

# TERRESTRIAL LOCOMOTION IN THE BLACK-BILLED MAGPIE: KINEMATIC ANALYSIS OF WALKING, RUNNING AND OUT-OF-PHASE HOPPING

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## Summary

The inter-limb kinematic patterns of walking, running and out-of-phase hopping in black-billed magpies (*Pica pica*) were studied using high-speed video recordings. The flexion/extension patterns of the joints were similar between the gait types, suggesting that the within-leg control of the angular excursions is similar. This result is further supported by the fact that running and hopping are alternative gaits at speeds higher than walking; however, magpies show a preference for hopping. Moreover, only small differences occur between the kinematic patterns of the two limbs during out-of-phase hopping, during which

the legs are believed to have different functions. The hindlimb kinematic patterns of magpies are like those of other flying and more terrestrial bird species; however, striking differences are found in comparison with humans at the level of the internal angles. This is probably due to the differences in the morphology and configuration of their legs.

Key words: kinematics, bipedal gait, terrestrial locomotion, black-billed magpie, *Pica pica*, running, hopping, walking.

## Introduction

Terrestrial locomotion in birds can involve several different gaits. Birds can walk, run or hop (in- or out-of-phase; Verstappen and Aerts, 2000), but most species use only one or two gait types. Several studies have already dealt with kinesiological aspects of these different gait types (energetics, see, Bamford and Maloiy, 1980; Brackenbury and Avery, 1980; Brackenbury et al., 1981, 1982; Cavagna et al., 1977; Fedak et al., 1974; Fedak and Seeherman, 1979; Muir et al., 1996; Pinshow et al., 1977; Roberts et al., 1997, 1998a; Taylor et al., 1971; Taylor, 1977; mechanics, see Alexander et al., 1979; Clark, 1988; Clark and Alexander, 1975; Fedak et al., 1982; Heglund et al., 1982a,b; Roberts et al., 1998b; Taylor et al., 1982; electromyography, see Jacobson and Hollyday, 1982a,b; Gatesy, 1999b; Weinstein et al., 1983; neurology, see Jacobson, 1980; Johnston and Bekoff, 1996; Steeves et al., 1987) but, compared with the wealth of studies dealing with mammalian locomotion, this number, and thus our knowledge of terrestrial bird locomotion, is relatively small.

Verstappen and Aerts (2000) analysed the spatio-temporal gait characteristics of walking, running and out-of-phase hopping in the black-billed magpie (*Pica pica*). With increasing speed, the three gait types do not occur successively as walking, trotting and galloping do in quadrupedal mammals. In magpies, walking is used at low velocities, and running and out-of-phase hopping are alternative gaits for higher speeds, with birds showing a preference for hopping. This is comparable with the situation in humans, hence the fact that humans prefer running at higher speeds (Caldwell and Whittall,

1995; Minetti, 1998). Verstappen and Aerts (2000) concluded that no intricate shifts in control and coordination are required for the gait transitions in magpies. They postulate that running emerges from 'over-powered' walking, and that hopping is like running but with a reduced phase difference between the limbs. From this, it follows that inter-limb kinematic patterns should be fairly similar over the different gait types. During out-of-phase hopping, the legs are not set down simultaneously. It is postulated that a different function might be present for the two legs (Verstappen and Aerts, 2000). Moreover, it is not obvious why the birds use running and hopping as alternative gaits and why they prefer hopping at higher speeds. In the light of the 'coupled oscillators for the legs' theory (see Kugler and Turvey, 1987; Peck and Turvey, 1997), it can be postulated that intrinsic features of the bird's build (e.g. body proportions) normally evoke out-of-phase hopping at speeds greater than walking, but that subtle changes in the initial state of the neuromuscular system are sufficient to shift the point at which walk–run coordination becomes unstable towards higher speeds (Verstappen and Aerts, 2000). To explain all these differences, more information on the detailed angular displacements of the leg and its segments over the course of a stride, i.e. the kinematics, in birds is needed.

The few studies on birds that concentrate on the detailed kinematics of the legs during terrestrial locomotion have mostly used conventional video recordings (50–60 frames s<sup>-1</sup>) (e.g. Dagg, 1977; Jacobson and Hollyday, 1982a; Johnston and Bekoff, 1992; Miller, 1937; Muir et al., 1996; Stolpe, 1932),

which may suffice for walking, but high-speed video recordings are essential for the faster gaits (running and hopping). Furthermore, analyses are often limited to one or two gaits (walking and/or running, e.g. Cracraft, 1971; Dagg, 1977; Jacobson and Hollyday, 1982a; Manion, 1984; Rylander and Bolen, 1974) or to a selection of joint angles (e.g. Dagg, 1977: only the ankle; Gatesy, 1999a: no ankle). To our knowledge, no study has compared quantitative data (internal and external angles) for hindlimb movements during walking, running and out-of-phase hopping in birds. The present study, therefore, aims to give a full kinematic description of the external and internal joint angles during walking, running and out-of-phase hopping in the black-billed magpie.

### Materials and methods

Initially, three hand-raised black-billed magpies (*Pica pica* L.) were trained for several months to move on a treadmill to gather high-speed recordings of complete locomotion cycles (strides) in close up. These locomotion bouts were very irregular and highly unrepeatable because the animals tended to flap their wings, so these results and this technique had to be discarded. The animals were therefore placed on a 6 m long outdoor running track where they were encouraged to move at different speeds to provide kinematic data over a range of speeds. To prevent slipping, the running track was covered with a thin layer of cork. To obtain a better view of the proximal hindlimb joints, the birds' feathers at the hip and knee joints were cut away a few days prior to filming. This did not seem to affect their behaviour in any way.

To obtain accurate information about the positions of the joints and the placing of the toes, high-speed video recordings (500 frames  $s^{-1}$ , NAC1000) were taken in close up. The camera settings were such that the image of the bird almost filled the screen. As a result, only parts of complete strides could be kept in the field of view, which means that the

overall picture of the locomotor cycle is compiled from several fragments. To give further support to the description of the angular displacement patterns of the hindlimb joints throughout a complete stride, the birds were also filmed at a wider view. For this purpose, a conventional camera (50 frames  $s^{-1}$ , Panasonic F15) was used.

In this study, gaits are distinguished by footfall patterns, so that they can be identified directly from the video recordings (see also Verstappen and Aerts, 2000). The onset of the stance phase coincides with the moment the hallux (=hind-toe, digit 1) touches the ground (see Figs 1B, 7). When the third digit leaves the ground, the recovery phase begins (see Figs 1B, 7). Walking is defined as a symmetrical gait with two double-support phases in each stride (=from the lift-off of a foot until the next lift-off of the same foot). During running, floating phases replace the double-support phases (high-speed filming is necessary to record these phases). Hopping, which also includes an aerial phase, is an asymmetrical gait and is thus easily differentiated from running. Out-of-phase hopping is also known as bipedal galloping (see Whittall and Caldwell, 1992; Caldwell and Whittall, 1995) or skipping (see Minetti, 1998). On the basis of the continuity of the gait and to obtain a velocity range, 28 walking, nine running and 32 out-of-phase hopping high-speed video sequences were selected for further analysis. From the conventional video recordings (50 Hz), seven walking sequences that included at least one complete stride were also analysed. This temporal resolution proved to be sufficient to obtain relevant additional data for the slowest gait. The velocity of the birds in each selected sequence was calculated by determining the slope of the linear regression of the forward displacement of the eye against time (all  $r^2 > 0.98$ ).

The circles in Fig. 1A mark the body points that were used for digitisation: bill tip (b), eye (e), neck (n), hip (h), knee (k), ankle (a), inter-phalangeal joint (i), and the distal ends of the hallux (ha) and the front-toes (f). These body points were always digitised on the side of the body closest to the camera.

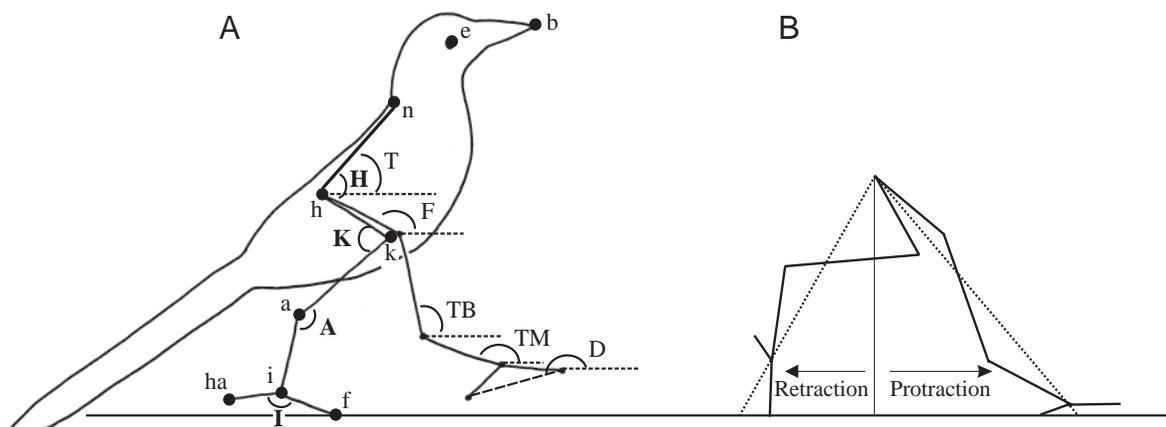


Fig. 1. (A) Outline of a magpie showing the points digitized (circles) and the external and internal angles. Lower case letters represent the body points: a, ankle; b, bill tip; e, eye; f, front toes; ha, hallux; h, hip; i, interphalangeal joint; k, knee; n, neck. Upper case letters represent the angles: A, ankle; D, digits; F, femur; H, hip; I, inter-toe; K, knee; T, trunk; TB, tibiotarsus; TM, tarsometatarsus. (B) Retraction and protraction angles of the leg.

In the case of the high-speed recordings, the coordinates of these body points were digitised at  $250 \text{ frames s}^{-1}$  using APAS software (Ariel Performance Analysis System, Ariel Dynamics Inc.). The sequences obtained using conventional video were digitised at  $50 \text{ frames s}^{-1}$  with custom-designed software. To reduce the error involved in the digitisation of the coordinates of the hip and knee (due to the presence of the wing feathers), an overlay stick model of the bird (based on X-ray photographs and video) drawn on a transparency was used. Whenever a joint was not clearly visible, this transparency was superimposed on the screen to locate it more precisely. Despite these precautions, the digitization errors for the hip, knee and ankle are expected to be larger than those for the other body points. However, none of the errors was so large that the angular patterns presented here are not a valid representation of the motions of the legs during locomotion.

In the present analysis, most attention was paid to the angular changes of the hindlimb segments during the stance phase for the following reasons. (i) It has previously been found that most of the metabolic cost during running in bipeds (birds and humans) is inversely correlated with the time available to generate force, i.e. the duration of the stance phase (Roberts et al., 1998b). (ii) Ground reaction forces act on the

hindlimb during this phase, leading to muscular and skeletal stresses much higher than those present during the recovery phase. (iii) Recovery phase duration is found to be independent of speed and to be similar for the three gaits, which suggests passive mechanical control (Verstappen and Aerts, 2000). For these reasons, high-speed sequences of primarily stance phases were used in further analysis.

After digitisation, the displacements (in m) of the coordinates against time were obtained. Next, time histories of angular displacements were calculated. A zero-phase-shift fourth-order Butterworth filter was used to remove noise from the angular displacement data. The external angles of the trunk, femur, tibiotarsus and tarsometatarsus were measured between these body segments and the horizontal (see Fig. 1A). The internal angles of the hip, knee and ankle were measured between two body segments (see Figs 1A, 7). The movements of the toes are expressed by an external angle measured between a line connecting digit 3 with the hallux and the horizontal, and by an internal angle measured between digit 3 and the hallux (inter-toe angle) (see Figs 1A, 7).

The angular displacement patterns can show several maxima and minima throughout a stride (e.g. see Fig. 2). These maxima/minima are coded according to the phase in which

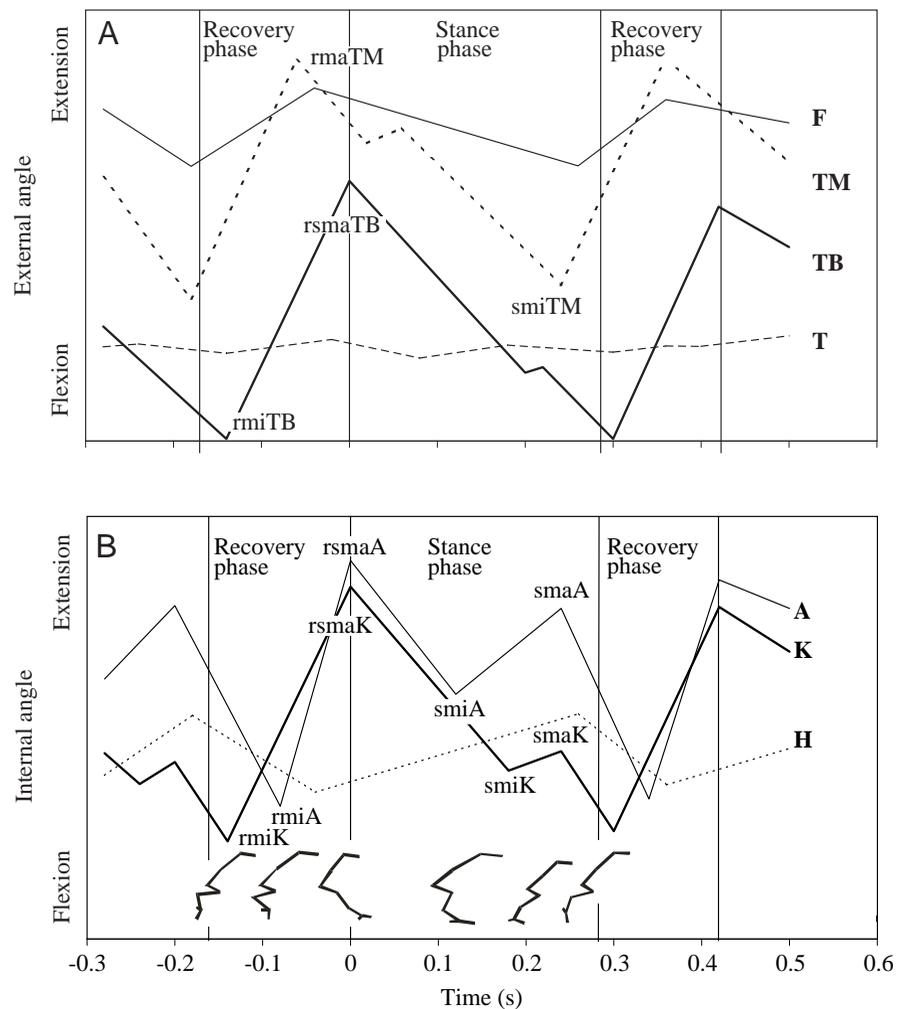


Fig. 2. Schematic representation of changes in external angles (A) and internal angles (B) with time for all gaits derived from real data (50 Hz). The stick figures, representing the leg closest to the camera, refer to the following angles/moments from left to right: rmiK, rmiA, onset of stance phase, smiA, smaA and onset of recovery phase. The abbreviations for the angles are defined in Fig. 1A. The maxima/minima in the measures are coded according to the phase in which they occur: r, recovery; s, stance; rs, recovery–stance transition; sr, stance–recovery transition; and also whether they represent maxima (ma) or minima (mi). See Materials and methods for further details.

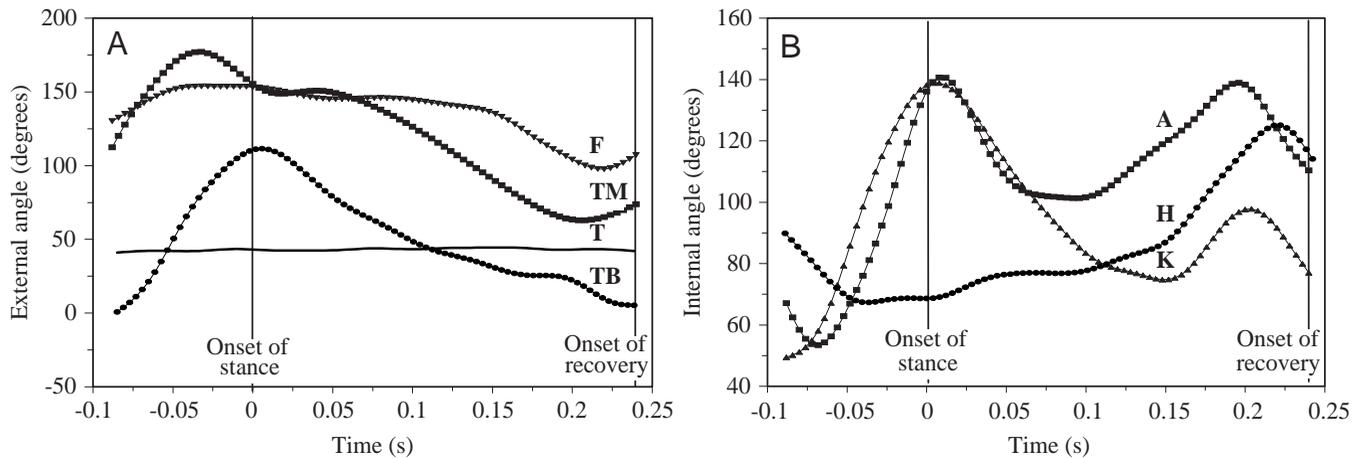


Fig. 3. External (A) and internal (B) angles recorded during the stance phase and part of the recovery phase during walking. Abbreviations are as in Fig. 1A.

they occur. The first letter of the code indicates the phase in which the maximum or minimum occurs: r for recovery, s for stance. The next two letters express whether it concerns a maximum (ma) or a minimum (mi). Upper case letters indicate the joint or leg segment (H, hip; K, knee; A, ankle; I, inter-toe; TB, tibiotarsus; TM, tarsometatarsus; D, digits; F, femur; T, Trunk). For example, rmiA is the minimum internal angle reached by the ankle during the recovery phase; smaTB is the maximal external angle reached by the tibiotarsus during the stance phase. If a minimum or maximum occurs at the transition from recovery to stance (or *vice versa*), it is indicated by 'rs' (recovery–stance transition) or 'sr' (stance–recovery transition) (e.g. rsmaA is the maximum angle reached by the ankle at the recovery–stance transition).

To determine whether the relative timing of the maxima/minima in a stride (divided into stance and recovery phases) changes with increasing velocity, both phase durations were set to 100%, with the start and end of each phase set at 0 and 100%, respectively. The correlation between the maxima/minima and relative timing and the velocity was

described using least-squares linear regression (Statistica 5.0). Analysis of covariance (ANCOVA) was used to compare maxima/minima and relative timings between the three gaits (Statistica 5.0).

During the asymmetrical hopping gait, the two legs apparently perform different functions: braking or propulsion. The angular displacements were therefore determined for the landing (first leg to make ground contact, first to leave the ground) and take-off (second leg to make ground contact, second to leave the ground) leg separately and then compared using *t*-tests (Statistica 5.0).

## Results

### General description

Flexion and extension patterns of the internal angles are accomplished through complex interactions of rotations of the different leg segments (external angles). Comparison of all the digitised sequences showed that the flexion–extension cycles were basically the same for walking, running and out-of-phase

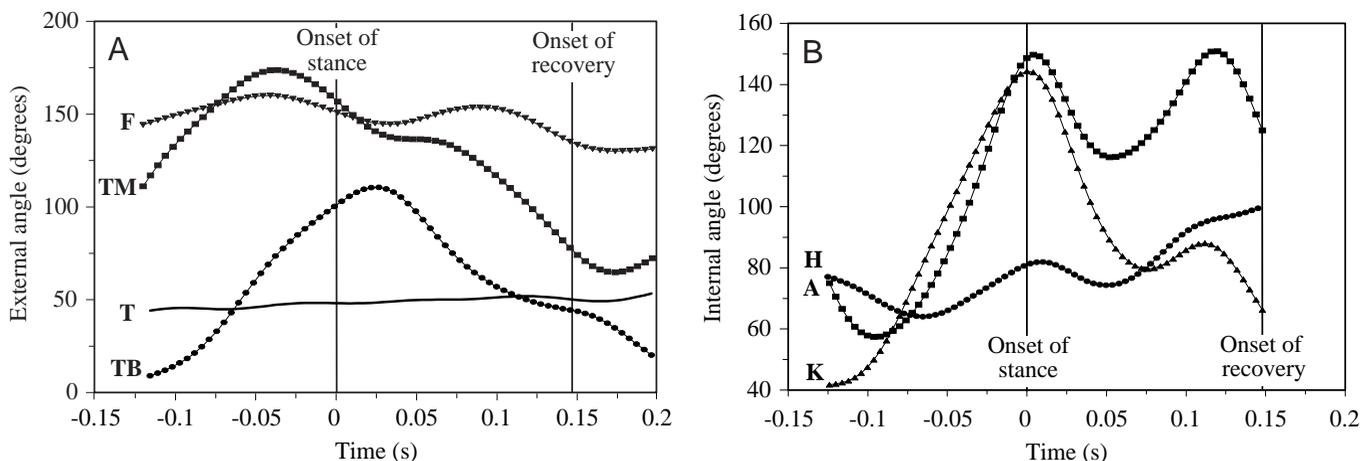


Fig. 4. External (A) and internal (B) angles recorded during the stance phase and part of the recovery phase during running. Abbreviations are as in Fig. 1A.

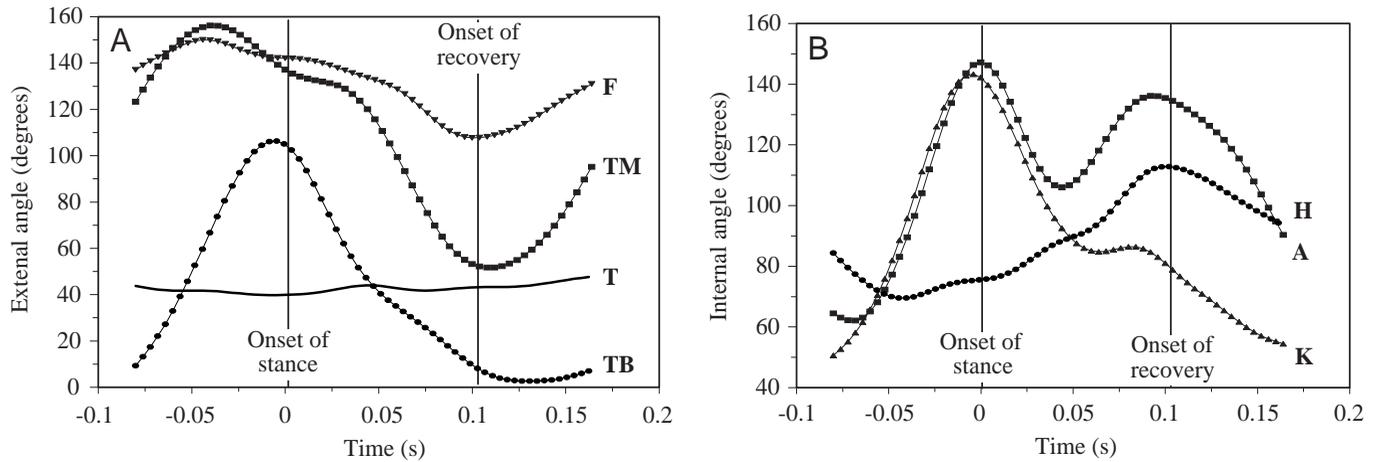


Fig. 5. External (A) and internal (B) angles recorded during the stance phase and part of the recovery phase during out-of-phase hopping: landing leg. Abbreviations are as in Fig. 1A.

hopping. However, the maximum/minimum angular values and their relative timing within the stance or recovery phases differed between the gaits (see below). Fig. 2 presents schematic representations of the observed angular displacements derived from sequences digitised at 50Hz. On the basis of Figs 2–6, a general description of these patterns of external and internal angles during the stance and recovery phases is given below.

#### Stance phase

At the onset of the stance phase, the knee and ankle start to flex. The knee generally continues to flex throughout the rest of this phase (a slight extension occurs just before the end of the stance phase because of a small temporary increase in the tibiotarsus angle, after which flexion is resumed). Near mid-stance, the ankle angle reaches a minimum (because of the rapid decrease in the tibiotarsus angle), after which it extends again. This extension is caused by the rapid decrease in the angle of the tarsometatarsus. At the late stance phase, just prior to the onset of recovery, the ankle starts to flex again as a result of a decrease in the tibiotarsus angle and an

increase in the tarsometatarsus angle. Although the angular displacements at the hip are small, the hip generally extends throughout the entire stance phase, extension reaching a maximum at approximately the transition from stance to recovery.

#### Recovery phase

The flexion of the ankle, knee and hip that started during the stance phase continues for the beginning of the recovery phase. The flexion of the knee reverses to rapid extension after approximately one-third of the recovery phase. At approximately mid-recovery, the ankle reaches a minimum value and starts to extend. The extension of the hip starts near the end of this phase, before the foot touches the ground. Because of the small changes in the trunk and femur angles, the angular displacements of the hip are small. The initial flexion of the knee is accomplished through a decrease in the tibiotarsus angle, and the initial flexion of the ankle is accomplished through a decrease in the tibiotarsus angle and an increase in the angle of the tarsometatarsus. The knee extends as a result of a

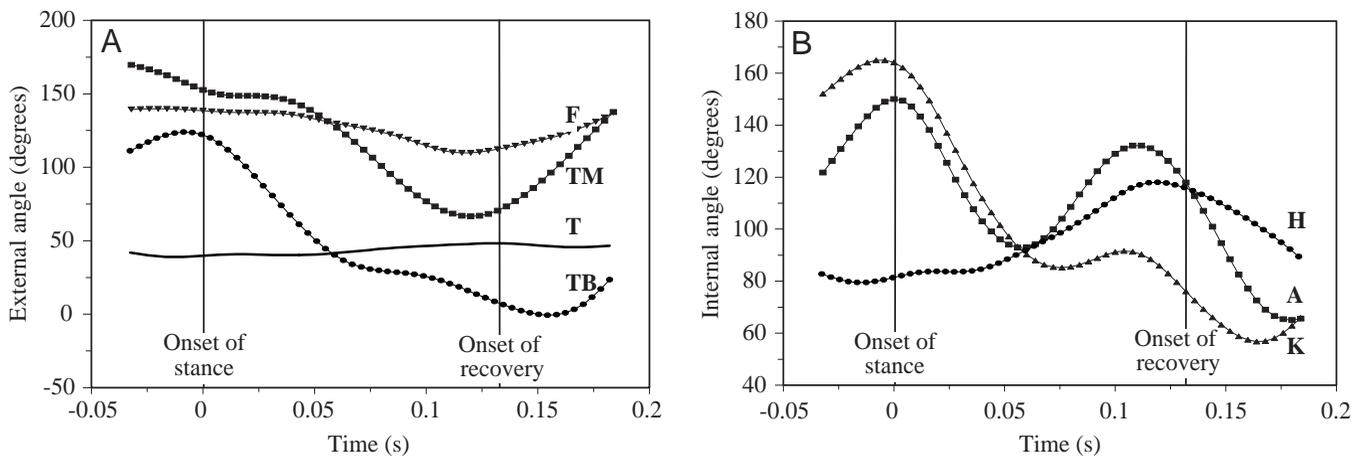


Fig. 6. External (A) and internal (B) angles recorded during the stance phase and part of the recovery phase during out-of-phase hopping: take-off leg. Abbreviations are as in Fig. 1A.

Table 1. Maxima/minima (in degrees) and relative timings (in %) of the angles measured for walking, running and hopping magpies

	Walking		Running		Hopping (landing leg)		Hopping (take-off leg)		Differences among means of intercepts		Differences among slopes	
	Mean	<i>N</i>	Mean	<i>N</i>	Mean	<i>N</i>	Mean	<i>N</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Maxima/minima (degrees)												
rmiK	50±12	20	*	5	*	6	45±13	14	2.58	0.07	2.58	0.07
rsmak	143±9	34	148±13	9	146±6	9	143±20	14	0.47	0.71		
smiK	72±12	26	79±13	6	70±13	10	92±14	22	10.72	0.00001		
smaK	85±17	26	89±15	5	85±20	8	103±15	21	5.09	0.003		
rmiA	62±10	22	64±13	8	76±9	7	70±9	10	4.01	0.01		
rsmaA	151±7	35	145±13	9	*	11	*	15	1.17	0.33	1.10	0.4
smiA	108±10	34	108±11	7	103±8	12	102±8	17	1.99	0.12		
smaA	142±10	28	144±25	6	138±16	12	152±11	19	3.33	0.03		
rmiTB	4±5	21	2±6	4	0±4	8	14±11	14	8.07	0.0002		
rsmaTB	116±6	35	115±8	9	*	9	120±10	14	3.12	0.03	2.65	0.06
rmaTM	173±7	30	*	9	155±11	6	172±26	10	3.58	0.02	2.67	0.06
smiTM	*	27	63±16	6	*	12	66±10	17	3.18	0.03	5.91	0.001
Relative timing (%)												
rmiK	27.3±7.9	16	‡	0	28.9	1	34.3	1				
rsmaK	3.5±2.6	26	‡	0	1.5±3.4	5	0.2±1.5	9	0.52	0.7	0.36	0.8
smiK	*	24	55.1±2.4	5	57.7±4.6	9	*	17	0.43	0.7	3.77	0.02
smaK	84.6±8.3	26	83.4±6.3	4	84.6±5.5	7	82.0±7.1	15	0.40	0.7		
rmiA	52.3±9.3	16	‡	0	44.4	1	48.6	1				
rsmaA	4.8±2.4	29	2.8±1.9	8	2.4±3.4	9	1.5±2.5	14	6.14	0.001		
smiA	44.1±8.3	27	41.4±4.4	7	42.8±3.4	11	*	17	0.29	0.8	1.76	0.27
smaA	86.8±6.0	27	84.0±6.0	5	*	11	89.4±3.0	14	2.03	0.1	2.86	0.05
rmiTB	16.2±9.6	16	‡	0	22.2	1	22.9	1				
rsmaTB	1.6±2.9	27	0.3±0.8	6	0.4±2.22	7	0±1.4	9	1.26	0.3		
rmaTM	72.7±5.1	16	‡	0	66.7	1	71.4	1			5.60	0.002
smiTM	90.0±2.3	27	93.7±5.0	5	96.5±3.1	10	*	14	4.17	0.01		

Values are means ± s.d., *N* is number of observations.

For an explanation of the abbreviations, see Figs 1 and 2 and Materials and methods.

*F* and *P* values in the last two columns are derived from analyses of covariance testing for differences among gaits. For variables that were affected by speed in one of the gaits, we compared the slopes and intercepts of the regression lines among gaits. For variables that did not change with speed, differences among means were tested by one-way ANOVA.

\*Means were not calculated because the variable depends on speed (see Table 2).

‡No data available.

rapid increase in the tibiotarsus angle, while the extension of the ankle is achieved by an increase in the tibiotarsus angle and a decrease in the tarsometatarsus angle. At the switch between the recovery and stance phases, the ankle and knee show maximal extension. As a result, the tibiotarsus angle is largest at this transition.

#### Effects of speed

Walking velocities between 0.5 and 1.2 m s<sup>-1</sup> were measured. The animals ran at velocities between 1.3 and 2.4 m s<sup>-1</sup> and hopped at velocities ranging from 1.1 to 2.3 m s<sup>-1</sup>.

#### Maxima/minima

For most of the angles measured, the maxima/minima were unaffected by speed (regression analysis, *P*>0.05; Table 1). Exceptions to this rule (Table 2) are discussed below.

The minimum angle reached by the tarsometatarsal segment

at the end of the stance phase (smiTM) during walking decreased significantly with speed (*r*<sup>2</sup>=0.3, *P*=0.003). From the regression equation (Table 2), increasing the walking velocity from 0.5 to 1.2 m s<sup>-1</sup> would result in a decrease in smiTM from 71 to 57°.

During the recovery phase of running, the minimum angle reached by the knee (rmiK, *r*<sup>2</sup>=0.85, *P*=0.03) and the maximum angle reached by the tarsometatarsus (rmaTM, *r*<sup>2</sup>=0.68, *P*=0.006) varied with speed. The respective regression equations (Table 2) predict that a change in running velocity from 1.3 to 2.4 m s<sup>-1</sup> would result in an increase in rmiK from 36 to 78° and an increase in rmaTM from 170 to 188°.

Four angles of the landing leg change with velocity during hopping. As in running, the minimum knee angle during the recovery phase (rmiK) increases with velocity (*r*<sup>2</sup>=0.79, *P*=0.02). Here, a speed increment from 1.1 to 2.3 m s<sup>-1</sup> is predicted to cause a change in rmiK from 30 to 84°. At the

Table 2. Intercepts and slopes of the linear least-squares regression lines relating maxima/minima and relative timings of angles to speed of locomotion

	Intercept	S.E.M.	Slope	S.E.M.	$r^2$	$P$
Maxima/minima						
Walking						
smiTM	81.9	5.3	-21.9	6.6	0.3	0.003
Running						
rmiK	-13.1	13.8	38.1	9.4	0.85	0.03
rmaTM	148.6	7.5	16.6	4.3	0.68	0.006
Hopping						
(landing leg)						
rmiK	-19.5	16.4	44.9	11.4	0.79	0.02
rsmaA	178.1	11.4	-18.9	7.1	0.44	0.03
rsmaTB	125.5	4.3	-8.9	2.7	0.6	0.01
smiTM	108.7	10.6	-31.6	6.5	0.7	0.0007
Hopping						
(take-off leg)						
rsmaA	168.5	10.1	-14.4	5.9	0.31	0.02
Relative timing						
Walking						
smiK	79.9	4.5	-21.3	5.4	0.41	0.0007
Hopping						
(landing leg)						
smaA	72.4	4.4	9.9	2.7	0.61	0.005
Hopping						
(take-off leg)						
smiK	80.3	8.4	-14.8	4.8	0.39	0.008
smiA	52.8	4.0	-5.6	2.3	0.28	0.03
smiTM	86.6	3.4	5.7	2.0	0.40	0.01

Also shown are the standard errors (S.E.M.) for both parameters, the coefficient of determination ( $r^2$ ), and its significance ( $P$ ).

Only those variables that were significantly affected by speed are shown.

For an explanation of the abbreviations, see Figs 1 and 2 and Materials and methods.

transition from recovery to stance phase, the maximum angles of the ankle (rsmaA,  $r^2=0.44$ ,  $P=0.03$ ) and the tibiotarsus (rsmaTB,  $r^2=0.60$ ,  $P=0.01$ ) decrease slightly with speed. An increase in velocity from 1.1 to 2.3 m s<sup>-1</sup> changes rsmaA from 157 to 135° and rsmaTB from 116 to 105°. The minimum angle reached by the tarsometatarsus during the stance phase (smiTM) decreases dramatically with increasing speed ( $r^2=0.70$ ,  $P=0.0007$ ). With a velocity increase from 1.1 to 2.3 m s<sup>-1</sup>, smiTM decreases from 74 to 36°. In the take-off leg, only rsmaA changes significantly with velocity ( $r^2=0.31$ ,  $P=0.02$ ). As for the landing leg, rsmaA decreases slightly with increasing locomotor speed in the take-off leg. It changes from 153 to 135° as the speed increases from 1.1 to 2.3 m s<sup>-1</sup>.

#### Relative timings

For most angles, the relative timing of the maxima and minima did not vary significantly with velocity (Table 1). Only

the exceptions to this rule (Table 2) are discussed below. Note that the observed relative timings for running are not related significantly to speed (Table 1); this may be partly due to the low number of observations for this gait type.

For walking, the only exception is the relative timing of the minimum knee angle during the stance phase (smiK,  $r^2=0.41$ ,  $P=0.0007$ ). As the velocity increases, this angle is reached earlier in the phase. At a velocity of 0.5 m s<sup>-1</sup>, it is reached after 70% of the stance phase, while at a velocity of 1.2 m s<sup>-1</sup>, the minimum occurs at 54% of the phase.

For the landing leg during hopping, the maximal ankle angle is attained at a later stage in the stance phase at higher speeds (smaA,  $r^2=0.61$ ,  $P=0.005$ ). The ankle reaches its maximal angle after 83% of the total duration of the stance phase at 1.1 m s<sup>-1</sup> and after 95% at 2.3 m s<sup>-1</sup>. In the take-off leg, speed modifies the relative timing of the minimal angle of the knee (smiK,  $r^2=0.39$ ,  $P=0.008$ ), of the ankle (smiA,  $r^2=0.28$ ,  $P=0.03$ ) and of the tarsometatarsus (smiTM,  $r^2=0.40$ ,  $P=0.01$ ) during the stance phase. At a hopping velocity of 1.1 m s<sup>-1</sup>, the minimum knee angle is reached after 64% of the total duration of the stance phase, while at 2.3 m s<sup>-1</sup>, it occurs after 46%. For a similar increment in velocity, the minimum ankle angle changes its relative timing from 47 to 40%, and the minimal tarsometatarsus angle changes its relative timing from 93 to 100%.

#### Differences between the kinematics of the landing and take-off leg during hopping

During hopping, the maxima/minima of the following four angles differ between the landing and the take-off leg (Table 1,  $t$ -tests): smaA,  $t_{29}=2.94$ ,  $P=0.006$ ; smiK,  $t_{30}=4.08$ ,  $P=0.003$ ; smaK,  $t_{27}=2.59$ ,  $P=0.02$ ; and rmiTB,  $t_{20}=3.33$ ,  $P=0.003$ . These minima and maxima have larger values in the take-off leg than in the landing leg. The average difference is approximately 14° for smaA and rmiTB, 18° for smaK and 22° for smiK. In addition, rsmaTB also takes higher values in the take-off leg than in the landing leg, regardless of the effect of speed (ANCOVA with speed as covariate, difference between legs:  $F_{1,20}=10.29$ ,  $P=0.004$ ). For the other angles, the difference between the landing and take-off leg was not significant ( $t$ -tests or, if angles change with speed, ANCOVAs: all  $P>0.08$ ). None of the relative timings differed significantly between the two legs ( $t$ -tests or ANCOVAs, all  $P>0.1$ ).

#### Differences between gait types

##### Maxima/minima

Analysis of covariance suggested substantial variation among gaits in smiK, smaK and rmiTB and smaller differences in rsmaTB, smiTM and smaA (Table 1). However, *post-hoc* comparisons show that most of the variation in these angles is due to the aberrant behaviour of the take-off leg during hopping. The values for smiK, smaK, smaA and rmiTB are all similar for walking, running and the landing leg during hopping, but are higher for the take-off leg. Values for rmaTM attained during walking do not differ from those for the take-off leg during hopping, and both are similar to the range of

Table 3. Mean values of the hip, femur and trunk (pelvic pitch) angles during the stance phase

	Walking		Running		Hopping			
					Landing leg		Take-off leg	
	Mean	<i>N</i>	Mean	<i>N</i>	Mean	<i>N</i>	Mean	<i>N</i>
Hip angle (degrees)	82.1±8.0	27	82.1±7.4	5	93.5±17.8	10	94.9±12.7	16
Femur angle (degrees)	142.1±9.5	27	141.7±13.9	5	135.0±15.4	8	137.5±14.3	18
Trunk angle (degrees)	44.3±7.2	27	46.0±10.3	5		49.2±6.6		21

Values are means ± s.d., *N* is number of observations.

rmaTM observed in birds running at speeds between 1.3 and 2.4 ms<sup>-1</sup>. However, lower values of rmaTM are noted for the landing legs in hopping magpies. Differences in the speed-dependence of smiTM among gaits prevent direct comparisons. The minimal tarsometatarsus angle during the stance phase (smiTM) does not change with speed during running and in the take-off leg, but decrease slightly during walking and in the landing leg. Finally, rmiA does not differ between walking and running and in the take-off leg, but attains slightly higher values in the landing leg of hopping magpies.

#### Relative timings

The relative timings of rsmaA are similar for walking and running birds and for the landing leg during hopping. However, the maximum is reached at an earlier stage by the take-off leg during hopping. The timing of smiK during running and for the landing leg is similar and, as indicated above, independent of speed in these cases. During walking, and for the take-off leg, smiK occurs earlier in the stance phase at higher speeds. The effect of speed is somewhat greater during walking. The minimal tarsometatarsus angle (smiTM) occurs relatively early in the stance phase in walking and running birds, and significantly later in the landing leg during hopping. For the take-off leg, the timings for smiTM span the range of timings in the other gaits, depending on speed. At low speeds (approximately 1 ms<sup>-1</sup>), smiTM timings for the take-off leg are similar to those of walking and running magpies, while at high speeds (approximately 2 ms<sup>-1</sup>), the timings are closer to that of the landing leg.

#### Hip, femur and trunk

The mean trunk angle during the stance phase of walking is

slightly smaller than that during running (44.3 versus 46.0°), but differs significantly from that during hopping (49.2°; *t*-test, *t*<sub>46</sub> = -2.39, *P* = 0.02). The mean femur angle during the stance phase does not differ significantly between walking, running and both legs during hopping (Table 3). The mean hip angle, in contrast, is similar during walking and running (82.1°), but differs between these two gaits and in the take-off leg during hopping (walk-hop, *t*-test, *t*<sub>41</sub> = -3.02, *P* = 0.006; run-hop, *t*-test, *t*<sub>19</sub> = -2.23, *P* = 0.047).

#### Movement of the toes

When a magpie sets its foot down, it does so by placing the hallux on the ground first (external angle approximately 200°, internal angle approximately 145°, Fig. 7). Next, the front toes are set down, and the plantar surface of the toes then makes contact with the ground. The external angle decreases to approximately 180° and the internal angle increases to approximately 160°. As the bird lifts its foot for the recovery phase, it is unrolled, with the hallux leaving the ground first and the third digit last. At the last moment before the recovery phase begins, the external angle measures approximately 110°, and the internal angle approximately 130°. During the recovery phase, the external and internal angles reach values of approximately 90° and approximately 80°, respectively. This movement pattern is similar for walking, running and out-of-phase hopping.

#### Movement of the whole leg (protraction and retraction)

The protraction angle (Fig. 1B) remains constant as the speed increases during walking, running and hopping (walking, 49±5.2°, *N* = 25; running, 43±4.0°, *N* = 11; landing leg, 43±5.1°, *N* = 11; take-off leg, 53±4.6°, *N* = 14) (means ± s.d.). In contrast, the retraction angle (Fig. 1B) increases with

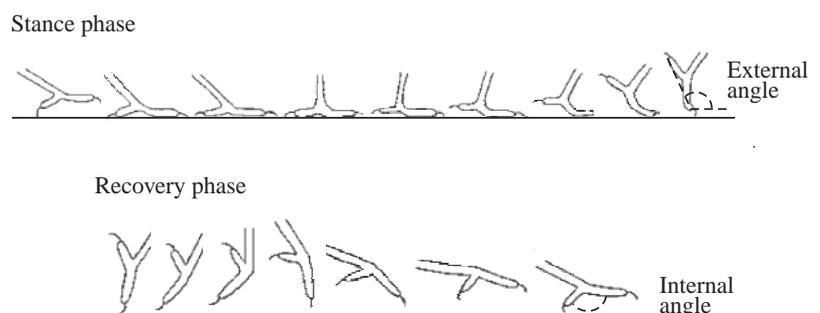


Fig. 7. Movements of the toes during the stance and recovery phases.

increasing velocity (linear regression, Quattro Pro). Over the velocity range of walking ( $0.5\text{--}1.2\text{ m s}^{-1}$ ), the retraction angle of the leg increased from  $27$  to  $41^\circ$  ( $r^2=0.32$ ,  $P_{\text{slope}}=0.0033$ ). As the running speed increases from  $1.3$  to  $2.4\text{ m s}^{-1}$ , this angle increases slightly from  $30$  to  $39^\circ$  ( $r^2=0.80$ ,  $P_{\text{slope}}=0.03$ ). For the landing leg during hopping, an increase in velocity from  $1.1$  to  $2.3\text{ m s}^{-1}$  doubles the retraction angle from  $28$  to  $56^\circ$  ( $r^2=0.73$ ,  $P_{\text{slope}}=0.00057$ ). The retraction angle for the take-off leg tended to increase (from  $20$  to  $32^\circ$ ) with increasing velocity, although not significantly so ( $r^2=0.22$ ,  $P_{\text{slope}}=0.05$ ).

### Discussion

Verstappen and Aerts (2000) proposed that the three gait types used by black-billed magpies are the result of the same control mechanisms and thus are highly comparable. Running is therefore an over-powered style of walking, and hopping is equivalent to running but with an altered phase shift between the legs. This hypothesis leads to the prediction that the within-leg control of the angular excursions will be identical and thus that the kinematic patterns of the three gaits should be fairly similar. The latter prediction seems to be confirmed by the present results.

A stride consists of two phases: a stance (ground contact) phase and a recovery (swing) phase. At the onset of the stance phase, the leg that touches the ground is almost completely extended and is placed on the ground in front of the body's centre of mass. The body is thus decelerated (braking). Assuming an analogy between magpies and the quail *Coturnix japonica* (Clark and Alexander, 1975), the leg is actively flexed when the ground reaction force passes anterior to the knee early in the stance phase. However, muscles act to prevent or counteract this flexion (for electromyography of terrestrial bird locomotion, see Jacobson, 1980; Jacobson and Hollyday, 1982a,b; Gatesy, 1999b). In the magpie, a slight hip flexion sometimes occurs early during the stance phase (probably resulting from the external forces; see above), but the hip generally starts to extend at the end of the recovery phase and continues to do so during the entire stance phase. The knee and ankle both flex. In the chicken *Gallus domesticus* (see Jacobson, 1980; Jacobson and Hollyday, 1982a) and in the guineafowl *Numida meleagris* (Gatesy, 1999b), it was found that these movements are counteracted by muscle activity. During stance, the magpie's leg displaces backwards relative to the body. As soon as the body's centre of mass passes over the foot, the body is accelerated (propulsion). Throughout the ongoing knee flexion, the leg continues to move relatively backwards, while the hip and particularly the ankle stretch to cause acceleration. Knee flexion lasts until the next recovery phase and initiates the lift-off of the foot. Ankle and hip flexion at the end of the stance phase also aid in lifting the foot. Near the end of the stance phase, the ongoing knee flexion is briefly interrupted by a small extension (smaK, Fig. 2B), after which knee flexion is resumed again. This brief extension–flexion pattern is also observed in pigeons *Columba livia* (Cracraft, 1971), chickens (Jacobson and Hollyday, 1982a; Johnston and

Bekoff, 1992; Manion, 1984; Muir et al., 1996) and guineafowl (at high velocities, Gatesy, 1999b). According to the latter author, activity of the musculus femorotibialis causes this extension, and its magnitude is correlated with the degree of hip extension. In the magpie, this knee extension is positively related to hip extension during walking and for the take-off leg during hopping.

During the recovery phase, the switch from flexion to extension in the three joints does not happen simultaneously. First the knee, then the ankle and finally, just before the next stance phase, the hip extend. Because of the configuration of the bird's leg, the hip must remain flexed so that the leg does not touch the ground. The forward movement of the parts of the leg below the knee is mainly the result of the rapid extension of the knee. If the ankle were to extend simultaneously with the knee, the toes would touch the ground during leg protraction. Therefore, ankle extension starts later in the phase, mainly to allow extension of the leg as far as possible before the next stance phase. In humans, maximum hip flexion angle is also reached at the end of recovery, but in this case, the protraction of the leg is achieved primarily by angular displacements in the hip (Borghese et al., 1996; Sutherland et al., 1994).

Some of the maximum and minimum angular values reached by the joints and segments are related to speed. During walking, the minimal tarsometatarsus angle at the end of the stance phase decreases with increasing velocity. As a result, step length is expected to increase as the bird walks faster, as described by Verstappen and Aerts (2000).

During running, the minimal knee angle at the beginning and the maximal tarsometatarsus angle at the end of the recovery phase correlate positively with speed. In the landing leg during hopping, the minimal knee angle during the recovery phase also correlates positively with velocity. At the transition from recovery to stance phase, the maximal ankle and tibiotarsus angle both decrease with speed. These latter angular changes probably decrease the stiffness of the leg as it becomes more flexed, which reduces the impact at touch-down. In the take-off leg, only the maximal ankle angle at the transition from recovery to stance phase decreases with speed. As in the landing leg, this causes a decrease in leg stiffness at the beginning of the stance phase. In walking/running guineafowl, there is a change in the maximum knee angle before touch-down with velocity (Gatesy, 1999a). In magpies, this angle does not change with velocity in either of the three gait types.

It is remarkable that, during the recovery phases in running and for the landing leg during hopping, the knee flexes less when the locomotor speed increases. This implies that the foot is lifted less high above the ground during the forward swing of the leg. Consequently, it is conceivable that, at higher speeds, the toes would touch the ground, which seems unfavourable from the point of view of stability. During hopping, however, the body is launched into the air, so that the potential danger of touching the ground is reduced. It might be concluded that the foot is lifted no more than strictly required, resulting in the observed reduced knee flexion at higher speeds.

However, during running, the vertical oscillations of the centre of mass remain very small (groucho running; McMahon, 1985), and reduced knee flexion can be expected finally to result in the feet touching the ground, unless alterations in the relative timing of changes in the hip and ankle angles compensate for this negative effect. However, these angles show no significant velocity-related changes. It may be that the minimal knee angle during the recovery phase is highly variable from step to step, being determined by the details of the take-off conditions. Given the light weight of the leg segments distal to the knee, the leg configurations can have only limited effects on the swing characteristics of the leg. If this is true, the significant relationship between knee angle and locomotor speed during recovery might be an accidental consequence of the limited number of trials.

The joint movements described here for magpies are comparable with those of other bird species such as the chicken (Jacobson, 1980; Jacobson and Hollyday, 1982a; Johnston and Bekoff, 1992; Manion, 1984; Muir et al., 1996), the pigeon (Cracraft, 1971), the guineafowl (Gatesy, 1999a, only hip and knee) and the silver gull *Larus novaehollandiae* (Dagg, 1977, only the ankle). In two studies of the chicken (Jacobson and Hollyday, 1982a; Johnston and Bekoff, 1992), the ankle angle is fairly constant during the stance phase, while in the magpie, in other studies of the chicken (Jacobson, 1980; Manion, 1984), in the pigeon (Cracraft, 1971) and in the silver gull (Dagg, 1977), there are clear flexion and extension movements. Gatesy (1999a) found that the pelvic pitch (the position of the trunk with respect to the horizontal) of walking/running guineafowl decreased with increasing velocity. In magpies, pelvic pitch changes very little when the birds change from a walk to a run or a hop (see Table 3).

Birds are digitigrade, i.e. they stand on their toes. Toe morphology shows adaptations to the habitat utilised by a species. For example, in running birds such as the chicken, the hallux is reduced in size (see Figs 42 and 43 in Manion, 1984), and in the ostrich, it is no longer present (Alexander, 1985). Magpies, like most other birds, are facultatively terrestrial, so their toes have an important role in perching. The four toes are well developed and are placed in a configuration of three front toes and one hind toe (hallux) (Verstappen et al., 1998). The external toe angle is defined as the angle between the sole of the toes and the horizontal, and the internal toe angle is the angle between the front toes and the hallux (Figs 1A, 7). During stance, the internal toe angle is maximal. As the ankle starts to flex at the onset of recovery, tension will act on the tendons of the toe flexors such that, as soon as the toes leave the ground, rapid toe flexion occurs. Halfway through the recovery, the ankle joint and the toes start to extend. Since ankle extension unstrains the toe flexor tendons, toe extension can occur passively. It cannot, however, be excluded that this passive extension is aided by activation of the musculus extensor digitorum longus (extension of front toes) and the musculus extensor hallucis longus (extension of the hallux). In contrast to the chicken (Jacobson, 1980), the toes are not set down simultaneously. In the pigeon (Cracraft, 1971) and the

magpie, the hallux touches the ground just before the front toes do, followed by contact of the plantar surface of the foot with the ground (see Fig. 7). During the present experiments, the running track was covered with a thin layer of cork. Variations in the movement pattern of the toes may occur because of the nature of the surface on which the birds move.

Humans are also efficient bipeds. Although humans and birds use the same type of locomotion and show adaptations to it, differences in leg morphology are striking. It is common knowledge that elongation of the distal leg segments increases the step/stride length, which in turn leads to the possibility of velocity increasing. Birds use this mechanism to a great extent. (i) In birds, because of the relatively short femur, the knee is located next to the trunk. (ii) The ankle joint in humans lies between the tibia/fibula and the tarsal bones. In birds, the tibia is fused with the proximal tarsal bones, and the metatarsal bones are fused with the distal tarsal bones. Therefore, the ankle lies between the elongated tibiotarsus and tarsometatarsus and bends in the same way as the ankle does in humans. The position of a bird's ankle in the leg is comparable with that of a human's knee. (iii) Although a human foot is relatively long, it does not add to the leg length. The foot configuration in birds is changed such that the leg length is increased markedly by the foot. The elongated tarsometatarsus does not touch the ground during the stance phase, only the toes (phalanges) do. By moving on the tips of their toes, birds add both length and an important joint (interdigital joint, see for example Verstappen et al., 1998) to the leg.

The overall patterns of changes in internal and external angles in walking, running and hopping magpies were relatively constant between trials and even between gait types, in contrast to the large inter- and intra-individual variation found for the hip and ankle angles in walking humans (Borghese et al., 1996). The major patterns of change in external angles are comparable between magpies and humans (Borghese et al., 1996). However, for the internal angles, some differences are seen. In magpies, the hip angle extends throughout the stance phase. In humans, this is not always the case because, in some individuals, the hip shows a flexion-extension movement (Borghese et al., 1996). At touch-down, a human slightly flexes the knee, then extends it again; near the start of recovery, another flexion of the knee occurs (Borghese et al., 1996; Vaughan, 1984; Winter, 1984). In magpies, the knee flexes throughout the stance phase (sometimes with a small extension, see above). At touch-down, the human ankle continues to extend slightly as a result of the previous recovery phase, but then flexes, extending again towards the start of the recovery phase (Borghese et al., 1996; Vaughan, 1984; Winter, 1984). When humans run, the ankle starts to flex immediately at touch-down (Vaughan, 1984). In magpies, this maximal ankle angle can occur at the transition from the recovery to the stance phase or at the beginning of the stance phase. There was no significant relationship between the relative timing of maximal ankle angle and velocity. Upon recovery, the human ankle flexes markedly and then extends again, but the extension is less pronounced than during the

stance phase (Borghese et al., 1996; Vaughan, 1984; Winter, 1984). In magpies, the extensions towards the end of the stance and the recovery phases were of equal magnitude. The differences between humans and magpies are probably caused by the relative positions of the joints in the leg (see above) and by posture. The leg movements in birds are mainly influenced by extension and flexion of both the knee and ankle (movements of the tibiotarsus and tarsometatarsus); in humans, leg movements rely mostly on the angular displacements of the hip and knee (movements of the femur and tibia/fibula). The posture of the trunk differs between humans and magpies, and this probably causes differences in angular displacements of the legs and their segments. Humans keep their trunk upright, whereas in magpies it is at an inclination of approximately  $45^\circ$  with the horizontal. In both bipeds, the trunk is held relatively stable during locomotion.

Movements of the leg segments result, of course, in movements of the entire leg. Legs can be protracted (move forwards) or retracted (move backwards). In contrast to humans, who increase the protraction angle of their legs with velocity within a gait type (Gatesy and Biewener, 1991), magpies keep this angle fairly constant with increasing velocity and even over the different gaits. Gatesy (1999a) reports a constant protraction angle of approximately  $46^\circ$  for walking and running guineafowl, which agrees well with the values found here for walking, running and hopping magpies (approximately  $45^\circ$ ). The only exception is for the take-off leg during hopping. The protraction angle of this leg is somewhat larger (approximately  $53^\circ$ ). The magnitude of the protraction angle could be limited by the small angular excursions of the hip in magpies.

#### *Running and out-of-phase hopping*

In addition to the differences in leg morphology, there are noticeable differences in the use of the three gait types between magpies and humans. At a Froude number (dimensionless velocity, Alexander, 1992) of approximately 0.5, magpies and humans stop walking and switch to a faster gait (Verstappen and Aerts, 2000; Alexander, 1992). Whittall and Caldwell (1992) described the spatio-temporal gait characteristics and kinematics of running and galloping in humans. They found that, when humans increase their speed, they change from walking to running. In some circumstances, galloping occurs (also known as skipping, see Minetti, 1998), but running is definitely the preferred gait. The voluntary speed achieved by galloping humans is generally lower than that during running (Caldwell and Whittall, 1995). The authors argued that the relationship between running and galloping in humans is not directly comparable with analogous relationships existing in other animals. Verstappen and Aerts (2000) showed that magpies walk at low speeds and that, like humans, they change their gait to either running or hopping at higher speeds. Two differences between magpies and humans concerning the gait types selected are noteworthy: (i) magpies prefer hopping at higher speeds and (ii) the voluntary speed of running in magpies is lower than that of hopping.

Why magpies prefer hopping and why running is used at lower speeds than hopping cannot be determined from the present kinematic results because we have found that running and hopping are very similar gait types. Future research recording ground reaction forces might provide answers to these questions.

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#### References

- Alexander, R. McN. (1985). The legs of ostriches (*Struthio*) and moas (*Pachyornis*). *Acta Biotheoretica* **34**, 165–174.
- Alexander, R. McN. (1992). *Exploring Biomechanics. Animals in Motion*. New York: Scientific American Library.
- Alexander, R. McN., Maloiy, G. M. O., Njau, R. and Jayes, A. S. (1979). Mechanics of running of the ostrich (*Struthio camelus*). *J. Zool., Lond.* **187**, 169–178.
- Bamford, O. S. and Maloiy, G. M. O. (1980). Energy metabolism and heart rate during treadmill exercise in the marabou stork. *J. Appl. Physiol.* **49**, 491–496.
- Borghese, N. A., Bianchi, L. and Lacquanti, F. (1996). Kinematic determinants of human locomotion. *J. Physiol., Lond.* **494**, 863–879.
- Brackenbury, J. H. and Avery, P. (1980). Energy consumption and ventilatory mechanisms in the exercising fowl. *Comp. Biochem. Physiol.* **66A**, 439–445.
- Brackenbury, J. H., Avery, P. and Gleeson, M. (1981). Respiration in exercising fowl. I. Oxygen consumption, respiratory rate and respired gases. *J. Exp. Biol.* **93**, 317–325.
- Brackenbury, J. H., Gleeson, M. and Avery, P. (1982). Respiration in exercising fowl. III. Ventilation. *J. Exp. Biol.* **96**, 315–324.
- Caldwell, G. E. and Whittall, J. (1995). An energetic comparison of symmetrical and asymmetrical human gait. *J. Motor Behav.* **27**, 139–154.
- Cavagna, G. A., Heglund, N. C. and Taylor, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **223**, 243–261.
- Clark, B. D. (1988). Mechanics and control of the hindlimb of bobwhite quail running and landing on substrates of unpredictable mechanical stiffness. PhD dissertation, University of Illinois, Chicago.
- Clark, J. and Alexander, R. McN. (1975). Mechanics of running by quail (*Coturnix*). *J. Zool., Lond.* **176**, 87–113.
- Cracraft, J. (1971). The functional morphology of the hind limb of the domestic pigeon, *Columba livia*. *Bull. Am. Mus. Nat. Hist.* **144**, 175–265.
- Dagg, A. I. (1977). The walk of the silver gull (*Larus novaehollandiae*) and of other birds. *J. Zool., Lond.* **182**, 529–540.
- Fedak, M. A., Heglund, N. C. and Taylor, C. R. (1982). Energetics and mechanics of terrestrial locomotion. II. Kinetic energy changes of the limbs and body as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **79**, 23–40.
- Fedak, M. A., Pinshow, B. and Schmidt-Nielsen, K. (1974). Energy cost of bipedal running. *Am. J. Physiol.* **227**, 1038–1044.

- Fedak, M. A. and Seeherman, H. J.** (1979). Reappraisal of energetics of locomotion shows identical cost in bipeds and quadrupeds including ostrich and horse. *Nature* **282**, 713–716.
- Gatesy, S. M.** (1999a). Guineafowl hind limb function. I. Cineradiographic analysis and speed effects. *J. Morph.* **240**, 115–125.
- Gatesy, S. M.** (1999b). Guineafowl hind limb function. II. Electromyographic analysis and motor pattern evolution. *J. Morph.* **240**, 127–142.
- Gatesy, S. M. and Biewener, A. A.** (1991). Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J. Zool., Lond.* **224**, 127–147.
- Heglund, N. C., Cavagna, G. A. and Taylor, C. R.** (1982a). Energetics and mechanics of terrestrial locomotion. III. Energy changes of the centre of mass as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 41–56.
- Heglund, N. C., Fedak, M. A., Taylor, C. R. and Cavagna, G. A.** (1982b). Energetics and mechanics of terrestrial locomotion. IV. Total mechanical energy changes as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 57–66.
- Jacobson, R. D.** (1980). Studies on the neural control of locomotion in the chick. PhD dissertation, University of Chicago, Illinois.
- Jacobson, R. D. and Hollyday, M.** (1982a). A behavioral and electromyographic study of walking in the chick. *J. Neurophysiol.* **48**, 238–256.
- Jacobson, R. D. and Hollyday, M.** (1982b). Electrically evoked walking and fictive locomotion in the chick. *J. Neurophysiol.* **48**, 257–270.
- Johnston, R. M. and Bekoff, A.** (1992). Constrained and flexible features of rhythmical hindlimb movements in chicks: kinematic profiles of walking, swimming and airstepping. *J. Exp. Biol.* **171**, 43–66.
- Johnston, R. M. and Bekoff, A.** (1996). Patterns of muscle activity during different behaviors in chicks: implications for neural control. *J. Comp. Physiol. A* **179**, 169–184.
- Kugler, P. N. and Turvey, M. T.** (1987). *Information, Natural Law and the Self-Assembly of Rhythmic Movement*. Hillsdale, NJ: Erlbaum.
- Manion, B. L.** (1984). The effects of size and growth on hindlimb locomotion in the chicken. PhD dissertation, University of Illinois, Chicago.
- McMahon, T. A.** (1985). The role of compliance in mammalian running gaits. *J. Exp. Biol.* **115**, 263–282.
- Miller, A. H.** (1937). Structural modifications in the Hawaiian goose (*Nesochen sandvicensis*): a study in adaptive evolution. *Univ. Calif. Publ. Zool.* **42**, 1–80.
- Minetti, A. E.** (1998). The biomechanics of skipping gaits: a third locomotion paradigm? *Proc. R. Soc. Lond. B* **265**, 1227–1235.
- Muir, G. D., Gosline, J. M. and Steeves, J. D.** (1996). Ontogeny of bipedal locomotion: walking and running in the chick. *J. Physiol., Lond.* **493**, 589–601.
- Peck, A. J. and Turvey, M. T.** (1997). Coordination dynamics of the bipedal galloping pattern. *J. Motor Behav.* **29**, 311–325.
- Pinshow, B., Fedak, M. A. and Schmidt-Nielsen, K.** (1977). Terrestrial locomotion in penguins: it costs more to waddle. *Science* **195**, 592–594.
- Roberts, T. J., Chen, M. S. and Taylor, C. R.** (1998a). Energetics of bipedal running. II. Limb design and running mechanics. *J. Exp. Biol.* **201**, 2753–2762.
- Roberts, T. J., Kram, R., Weyand, P. G. and Taylor, R. C.** (1998b). Energetics of bipedal running. I. Metabolic cost of generating force. *J. Exp. Biol.* **201**, 2745–2751.
- Roberts, T. J., Marsh, R. L., Weyand, P. G. and Taylor, R. C.** (1997). Muscular force in running turkeys: the economy of minimizing work. *Science* **275**, 1113–1115.
- Rylander, M. K. and Bolen, E. G.** (1974). Analysis and comparison of gaits in whistling ducks (*Dendrocygna*). *Wilson Bull.* **86**, 237–245.
- Steeves, J. D., Sholomenko, G. N. and Webster, D. M. S.** (1987). Stimulation of the pontomedullary reticular formation initiates locomotion in decerebrate birds. *Brain Res.* **401**, 205–212.
- Stolpe, M.** (1932). Physiologisch-Anatomische untersuchungen über die hintere Extremität der Vögel. *J. Orn.* **2**, 161–247.
- Sutherland, D. H., Kaufman, K. R. and Moitza, J. R.** (1994). Kinematics of normal human walking. In *Human Walking* (ed. J. Rose and J. G. Gamble), pp. 23–44. Baltimore: Williams & Wilkins.
- Taylor, C. R.** (1977). The energetics of terrestrial locomotion and body size in vertebrates. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 127–141. London: Academic Press.
- Taylor, C. R., Dmi'el, R., Fedak, M. and Schmidt-Nielsen, K.** (1971). Energetic cost of running and heat balance in a large bird, the rhea. *Am. J. Physiol.* **221**, 597–601.
- Taylor, C. R., Heglund, N. C. and Maloiy, G. M. O.** (1982). Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 1–21.
- Vaughan, C. L.** (1984). Biomechanics of running gait. *Crit. Rev. Biomed. Eng.* **12**, 1–48.
- Verstappen, M. and Aerts, P.** (2000). Terrestrial locomotion in the black-billed magpie. I. Spatio-temporal gait characteristics. *Motor Control* **4**, 150–164.
- Verstappen, M., Aerts, P. and De Vree, F.** (1998). Functional morphology of the hindlimb musculature of the black-billed magpie, *Pica pica* (Aves, Corvidae). *Zoomorph.* **118**, 207–223.
- Weinstein, G. N., Anderson, C. and Steeves, J. D.** (1983). Functional characterization of limb muscles involved in locomotion in the Canada goose, *Branta canadensis*. *Can. J. Zool.* **62**, 1596–1604.
- Whitall, J. and Caldwell, G. E.** (1992). Coordination of symmetrical and asymmetrical human gait: kinematic patterns. *J. Motor Behav.* **24**, 339–353.
- Winter, D. A.** (1984). Kinematic and kinetic patterns in human gait: variability and compensating effects. *Human Movement Sci.* **3**, 51–76.