species including pigeons (Rayner, 1991*b*), because only birds with wings of comparatively high aspect ratio are reported to use a continuous-vortex gait during fast, steady-speed flight (Spedding, 1987*b*, 1992; Rayner, 1988, 1991*b*; Pennycuick, 1988; Norberg, 1990).

The wingtips, but not the wrists, in pigeons were progressively more adducted at mid-upstroke as speed increased from 12 to 20 m s^{-1}. This behavior was probably in response to the negative thrust which results from lift production during upstroke (Spedding, 1987*b*, 1992; Pennycuick, 1988; Rayner, 1988, 1991*b*, 1993, 1995; Norberg, 1990) and was facilitated by the different functions of the secondaries and the primaries in the wing first proposed by Storer (1948). During the wingbeat cycle of the continuous-vortex gait, the secondaries are continuously loaded and are thus a source of lift throughout the wingbeat, whereas the primaries are cyclically loaded and unloaded (Spedding, 1987*b*, 1992; Pennycuick, 1988; Rayner, 1988, 1991*b*, 1993, 1995; Norberg, 1990). Profile and parasite drag on the bird's wings and body increase with airspeed, so that generating positive horizontal thrust becomes progressively more important (Pennycuick, 1968*b*, 1975, 1989*a*; Rayner, 1979, 1985, 1988, 1991*b*). Consequently, progressive reduction of wingspan but not wristspan during upstroke is essential for generating a net positive thrust of sufficient magnitude to overcome drag (Rayner, 1988, 1991*b*, 1993, 1995).

Interestingly, the proportion of the wingbeat spent in downstroke was less than 50 % during flight at 20 m s^{-1} in the pigeon. This seems unusual because negative thrust during upstroke would retard the bird at the expense of overcoming the high parasite and profile drags at this speed (Pennycuick, 1968*b*, 1975, 1989*a*; Scholey, 1983; Rayner, 1979, 1988, 1991*b*). One explanation for this anomalous result is that the pigeons could have been changing aspects of their wing kinematics, including angle of attack and camber of the wing, which we did not study. Measuring these variables requires more complex three-dimensional analysis (e.g. Aldridge, 1986) than was attempted in the present study.

Because of negative thrust during upstroke, the continuous-vortex gait would be of assistance to a bird wishing to decelerate (Rayner, 1988, 1991*b*, 1993, 1995); thus, it makes sense that both species used a continuous-vortex gait when decelerating. The pigeon used a continuous-vortex gait for steady-speed flight at 14 m s^{-1}, and it continued to use this gait for deceleration at that speed (Figs 4, 8, 9B, 12). Nonetheless, its kinematics changed from steady-speed flight at the same speed, because both wingbeat amplitude and frequency decreased. Also, the wingtips remained much more distal during upstroke. Magpies never employed a continuous-vortex gait during steady-speed flight (Figs 3, 7, 9A); thus, their use of this gait for deceleration at 10 m s^{-1} was associated with significant kinematic changes from the steady-speed kinematics including a decrease in wingbeat amplitude and frequency and increases in wing- and wristspans at mid-upstroke (Fig. 11). As for our previous discussion of the acceleration kinematics in each species (see Vortex-ring gait, above), the changes in kinematics for deceleration at one speed do not necessarily represent the changes that would occur when decelerating at other speeds (Rayner, 1988, 1991*b*, 1993, 1995).

Modulation of the wingbeat frequency and amplitude is a well-known characteristic of magpie flight in the wild (Rayner,

1985; Olson and Dial, 1992; Olson, 1993), and our data illustrate that the behavior in this species can be described in terms of switching between a vortex-ring gait during accelerative and steady-speed phases and a continuous-wake gait (or non-flapping phase) during decelerative phases. From the present study (Figs 7, 11) and that of Olson (1993), it seems that wingbeat frequency, wingbeat amplitude and the force of muscle contraction are greater during the use of a vortex-ring gait in the magpie than during the use of the continuous-vortex gait; thus, magpies appear to use gait modulation to vary mechanical power output. Recognizing that the unique flight behavior of the magpie can be described in terms of gait selection may help to model power output for the flight of this species (Rayner, 1985, 1991*b*).

Correspondence between flapping and non-flapping gaits

Our observations of magpies and pigeons support the general conclusion that the use of flap-bounding flight seems to be related to the frequent use of the vortex-ring gait (Rayner, 1991*b*, 1993, 1995), which may in turn be related to the presence of low-aspect-ratio, rounded wings (Scholey, 1983; Rayner, 1991*b*, 1993, 1995). The wing- and wristspans at mid-upstroke did not vary appreciably with speed in the magpie (Fig. 9A), illustrating a lack of flexibility in upstroke kinematics which Rayner (1985) predicted should be evident in birds that use flap-bounding flight. However, there was a dramatic difference between spans during glides compared with bounds in the magpie (Fig. 14A), and wing- and wristspans during bounds were quite similar to wing- and wristspans exhibited during upstroke of the vortex-ring gait (i.e. at all steady-speed flight speeds and during acceleration) in this species (Fig. 9A).

The mid-upstroke wing- and wristspans in the pigeon changed dramatically with speed (Fig. 9B), suggesting greater flexibility in upstroke kinematics compared with the magpie, and this species progressively flexed its wings during glides (Fig. 14B). The pattern of progressive wing flexion with glide speed in pigeons is already known from the work of Pennycuick (1968*a*) and seems to be representative of the pattern exhibited by many birds that glide extensively (Hankin, 1913; Tucker and Parrott, 1970; Tucker, 1987, 1992; Tucker and Heine, 1990). However, our data are the first to illustrate the remarkable similarity between mid-upstroke wing- and wristspans exhibited in the continuous-vortex gait of the pigeon (from 12 to 20 $m\,s^{-1}$) and the wing- and wristspans for glides at the corresponding speeds (Figs 9B, 14B). These similarities probably represent shared aspects of lift production by the wings.

Magpies increased the percentage of bounds among non-flapping phases as flight speed increased (Fig. 13). This pattern is similar to the trend that budgerigars and starlings exhibit (Tobalske and Dial, 1994; Tobalske, 1995) and probably represents an attempt to minimize energy expenditure per unit time relative to continuous flapping. Using mathematical models, various authors report that flap-gliding should be less costly in terms of mechanical power output than continuous flapping at slow speeds and that flap-bounding should offer savings compared with continuous flapping at fast speeds (Lighthill, 1977; Rayner, 1977, 1985; Alexander, 1982; DeJong, 1983; Ward-Smith, 1984*a*,*b*).

Why do certain species such as the pigeon progressively flex their wings and others such as the magpie shift from intermittent glides to intermittent bounds (Figs 13, 14)? Rayner (1977, 1985) predicts that many small birds are constrained by their muscle physiology (homogeneity of fiber types and thus range of efficient contractile velocities) and wing kinematics to the use of a single flapping ‘gear’ so that intermittent bounds are the only means available for varying power output. According to this ‘fixed-gear’ hypothesis, larger birds have other ways to vary power output, including varying motor-unit recruitment and wing kinematics, so that intermittent bounds are not needed and intermittent glides are more efficient (Goldspink, 1977; Rayner, 1977, 1985). Consistent with the fixed-gear hypothesis, pigeons changed flapping gaits (upstroke kinematics) according to flight speed during steady flight whereas magpies did not (Figs 3, 4, 7–9), and the pectoralis muscle of pigeons is more heterogeneous in terms of histological staining than that of the magpie, indicating a greater range of efficient contractile velocities (Rosser and George, 1986*a*; N. E. Olson, B. W. Tobalske and K. P. Dial, unpublished observations). However, our data show that magpies were capable of changing gait (and thus upstroke kinematics) to decelerate and were thus not contrained to use only one gait (Fig. 11). Neither species possesses slow-twitch muscle fibers in their pectoralis which would be the most economical type for isometric contraction during a glide (Goldspink, 1977, 1981; Rayner, 1977, 1985; Goldspink *et al*. 1978; Rosser and George, 1986*a*,*b*; Meyers, 1993; Tobalske and Dial, 1994; Tobalske, 1995).

An ‘adverse-scaling’ hypothesis provides an alternative explanation for the non-flapping kinematics exhibited by magpies and pigeons. This idea is based on the assumption of adverse scaling of available mass-specific power for flap-bounding flight (Rayner, 1977, 1985; DeJong, 1983; Tobalske, 1996). Rather than being constrained by their body mass to use flap-bounding, as implied by the fixed-gear hypothesis (Goldspink, 1977; Rayner, 1977, 1985), it may be that only relatively small birds have sufficient mass-specific power available from their flight muscles to use flap-bounding and that larger birds are unable to use intermittent bounds in spite of the potential that such non-flapping phases offer for reducing metabolic and mechanical power output. Flapping flight requires an enormous expenditure of energy per unit time (Tucker, 1973; Goldspink, 1981; Hudson and Bernstein, 1983) and, during bounds, periods of no muscle activity in the primary flight muscles could offer subtantial savings in metabolic energy (Tobalske and Dial, 1994; Tobalske, 1995). As mechanical power output is predicted to be smaller during flap-bounding than during continuous flapping at fast speeds (Lighthill, 1977; Rayner, 1977, 1985; Alexander, 1982; DeJong, 1983; Ward-Smith, 1984*a*,*b*), the potential for savings in metabolic and mechanical power would seem to be worthwhile for any species choosing to fly fast, regardless of body mass.

With increasing body size, the mass-specific power required for sustained flapping flight increases (Pennycuick, 1968*b*;

Rayner, 1977, 1985; Marden, 1987, 1994; Ellington, 1991). Current empirical evidence shows that the mass-specific maximum (burst) power output matches this increase (Marden, 1987; Ellington, 1991), but that sustainable flight performance (lift per unit power produced; Marden, 1994) and acceleration ability (DeJong, 1983) both scale negatively with body mass. The adverse scaling of these two variables, and perhaps of sustainable mass-specific power available from the muscles (Rayner, 1977, 1985), in relation to the mass-specific power required for sustained flapping flight should provide an upper limit above which larger birds should have insufficient power or acceleration ability to generate enough lift during flapping to counteract the loss of altitude incurred during bound phases (DeJong, 1983; Rayner, 1977, 1985). Patterns of muscle activity (isometric contractions) reveal that weight is supported during intermittent glides (Tobalske and Dial, 1994; Tobalske, 1995), much as in prolonged glides (Goldspink *et al*. 1978; Spedding, 1987*a*; Meyers, 1993); thus, larger species could glide to benefit from the known lower in metabolic costs of gliding (Goldspink, 1981) and presumed lower mechanical costs of flap-gliding (Rayner, 1977, 1985; Ward-Smith, 1984*b*) relative to those of continuous flapping flight.

The percentage of bounds relative to glides, within a given flight speed, decreases as a function of increasing body mass among budgerigars, starlings and magpies (Tobalske and Dial, 1994; Tobalske, 1995; Fig. 13). This pattern among species may directly reflect the adverse scaling of the power available from the flight muscles relative to the power required to use flap-bounding flight and leads us to suggest that pigeons, with a body mass double that of magpies (Table 1), were limited to gliding as their only means of reducing metabolic and mechanical power output during non-flapping phases (Fig. 14A). In other words, they could not use intermittent bounds because of their large body mass.

Using empirical evidence of acceleration ability and mathematical modelling, the proposed limit for the ability to flap-bound is predicted to be near 100 g (Rayner, 1977, 1985; Dejong, 1983). Our observations of intermittent bounds in the magpie, with a body mass of 175 g (Table 1), show that this estimate may be slightly low. The use of intermittent bounds in the magpie may have been facilitated by the reduced power costs for flight within the flight chamber of the wind-tunnel in comparison with those during free flight (Rayner, 1993, 1994; see below). However, certain woodpecker species continue to use intermittent bounds in free flight up to a body mass of approximately 300 g (Tobalske, 1996), so the size limit for the ability to flap-bound may be only slightly lower than the average body mass of the pigeon at 350 g (Table 1).

Effects of the wind-tunnel

The aerodynamic properties of the wind-tunnel are expected to alter the power required for flight at a given speed in comparison with free flight at the same speed and in the absence of ground effects (Rayner, 1991*a*, 1993, 1994). These differences could be very important if the cross-sectional dimensions of the flight chamber are relatively small compared with the wingspan and frontal body area of the animal – as is the case in our study. The ratio of the height H of the (square cross section) flight chamber to wingspan b ($H/2b$; Rayner, 1994) was 1.2 in the pigeon and 1.3 in the magpie, and the body mass (thus probably frontal area for the body) of the pigeons was greater than that of the magpies (Table 1). Consequently, any wind-tunnel effects were likely to have been more pronounced for the pigeon than for the magpie. The effects of the wind-tunnel increase if an animal flies in regions other than the altitudinal center of the flight chamber (Rayner, 1993, 1994), which was the case for the magpies at slow and intermediate speeds and for the pigeons at intermediate flight speeds.

Wind-tunnel effects are caused by recirculation of lift vortices due to the walls of the flight chamber, the flow characteristics in the boundary layer adjacent to the wind-tunnel walls and blocking effects caused by the frontal body area of the animal disrupting the laminar flow of air (Rayner, 1993, 1994). Our study was not designed to test the predicted effects of the flight chamber on behavior and performance during flight, but models of such effects provide estimates that should be taken into account when interpreting our results. In a closed, square wind-tunnel, such as the one we used, the power requirements should be smaller than for free flight at the same speed, and characteristic speeds such as ‘preferred’ flight speed, minimum power speed (V_{mp}) and maximum range speed (V_{mr}) should be slower than in free flight (Rayner, 1993, 1994). Taking the wingspans and behaviors of the birds and the dimensions of the flight chamber into account, Rayner’s (1994) model predicts that both species should have experienced between 27 and 31 % reductions in power and between 10 and 14 % reductions in speed for V_{mp} and V_{mr}, respectively, relative to free flight in the absence of ground effects (Rayner, 1991*a*).

The most obvious effect of the wind-tunnel on flight behavior in this study was that pigeons used flap-gliding flight, particularly at intermediate flight speeds, even though this species does not regularly exhibit such behavior in the wild. Pigeons may generally avoid flying at intermediate speeds in the wild (i.e. they may quickly accelerate and decelerate between take-off and fast cruising flight), but it is more likely that their behavior was in response to the reduced power costs for flight in the flight chamber. Flap-gliding flight can represent a reduced mechanical power output relative to continuous flapping (Rayner, 1985; Ward-Smith, 1984*b*). The wood pigeon *Columba palumbus* commonly exhibits flap-gliding in the wild (B. W. Tobalske and K. P. Dial, unpublished observations); perhaps this species would be useful for a combined wind-tunnel and field study to evaluate wind-tunnel effects.

The manner in which a closed wind-tunnel affects the use of flapping gaits has not been estimated. Rayner’s (1994) suggestion that characteristic airspeeds in closed flight chambers should be slower than in comparison with free flight may mean that the kinematics we observed at a given airspeed actually corresponded to the kinematics at faster airspeeds in free flight. For example, given the 10–14 % decreases in characteristic airspeeds we calculated for both pigeons and magpies using Rayner’s (1994) model, the kinematics we

observed in the birds at $10\,m\,s^{-1}$ may be representative of the kinematics exhibited at 11 or $12\,m\,s^{-1}$ in the wild. Studies comparing wind-tunnel flight with free flight over a similar range of speeds would obviously be worthwhile for testing such predictions, but it is difficult to motivate a species to fly over a range of speeds in the absence of a variable-speed wind-tunnel.

Future studies

Several directions may be worthwhile for future studies of gait selection in birds. To document fully the relationships between kinematics and the structure of vortex wakes, detailed wing kinematics over a range of speeds should be recorded simultaneously with data on the aerodynamic functions of the wings. Such efforts may require adaptation of vortex-measurement techniques for use in a wind-tunnel, perhaps using smoke instead of neutrally buoyant bubbles or with pitot tubes mounted behind the animal (e.g. Pennycuick *et al.* 1992). Another possibility would be to use micro-strain gauges on the feather shaft to record changes in force on the feathers (e.g Dial *et al.* 1994). Important improvements in our understanding of gait selection in the context of the ecology of the animal would probably result from field studies that couple measurements of kinematics, flight speeds and other behaviors such as foraging (e.g. Pennycuick, 1989*b*, 1990; Tobalske, 1996). The use of telemetry equipment to transmit data from micro-accelerometers or micro-airspeed indicators mounted on the flying animal seems promising for obtaining instantaneous flight speeds; methods that are more established for measuring the airspeeds of flying animals involve the use of an ornithodolite (Pennycuick, 1982, 1989*b*, 1990) or Doppler radar (Lanyon, 1962; Schnell, 1965; Pye, 1981; Evans and Drickamer, 1994) and may require time intervals that are too long to be of use in a within-wingbeat analysis. Lastly, coupling studies of flight in the wind-tunnel with studies of free flight either in the laboratory or in the field would be valuable for testing the predicted effects of the wind-tunnel on flight performance and gait selection (Rayner, 1993, 1994).

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