Mechanics of wing-assisted incline running (WAIR)

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Summary

A recently discovered locomotor behavior, wing-assisted incline running (WAIR), allows fully volant animals to 'run' up vertical obstacles. Such a task would appear to be especially formidable for bipeds, yet WAIR is used preferentially by ground-dwelling birds, specifically chukar partridge *Alectoris chukar*, to reach refugia. The basic locomotor mechanics that enable this behavior are not fully understood. For instance, are there functional differences at the level of the wing during WAIR and free flight, and do the hindlimbs actively participate in propulsion during WAIR? To investigate wing function during these activities we used accelerometry to compare the instantaneous whole-body acceleration during WAIR and ascending free flights at a similar climb angle. Throughout a substantial portion of the wingbeat cycle, chukars engaged in WAIR experienced an acceleration oriented towards the substrate, whereas during ascending free flights the acceleration of the center of mass was parallel to the direction of travel. We investigated whether the animals were using their hindlimbs for propulsion, rather than for some other function (e.g. to maintain balance), by measuring ground reaction forces (GRF) during bouts of WAIR. Estimates of the contribution of the hindlimbs towards the vertical external work done by the bird were 98±8% of the total at an incline of 60° (the steepest angle that birds were able to negotiate without the use of their forelimbs). During vertical (90°) bouts of WAIR the hindlimb contribution was 37±5% of the total external work. Yet, the magnitude of the peak GRF at 90° was 175% of the value generated during level walking, revealing that birds engaged in WAIR do generate sizeable hindlimb forces even during vertical ascents. These data support the hypothesis that forelimbs are enabling hindlimb function, and we argue that this represents a locomotor strategy which may have been used by proto-birds during the evolution of flight.

Movies available on-line

Introduction

Despite a long history of study (e.g. Lilienthal, 1889) and an appreciable understanding of biological wings (Pennycuick, 1968; Kokshaysky, 1979; Rayner, 1979a,b; Spedding et al., 1984; Ellington et al., 1996; Dickinson et al., 1999; Hedrick et al., 2002; Spedding et al., 2003a,b), our knowledge of the activities supported by these wings continues to expand. A recently described behavior, wing-assisted incline running (WAIR), documents the use of wings to enable bipedal ground birds to 'run' up vertical surfaces (Dial, 2003). This challenging and unexpected activity requires that in contrast to the traditional function of supplying thrust in the direction of travel and lift to support body weight, the wings of ground birds act to enhance hindlimb function (Dial, 2003). Specifically, the WAIR hypothesis suggests that during a substantial portion of the wingbeat cycle the wings of ground birds act to accelerate these animals towards the substrate.

WAIR has been documented in the juveniles and adults of four species of ground birds, and involves the simultaneous use of flapping wings and running legs to ascend steep inclines (Dial, 2003). WAIR permits extant ground birds, and may have permitted proto-birds, to use their hindlimbs more effectively in retreat to elevated refuges (cliffs, boulders, trees, etc.). It has been hypothesized that as these animals negotiate precipitous inclines (>60°), they alter their normal flight stroke to develop aerodynamic forces that secure the animal's feet upon the substrate, essentially functioning like the spoiler on a racecar, to enhance traction (Dial, 2003).

From previous work (Dial, 2003) we knew that chukars *Alectoris chukar* engaged in WAIR were able to run up vertical obstacles. We also knew that hatchlings as young as 3 days old use their partial wings to assist ascents, and that week-old hatchlings could ascend inclines unmatched by manipulated individuals whose flight feathers had been removed. Yet on a smooth inclined substrate there were no measurable performance differences between experimental groups, suggesting that the winged animals were not simply flying up the incline. Further, the reported preliminary measures of instantaneous acceleration from birds engaged in WAIR (Dial,

2003) suggest that during the late stages of the wing's downstroke, the birds' center of mass (COM) experiences an acceleration that is directed towards the substrate. Despite the relevance of these observations to discussions on the evolution of bird flight and the likely importance of WAIR to the natural history of ground birds in general, much remains unknown about this form of locomotion.

In this paper, we address the mechanics of WAIR through
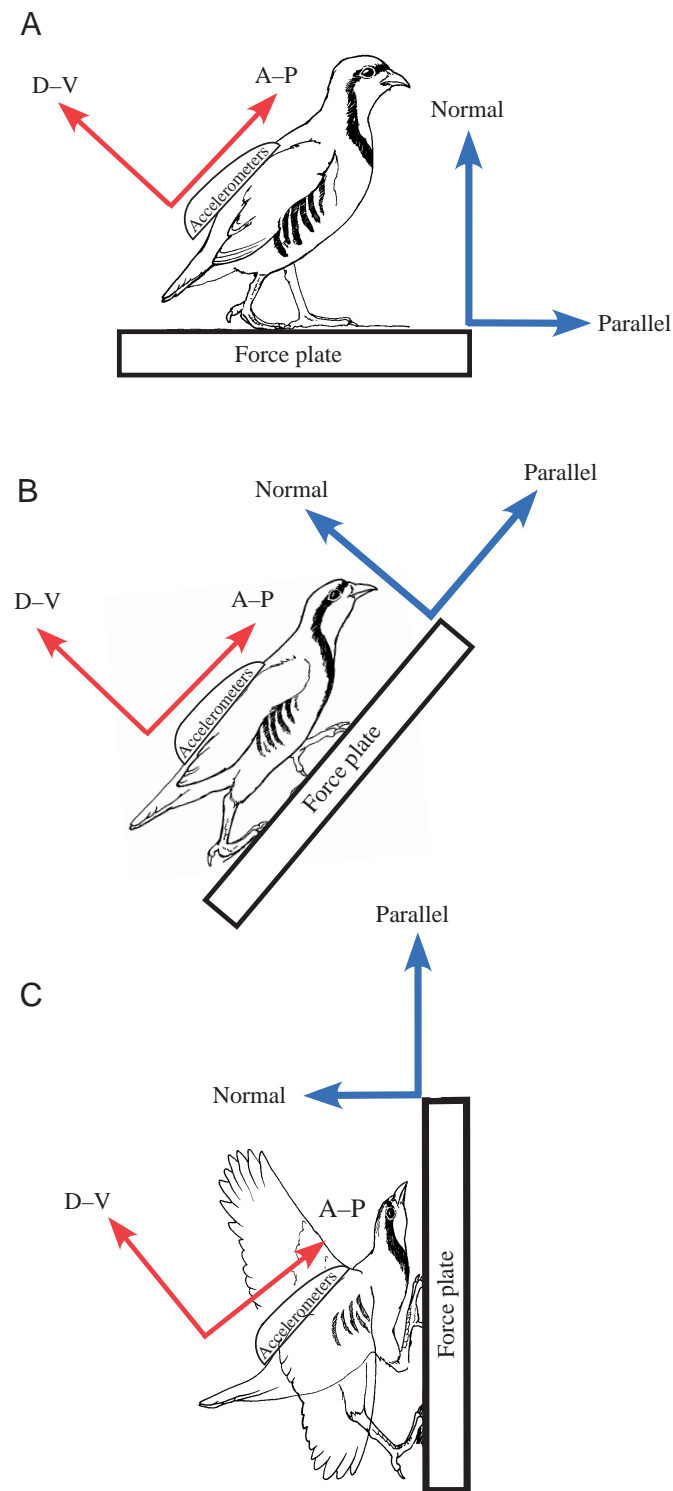
two primary questions. First, do the wings of chukars perform distinct functions during WAIR and free flight? The only published data of whole-body acceleration during WAIR (Dial, 2003) do not permit this critical comparison. Second, if differences in wing function exist between WAIR and free flight, do the wings enable the hindlimbs to generate large ground reaction forces (GRFs) when animals negotiate precipitous inclines? In other words, do the hindlimbs of these animals generate useful forces during ascents, or do they instead perform a non-propulsive role (e.g. balance)?

To evaluate the hypothesis that during WAIR ground birds use their wings to adhere themselves to the substrate to improve hindlimb function, we measured the instantaneous acceleration of the COM during WAIR and during free flight at a similar climb angle. Since acceleration is the only vector component of the total force, the direction of the acceleration of the COM is the same as the direction of total force. We predicted that during a substantial portion of the wingbeat cycle the acceleration of the birds' COM would be directed towards the substrate during WAIR, but not during flight.

To determine the extent to which hindlimbs are active during bouts of WAIR, we mounted a force platform in a ramp that could be inclined to angles between horizontal (0°) and vertical (90°) (Fig. 1). Thus, we would be able to measure the GRF generated during foot strikes as the birds engaged in WAIR over steep incline angles, including vertical. We specifically hypothesized that hindlimb force generation would provide a substantial portion of the required external work at all inclines, including 90° (Fig. 1).

Materials and methods

Animals and training

Four wild-type, captive bred, adult chukar partridges *Alectoris chukar* Gray 1830 (672.5±43 g, mean ± S.E.M.) were obtained from a local dealer. Chukar partridge are an Old World species, introduced in North America as a game bird and now established in the rocky, arid, mountainous areas of the western United States (McGowan, 1994). We make the assumption that the recordings and behaviors observed from our captive bred chukars are representative of this species as a whole. Animals were housed in an outdoor aviary 6.2 m (width) × 15.2 m (length) × 3.9 m (height). During the

Fig. 1. The relationship between the frames of reference of the instruments during the experiments (A, level; B, inclined; C, vertical) and the global frame of reference. The force plate is sensitive in the normal plane (perpendicular to the plate) and in the parallel plane (plane of motion). The accelerometers are sensitive to acceleration in the dorso–ventral (D–V) plane and the anterior–posterior (A–P) plane, relative to the bird's back. During inclined WAIR (B), weight support is no longer measured from a single axis. Both during a single wing beat and across different inclines, the changing orientation of the bird's back requires that the accelerometers be analyzed from within the bird's frame of reference (i.e. the A–P and D–V planes).

experimental period, June 2002 through December 2002, birds were given food and water *ad libitum*.

Birds were trained to ascend an inclined treadmill, the speed of which was selected to slow but not eliminate the animal's rate of climb. The birds were also trained to run up a ramp housing a force platform that could be inclined at angles between horizontal and vertical. Finally, the chukars were trained to take off on command from a marker and to fly at an angle to a platform.

Data acquisition

Accelerometers

To investigate whole-body instantaneous accelerations during WAIR and free flights, we employed two separate protocols. During both protocols the recording from, and harnessing of, the accelerometers were identical. The WAIR protocol required birds harnessed with the accelerometers to ascend a treadmill inclined to 52°. This permitted accelerometer recordings from a series of consecutive wing beats, but did not ensure that birds achieved or maintained a steady velocity. The treadmill was used specifically to lengthen the duration of the bout of WAIR, not to achieve a steady state condition.

The free-flight protocol required birds harnessed with the accelerometers to fly with a climb angle similar to that imposed during the treadmill-induced WAIR. Birds were trained to fly on command to an elevated perch 2.3 m high. They were placed at a horizontal distance of 1.6 m from the base of the perch so that their average climb angle was similar to the angle of inclination of the treadmill (i.e. 52°).

Two uni-axial accelerometers (EGAX-10, Entran, Fairfield, NJ, USA) with a sensitivity range of ±10 times the acceleration due to gravity (*g*) were aligned orthogonally and fused with self-catalyzing cyanoacrylate. The two accelerometers (mass 0.5 g each without leads) were mounted in foam and secured with athletic tape to form a package that could be mounted on the back of the animals. The dimensions of this 'backpack' were 3 cm × 1.5 cm with a height of 1.5 cm. Two bound strands of four-lead shielded lightweight cable (Cooner Wire, Chatsworth, CA, USA) exited the backpack and connected the accelerometers to an amplifier and power supply (Vishay 2100 system strain gauge conditioner and amplifier, Measurements Group, Inc., Raleigh, NC, USA). The analog signals from the strain gauge amplifier were acquired to a computer through a 16-bit A/D board (Digidata 1322A, Axon Instruments, Inc., Union City, CA, USA) at 3333.3 Hz, using Axoscope 8.1 software. Short tabs of tape extended from the long axes of the backpack and were securely sutured to the bird's intervertebral ligaments. The most posterior portion of the backpack lay immediately anterior to the synsacrum; this location was 3 cm dorsal and 3 cm posterior to the COM of the carcass of an adult chukar. Our choice of attachment site was based on this location's close proximity to the COM and the strong inter-vertebral ligaments to which the backpack could be attached without influencing the animal's performance. This site also ensured the alignment of the accelerometers with the standard anatomical body axes, such that one accelerometer lay in the anterior–posterior (A–P) plane while the second accelerometer lay in the dorso–ventral (D–V) plane. We assume that the location described above experiences accelerations that are representative of those of the true center of mass throughout the course of the wingbeat cycle.

The accelerometers were calibrated at the end of each recording session by alternately placing them in orientations where they were parallel and then orthogonal to the acceleration due to gravity. This process was repeated at least six times and the mean voltage difference between the two orientations was determined to be the voltage output produced by an acceleration of 9.8 m s^{-2}.

Force platform

A force plate (25 cm × 10 cm), previously described by Biewener (1983), was used to measure GRFs over different inclines during WAIR. The force plate was mounted flush in a moveable ramp, and overlaid with 50-grit sandpaper to reduce slippage. The force plate uses strain gauges in a Wheatstone bridge circuit to give separate voltage outputs proportional to the normal (two channels, fore and aft) and to the parallel (a single channel) components of the force acting on it. The strain gauges were powered by a Vishay 2100 system strain gauge conditioner and amplifier (Measurements Group, Inc., Raleigh, NC, USA). Analog signals from the amplifier were converted to digital through the same 16-bit A/D board we described above.

The force-plate channels sensitive to the normal component of force were calibrated by placing ten different masses (range 0.040–2.245 kg) at 2 cm increments along the length of the plate to establish a relationship between foot-strike position and the fore or aft channel most sensitive to pressure at that location. The channel sensitive to parallel force was calibrated by tilting the force plate by 90° and then suspending seven masses (range 0.05–2.00 kg) attached to the center of the plate by an inelastic cord. During testing with static weights at angles where a weight would remain stationary on the force plate (between 30° and 45°). we were able to predict the mass of known weights to within 2.2±0.5%, mean ± standard deviation (S.D.).

During recording sessions the angle of inclination of the force plate was increased in 10° increments between 60° and 90°. Only trials with a single foot strike where the entire foot was on the force plate were included in the analysis (a representative trial is reproduced in Fig. 2). Throughout these experiments we make the assumption that the wake produced by the animal's wings during WAIR does not influence the recordings of the force plate. We justify this assumption with the knowledge that the width of the force plate was only slightly larger than the width of the animal's body 10 cm *vs* 9 cm, and that the chukar's wing length of 24 cm is sufficiently long, relative to the width of the plate, that vortices shed by these structures are likely to occur lateral to the forceplate.

High-speed video recordings

Simultaneous high-speed video recordings (Redlake Masd Inc., PCI 500, 250–500 frames s^{-1}, shutter speed 1/2500–1/5000) were obtained during all experiments, using two internally synchronized cameras placed lateral to the path of motion. One of the cameras supplied detailed images of the force-plate strike during runs, or lift-off during flights. The second camera provided a wide-angle image to allow whole-body velocity measurements over the entire run. For each run, the video recordings were terminated by an external trigger that permitted synchronization of video recordings with the accelerometer and force-plate data.

Data analysis

Frames of reference

Both the accelerometers and the force plate have axes of direct measurement that are dependent on the orientation of the instruments during the experimental protocol (Fig. 1). For both the force plate and the accelerometers the component axes were summed to yield a resultant vector in the frame of reference of the instrument. To compare resultant vectors obtained during different experimental conditions (e.g. across inclines), the calculated vectors were rotated from the frame of reference of the instrument to the global frame of reference. Vectors with an orientation of 0° or 360° were parallel to the unit vector (0,1). The degree of rotation was determined from the orientation of the measuring device at the moment of interest.

Accelerometer data

The accelerometer data were zeroed to eliminate DC offset and filtered with an interpolative smoothing spline in Igor Pro version 4.0 (Wavemetrics, Inc., OR, USA) before further

analysis, which was performed in Microsoft Excel 2000 (Microsoft Corp., Redmond, WA, USA). The orientation of the accelerometers throughout the trial was determined from the video recording by digitizing a line parallel to the bird's back (Video point 2.1, Lenox Softworks, Lenox, MA, USA and Microsoft Excel 2000). The calibrated recordings from the A–P and D–V component accelerometers (Fig. 2) were combined to obtain a resultant acceleration vector. The orientation of this vector was adjusted to the global frame of reference, by a rotation that depended on the angle of inclination of the bird's back. The unit vector (0,1) was added to the resultant vector so that by convention, the accelerometers would read 1 g oriented at 360° for a motionless bird resting on the floor.

The mismatch in sampling frequency between the accelerometer data and the high-speed video, typically 3333.3 and 500 Hz, respectively, was overcome by averaging the resultant acceleration vectors collected in the time interval between two video frames and assigning the average vector a time value that would correspond to the first frame. Following this calculation we obtained measurements of the magnitude and direction of the acceleration of the COM that correspond directly to each image recorded by the high-speed video cameras.

Kinematic data were obtained from the video recordings corresponding to the analyzed portion of each trial. We noted the instant of each start of downstroke (SDS) and each end of downstroke (EDS) kinematic event that occurred within the analyzed portion. We determined the downstroke and upstroke transitions based on the movements of the bird's wrist. From these data the video frames falling midway and two-thirds of the way between SDS and EDS were determined and labeled mid-downstroke (MDS) and two-thirds downstroke (0.66DS). The frames falling one-third and mid-way between the kinematic events EDS and the following SDS were identified as one-third upstroke (0.33US) and mid-upstroke (MUS).

Force-plate data

The inclination of the force platform during each trial was determined from the video recordings by digitizing a line parallel to the force platform. The force-platform data were also zeroed to eliminate DC offset and filtered with an interpolative smoothing spline in Igor Pro version 4.0 (Wavemetrics, Inc.) before further analysis, which was performed in Microsoft Excel 2000. The normal force component was calculated through a position-dependent, weighted average between the calibrated fore and aft channels using the digitized location of the foot on the plate. The parallel force component was converted from volts (V) to Newtons (N) using the calibration algorithm previously described for the parallel force channel. The normal and parallel components of the GRF (Fig. 2) were summed
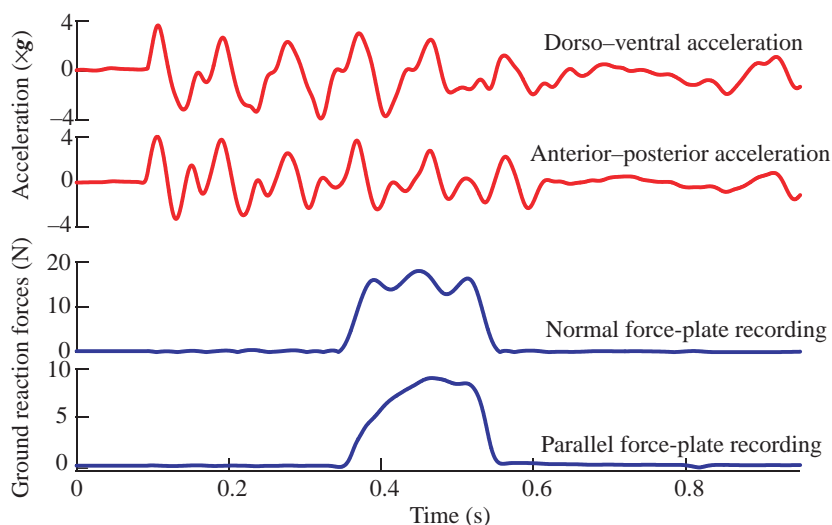

Fig. 2. Representative and simultaneous acceleration and force-plate data, from a chukar (mass 683.7 g) engaged in wing-assisted incline running, on a 70° incline. The D–V and A–P accelerometer signals have been conditioned and calibrated in multiples of the acceleration due to gravity (g). The force-plate ground reaction signals (N) have also been conditioned and converted.

to yield the GRF. The orientation of this vector was rotated by the angle of the incline to obtain vectors in the global frame of reference. The GRF vectors calculated for the time interval between successive video frames were averaged and assigned to the preceding video frame, in order to achieve a single GRF value that corresponds to each video frame.

Contribution of wings and hindlimbs to vertical work

Using a combination of the force-plate data and the high-speed video recordings we estimated the percentage of the external work done against gravity (i.e. vertical work) by the hindlimbs. The mechanics and assumptions of this calculation are based on the methodology described by Cavagna (1975) and are presented in Appendix I. Briefly, we considered only the vertical components of force, velocity and displacement during these calculations. We then compared the amount of external work done by the bird's COM to the magnitude of the cross product of the force measured by the force plate and the distance the COM moved during the application of the force. The fraction of the work attributed to the hindlimbs was estimated for all four experimental inclines (i.e. 60–90°).

The portion of the vertical work contributed by the wings was determined by subtracting the percentage of work done by the legs from 1.0. We reasoned that work was being performed either by the wings, or by the legs, and therefore the sum of the vertical work from each locomotor module must add to 1.0.

Statistics

Throughout the paper means ± standard error of the mean (S.E.M.) are reported. Calculation of the mean and standard error of directional data require techniques specific to this form of data in order to overcome the mathematical problem of finding the average between the two adjacent directions 359° and 0°. Here the standard error of the directional data was determined by transforming the vector in question to a unit vector with the same heading. The vector addition of all of the unit vectors within the sample permitted determination of the mean direction. The S.E.M. was calculated by dividing the estimated angular standard deviation (angular dispersion) by the square root of the number of observations (Butler, 1992). For the accelerometer data, the mean magnitude and orientation for the six kinematic events of interest were calculated for each recorded bout of WAIR and climbing flight. The means for each bout were then pooled to obtain an individual animal's mean, which were then combined to produce the reported means ± S.E.M.

Results

All of the birds consistently elected to use WAIR over free flight to reach the elevated refuge. Throughout the data acquisition of the force-plate and treadmill-induced WAIR protocols, we recorded well over 60 individual bouts of WAIR. On only two occasions during these recording sessions did a chukar choose to fly to the elevated refuge rather than to use WAIR.

Accelerometry during WAIR

The trends generated from the mean values of the resultant instantaneous acceleration measured from three birds, over nine runs and 121 individual wing beats (Table 1, and Fig. 3A–F). can be divided into three temporal categories. During the first portion of the downstroke (Fig. 3A), acceleration vectors were generally large and oriented upwards and in the direction of travel (SDS 2.8±0.2 g, 9±15°). The second functional division occurred during the late stages of downstroke (Fig. 3C,D) where the acceleration of the COM was directed towards the substrate (0.66DS 1.7±0.2 g, 111±13°). During the upstroke period (Fig. 3E,F) the acceleration was generally small and directed towards the ground (MUS 0.7±0.3 g, 187±24°). The standard errors surrounding the mean orientation of the acceleration vector illustrate the portions of the wingbeat cycle that were generally more stereotypical. Following this criterion, the middle through late downstroke periods were the least variable portions of the wingbeat cycle.

Table 1. *Instantaneous acceleration of the COM during wing-assisted incline running and during ascending flight*

	Acceleration vector			
	During WAIR		During flight	
Wing position	Magnitude (g)	Orientation (degrees)	Magnitude (g)	Orientation (degrees)
Start of downstroke (SDS)	2.8±0.2	9±15	3.0±0.2	327±8
Middle of downstroke (MDS)	2.0±0.2	15±17	2.0±0.3	61±22
Second third of downstroke (0.66DS)	1.7±0.2	121±15	3.8±0.2	86±8
End of downstroke (EDS)	2.2±0.2	111±13	2.9±0.1	72±7
First third of upstroke (0.33US)	0.8±0.2	163±17	1.1±0.3	142±36
Middle of upstroke (MUS)	0.7±0.3	187±24	0.2±0.3	263±45

COM, center of mass; WAIR, wing-assisted incline running.

Values are means ± S.E.M. (N=121 wingbeats, from 3 birds, during WAIR; N=57 wingbeats, from 4 birds, during ascending flight). These same values are presented graphically in Fig. 3.

During the second half of downstroke the orientation of the acceleration vector is directed towards the substrate during running, and in line with the direction of travel during flight (wing positions 0.66DS through EDS).
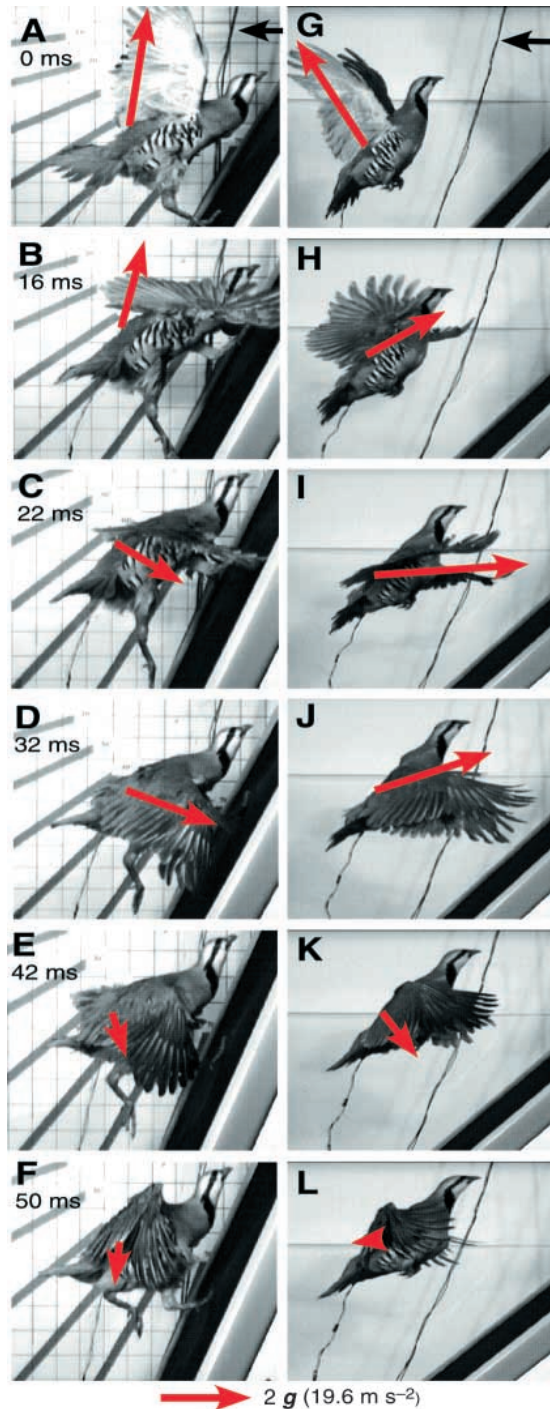
Fig. 3. The average instantaneous acceleration of the center of mass measured during WAIR (A–F) and during free flight at a similar angle (G–L). Red arrows represent the magnitude and direction of the instantaneous acceleration, calculated as the resultant vector from the A–P and D–V component accelerometers. The orientation of the acceleration vector during the late stages of downstroke (C,D and I,J) differs between WAIR and free flight. We propose the acceleration during WAIR acts to push the animal against the substrate in order for the legs to contribute a portion of the forces required for movement. The black arrows in A and G denote the cable connecting the accelerometers to the recording equipment.

Accelerometry during free flight

The mean values of the resultant instantaneous acceleration were generated from four birds, ten flights, and a total of 57 individual wing beats (Table 1, Fig. 3G–L). During the early stages of downstroke (Fig. 3G), the acceleration vector is large and oriented upwards (SDS 2.0 ± 0.3 g, $327\pm8°$) in a manner consistent with this phase of the wing beat generating much of the required lift. Through the middle to end stages of downstroke (Fig. 3I,J) the orientation of the acceleration is directed parallel to the direction of travel (0.66DS 3.8 ± 0.2 g, $72\pm7°$), unlike during WAIR. The upstroke portion of the wing beat (Fig. 3K,L) is characterized by small accelerations that are oriented approximately anti-parallel to the direction of travel (MUS 0.2 ± 0.3 g, $263\pm45°$), suggesting that this portion of the wing beat is not active in thrust generation. Similar to WAIR, the standard error of the mean orientations consistently showed the late stages of the downstroke period to be the least variable in orientation.

Force platform

Ground reaction force

The mean values of peak ground reaction force (GRF), expressed as multiples of the individual animal's body weight (M_b) measured over the five experimental inclines (Table 2), were all greater than those generated during fast level walks (1.5 m s^{-1}). These results indicate that at all of the experimental inclines, including the vertical, chukars were able to generate large forces against the substrate. Additionally, no decelerative phase was measured from the parallel force axis during inclined bouts of WAIR (Fig. 2). During level walks we did observe a braking phase during foot contacts.

Despite the normal axis' reduced role in weight support and vertical propulsion as incline angle was increased, the

Table 2. *Mean values of peak ground reaction forces (GRF) expressed as multiples of the birds' body weight measured over five experimental inclines*

Incline angle (degrees)	N	Peak GRF	
		Magnitude (multiples of M_b)	Orientation (degrees)
0 (horizontal)	5	1.47 ± 0.22	344 ± 7
60	10	3.32 ± 0.14	327 ± 3
70	10	2.62 ± 0.15	326 ± 3
80	8	2.42 ± 0.19	317 ± 4
90 (vertical)	5	2.61 ± 0.29	302 ± 5

N, number of observations; M_b, body weight.

Values are means ± S.E.M.

Peak GRF during incline running: horizontal values were from fast walks (1.49 ± 0.04 m s^{-1}).

Although the magnitude of peak GRF decreases with angle of incline, during vertical running (90°) the magnitude of the GRF is nearly twice that of level walking. The level walks are included for comparison; however, during each observation the birds were decelerating slightly.

magnitude of the force exerted in the normal plane remained larger than that of the parallel axis (Fig. 4). When expressed as a fraction of the peak GRF, the lowest value measured by the normal axis was 79% of the GRF, indicating even during steep ascents the animals were applying large forces in a manner consistent with the development of traction (Fig. 5).

Contribution of hindlimbs and wings to vertical work

During runs at 60°, an angle at which chukars generally did not engage in WAIR, our estimate of the contribution of the hindlimbs to the external vertical work was 98±8% (Fig. 6A). During bouts of WAIR at 70° and 80°, the estimated

contribution of the hindlimbs to the required vertical work decreased to 64±5% and 51±6%, respectively. During wing-assisted vertical ascents we estimate the contribution from the legs to be the lowest of any of the experimental inclines at 37±5%.

During ascents of 60° we estimate that the wings contributed 5±2% of the observed external vertical work (Fig. 6B). During bouts of WAIR at 70°, 80° and 90°, the contribution from the wings to the observed external vertical work increased to
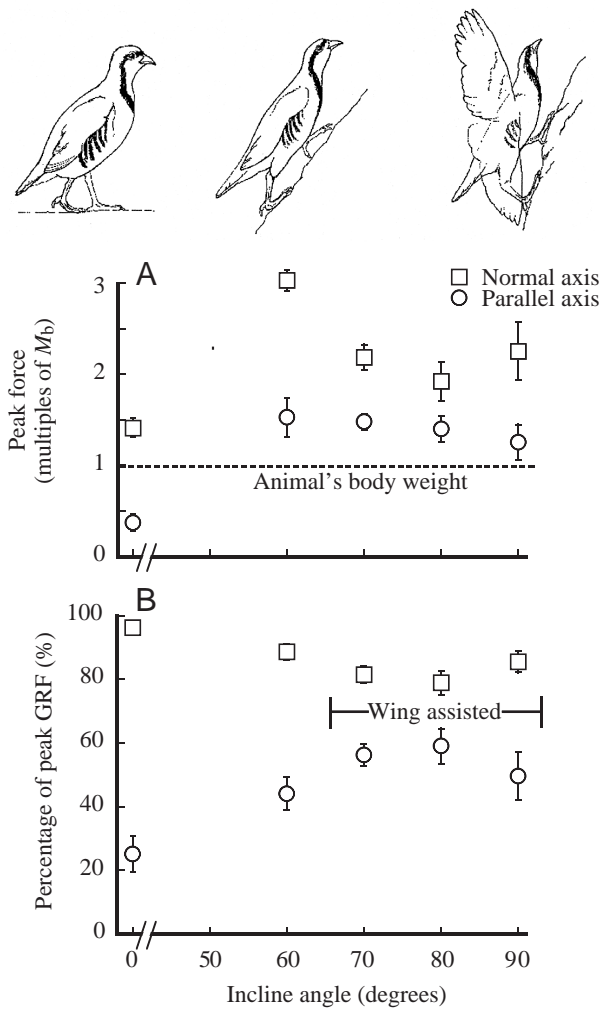

Fig. 4. During ascents (body postures shown above), both the normal (squares) and parallel (circles) components of the ground reaction force (GRF) show large increases over level walking values (A). The relative importance of the parallel axes to the peak GRF increases with the angle of ascent (B). The high forces in the normal plane during WAIR are consistent with the development of high frictional forces, which permit hindlimb propulsion. The magnitude of the GRF decreases during climbs when the wings are used to assist locomotion, generally angles greater than 60°. In B the sum of the percentage of peak GRF for each component does not equal 100%; rather vector addition requires the squares of the components to sum to the square of the GRF.
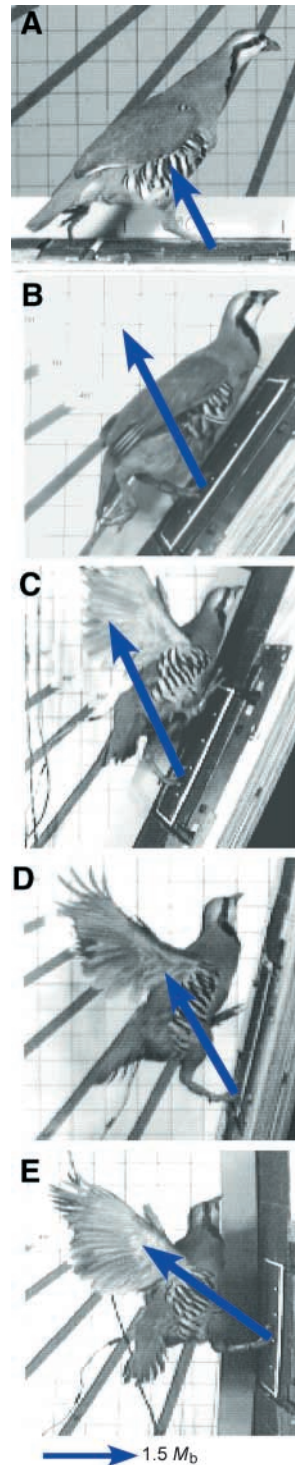

Fig. 5. The magnitude and orientation (length and direction of the blue arrows) of the peak ground reaction force (GRF) from representative runs of different inclination. (A) Peak GRF during fast walking on the level. During this trial the animal was decelerating slightly, and not maintaining a steady velocity. (B–E) Peak GRF for the illustrated runs at 60°, 70°, 80° and 90°, respectively. During wing-assisted running (C–E) the magnitude of the GRF is less than at 60°, where wings are generally not used. Despite the pattern shown between wing position and the instance of peak GRF shown in C–E, during sustained bouts of WAIR on an inclined treadmill we found no relationship between footfall and wing position. M_b, body weight.
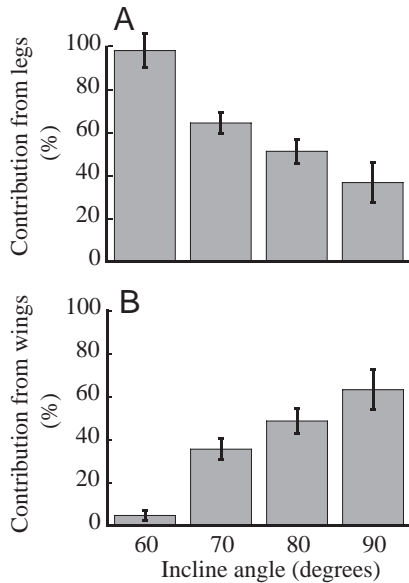
Fig. 6. The calculated fraction of vertical mechanical work done on the center of mass (COM) during locomotion across different inclines by the legs (A) and wings (B). At 60° chukars rarely use their wings, and the magnitude of the vertical component of the ground reaction force is sufficient to provide the motion in this plane. Over steeper inclines the vertical component of the GRF is no longer sufficient to provide the energy required of vertical motion, thus the difference must be attributed to the wings.

overcome the reduction in contribution from the hindlimbs, and was 35±5%, 49±6% and 63±5%, respectively.

Discussion

In this study we posed two questions pertaining to the locomotor mechanics of WAIR in galliform birds. (1) Do the wings of chukars function differently during WAIR and free flight, and (2) do their hindlimbs generate substantial and useful propulsive forces during these ascents? We affirmed the first question by refining and updating a technique to measure instantaneous acceleration, a vector quantity that is parallel to the total force experienced by an animal's COM. These new data permitted simultaneous evaluation of the accelerations experienced by the COM and of the corresponding wing kinematics. We addressed the second question by mounting a force plate into a variably inclined ramp to obtain the first inclined values of ground reaction force as animals negotiated the precipitous inclines of interest. Our measures of GRF reveal that during these ascents peak force production is at least 50% greater at all inclines than during horizontal walking at nearly 1.5 m s^{-1} (Table 2 and Fig. 5).

Accelerometers

The potential use of accelerometers in studies of locomotion has long been recognized (Cavagna et al., 1963; Morris, 1973). However, their use has not been widespread (van den Bogert et al., 1996). Further, published efforts focused on bird flight

are limited to the single work of Bilo and colleagues (Bilo et al., 1985), who mounted two accelerometers onto the ventral aspect of the body of pigeons (*Columbia liva*) flying within a wind tunnel in order to measure acceleration in the axes of thrust (horizontal plane, during level flight) and lift (vertical plane, during level flight). These authors did not, however, combine the thrust and lift components to determine a resultant vector as we have done (A–P and D–V component accelerometers), and thus the interpretation of their data is rather difficult. Our approach not only estimates the resultant instantaneous acceleration, but also combines these data with wing kinematics (Fig. 3) and relies heavily on the technological advances that have occurred since the pioneering efforts of these scientists. For instance, the use of high-speed digital video recordings, the ease of converting analog signals to digital files, and the subsequent analysis of large volumes of digital files, have greatly reduced the time commitment that would have been required of the original authors.

We feel that the use of accelerometers in a manner similar to that reported here will provide functional morphologists and experimental biologists with an additional tool to investigate the timing and magnitude of biologically relevant forces. This technique is likely to be particularly appealing to those investigators who focus on modes of locomotion for which the force exerted against the environment is not easily measured (i.e. movement in a fluid). Although the technique is relatively straightforward, our results, as well as others generated under similar conditions, do not permit distinction between aerodynamic and inertial forces. Nevertheless, by incorporating detailed three-dimensional kinematics it may be possible to estimate the inertial forces and to subtract these estimates from the measured values of whole-body acceleration to determine the magnitude and direction of the resultant aerodynamic force.

Instantaneous acceleration during free flight

During free flight (Movie 1) the integration of the instantaneous acceleration with the kinematic data revealed three general patterns. First, the large upwardly directed acceleration during the start of downstroke (Fig. 3A) suggests that a phenomenon similar to the 'fling' portion of the 'clap and fling' mechanism (Weis-Fogh, 1973) may counteract the Wagner effect and allow lift production to be generated early in the downstroke. Second, the relatively rapid decrease of the magnitude of the acceleration vector during the late stages of downstroke (Fig. 3D) may be caused by the sudden transfer of momentum into the wake of the bird (i.e. the shedding of a vortex ring). Third, during the upstroke portion of the wing beat the values of instantaneous acceleration are only mildly directed upwards, suggesting that the upstroke kinematics (Fig. 3F) used during these flights were only slightly aerodynamically active. The results presented here provide empirical support for these predictions that follow from aerodynamic theory (Weis-Fogh, 1973; Spedding et al., 1984; Rayner, 1979c); however, it should be clear that inferring fluid flow would most accurately be accomplished by the

visualization of fluid dynamics (e.g. DPIV; Spedding et al., 2003a,b; Rosen, 2003).

Instantaneous acceleration, WAIR

The measurements of instantaneous acceleration during free flight and WAIR suggest that the wings function differently during these two modes of locomotion. During the majority of the downstroke the orientation of the acceleration vectors was different between free flight and WAIR (Fig. 3). The orientation of the acceleration vectors measured during WAIR are towards the substrate during the second half of the downstroke, whereas during ascending flights the acceleration vectors are generally oriented parallel to the direction of travel, as would be expected.

Although we are unable to address whether the forces responsible for the observed acceleration are inertial or aerodynamic, their outcome is clear: chukars engaged in WAIR can climb very steep inclines, including vertical obstacles (Fig. 5). This ability is shared with few other tetrapods, none of whom are bipeds, and those that are capable of such precipitous ascents generally possess specialized, derived morphological features to accomplish this task (Autumn et al., 2000, 2002; Ji et al., 2002). In contrast, galliform species appear to co-opt existing locomotor machinery in a manner that has only recently been appreciated. The major requirement for the use of WAIR appears to be the animal's ability to achieve stance periods without slipping in order to allow hindlimb propulsion. To reduce skidding on a surface, either the normal force (also referred to as the loading force) or the frictional coefficient between the interacting surfaces must be altered. By incorporating WAIR into their locomotor behavior (Movie 2), chukars appear to be adding effective weight to their hindlimbs to increase the normal component of friction. Previously, Dial (2003) described how fully volant chukars attempting to climb a smooth surface would engage in WAIR in a futile attempt to climb even modest inclines, strongly suggesting that these birds are committed to WAIR even though they are fully capable of flight. These observations further suggest that the amount of effective weight that chukar wings are capable of generating is insufficient to overcome an experimentally reduced friction coefficient.

Hindlimb function during WAIR

Our second hypothesis asked whether the hindlimbs were active in generating useful propulsive forces. Our measurements of peak ground reaction force during WAIR reveal that the hindlimbs do generate sizeable forces at all of the experimental inclines (Movie 3). Despite the decreasing trend of peak GRF with increasing incline angle (Table 2 and Fig. 5) the lowest value of peak GRF was 2.4 times the animal's body weight. Our estimates of the relative contribution of the wings and hindlimbs to the total vertical work (Fig. 6) further suggest that these large GRFs were responsible for a substantial portion of the required work on all inclines. The relatively low contribution (i.e. 37%) of the

hindlimbs to the total external work during vertical runs was due to the high power requirements of these ascents rather than a dramatic decrease in force production at this incline. The correspondingly high contribution from the forelimbs during vertical ascents agrees well with previous results (Dial, 2003), which demonstrated that chukars with experimentally reduced wings were unable to use WAIR to ascend vertical substrates, implicating the importance of wings to ascents at these steep inclines.

When the components of the GRF were evaluated independently we did not observe a decelerative phase in the parallel component during bouts of WAIR. The absence of a breaking force during accelerative runs has been previously identified in humans (Cavagna et al., 1971) and turkeys (Roberts and Scales, 2002), and may represent a relatively common strategy during activities that require high power outputs (i.e. the accelerative runs they report, and the vertical ascents we document here).

Significance and ubiquity of WAIR

Following hatching, precocial species of birds rely almost entirely on their hindlimbs to move rather than their as-yet-undeveloped wings (e.g. Oken, 1837; Starck and Ricklefs, 1998). Nevertheless, these animals recruit their partial wings from the first day of hatching by flapping the forelimbs when required to negotiate even modest inclines (Dial, 2003). Throughout their development, these birds use their forelimbs and hindlimbs in combination to permit escape to elevated refuges (Dial, 2003). WAIR may be common to other ground birds in general, and specifically to other similar clades such as the tinamous of South America and the megapodes (also galliformes) of Australia.

The strategy of employing partially grown and non-flight-capable wings to enhance hindlimb function may also be common to altricial species of birds. Altricial birds may use WAIR during the brief post-fledging period when these animals are developing their aerial skills but are unable to depend entirely upon aerial locomotion. Another opportunity for the use of WAIR is provided by members of the Strigidae (typical owls), who are known to leave their nests well before they are capable of flight (referred to as branching; Marks et al., 1999); however, details of this locomotor behavior have yet to be described. Further, the frequency with which other altricial chicks fall from their nests and their ability to reach the safety provided by elevated refuges such as bushes, trees, and cliffs, are additional examples of the potential use and importance of WAIR. Whether these animals engage in WAIR during some or any of their life history is currently unknown, but studies of this type would represent an exciting merger between biomechanics and natural history.

Evolutionary aspects of WAIR

For more than a century, discussions on the origin of avian flight have been confined to the arboreal–cursorial dichotomy (i.e. tree-down *versus* ground-up hypotheses). Despite volumes of publications (e.g. Feduccia, 1996; Chatterjee, 1997; Paul,

2002) and exquisite fossil finds (e.g. Sereno and Rao, 1992; Zhou and Wang, 2000; Zhang and Zhou, 2000; Norell et al., 2002; Xu et al., 2003), few intellectual advances have been made to alter the initial framework for either the arboreal (Marsh, 1880; Heilmann, 1926; Bock, 1985; Rayner, 1991; Pennycuick, 1986; Norberg, 1985; Xing et al., 2000) or cursorial theses (Williston, 1879; von Nopsca, 1907; Ostrom, 1974; Caple et al., 1983; Burgers and Chiappe, 1999). The lack of substantial progress to resolve this impasse may be due to the following. First, the lack of credible and incremental adaptive transitional stages from wingless, to intermediate-winged, to full-winged powered fliers. Second, our inability to identify plausible models using extant taxa to reveal transitional forms employing proto-wings leading to powered-flapping wings. And third, our failure to provide meaningful empirical results based on living forms as models, rather than depending on theoretical and computational models to validate either flight thesis. More recently, an increasing number of scientists recognize the inherent difficulty in supporting, or falsifying, the arboreal–cursorial dichotomy, and have instead focused attention on understanding aspects of the origin of flight that lie beyond the confines of this dichotomy (e.g. Jenkins, 1993; Padian and Chiappe, 1998; Padian, 2001a; Burgers and Padian, 2001). We believe the present study incorporates the latter philosophy in an effort to further advance our knowledge of the avian trajectory towards flight.

The empirical results reported here and previously (Dial, 2003) suggest that WAIR provides a model identifying incremental adaptive plateaus by which the evolution of flight may have occurred. We propose that WAIR provides a logical framework by which the proto-wings of avian precursors may have offered adaptive benefits to their owners, despite being incapable of flapping aerial flight. The identification of transitional stages is a crucial element towards elucidating the trajectory leading to the evolution of complex morphological traits (Bock, 1965, 1985). Despite the logical application of WAIR to the evolution of flight, however, many questions still remain unanswered.

The importance of WAIR to the origin and evolution of flight is clearly not a directly testable hypothesis. Nevertheless, WAIR does demonstrate how transitional stages of proto-wings may have been adaptive, particularly to small bipedal cursors. Future studies that address the aerodynamic and biomechanical requirements necessary for WAIR, such as the minimum required wingbeat frequency, wing geometry and the potential role of ground effect, will provide a more complete empirical picture of how proto-wings may have functioned during the evolution of flight. Additionally, phylogenetic analyses, based on relevant traits and states, will provide a further test of WAIR's relevance or consistency to discussions on the evolution of flight (Padian, 2001b).

Conclusions

Our measurements of the orientation of the whole-body acceleration vectors and the magnitudes of the ground reaction force vectors during WAIR at steep incline angles support our original hypothesis, that forelimb function acts to enhance hindlimb propulsion. The reliance on this strategy by both juvenile and adult chukars, its potential use by many other avian species, and its possible role in the evolution of flight, all illustrate the importance of this non-steady-state locomotor event to the life history of birds. These non-intuitive results highlight the flexibility of the avian wing, underscoring the importance of continued empirical investigation into the force-generation capabilities and movements of this structure, and the incorporation of natural animal behaviors into aerodynamic models. Moreover, we hope our empirical results stimulate discussions and experimentation on the origin of avian flight by supplanting the intractable arboreal–cursorial debate with alternative, testable hypotheses. The recruitment of the forelimbs, and the subsequent mechanics that permit chukars to run up vertical obstacles, may also have allowed early birds to escape to elevated refuges, as extant galliformes do, and thus provided the mechanism by which the trajectory towards avian flight may have proceeded.

Appendix

Calculation of the hindlimb contribution to vertical work

Estimates of the hindlimb contribution to the external mechanical work performed in the vertical direction were generated by calculating the ratio of mechanical work done on the COM to the amount of physical work attributed directly to the hindlimb, as measured from the force plate and high-speed video recordings (hindlimb external work). Throughout the following calculation we have used only the vertical components of the ground reaction force, velocity and displacement.

Total mechanical work on the body

The magnitude of the total external mechanical work done on the COM was determined by:

$$Work_{total} = \Delta E_{Potential} + \Delta E_{Kinetic} , \qquad (A1)$$

which can be expanded to:

$$Work_{total} = \Delta mgh + \Delta \tfrac{1}{2}mv^2 , \qquad (A2)$$

where m is the mass of the animal in kg, $\boldsymbol{g}$ is the acceleration due to gravity, h is the height gained by the animal in m, and v is the velocity of the animal (m s^{-1}). In practice, the height gained by the animal was the displacement of the COM determined from digitizing the high-speed video recording during the period that began with foot contact on the force plate and ended at foot down of the other foot (off-foot). The velocity of the COM was determined from the same digitized portion of the video recording from which the displacement (h) data was obtained.

Hindlimb external work

The magnitude of the hindlimb external work was determined by summing the trapezoidal integral of a plot of net vertical force (net F_v) and the displacement of the COM during

force generation (i.e. during stance on the force plate). The displacement of the COM during force application was defined as the displacement of the COM during the time period between touch-down on the force plate, and either toe-off from the force plate, or touch-down of the off-foot, whichever occurred first.

To determine only the portion of the vertical force (F_v) that was responsible for the external mechanical work (net F_v), the portion of the vertical force responsible for weight support was subtracted prior to the calculation of the integral. Since it was not possible to zero the force plate with the subject animals standing quietly on the force plate at the incline angles of interest (Cavagna, 1975), we estimated the portion of the F_v that was required to support the animal's body weight (M_b). To perform this calculation two assumptions were made. First we assumed that chukars engaged in WAIR relied equally on their right and left feet. Second, over a period of one stride the portion equal to weight support must average $1 \times$ body weight. We measured the total duration of stance from each foot during a single stride, as well as the stride duration, and then calculated the percentage of the stride during which foot contact was occurring (stance percentage). We then performed the following subtraction:

$$\text{net}F_v = F_v - [(\text{stance percentage}^{-1})/2] \cdot M_b , \quad (A3)$$

followed by the calculation of the trapezoidal integral of a graph of the net F_v *vs* the displacement (d) of the COM during force application:

$$\text{Hindlimb work} = \sum_{i=1}^{n} \text{net}F_{vi} \cdot d_i , \quad (A4)$$

which expands to:

$$\text{Hindlimb work} = \sum_{i=1}^{n} |\text{net}F_{vi}| \cdot |d_i| \cdot \cos\theta , \quad (A5)$$

where θ is the angle between the two vectors. Since throughout this calculation we have only considered the vertical components of these forces and displacements, the angle between them is $0°$, and thus the term $\cos\theta$ is equal to 1. As a result Eq. A5 becomes:

$$\text{Hindlimb work} = \sum_{i=1}^{n} |\text{net}F_{vi}| \cdot |d_i| . \quad (A6)$$

It then becomes possible to evaluate the ratio of hindlimb external work to total mechanical work.

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