

RESEARCH ARTICLE

Comparative intralimb coordination in avian bipedal locomotion

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SUMMARY

Analyses of how intralimb coordination during locomotion varies within and across different taxa are necessary for understanding the morphological and neurological basis for locomotion in general. Previous findings suggest that intralimb proportions are the major source of kinematic variation that governs intralimb coordination across taxa. Also, independence of kinematics from habitat preference and phylogenetic position has been suggested for mammals. This leads to the hypothesis that among equally sized bird species exhibiting equal limb proportions, similar kinematics can be observed. To test this hypothesis, the bipedal locomotion of two distantly related ground-dwelling bird species (*Eudromia elegans* and *Coturnix coturnix*) and of a less terrestrial species (*Corvus monedula*) was investigated by means of a biplanar high-speed X-ray videographic analysis. Birds exhibited similar intralimb proportions and were filmed over a broad range of speed while moving on a treadmill. Joint and limb element angles, as well as pelvic rotations, were quantified. Regarding fore–aft motions of the limb joints and elements, a congruent pattern of intralimb coordination was observed among all experimental species. The sample of species suggests that this is largely independent of their habitat preference and systematic position and seems to be related to demands for coping with an irregular terrain with a minimum of necessary control. Hence, the initial hypothesis was confirmed. However, this congruence is not found when looking at medio-lateral limb motions and pelvic rotations, showing distinct differences between ground-dwellers (e.g. largely restricted to a parasagittal plane) and *C. monedula* (e.g. increased mobility of the hip joint).

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/215/23/4055/DC1>

Key words: X-ray videography, birds, kinematics, terrestrial locomotion.

Received 19 January 2012; Accepted 9 August 2012

INTRODUCTION

Analyses of how intralimb coordination during locomotion varies within and across different taxa are necessary for understanding the morphological and neurological basis for locomotion in general. When combined with an explicit phylogenetic hypothesis, such an analysis further holds important information about the evolution of movement patterns from a common ancestor to extant representatives of a taxon (Gatesy, 1990; Hutchinson and Allen, 2009; Gatesy and Pollard, 2011). Numerous studies have shown that differences in locomotor behavior are often linked to differences in habitat use and morphology (e.g. Fuller et al., 2011). However, studies focusing on intralimb coordination during locomotion that compare species that are characterized by differences in morphology and ecology are not as common outside of mammals. Such comprehensive studies are needed to disentangle the various factors that are related to differences in form and function and, ultimately, the variation in performance during, for example, predator avoidance, foraging or social behaviors.

Intralimb kinematics of tetrapods are commonly quantified as the excursion of limb elements or the angular movements of limb joints (i.e. between limb elements), both in 2-D and in 3-D (e.g. Fischer et al., 2002; Gatesy, 1999a; Irschick and Jayne, 1999; Jenkins and Weijjs, 1979; Verstappen et al., 2000). By means of computational modeling of different bird species, Gatesy and Pollard (Gatesy and Pollard, 2011) recently demonstrated that

variation in the relative proportions and the degree of crouch within the limb impose a geometric constraint on angular excursions leading inevitably to differences in kinematics across species. Furthermore, it has been shown that small to medium-sized mammals of differing phylogenetic position but with highly similar intralimb proportions exhibit a generalized kinematic pattern (Fischer et al., 2002; Schmidt and Fischer, 2009). Whereas the variation in the degree of crouch is generally related to body size (e.g. Gatesy and Biewener, 1991; Reilly et al., 2007), a comparative study of domestic dogs (32 breeds) ranging from the small Chihuahua to the large great Dane has shown that both intralimb proportions and intralimb kinematics stay virtually the same despite a 30-fold increase of body mass (Fischer and Lilje, 2011). These findings suggest that intralimb proportions themselves are the major source of kinematic variability across parasagittally striding tetrapods and that intralimb coordination is surprisingly little influenced by phylogeny and habitat preference. We therefore hypothesize that among equally proportioned and similar sized bird species, hindlimb kinematics will be very similar as well. If corroborated, according to actualism this result would also have a bearing on the inference of locomotor characteristics of fossil species. Here we approach this hypothesis by analyzing the hindlimb kinematics of three distantly related bird species representing two differing types of habitat preference.

Intralimb coordination of three distantly related small bird species was accurately quantified using high-definition, biplanar high-speed

X-ray videography. Small bird species exhibiting similar intralimb proportions and hip height and also having a similar body mass range (compared with the entire range of body mass found within Aves) but being different in habitat preferences, i.e. differing ecological specializations, were chosen for the analysis, in order to estimate the influence of ecological specialization and phylogenetic position on intralimb coordination. In a first step, two distantly related ground-dwelling species (*Eudromia elegans*, Tinamidae, Tinamiformes; *Coturnix coturnix*, Phasianidae, Galliformes) were compared. Phylogenetic position and the fossil record suggest convergent evolution of the ground-dwelling mode of life in both species (Houde and Olson, 1981; Houde, 1986; Mayr and Weidig, 2004; Kriegs et al., 2007; Mayr, 2009). In order to distinguish between limb behavior specific to ground-dwelling species and more common principles of avian terrestrial locomotion, a third and less terrestrially adapted species was included in the analysis (*Corvus monedula*, Corvidae, Passeriformes). Jackdaws exhibit many different locomotor behaviors, including striding and hopping on the ground, moving on thin branches and hopping from one branch to another, and even climbing (Haffner, 1993). The possible influence of phylogeny on a behavior can largely be controlled by choosing only distantly related experimental species. However, adaptive significance can be identified by comparing distantly related taxa that have convergently adapted to a particular habitat (terrestrial, e.g. *E. elegans* and *C. coturnix*) with species predominantly adapted to a different habitat (arboreal, e.g. *C. monedula*). Currently, knowledge of intralimb coordination of avian terrestrial locomotion is restricted to guinea fowl (Gatesy, 1999a; Gatesy, 1999b), chicken (Jacobson and Hollyday, 1982; Manion, 1984; Muir et al., 1996), quail (Reilly, 2000; Abourachid et al., 2011), pigeon (Cracraft, 1971), magpie (Verstappen et al., 2000) and several Struthioniformes (e.g. Abourachid and Renous, 2000; Jindrich et al., 2007; Rubenson et al., 2007; Smith et al., 2010). Although Gatesy (Gatesy, 1999a) demonstrated the necessity of applying X-ray technology for an accurate and reproducible analysis of the kinematics of avian terrestrial locomotion, very few studies have since used this method in analyses of avian bipedalism (Abourachid et al., 2011; Provini et al., 2012). As proximal segments and joints, as well as the pelvis, are obscured by feathers, wings and musculature, X-ray videography is crucial to the precise quantification of avian hindlimb kinematics (Gatesy, 1999a; Abourachid et al., 2011).

MATERIALS AND METHODS

Animals and experimental protocol

The centerpiece of the present study was an X-ray videographic analysis, because only this technique allows for highly precise capture of bony landmarks without serious manipulation of the experimental animals. Spatio-temporal and kinematic data were obtained from two adult elegant-crested tinamou [*Eudromia elegans* (Saint-Hilaire 1832)], weighing 540 and 670 g, respectively; four adult European quail [*Coturnix coturnix* (Linnaeus 1758); breeding quail], weighing between 270 and 290 g; and three adult European jackdaw [*Corvus monedula* (Linnaeus 1758)], each weighing 240 g. Average hip height during stance was 130 mm in the tinamous, 110 mm in the jackdaws and 90 mm in the quail. The Committee for Animal Research of the State of Thuringia, Germany, approved all animal care and experimental procedures. Animals were hand-raised (jackdaws) or obtained as immature.

Birds were habituated to the experimental setup by positive conditioning. Animals were trained over 4 weeks to move on a motorized treadmill in front of X-ray image intensifiers with relatively constant speed. A Plexiglas box (240×48×48 cm)

prevented escape of the birds but did not interfere with the locomotion of the animal (Fig. 1). The treadmill was custom-built in order to allow for biplanar X-ray recording and to reduce scattered X-rays. The treadmill belt (200×40 cm) was underpinned by a support made out of compressed wood, and within the middle portion of the treadmill frame, metal components were omitted as much as possible. The maximum speed of the treadmill was 5.95 m s⁻¹.

Data recording and X-ray videography

Kinematics were recorded simultaneously. Birds were filmed at the custom-built, state-of-the-art high-speed biplanar X-ray videography facility housed at the Institut für Spezielle Zoologie und Evolutionsbiologie of the Friedrich-Schiller-Universität Jena, Germany (Fig. 1). The digital system is based on the high-end X-ray device NeuroStar™ (Siemens AG, Erlangen, Germany). It allows for synchronous biplanar X-ray recordings on two 20–40 cm image intensifiers and the recording of two additional synchronous standard light high-speed cameras (SpeedCam Visario g2, Weinberger, Erlangen, Germany). Television screens allowed for monitoring activity during experiments from outside the experimental room (the treadmill was operated by a remote control). Avian terrestrial locomotion was recorded at 1000 frames s⁻¹ using maximum resolution (1536×1024 pixels) from lateral and ventro-dorsal projection simultaneously. Animals were filmed at 40 kV and between 70 and 100 mA. Raw video data (vr2) were filtered (gamma correction, contrast, sharpness) and subsequently converted into the conventional audio video interleave (AVI) format.

Data analysis

Eighty to 100 complete stride cycles for each species were analyzed. Only velocities the animals were easily willing to perform were recorded and analyzed. Elegant-crested tinamou moved at speeds between 0.2 and 2.15 m s⁻¹, and quail and jackdaw moved at 0.2–1.2 m s⁻¹. Motion analysis was performed using SimiMotion 3D (SIMI Reality Motion Systems, Unterschleissheim, Germany). The software allows for 3-D calibration, interactive digitalization of bony landmarks and calculation of the kinematic parameters of interest. Skeletal landmarks used in this study are shown in Fig. 2. After calibration, every tenth to twentieth frame was manually digitized in each of the two planes. Data between these frames were spline-interpolated. Subsequently, SimiMotion 3D calculates either 2-D or 3-D coordinates, which are needed to obtain angles for kinematic parameters. Parallax was corrected by calibration of the recordings before calculation of coordinates and angles. Furthermore, a calibration cube enabled a definition of the three direction in space (*x*, *y*, *z*-axes) for the coordinate system. The calculated data were exported into MS Excel (Microsoft, Redmond, WA, USA), SPSS (IBM, Armonk, NY, USA) and MATLAB (The MathWorks, Natick, MA, USA) for further analysis. To test for accuracy of the digitization, we digitized the 20 consecutive frames and calculated the joint and element angles of the five trials. This procedure was repeated five times for the same 20 frames. The standard deviation between the angles of each frame from the five trials was calculated. The mean of the 20 standard deviations obtained was used as a measure of accuracy. The standard deviation between the angles of the five trials was constantly less than 1 deg; therefore, the error of digitization is negligible.

Analyzed parameters

Speed was calculated by adding or subtracting animal speed to or from treadmill speed, respectively. Animal speed was quantified by the distance the apophysis furculae travelled during one stride and

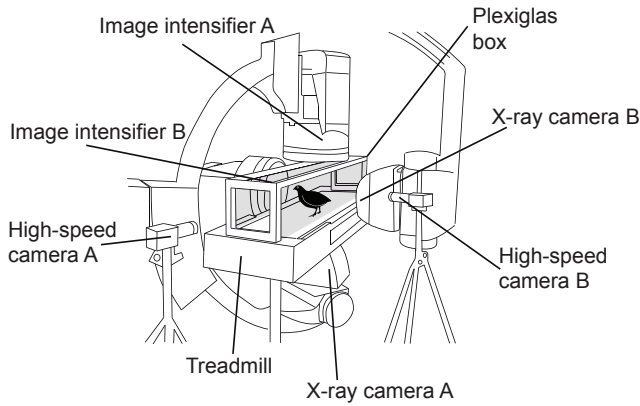


Fig. 1. Experimental setup.

is reported in ms^{-1} . Touch-down is defined as the moment the anterior tip of the third toe touches the ground and lift-off represents the moment that the toe loses contact with the substrate.

To facilitate comparison among different sized species at an equivalent speed, speed was normalized for differences in body mass into dimensionless variables (Alexander and Jayes, 1983; Gatesy and Biewener, 1991). Froude number (Fr) was obtained by calculating the following formula: $V^2/(gh)$, where V is absolute speed, g is gravitational acceleration (9.81 ms^{-2}) and h is a characteristic quantity. Instead of using hip height as a characteristic quantity we choose the cube root of body mass (kg) as it does not change over the stride cycle (Studel-Numbers and Weaver, 2006). Additionally, the following spatio-temporal gait parameters were calculated: stride duration (duration from touch-down to subsequent touch-down), stance duration (duration from touch-down to lift-off), swing duration (duration from lift-off to touch-down), stride frequency (strides per unit time), duty factor (relative fraction of step length of the entire stride length), stride length (speed multiplied by stride duration), step length (speed multiplied by stance duration) and swing length (speed multiplied by swing duration). For a better comparison and presentation of kinematic data, relative values of stride length and step length were calculated as the absolute value divided by the cube root of body mass (Abourachid, 2001).

Skeletal landmarks defining anatomical limb joint and element angles are shown in Fig. 2. Protraction and retraction angles of the limb were measured at touch-down and lift-off, respectively, between a line connecting the tip of the third digit and the proximal pivot and the vertical line originating at the proximal pivot (Gatesy and Biewener, 1991). Limb joint angles were measured on the flexor side of each joint, except for the tarsometatarso-phalangeal (TMTP) joint, which was measured on the extensor side (Fig. 2). We quantified both 2-D and 3-D limb joint angles as well but chose to present only 2-D angles – projected on the parasagittal plane – for two reasons: on the one hand, 2-D and 3-D limb joint angles differ between 1 and 2 deg on average, and discussing both values does not provide further valuable information; on the other hand, discussing 2-D data permits comparison with other species investigated previously. Limb element angles were calculated with several approaches. To determine the significance of the movement of an individual limb element for progression and to calculate its individual relative contribution to step length, limb element angles were projected on a parasagittal plane and were measured relative to the horizontal (Fig. 2). In order to ascribe importance to out-of-parasagittal-plane movement of limb elements, abduction and adduction angles were measured and compared among species.

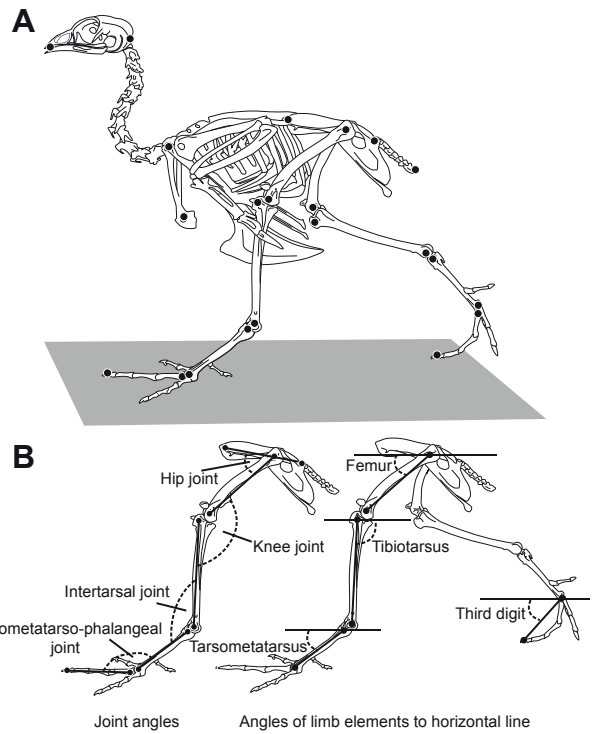


Fig. 2. (A) Skeletal landmarks and (B) calculated limb joint and limb element angles from the X-ray videographic locomotion analysis.

Abduction is defined as the movement of the distal end of a limb element away from the plane of relevance. Femoral abduction angle was measured in two ways. First it was measured as the 3-D angle relative to the sagittal plane of the pelvis; therefore, an anatomical coordinate system was chosen. Computation was rather simple, as movements of the pelvis relative to the thoracic spine can be ruled out, and the pelvis provides enough anatomical landmarks to define two vectors for calculation. Femoral abduction was calculated based on the following formula:

$$\text{Abduction (femur)} = 90 - \arccos \left(\frac{\vec{b} \cdot \vec{n}}{|\vec{b}| |\vec{n}|} \right), \quad (1)$$

where \vec{b} is the vector of the femur and \vec{n} is the normal vector of the sagittal plane of the pelvis (C. Krause and M.S.F., unpublished data). To assess out-of-parasagittal plane movements of the all limb elements, the angle of abduction and adduction of the femur, tibiotarsus, tarsometatarsus and third digit was calculated by means of a global coordinate system and was measured three-dimensionally relative to the x - z plane, which is equitable with the direction of travel.

Pelvic pitch was measured relative to the horizontal from lateral projection. Pelvic yaw was determined relative to a fore-aft line from a ventro-dorsal projection. Pelvic roll was calculated as the 3-D angle between a line connecting both acetabuli and the x - y plane.

By means of the limb joint and limb element angles that were projected on a parasagittal plane (aside from the complete and graphically given pattern of motion), the following kinematic parameters were determined and statistically analyzed: touch-down angle, lift-off angle, mid-stance angle, and maximum and minimum joint excursion during stance and swing. The effective angular displacement as the difference between touch-down and lift-off

angle, as well as the stance amplitude as the difference between the maximum and the minimum value, were determined in order to calculate the ratio between both values. This ratio defines the coefficient of stance phase (CSP) of the limb joints (Fischer et al., 2002). The CSP is a measure of the role of a joint in adjusting functional limb length and thus the contribution of a joint to limb compliance. The lower the CSP of a particular joint the higher its yield during weight bearing. The 'overlay method' (Fischer and Lehmann, 1998) provides a means of assessing how much the excursion of a limb element contributes to body propulsion or step length (its proper motion). This method considers that only angular movement of a limb element within its proximal adjacent joint and its pivot height determine its contribution to step length. Except for the most proximal limb element (femur), the amplitude of excursion of all limb elements is a product of both their proper motion and the passive displacement generated within the pivots of the more proximal limb elements. The 'overlay method' can dissociate these two components of amplitude by overlaying the configuration of the proximal element in frame one onto frame two and so on, without changing angles in the more distal joints. The difference between the horizontal excursion of the tip of the third toe (frame one) and at instant $i+1$ (frame two) is the horizontal distance caused by the movement of the relevant element. The absolute contribution of each element to step length is given as the summation of all single-frame calculations. The contribution of the remaining elements to forward motion is calculated in the same way, except that the angular movement achieved by sagittal rotation of the more proximal elements is subtracted.

The angle of attack is defined as the angle at touch-down between a line connecting the center of mass (CoM) and the tip of the third digit and the substrate (Hackert et al., 2006). To be able to calculate the angle of attack, the position of the CoM has to be determined. After euthanizing experimental animals (except for jackdaws, where dead specimens were provided), birds were weighed and subsequently disarticulated into the following component parts: head/neck, trunk, thigh, shank, lower leg (tarsometatarsus) and digits. The location for disarticulation corresponds to anatomical landmarks used for manual digitization (Fig. 2). Therefore, component parts can be reconstructed with coordinates from the kinematic data analysis. The mass of component parts relative to overall body mass was determined. To obtain the length of elements and the relative position of the CoM of individual component parts, the longitudinal length of elements was sized with a digital caliper and the CoM of the element in question was measured five times with a pendulum. The complete morphometric data set and coordinates obtained from the kinematic analysis using SimiMotion 3D were imported into MATLAB and analyzed with a custom-written MATLAB script (M. Maus, Locomotion Laboratory, Technische Universität, Darmstadt, Germany).

Intralimb proportions were also measured using SimiMotion 3D and were as follows: *E. elegans*, femur 27%, tibiotarsus 36%, tarsometatarsus 22% and third toe 15%; *C. coturnix*, femur 28%, tibiotarsus 33%, tarsometatarsus 20% and third toe 18%; and *C. monedula*, femur 20%, tibiotarsus 36%, tarsometatarsus 24% and third toe 20%.

Means, standard deviations and the range of variation are given. Subsequently, data were ln-transformed for further analysis. Quantitative correlations of kinematic variables with locomotor speed were calculated using least-square regression ($\ln y = \ln x b + a$). The significance level was $P < 0.05$. The coefficient of determination (R^2) and the coefficients a (y -intercept) and b (slope) and their standard error are also given in the tables.

To compare kinematics statistically, a one-way fixed-factor ANOVA of selected kinematic parameters was performed. Only kinematics within an equal velocity range among species were analyzed ($Fr = 0.018$ – 0.11). To check for speed effects, the velocity range was divided into two ranges, one below $Fr = 0.06$ and one above $Fr = 0.06$. In order to test for homogeneity of variances of the sample sets, Levene's test was performed prior to the ANOVA. If variances differed significantly, the Welch test was preferred instead of the ANOVA (Nachtigall and Wirtz, 2004). As ANOVA indicates only whether means among groups differ significantly but does not reveal which groups differ, *post hoc* tests were performed subsequently to the ANOVA. To test which group means were significantly different from each other, we used the GT2 method (Hochberg, 1974), if variances were homogeneous. In the case of heteroscedastic samples, the Tamhane-T2 test was used instead of the GT2 method.

RESULTS

Eighty to 100 successive stride cycles of each species within a broad speed range were analyzed (*E. elegans*, 0.2 – 2.2 ms^{-1} ; *C. coturnix*, 0.2 – 1.2 ms^{-1} ; *C. monedula*, 0.2 – 1.1 ms^{-1}).

Intralimb coordination of hindlimb elements

The trajectory of the angular movements of the hindlimb elements is monophasic in all species. The displacement of the segments consists mainly of retraction during stance, whereas segments are protracted during most of swing. Retraction of all segments in all species starts when the limb is already in swing phase. The relative timing of the onset of protraction differs between segments, but not between species. Femoral and tarsometatarsal protraction already begins in late stance, whereas protraction of the tibiotarsus and the third toe is initialized during early swing (Fig. 3).

Femur

The amplitude of femoral displacement has the smallest value of all segments. Femoral retraction starts after 50% of swing and lasts until 85–95% of stance. It is interrupted by a small gravity-induced protraction that starts with touch-down and its amplitude is ~ 5 deg, but this small protraction is not found in quail. In all species, touch-down angle of the femur is between 20 and 35 deg below the horizontal. Only in jackdaw is a marginal but significant correlation between femoral touch-down angle and velocity found. Lift-off angle of the femur was speed-dependent in all species investigated and strongly increases over the entire speed range analyzed (Table 1). Nevertheless, femoral displacement angle never goes above 90 deg from the horizontal. While the displacement of the femur contributes only minor to stance progression during slow trials, its contribution increases up to 30% and even more during the fastest stride cycles analyzed in all species (Fig. 4).

Tibiotarsus

Retraction of the tibiotarsus accounts for most of the stance progression at all speeds and in all species investigated. However, its relative contribution decreases with speed, because the femur and the tarsometatarsus become more important for stance progression with increasing speed and the angular proper movement of the tibiotarsus does not increase beyond $Fr = 0.08$ (Fig. 4). In tinamou the contribution of the tibiotarsus to stance progression abruptly decreases to $\sim 50\%$ beyond $Fr = 0.08$. The displacement of the tibiotarsus consists of a continuous retraction during stance. Protraction is initiated after 5–15% of swing. In the ground-dwelling birds, the protraction starts later with increasing velocity. In contrast, in jackdaw the timing of the onset of protraction is

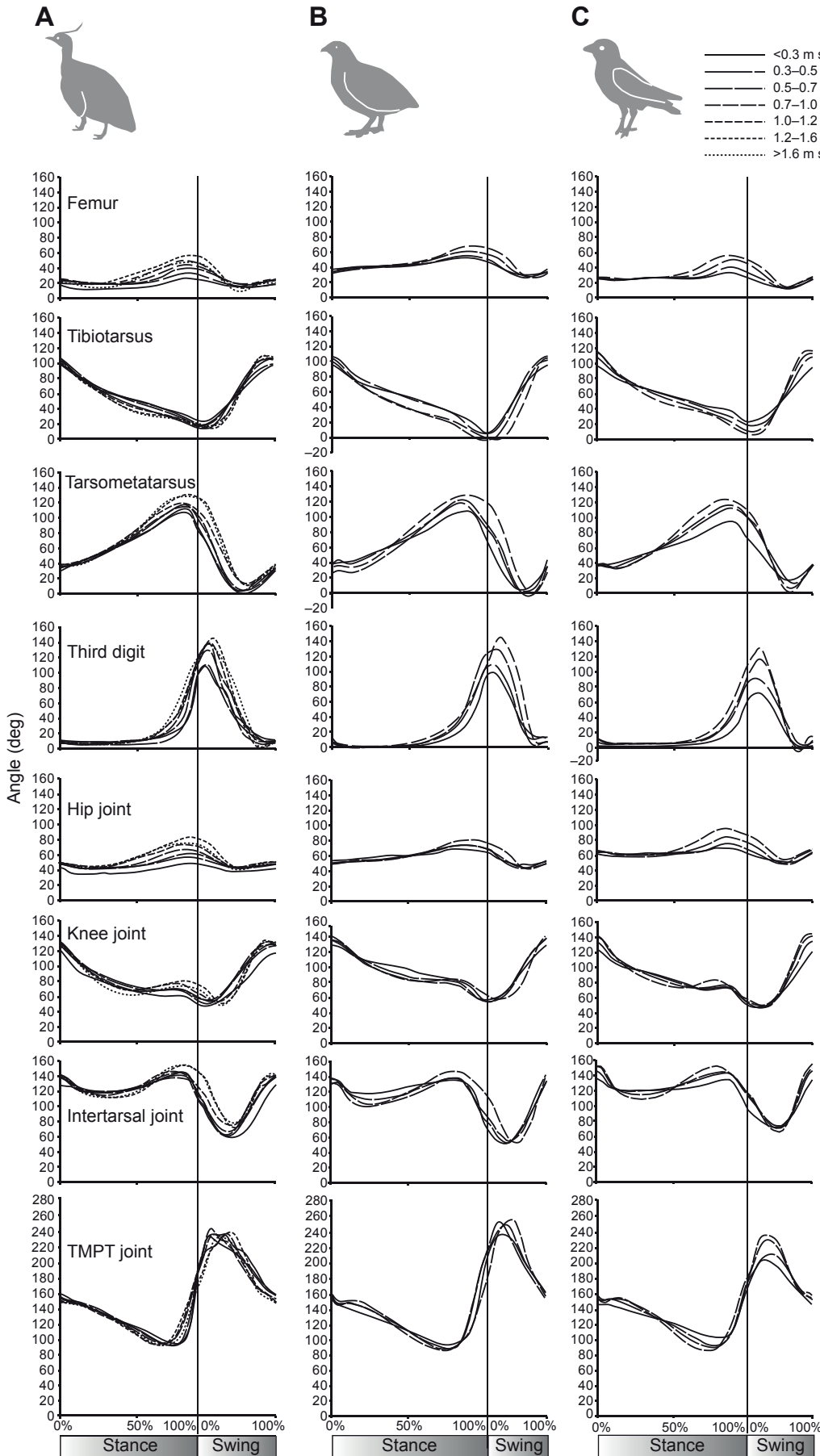


Fig. 3. Each line represents mean values of 12–20 stride cycles each speed range of hindlimb joint and element angles of (A) *Eudromia elegans*, (B) *Coturnix coturnix* and (C) *Corvus monedula*. Duration of stance and swing is normalized for duration at $Fr=0.08$.

Table 1. Kinematic parameters of limb element angles and their relation to speed

Limb element		N	Angle (deg)	Range (deg)	R ²	b	a	
<i>Eudromia elegans</i>								
Femur	Touch-down	93	23.1±2.9	16.2–29.6	0.04	0.045±0.023	1.36±0.006	
		94	42.5±7.6	23–60.8	0.726**	0.31±0.02	1.63±0.005	
	Midstance	94	21.9±5.8	9.8–40.4	0.274**	0.232±0.039	1.34±0.01	
		93	45.6±7.8	25.1–65.6	0.632**	0.281±0.023	1.66±0.006	
	Min	93	16.6±3.6	8.3–23.5	0.003	–0.024±0.045	1.2±0.011	
		94	18±3.4	11.1–25.8	0	0±0.036	1.24±0.009	
	Tibiotarsus	Touch-down	94	103.9±3.6	94.5–111.7	0.094**	0.02±0.006	2.02±0.002
		Lift-off	94	46.5±5.3	32.4–57.3	0.717**	–0.206±0.014	1.7±0.003
		Midstance	94	103.9±3.6	94.5–111.7	0.094**	0.02±0.006	2.02±0.002
		Min	94	17.9±3.4	11.1–25.8	0	0±0.036	1.24±0.009
	Tarsometatarsus	Touch-down	94	35.4±3.1	27.8–43.4	0.206**	0.073±0.015	1.55±0.004
		Lift-off	94	105±15.9	65.1–132.1	0.759**	0.259±0.015	2.03±0.004
		Midstance	93	73.2±3.6	62.1–81.5	0.318**	0.056±0.009	1.87±0.002
		Max	93	119.7±8.8	98.4–136.5	0.566**	0.101±0.009	2.08±0.002
	Digitus III	Touch-down	81	8.5±3.0	1.2–15.8	0	–0.003±0.098	0.887±0.025
		Lift-off	90	116.4±11.2	86.7–142.2	0.395**	0.133±0.015	2.071±0.004
Midstance		92	8.6±2.7	1.1–16.8	0.011	0.074±0.074	0.912±0.019	
Max		77	115.6±11.6	86.7–142.2	0.358**	0.114±0.018	2.07±0.007	
	Min	78	4.3±1.4	0.6–8.1	0.009*	–0.085±0.1	0.588±0.025	
<i>Coturnix coturnix</i>								
Femur	Touch-down	97	31.3±2.9	20.8–41.3	0	–0.005±0.031	1.49±0.009	
	Lift-off	94	53.3±5.7	32.7–70	0.297**	0.181±0.029	1.77±0.008	
	Midstance	80	40.9±2.7	31.7–48.1	0.008**	0.023±0.027	1.62±0.007	
	Max	80	59.5±4.5	42.3–71.8	0.391**	0.159±0.023	1.8±0.006	
	Min	82	31.1±2.6	24.1–41.4	0.02	0.046±0.037	1.498±0.01	
Tibiotarsus	Touch-down	98	99.9±6.1	82–111.4	0.123**	0.048±0.013	2.01±0.004	
	Lift-off	94	–3.1±4.8	12.1 to –16.3	0.145**	–0.031±0.008	2.27±0.002	
	Midstance	82	36.8±6.3	22.3–56.1	0.224**	–0.262±0.055	1.5±0.014	
	Max	82	100.4±5.6	82.6–111.4	0.128**	0.054±0.016	2.01±0.004	
Tarsometatarsus	Touch-down	96	–3.3±4.7	12.8 to –16.3	0.101	0.028±0.009	2.27±0.002	
	Lift-off	87	27.7±4.3	16.6–45	0.007	–0.043±0.053	1.43±0.016	
	Midstance	80	97.6±17.9	55.9–126.7	0.695**	0.377±0.027	2.06±0.008	
	Max	80	73.7±5.3	58.4–87.3	0.188**	0.092±0.021	1.884±0.006	
Digitus III	Touch-down	80	123.9±10	100.7–149.7	0.299**	0.127±0.022	2.12±0.006	
	Lift-off	82	25.9±4.6	8.7–43.2	0	–0.014±0.087	1.39±0.023	
	Touch-down	91	6.2±2.8	0–15	0.103*	–0.501±0.16	0.598±0.049	
	Lift-off	85	114.9±11.6	83–138.1	0.089	0.078±0.027	2.073±0.008	
Digitus III	Midstance	79	3.9±1.3	0.9–7.3	0.169**	0.462±0.117	0.644±0.032	
	Max	73	111.3±9.1	83–131.3	0.061	0.057±0.027	2.07±0.007	
	Min	77	0.4±0.5	0–2	0.001	–0.412±1.958	–3.351±0.532	
<i>Corvus monedula</i>								
Femur	Touch-down	79	26.6±2.6	19.8–36.4	0.127**	0.092±0.027	1.45±0.009	
	Lift-off	79	40.5±10.2	20.4–69.2	0.584**	0.506±0.049	1.73±0.016	
	Midstance	79	28.2±3.7	19.1–38.7	0.108**	0.118±0.039	1.48±0.012	
	Max	79	49.7±9.7	25.1–78.5	0.534**	0.388±0.041	1.79±0.013	
	Min	79	23.5±2.7	17.4–33.5	0.164**	0.125±0.032	1.4±0.01	
Tibiotarsus	Touch-down	79	110.6±5.2	92.2–119.4	0.421**	0.089±0.012	2.07±0.004	
	Lift-off	79	13.5±5.9	4.2–36.7	0.363**	–0.726±0.109	0.885±0.035	
	Midstance	79	51.3±5.9	38.4–62.6	0.484**	–0.21±0.024	1.65±0.008	
	Max	79	110.6±5.2	92.2–119.4	0.421**	0.089±0.012	2.07±0.004	
Tarsometatarsus	Touch-down	79	13.5±5.9	4.2–36.7	0.363**	–0.726±0.109	0.885±0.035	
	Touch-down	79	36.1±2.6	27.3–42.2	0.001	0.008±0.024	1.55±0.008	
	Lift-off	75	98.2±11	64.2–119.3	0.728**	0.298±0.021	2.07±0.007	
	Midstance	79	70.5±5.4	54.7–81.8	0.534**	0.149±0.016	1.89±0.005	
Digitus III	Touch-down	74	116±7.6	91–132.6	0.826**	0.187±0.01	2.12±0.003	
	Min	74	32.4±2.8	25.2–40	0.127**	–0.083±0.026	1.5±0.008	
	Touch-down	77	8.1±4.3	0.1–21.2	0.236**	1.54±0.32	1.19±0.103	
	Lift-off	72	95.7±14.1	56.4–118.8	0.694**	0.331±0.026	2.07±0.009	
Digitus III	Midstance	78	6±1.7	1.6–11.3	0.301**	0.462±0.117	0.644±0.032	
	Max	71	95.8±14.2	56.4–118.8	0.694**	0.057±0.027	2.07±0.007	
	Min	71	3±1.3	0.1–6	0.327*	–0.412±1.958	–3.351±0.532	

N, number of trials.

Angles are presented as means ± s.d.

Regression equation: $\ln y = \ln b x + a$, where x is speed; coefficients are presented ± s.e.* $P < 0.05$; ** $P < 0.01$.

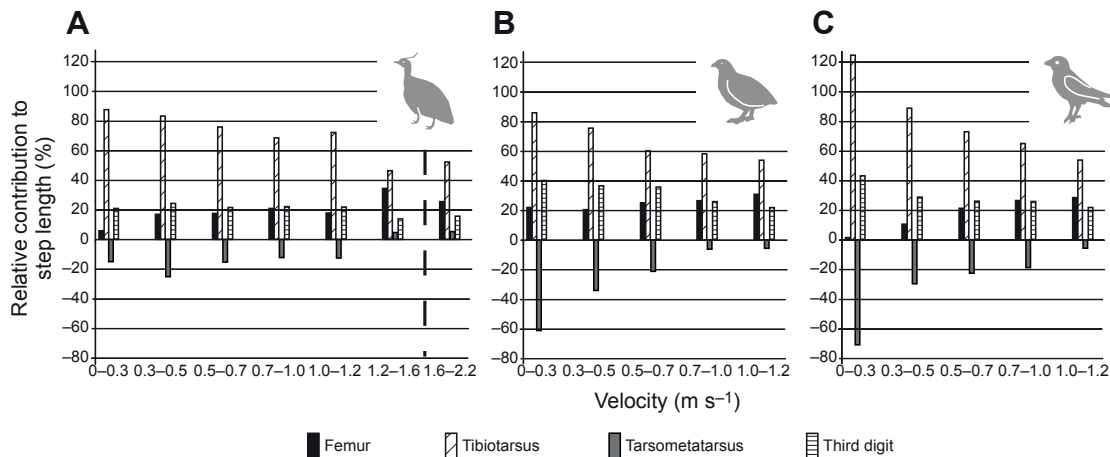


Fig. 4. Relative contribution (%) of the femur, tibiotarsus, tarsometatarsus and third digit to step length of (A) *Eudromia elegans*, (B) *Coturnix coturnix* and (C) *Corvus monedula*.

constant (Fig. 3). Retraction of the tibiotarsus starts after 95% of swing. Tibiotarsal touch-down angle is speed dependent in the investigated species, decreasing slightly with increasing speed (Table 1). Lift-off angle increases until $Fr=0.08$ is reached but decreases beyond. In quail, lift-off angle is almost equal to horizontal, whereas in tinamou and jackdaw, this element is lifted off the ground ~ 20 deg before reaching the horizontal.

Tarsometatarsus

Retraction of the tarsometatarsus starts after two-thirds of swing. It lasts until very late stance (Fig. 3). Touch-down angle is in matched-motion with the femur. This does not hold true for the lift-off angle, which is speed dependent, and whose increase with velocity has the steepest slope of all segmental lift-off angles (Table 1). The tarsometatarsus contributes positively to step length only in the second half of stance, when its pivot elevates. In all species, its overall contribution to progression is negative, and, particularly at the lowest velocities recorded, a negative contribution of up to -60% has to be compensated by the other limb segments. Only in tinamou is there a positive contribution of the tarsometatarsus to step length, not exceeding $5\text{--}6\%$ observed at the highest speeds found (Fig. 4). The negative to positive change of this bone's contribution to step length goes along with the sudden drop of tibiotarsal contribution beyond $Fr=0.08$.

Digitus III

In the first $5\text{--}50\%$ of stance, the four phalanges of the third toe are in contact with the ground. After the first half of stance, the third toe starts to lift off the ground, beginning with the first phalanx and ending with the fourth. In the second half of stance, when its pivot is raised off the ground, the third toe positively contributes up to $20\text{--}30\%$ to step length (Fig. 4). This amount decreases with increasing velocity of the animals. Retraction switches to protraction after $5\text{--}15\%$ of swing. With increasing velocity, the maximal value of the retraction appears later in swing in the ground-dwelling birds, but not in jackdaw. The amplitude of third toe displacement is lower in jackdaw than in quail or tinamou. After 90% of swing, retraction of the third toe is renewed (Fig. 3). Although the maximal value of displacement of the third toe within the stride cycle is speed-dependent in all species, its lift-off angle correlates with velocity only in tinamou and jackdaw. In all species, the slope of the lift-off angle significantly decreases beyond $Fr=0.08$. Although the

touch-down angle of the third toe slightly decreases in the ground-dwellers, it significantly increases in *C. monedula* (Table 1).

Medio-lateral motions of limb elements

There exist distinct interspecific differences in the pattern of abduction and adductional movements of the hindlimb segments. This holds particularly true for the femur of the ground-dwelling species and the jackdaw (Fig. 5, supplementary material Fig. S1). The femur is abducted throughout the whole stride cycle. In the ground-dwelling species, it is only slightly abducted from the sagittal plane throughout stance and swing, whereas in jackdaw, it is consistently abducted $20\text{--}30$ deg from the sagittal plane. Considering the abduction of the femur from the sagittal plane of the pelvis, in jackdaw there exist some distinct intraspecific differences most distinct between individual 1 and individual 2. In individual 2, the femur becomes abducted to nearly 50 deg throughout stance, whereas in individual 1, the femur is held almost constant. This variance is due to intraspecific differences in pelvic rotations within the analyzed specimens of jackdaw. If one looks at the pattern of femoral abduction with regards to the direction of travel, the interspecific differences vanish and femoral abduction increases throughout stance from 14 deg at touch-down to 40 deg at lift-off on average. In the ground-dwellers, the femur is held almost constantly 15 deg adducted from the $x\text{--}z$ plane. In all species, the tibiotarsus is adducted from the $x\text{--}z$ plane throughout the whole stride but undergoes abduction in the last third of stance. In tinamou and quail, flexion of the knee is coupled to adduction of the tibiotarsus against the femur. In jackdaw, this specific movement does not become evident, and tibiotarsal abduction and adduction are brought about passively by the movements within the hip joint. Tinamou differs from quail and jackdaw in the medio-lateral posture of the tarsometatarsus and the third toe. While in quail and in jackdaw both elements are held only marginally abducted from the $x\text{--}z$ plane, in tinamou both segments in their movements are abducted between 10 and 15 deg from this plane.

Intralimb coordination of hindlimb joints

The flexion/extension pattern of the knee and intertarsal joints is biphasic throughout the stride cycle whereas the trajectory of the movement of the hip and the TMTP joint is monophasic (Fig. 3). In all species, extension of all joints starts before touch-down. Extension and flexion of the joints are synchronized neither during

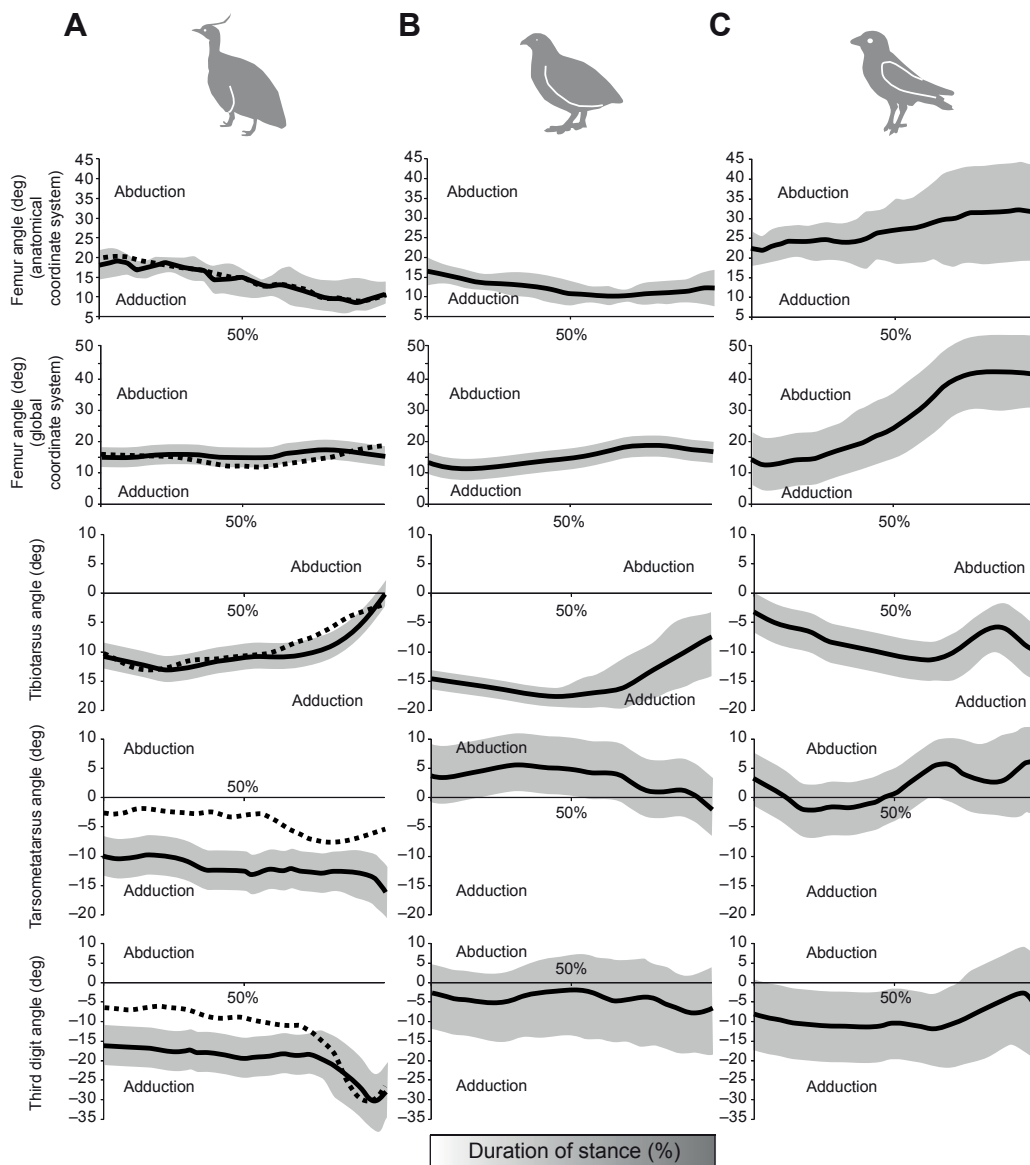


Fig. 5. Medio-lateral movements of hindlimb elements during stance in (A) *Eudromia elegans*, (B) *Coturnix coturnix* and (C) *Corvus monedula*. Femoral abduction angle is calculated relative to the sagittal plane of the pelvis (anatomical coordinate system) and to the x - z plane (global coordinate system). All other limb elements were calculated within a global coordinate system. Curves represent the mean of all analyzed stride cycles. The dashed line in *Eudromia elegans* represents medio-lateral movements during running.

swing nor during stance, although change from extension to flexion at the end of stance occurs almost simultaneously. In swing phase, joints flex in the following order: knee, TMTP joint, intertarsal and then hip. In all species, maximum extension is reached by the hip joint after 90% of stance, in the knee joint after 90% of swing, in the intertarsal joint either after 95% of swing or after 85% of stance, depending on the velocity at which the animal is moving, and in the TMTP joint after 25% of swing. Except for the TMTP joint, maximum flexion occurs in all joints during swing in order to lift feet far enough off the ground. In all joints but the knee joint, the amplitude of angular joint motion during stance is higher than the effective joint motion between touch-down and lift-off (Fig. 3).

Hip

Right after touch-down, the hip joint undergoes gravity-induced flexion (Fig. 3). The amplitude of this flexion amounts to an average of 5 deg in tinamou and jackdaw, and in quail it is marginal and amounts to less than 1 deg. The CSP indicates the degree of horizontal *versus* vertical joint work. A CSP value of less than 50% indicates that joint work is contributing mainly to vertical stretching and bending of the limb and not to forward progression of the animal

(Fischer et al., 2002). Although the trajectory and amplitude of joint excursion are largely similar between species, the mean CSP differs because the effective angular displacement differs. This is due to a varying relationship between maximal joint extension and lift-off, caused by the differing lengths of the femur and the distal segments among species. Therefore, in jackdaw, hip joint excursion during stance contributes less to the animal's forward progression than in the ground-dwellers. Touch-down angle is independent of speed in all of the species investigated. Lift-off angle, in contrast, is speed-dependent (Table 2).

Knee

The CSP of the knee joint consistently amounts to 100% in all species because its stance amplitude and effective angular displacement during stance are nearly equal (Table 2). This points to the exclusive role of the knee joint for generating forward progression. Only in tinamou does the CSP decrease to 75% when running at highest velocity. During the first half of stance, the knee joint is continuously flexed. Subsequently, flexion is interrupted by a small but speed-dependent extension of the knee that lasts until 80% of stance is finished. During the last 20% of stance, the knee

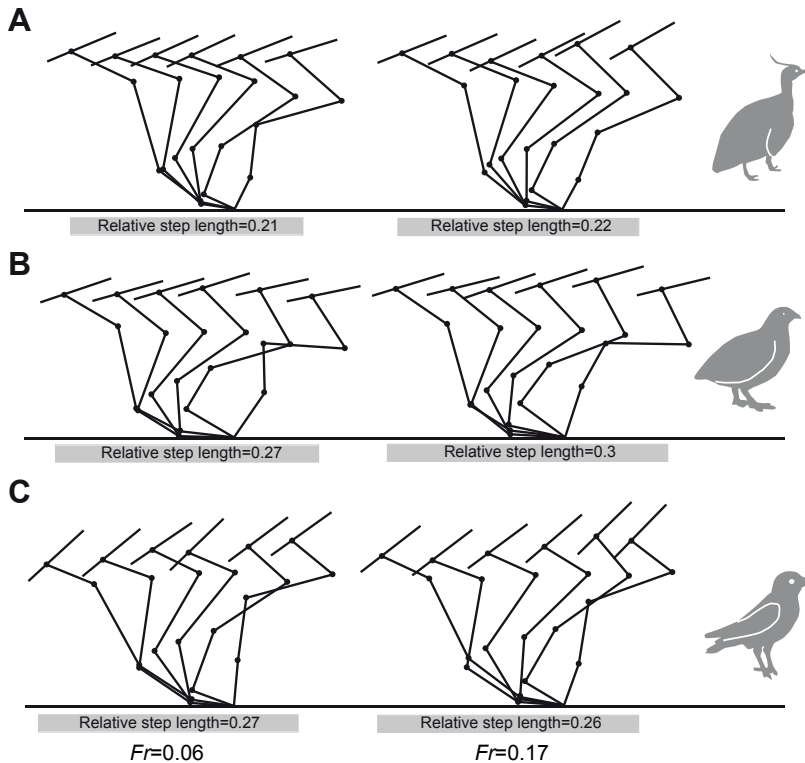


Fig. 6. Limb element positions during stance in (A) *Eudromia elegans*, (B) *Coturnix coturnix* and (C) *Corvus monedula* at relative speeds of $Fr=0.06$ and $Fr=0.17$. The length of the gray bar at the bottom of each stick figure represents the relative step length that was attained.

undergoes flexion again. This holds true for all species investigated. In all species, the amplitude of knee joint excursion decreases beyond $Fr=0.08$. In contrast to jackdaw, with an increase of knee joint amplitude below $Fr=0.08$, in the ground-dwelling birds, knee amplitude is almost constant below $Fr=0.08$. Lift-off angle of the knee joint significantly increases exclusively below $Fr=0.08$, whereas it decreases above $Fr=0.08$. Touch-down angle of the knee is positively speed-dependent in quail and jackdaw.

Intertarsal

The trajectory of joint excursion of the intertarsal joint is biphasic with one maximum at the beginning of stance and the other after 85% of stance (Fig. 3, Table 2). The lift-off angle of the joint is speed-dependent. Only in tinamou running at velocities higher than $Fr=0.08$ are lift-off angles with values higher than the touch-down angle observed. A higher lift-off than touch-down angle means an elevated pivot of the tarsometatarsus at the end of stance. Hence, only in tinamou running at high speeds can a positive contribution of the tarsometatarsus to step length be observed. The CSP of the intertarsal joint significantly decreases in all species with increasing speed, meaning an increasing importance of the joint for compensation of vertical body displacement. This seems paradoxical as the tarsometatarsus becomes increasingly important for generating step length with increasing speed, but points to the relevance of the independent consideration of joint and segment motions. The increasing lift-off angle indicates increasing non-progressive vertical work of the intertarsal joint, but simultaneously implies an elevation of the tarsometatarsal pivot that accounts for positive contribution of the bone to step length.

TMTP joint

The TMTP joint strongly extends during the second half of stance. Its relevance for forward progression is only marginal, although the third toe contributes consistently 20% and more to step length. The

trajectory of TMTP joint excursion is monophasic. In contrast to the other limb joints, flexion of the TMTP joint is less marked during swing than during stance. It undergoes the largest excursions of all limb joints. The amplitude of joint excursion is distinctly smaller in jackdaw than in ground-dwelling birds. Exclusively in jackdaw, lift-off angle of the TMTP joint is independent of speed. Touch-down angle significantly increases with speed in jackdaw but decreases in quail and tinamou (Table 2).

Kinematic parameters of joint excursions during swing are given in supplementary material Table S1.

Pelvic motions

Pelvic posture in quail is almost horizontal, whereas in jackdaw it is distinctively more steeply pitched. Pelvic pitch is biphasic during stance in all species, but at the highest speeds analyzed it becomes monophasic during stance, as the second maximum marks the beginning of swing in running birds. Touch-down angle is always greater than lift-off angle. Amplitude and effective angular displacement of pelvic pitch are similar among species (Table 3). The amplitude of pelvic pitch decreases with speed in jackdaw and quail and is constant in tinamou. Touch-down angle is positively speed-related in tinamou, significantly decreases with speed in quail, and is independent of speed in jackdaw. Lift-off angle is speed-related (positively) exclusively in tinamou.

Pelvic roll shows similar effective angular displacement and amplitude among the species investigated and is positively speed-dependent. Looking at the left limb during the first 10% of stance, the pelvis still rolls to the right side. Subsequently, it rolls to the left side, having a level posture after 50% of swing of the right limb. The pelvis rolls to the left side until 95% of stance is finished.

Although the procedure and extent of pelvic pitch and roll are similar among species, there exist distinct differences among species regarding pelvic yaw (Table 3, supplementary material Fig. S1). In the ground-dwelling birds, the extent of medio-lateral rotations of

Table 2. Kinematic parameters of limb joint angles and their relation to speed during stance

Limb joint		N	Angle (deg)/CSP (%)	Range	R ²	b	a
<i>Eudromia elegans</i>							
Hip	Touch-down	91	47.3±3.2	38.5–56	0.039	0.026±0.014	1.68±0.003
	Lift-off	92	66.5±8.7	44.1–86.8	0.72**	0.24±0.016	1.8±0.004
	Max	90	70.1±8.7	45.4–92.5	0.61**	0.221±0.019	1.84±0.004
	Min	90	40±3.6	30.7–52	0.19**	0.076±0.017	1.6±0.004
	CSP	90	62±16	4–100	0.51**	0.588±0.06	–0.23±0.014
Knee	Touch-down	92	127.7±4.1	112–138.7	0.008	0.006±0.007	2.1±0.002
	Lift-off	93	61.6±7.9	47.7–80.6	0.548**	0.194±0.018	1.79±0.004
	Max	92	127.8±4.2	112–138.7	0.008	0.006±0.007	2.1±0.002
	Min	92	59.1±6.2	47.7–78.6	0.32**	0.117±0.018	1.77±0.004
	CSP	92	96±6	75–100	0.344**	–0.09±0.013	–0.02±0.003
Intertarsal	Touch-down	93	139.7±4.6	124.7–148	0.084**	0.019±0.006	2.15±0.001
	Lift-off	92	125.4±15.8	89.3–157	0.615**	0.202±0.017	2.1±0.004
	Max	92	148±6.8	134–162.6	0.285**	0.048±0.008	2.17±0.002
	Min	92	110.8±5.2	89–123.6	0.03	0.016±0.01	2.05±0.002
	CSP	92	53±35	1–100	0.365**	–1.5±0.209	–0.53±0.047
TMTP joint	Touch-down	82	152.3±5.5	126.9–164	0.157**	–0.03±0.008	2.2±0.002
	Lift-off	90	191.1±16.5	130–221	0.201**	–0.08±0.017	2.28±0.004
	Max	81	191.3±16.4	150–221	0.212**	–0.08±0.018	2.28±0.004
	Min	79	91±6	76–105	0.035	–0.03±0.015	1.96±0.003
	CSP	79	38±12	4–56	0.079*	–0.29±0.111	–0.47±0.025
<i>Coturnix coturnix</i>							
Hip	Touch-down	80	47.2±3.2	34.4–56.6	0.01	–0.03±0.029	1.67±0.008
	Lift-off	86	67.7±6	48.7–83.8	0.268**	0.134±0.024	1.86±0.007
	Max	74	74±4.8	61–87.4	0.307**	0.108±0.019	1.9±0.005
	Min	74	46.2±3.5	30.5–56.4	0.006	–0.02±0.036	1.66±0.01
	CSP	74	75±14	31–100	0.234**	0.282±0.06	–0.08±0.017
Knee	Touch-down	85	132.4±6.1	111.1–148	0.111**	0.046±0.014	2.13±0.004
	Lift-off	86	51.7±4.7	35.4–72	0.044	0.08±0.041	1.72±0.012
	Max	77	132.6±5.8	114.8–148	0.094**	0.04±0.014	2.13±0.004
	Min	77	51.4±4.8	35.4–72	0.059**	0.099±0.046	1.72±0.012
	CSP	77	100±1	97–100	0.056*	0.004±0.002	–0.001±0.001
Intertarsal	Touch-down	84	128.8±8	98.6–153	0.034	0.036±0.021	2.12±0.006
	Lift-off	81	94.5±15.4	60.1–126.8	0.639**	0.316±0.027	2.04±0.008
	Max	72	141.9±8.2	120.5–161	0.134**	0.059±0.018	2.16±0.005
	Min	72	88±9.5	60.1–110.9	0.442**	0.199±0.027	1.98±0.007
	CSP	72	62±23	9–100	0.256**	–0.63±0.129	–0.4±0.036
TMTP joint	Touch-down	80	157.7±5.8	138–174	0.062*	–0.02±0.01	2.19±0.003
	Lift-off	81	197.3±20.5	152–260.5	0.319**	–0.14±0.023	2.26±0.007
	Max	69	196.5±18.9	154–260.5	0.345**	–0.14±0.024	2.26±0.007
	Min	71	83.7±5.1	67–95	0.072*	–0.05±0.024	1.9±0.007
	CSP	69	32±13	1–52	0.199**	–0.82±0.201	–0.74±0.056
<i>Corvus monedula</i>							
Hip	Touch-down	78	62.4±3.5	51.9–70	0	0.002±0.017	1.8±0.006
	Lift-off	79	73.2±9.5	53.1–93.6	0.528**	0.243±0.026	1.93±0.008
	Max	78	83.9±9.5	64.8–105.2	0.574**	0.224±0.022	1.98±0.007
	Min	78	56.5±2.8	48–63	0.007	–0.01±0.015	1.75±0.005
	CSP	78	38±20	1–80	0.075**	0.653±0.263	–0.35±0.086
Knee	Touch-down	78	137±6.5	117–147	0.481**	0.09±0.011	2.16±0.003
	Lift-off	79	54±7.2	41.8–78.3	0.227**	0.156±0.033	1.77±0.011
	Max	78	137±6.4	118–147	0.479**	0.089±0.011	2.16±0.003
	Min	78	54±7	41.8–73	0.268**	0.167±0.032	1.78±0.01
	CSP	78	100±1	92–100	0.007	–0.002±0.003	0±0.001
Intertarsal	Touch-down	79	146.3±6.7	128.8–158	0.26**	0.064±0.012	2.18±0.004
	Lift-off	78	110.5±10.5	81.1–130	0.326**	0.141±0.023	2.08±0.008
	Max	77	149.6±6.9	130–165	0.662**	0.098±0.008	2.2±0.003
	Min	77	105.9±7.4	81–124	0.092	0.058±0.021	2.04±0.007
	CSP	77	83±20	13–100	0.19**	–0.42±0.101	–0.22±0.033
TMTP joint	Touch-down	77	152.2±5	137–165.5	0.183**	0.036±0.009	2.2±0.003
	Lift-off	75	167.4±10.5	110.9–208	0.021	–0.06±0.051	2.2±0.017
	Max	72	179±11.8	154.5–208	0.025	0.026±0.02	2.26±0.007
	Min	72	88.7±5.7	77–103.6	0.552**	–0.13±0.013	1.9±0.004
	CSP	72	29±11	2–48	0.042	–0.31±0.178	–0.68±0.06

N, number of trials; CSP, coefficient of stance phase; TMTP, tarsometatarso-phalangeal.

Angles and CSP values are presented as means ± s.d.

Regression equation: $\ln y = \ln b x + a$, where x is speed; coefficients are presented ± s.e.

* $P < 0.05$; ** $P < 0.01$.

Table 3. Kinematic parameters of pelvic rotations and their relation to speed during stance

Pelvic rotation		N	Angle (deg)	Range	R ²	b	a
<i>Eudromia elegans</i>							
Pitch	EAD	89	2.7±2.1	0.1–9.6	0.022	0.2256±0.046	0.299±0.212
	Amplitude	93	6.6±1.6	2.7–11.9	0.046*	0.805±0.011	0.107±0.052
Roll	EAD	86	11.4±5.8	0.1–22.2	0.475**	0.985±0.026	1.06±0.12
	Amplitude	86	15.9±4.2	5.1–25.3	0.702**	1.19±0.007	0.472±0.034
Yaw	EAD	83	2.6±2.1	0.1–10.3	0.032	0.208±0.052	0.41±0.253
	Amplitude	83	5.4±1.8	1.5–12.4	0.015	0.7±0.015	0.081±0.074
<i>Coturnix coturnix</i>							
Pitch	EAD	76	2.6±2.1	0.1–9.2	0.009	0.163±0.099	−0.292±0.362
	Amplitude	76	7.1±1.9	3.4–13.4	0.052*	0.788±0.025	−0.187±0.093
Roll	EAD	79	8.4±4.9	0.2–21.2	0.212**	1.02±0.061	0.995±0.224
	Amplitude	79	15.6±4.9	6.1–28.5	0.14**	1.23±0.023	0.29±0.084
Yaw	EAD	78	5.5±4	0.1–18.4	0.125**	0.352±0.085	−1.03±0.313
	Amplitude	78	9.4±3.8	3.7–21	0.06*	0.892±0.028	−0.226±0.103
<i>Corvus monedula</i>							
Pitch	EAD	55	3.8±1.2	0.1–13.8	0.014	0.43±0.197	0.365±0.522
	Amplitude	55	8.8±1.2	5.1–14.1	0.079	0.954±0.033	0.15±0.08
Roll	EAD	54	10.8±6.2	4.3–25.2	0.137**	1.111±0.049	0.405±0.141
	Amplitude	54	15.6±5.6	6.5–25.2	0.014	1.195±0.044	0.111±0.129
Yaw	EAD	54	12.1±7.4	1.6–30.7	0.19**	1.211±0.08	0.813±0.233
	Amplitude	54	19.3±8.2	5.7–45.7	0.023	1.287±0.05	0.162±0.146

N, number of trials; EAD, effective angular displacement between touch-down and lift-off; amplitude, value of angular displacement between maximum and minimum.

Angles are presented as means ± s.d.

Regression equation: $\ln y = \ln bx + a$, where x is speed; coefficients are presented ± s.e.

* $P < 0.05$; ** $P < 0.01$.

the pelvis is only marginal, whereas in jackdaw the effective angular displacement and particularly the amplitude of pelvic yaw are considerable. There exists a significant intraspecific difference in the extent of pelvic yaw among individual 1 and individual 2 of jackdaw, with the second bird showing in X-ray analysis a significantly higher excursion compared with individual 1.

Spatio-temporal parameters and whole limb angles

The majority of spatio-temporal gait characteristics are speed-dependent (except for swing duration in quail and jackdaw). Tinamou, quail and jackdaw increase speed by increasing stride length as well as stride frequency (supplementary material Table S2). The three species increase stride length particularly by increasing the retraction angle of the hindlimb. In all of the species investigated, the protraction angle at touch-down is almost constant or, in the case of tinamou, entirely independent of speed.

Angle of attack

In *E. elegans*, the mean ± s.d. angle of attack is 49±2.5 deg, varying between 45 and 54 deg; this value is 48±2.4 deg (43–54 deg) in *C. coturnix* and 47±1 deg (45–49 deg) in *C. monedula*. In all species, the angle of attack is always independent of speed. This is consistent with the invariable touch-down angles given above. Furthermore, the angle of attack is similar among species owing to a consistent position of the CoM among the species investigated.

ANOVA

Significant differences ($P < 0.05$) between experimental species and among velocity ranges are found in the majority of kinematic parameters subject to ANOVA (Table 4). No statistical significant differences were found only in the amplitude of hip excursion during stance and in most of the parameters concerning relative timing of joint maxima and minima. Table 4 shows results of *post hoc* comparisons of parameters between species, with no clear

picture emerging. However, in general, *E. elegans* exhibits smaller touch-down angles, joint amplitudes and pelvic excursion but higher lift-off angles than the other species. *Coturnix coturnix* moves with smaller touch-down and lift-off angles as well as smaller pelvic excursions compared with *C. monedula*, but exhibits higher amplitudes in the distal joints. Parameters describing femoral abduction also differ significantly among species ($P < 0.05$; Table 4).

DISCUSSION

Methodology and comparison of angular values

From a methodological perspective, the present study has shown that precise analyses of movements of the avian hindlimb and pelvis as a necessity require an application of X-ray videography, because the femur, tibiotarsus and pelvis are hidden underneath the skin, feathers and wings. To our knowledge, this is the first comparative study of avian terrestrial locomotion using X-ray videography. The study produced some distinct differences to preceding work using conventional video technique. To take a single example, Reilly (Reilly, 2000) reported a nearly immobile femur and hip joint in quail during the stance phase of locomotion. In the present study, a major result is that hip joint movement in quail during stance is substantial even at low velocities and also increases significantly with increasing locomotion speed. Maximum amplitudes of more than 30 deg could be attained. Hence, Reilly's conclusion that birds were showing two modes of limb functions, where smaller birds were characterized by a terrestrial locomotion using only three joints (showing no hip motions) and larger birds were characterized by a 'four-joint' limb at higher speeds (adding hip), is falsified. This is not at odds with the author's argumentation of size-related energetic constraints for smaller birds when switching from terrestrial locomotion to flying at a specific velocity, but rather shows that there are not two distinct modes of terrestrial locomotion, as hip excursions are also present during low velocities. The three-joint limb function is likely an artifact of applying conventional video

techniques unable to capture subtle hip motions, e.g. being obscured by the noise of skin movements (Filipe et al., 2006; Bauman and Chang, 2010). A rather continuous increase in hip motions when increasing speed can be expected for birds of all sizes (see below). This is supported by further X-ray videographic data on quail recently published by Abourachid et al. (Abourachid et al., 2011), who found hip extension during stance and whose overall results are consistent with our data on quail during slow locomotion.

A further comparison with other species requires accepting that treadmill locomotion parallels unrestrained locomotion, an idea that is already supported by data on mammals (Fischer, 1999; Herbin, et al., 2007; Matsas et al., 2000; Riley et al., 2007). Furthermore, in ostriches, only marginal differences occur by means of a slight variation in swing duration (Rubenson et al., 2004; Rubenson et al., 2007). Also, despite birds showing no head-bobbing during treadmill locomotion (Necker, 2007), the absence of this behavior likely will not influence kinematics because it does not demonstrably influence the position of the body's CoM (Fujita, 2002; Hancock, 2010).

As revealed by ANOVA (Table 4), the mean of most angular values significantly differs between species, although birds with similar limb proportions and hip height were chosen. By applying simple geometrical modelling, Gatesy and Pollard (Gatesy and Pollard, 2011) have shown how geometric constraints limit angular limb configuration. Constraints take effect on the distal end of a limb, e.g. because of the need for a relatively constant toe position in order to ensure stance phase stability, or on the proximal side because of restrictions in vertical oscillations of the CoM/relative hip height. Hence, kinematic angles are dependent on segment length in order to satisfy spatial requirements (Gatesy and Pollard, 2011), making comparison of absolute values not as straightforward as previously thought. Therefore, the further discussion focuses largely on the kinematic pattern and its relationship to speed rather than on a comparison of absolute values.

Conserved pattern of intralimb coordination in fore-aft motion and general principles in avian bipedalism

Flexion and extension of limb joints as well as protraction and retraction of limb elements are the motions of a limb that are primarily responsible for forward progression of a parasagittally striding animal and compensation for vertical fluctuations of its CoM (Fischer and Blickhan, 2006). Despite major differences in ecology, morphology (e.g. presence of hallux) and phylogenetic position, the overall pattern of joint flexion/extension and limb element translation was similar between the ground-dwellers and *C. monedula* (Fig. 6).

For all species investigated, ground-dwelling or less terrestrial, femoral and hip movements are important and indispensable for achieving step length, particularly at higher velocities. As in guinea fowl (Gatesy, 1999a; Gatesy, 1999b) the amplitude of femoral retraction and hip extension during stance becomes more important for forward progression at increasing velocities. Hip joint amplitude reaches mean values of 25–28 deg in all experimental species below a relative speed of just $Fr=0.08$. The angular value of femoral retraction approximates 90 deg at the highest speeds but never goes beyond this.

In all species, retraction of the tibiotarsus is the most important source of generating step length. This importance of knee movement for the displacement of the body as a peculiarity of avian bipedalism has been recognized previously by other authors (Cracraft, 1971; Jacobson and Hollyday, 1982; Manion, 1984; Gatesy, 1990; Gatesy, 1999a; Gatesy, 1999b; Reilly, 2000; Verstappen et al., 2000; Rubenson et al., 2007; Hutchinson and Allen, 2009). However, the excursion of knee flexion and proper motion of the tibiotarsus does

not increase beyond $Fr=0.08$. Knee movements reach their upper limit even at lower velocities in all of the birds analyzed. Hence, it is inevitable for the animal to increase hip movements to further raise step length beyond $Fr=0.08$. Although the amplification of hip joint amplitude is relatively small, the higher pivot of the hip compared with the knee provides a sufficient increase in step length.

Although an almost static intertarsal joint during stance phase has been reported by Reilly (Reilly, 2000) in quail and by Jacobson and Hollyday (Jacobson and Hollyday, 1982) in hens, its motion during stance is significant in the species investigated here. Its small CSP points to a high degree of non-progressive joint excursions that indicate the importance of the intertarsal joint for telescoping movements (compliance) of the limb. This holds also true for other small and medium-sized birds (up to the size of a chicken) investigated so far (Cracraft, 1971; Dagg, 1977; Manion, 1984; Muir et al., 1996; Verstappen et al., 2000). However, within Aves, motion of the intertarsal joint is clearly size-dependent, with large ratites showing nearly no motion in the joint during stance (Rubenson et al., 2007; Goetz et al., 2008; Schaller et al., 2009).

The small CSP of the TMTP joint indicates that excursion of this joint contributes only marginally to progression. Its distally adjacent digits are of great importance for generating step length. This is mainly due to the great length of the digits in birds, which is related to limb configuration and the location of the CoM, which is situated cranially to the hip joint (e.g. Gatesy, 1990; Hutchinson and Allen, 2009).

Furthermore, as in guinea fowl and other ground-dwelling birds (Gatesy and Biewener, 1991; Gatesy, 1999a), the majority of the intralimb kinematic parameters are highly speed-dependent, but limb configuration at touch-down is uniform and mainly independent of speed in tinamou, quail and jackdaw. Also the angle of attack is consistent and independent of speed. Hence, the increase of speed is a rather asymmetric procedure in the avian species investigated.

Therefore, the behavior of the avian hindlimb during terrestrial locomotion of small (and medium-sized) species is characterized by three general observations: (1) forward progression is achieved by the proximal limb elements with increasing importance of femoral movements at increasing velocities; (2) more distal elements contribute less to step length but are mainly involved in telescoping movements (compliance) of the limbs; and (3) the majority of parameters are speed-dependent, though limb configuration at touch-down relates to a lesser degree to speed, being uniform among species. So far, available data on large Struthioniformes (Abourachid and Renous, 2000; Rubenson et al., 2007; Goetz et al., 2008; Schaller et al., 2009; Smith et al., 2010) suggest that across the entire class Aves, it is mainly body size, leading to a differing degree of crouch and elongation of relative distal limb length, that constrains the kinematic pattern (Gatesy and Pollard, 2011) (A.S., B. M. Kilbourne and M.S.F., unpublished). Looking at small species exhibiting rather similar intralimb proportions, a consistent pattern of intralimb coordination can be observed, supporting the initial hypothesis. At least in the species analyzed here and also in guinea fowl (Gatesy, 1999a), magpie (Verstappen et al., 2000) and chicken (Manion, 1984), this common pattern is only slightly influenced by preferred habitat and phylogenetic position. Even obvious differences in anatomy, such as the presence of a hallux, do not influence this kinematic pattern. Hence, it can be assumed that rather similar intralimb proportions that are governing consistent intralimb coordination are related to a general demand to cope with the terrestrial substrate, particularly irregularities of the ground (Fischer and Blickhan, 2006; Jenkins, 1971). These irregularities are relatively greater for small sized taxa and pose major handicaps for

Table 4. Results of *post hoc* tests (following ANOVA) of selected kinematic parameters

Parameter	Froude=0.018–0.06			Froude=0.06–0.11		
	<i>E. elegans</i> – <i>C. coturnix</i>	<i>E. elegans</i> – <i>C. monedula</i>	<i>C. coturnix</i> – <i>C. monedula</i>	<i>E. elegans</i> – <i>C. coturnix</i>	<i>E. elegans</i> – <i>C. monedula</i>	<i>C. coturnix</i> – <i>C. monedula</i>
Touch-down hip	–0.0055	–0.2674	–0.2729	0.0674	–0.3053	–0.3726
Touch-down knee	–0.0133	–0.0516	–0.0383	–0.0134	–0.0944	–0.081
Touch-down intertarsal	–0.09247	–0.0389	–0.1314	0.1166	–0.0719	–0.1885
Touch-down TMTP	–0.0127	0.0224	0.0351	–0.0421	–0.0136	0.0284
Lift-off hip	–0.1028	–0.1669	–0.0641	–0.0335	–0.2372	–0.2037
Lift-off knee	0.1444	0.0868	–0.0576	0.1842	0.008	–0.1762
Lift-off intertarsal	0.2696	0.0258	–0.2438	0.2313	0.0432	–0.1881
Lift-off TMTP	–0.0304	0.1915	0.2218	–0.0153	0.1094	0.1247
Amplitude hip	–0.1412	–0.057	0.0842	–0.042	–0.0719	–0.0299
Amplitude knee	–0.1333	–0.1474	–0.0141	–0.1388	–0.1556	–0.0168
Amplitude intertarsal	–0.4716	–0.1033	0.3683	–0.556	–0.4043	0.1517
Amplitude TMTP	–0.1053	0.2261	0.3315	–0.1297	0.08	0.2097
Relative timing max. hip	0.0977	0.0707	–0.027	0.0348	0.0382	0.0034
Relative timing max. knee	0	0	0	0	0	0
Relative timing 1st max. intertarsal	0.0082	0.2516	0.2435	–0.3456	–0.1641	0.1815
Relative timing 2nd max. intertarsal	0.1015	0.0321	–0.0694	–0.129	–0.129	0
Relative timing max. TMTP	0	0	0	0	0	0
Relative timing min. hip	1.6527	0.2938	–1.359	1.4174	0.22	–1.198
Relative timing min. knee	0	0	0	0	0	0
Relative timing 1st min. intertarsal	0.162	0.1103	–0.0513	0.1834	0.0916	–0.0918
Relative timing 2nd min. intertarsal	0	0	0	0	0	0
Relative timing min. TMTP	–0.0477	0.0175	–0.0302	–0.0217	–0.0067	0.015
Amplitude pelvic pitch	–0.1738	–0.2788	–0.105	0.0193	–0.29	–0.3094
Amplitude pelvic roll	–0.4988	–0.4656	0.0332	–0.3144	–0.0621	0.2523
Amplitude pelvic yaw	–1.3039	–1.983	–0.6791	–2.0064	–2.8845	–0.8781

Given is the mean difference between species. Positive values indicate a larger mean of the particular parameter of the species stated first compared with the second in each column (negative values indicate smaller means). Bold numbers indicate a significantly smaller/greater value ($P < 0.05$).

parasagittally striding animals. It is not surprising that intralimb coordination is also consistent among small to medium-sized therian mammals, ranging across marsupials, primates, carnivores, artiodactyls, rodents and hyraxes (e.g. Fischer et al., 2002; Jenkins, 1971; Jenkins, 1974; Jenkins and Camazine, 1977; Jenkins and Weijjs, 1979; Rocha-Barbosa et al., 2005; Schmidt, 2005; Schmidt, 2008; Schmitt, 1999), and can even be recognized in the suspensory locomotion of sloths (Nyakatura et al., 2010). General demands for coping with terrestrial substrates (amongst others) are behaviors that simplify control, particularly at high velocities and at touch-down, when errors in position are most likely (Gatesy and Biewener, 1991), thereby explaining some of the interspecific consistency of parameters.

Using mathematical simulations, in recent years researchers have determined the intrinsic mechanical properties of the limb itself (proportions) and of its translations (kinematics) that provide self-stability. Self-stability implies stable locomotion in the presence of internal or external perturbations without the necessity of neural feedback dedicated to the perturbation (Seyfarth et al., 2001; Seyfarth et al., 2002; Fischer and Blickhan, 2006; Blickhan et al., 2007). Consistent element angles at touch-down and a homogenous angle of attack (CoM) are prerequisites for self-stability. Furthermore, retraction of limb segments before touch-down, as found in all species investigated, is another factor enhancing self-stability (Seyfarth et al., 2003). Another parameter enhancing the self-stable operation of segmented limbs across species might be the intralimb proportions themselves. Considering a tri-segmented parasagittally operating limb, mathematical simulations allow different limb configurations to move stably under the condition of a constant middle segment (Seyfarth et al., 2001). In fact, scaling studies of mammals and birds were able to show that the

tibia/humerus and the tibiotarsus have an almost constant ratio to total limb length across a large range of body mass, from the dormouse and finch to the buffalo and ostrich (Schmidt and Fischer, 2009) (A.S., B. M. Kilbourne and M.S.F., unpublished). Hence, besides the degree of crouch, which is also related to the demands of managing a highly 3-D terrain, the common principles of intralimb coordination and several consistent aspects of morphology are likely dedicated to allowing stable terrestrial locomotion under simple control. Further studies will show how limbs of species with aberrant intralimb proportions for their body mass (e.g. stilts, jacanas or loons) behave during terrestrial locomotion.

Medio-lateral motions of the limb, pelvic rotation and the habitat-related aspect of limb coordination

Although the pattern of fore–aft motion of the limb is similar among the species studied, there exist distinct differences within the patterns of medio-lateral limb and pelvic motions. Most striking is the highly abducted femur of jackdaws during the entire stride cycle and the strong abduction during the second half of stance. In contrast, in both of the ground-dwelling birds, the angle of femoral abduction and its amplitude are much smaller during the stride cycle than in jackdaws. In all, the translational movements of the hindlimb are more restricted to fore–aft motion in ground-dwellers. This is a principle already known for large terrestrial birds (Rubenson et al., 2007; Goetz et al., 2008) and cursorial mammals (Hildebrand, 1988), and it imparts longer relative stride lengths, as segment length can be translated more straightforward into stride length. In consequence of greater relative body width in jackdaws compared with ground-dwelling species (Gatesy, 1999a), the mean femoral abduction angle is greater in jackdaws. This affects pelvic yaw, as the minimal distance between both knee

joints is greater in jackdaws, and adduction of limb elements at the end of swing and early stance is insufficient to position the stance foot underneath the CoM. Therefore, pelvic yaw rotates the swing limb from a lateral position into a cranio-lateral position right before touch-down, and in the course of stance, pelvic yaw translates the CoM over the stance foot. Pelvic yaw is generated in the hip joints of jackdaws, which are characterized by an increased mobility. Such a hip joint is also convenient for fulfilling other locomotor behaviors common for jackdaw, such as climbing into breeding burrows and chimneys or for diagonally walking on thin branches and manipulating items, etc. The relatively minute pelvic movements found in quail and tinamou in the present study have also been found in guinea fowl, ostrich and other quail individuals (Abourachid et al., 2011; Gatesy, 1999a; Rubenson et al., 2007). Locomotion with minute pelvic motions, as in ground-dwellers and the rather waddling walk of Passeriformes or Anseriformes, do not represent different strategies of avian terrestrial locomotion. In actual fact, the pattern of pelvic yaw is the same in the ground-dwellers and the jackdaws, but the ratio between maximum body width and the interacetabular distance is different among species. The relatively narrow body of the ground-dwellers favors a rather low pelvic yaw and simultaneously supports a focus on the fore–aft motions of the limb of ground-dwellers.

Differences in medio-lateral limb coordination and morphological aspects such as body width between the ground-dwellers and jackdaws are due to an adaptation to effective terrestrial striding performance for the former and an adaptation to various 3-D habitats and dynamic volant locomotion for the latter. Data further suggest that these differences, such as in pelvic yaw and hip joint mobility, might help to compensate for the trade-off between the need of fore–aft motions under simplified control and differences in morphology and behaviour due to different habitat preferences.

Conclusions

Computational modeling shows that limbs are geometrically constrained systems (Gatesy and Pollard, 2011). This means that intralimb control depends on intralimb proportions. Hence, even slight variation in proportions and hip height, etc., potentially causes disparities in angular values among species or even conspecifics (see Table 4). However, regarding fore–aft motions, the pattern of intralimb coordination of bipedal locomotion is very similar among small birds, which is in concert with the initial hypothesis of this study. The similar pattern among the three experimental species chosen for this study allows us to conclude that among *E. elegans*, *C. coturnix* and *C. monedula*, intralimb coordination is barely influenced by habitat and phylogeny.

The general kinematics found here relate to the need to cope with an irregular terrain with a minimum of necessary control. However, this does not hold true for medio-lateral limb motions and pelvic rotations. These motions can serve as an indicator of the relevance of terrestrial locomotion in a species' mode of life. Notwithstanding other reasons, an increased mobility of the hip joint favors the ability to manage a strongly 3-D habitat such as a tree branch. In contrast, emphasis on fore–aft motion in ground-dwellers has likely evolved convergently and can therefore be seen as an adaptation for rapid bipedal locomotion.

ACKNOWLEDGEMENTS

We thank Dr Hans-Ulrich Peter for helping with raising jackdaws and Dr Christian Schloegl of the Konrad Lorenz Research Station for providing animal material

(jackdaw). We thank Moritz Maus for providing help with MATLAB. We are indebted to Dr John A. Nyakatura, Dr Tracy L. Kivell and Dr Brandon M. Kilbourne to provide helpful comments and insightful criticism to the manuscript.

FUNDING

This research was supported by a grant from the German Research Council (DFG) [FI 410/15-1 to M.S.F.].

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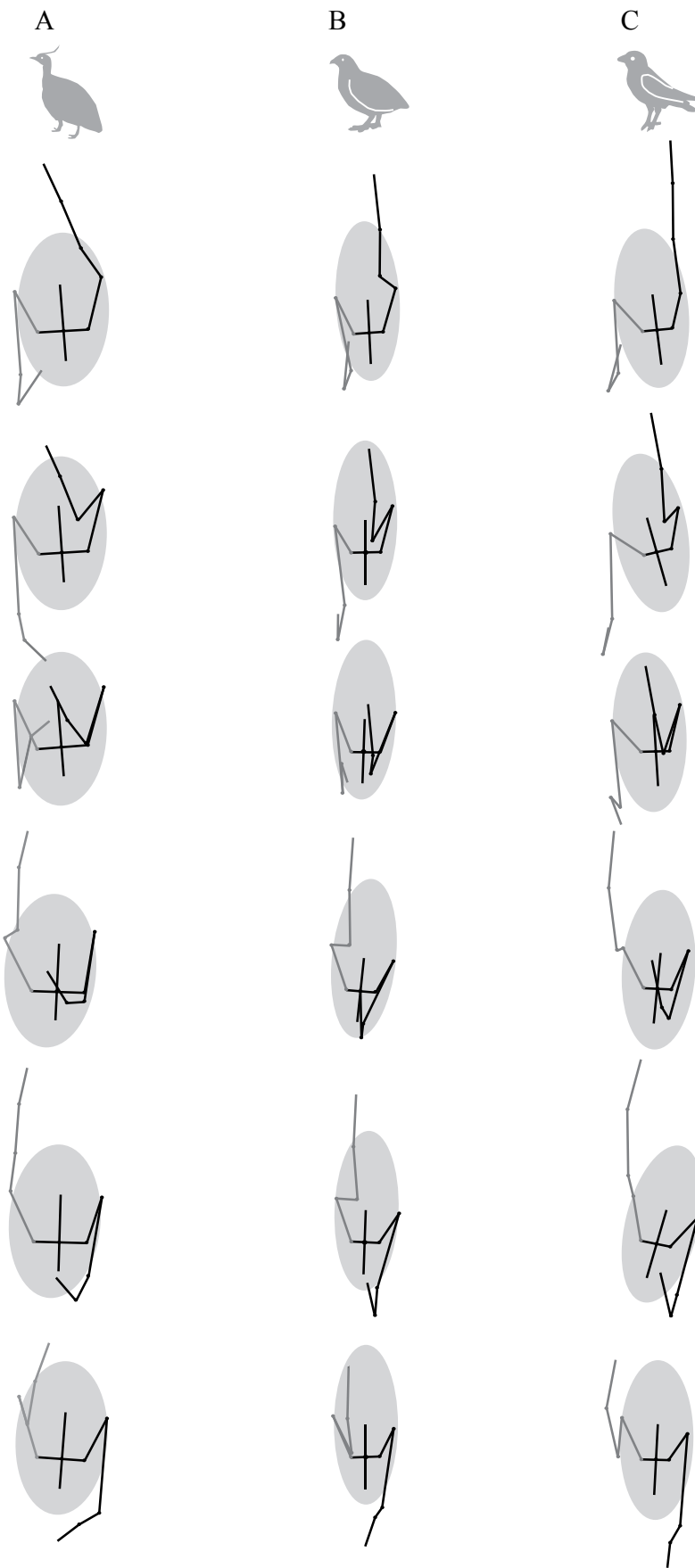


Fig. S1. Stick figures of the stance phase of the right limb (black) from ventro-dorsal perspective based on an X-ray videographic sequence (Fr=0.06). (A) *Eudromia elegans*, (B) *Coturnix coturnix* and (C) *Corvus monedula*.

Table S1. Kinematic parameters of limb joint angles and their relation to speed during swing

		N	Angle (deg)	Range (deg)	R ²	b	a
<i>Eudromia elegans</i>							
Hip	Max	94	65.4±8.5	44.2–86.8	0.73**	0.237±0.015	1.82±0.004
	Min	94	40.4±3	32.1–48.2	0.004	0.01±0.015	1.6±0.004
Knee	Max	93	130.9±5.2	107.2–144	0.451**	0.057±0.007	2.12±0.002
	Min	93	50.4±3.1	43.2–55.7	0.007	−0.01±0.012	1.7±0.003
Intertarsal	Max	91	141.4±5.7	124.7–157	0.448**	0.053±0.006	2.15±0.001
	Min	91	66.3±7.8	48.5–81.6	0.322**	0.137±0.021	1.83±0.005
TMTP joint	Max	93	244.4±7.3	224–263	0.015	0.007±0.006	2.39±0.001
	Min	92	156.5±12.8	126–203	0.001	−0.01±0.016	2.2±0.004
<i>Coturnix coturnix</i>							
Hip	Max	84	66.8±5.6	52.4–83.8	0.2**	0.103±0.023	1.847±0.007
	Min	84	40.8±3.4	30.4–53	0.143**	−0.1±0.027	1.59±0.008
Knee	Max	84	131.3±6.3	111.1–148	0.089**	0.04±0.014	2.13±0.004
	Min	84	48.9±3.7	33.3–63	0.004	−0.02±0.036	1.68±0.011
Intertarsal	Max	80	127.6±9	83.2–152.8	0.034*	0.041±0.024	2.11±0.008
	Min	80	51.6±5.1	32.3–70.5	0.006	−0.03±0.039	1.7±0.012
TMTP joint	Max	73	258.7±11.3	227.5–283	0.159**	0.05±0.014	2.42±0.004
	Min	73	157.2±6.4	133.6–172	0.1**	−0.03±0.011	2.19±0.003
<i>Corvus monedula</i>							
Hip	Max	80	73±8.8	57.8–93.6	0.481**	0.208±0.025	1.92±0.008
	Min	80	47.3±4.2	34.5–56.3	0.004	−0.02±0.029	1.67±0.01
Knee	Max	81	137.5±7.4	111–155	0.619**	0.119±0.01	2.17±0.003
	Min	81	46.9±4.7	38.5–67.8	0.068*	0.064±0.027	1.69±0.009
Intertarsal	Max	75	145.5±7.2	122.4–158	0.379**	0.084±0.013	2.19±0.004
	Min	75	70.1±3.5	60.2–77.6	0.134**	−0.05±0.014	1.83±0.005
TMTP joint	Max	70	222.5±12.9	192–250.7	0.607**	0.113±0.011	2.38±0.004
	Min	71	151.3±8.1	110.7187	0.013	0.018±0.019	2.18±0.007

N, number of trials; TMTP, tarsometatarso-phalangeal. Angle is given as mean ± s.d.

Regression equation: $\ln y = \ln b x + a$, where x is speed; coefficients are presented ± s.e.

* $P < 0.05$; ** $P < 0.01$.

Table S2. Spatio-temporal gait parameters and protraction and retraction angles of the species

Parameter	N	Mean (±s.d.)	Range	R ²	b	a
<i>Eudromia elegans</i>						
Stride duration (s)	101	0.36±0.12	0.22–0.75	0.968**	−0.527±0.01	−0.489±0.003
Stance duration (s)	97	0.24±0.11	0.10–0.56	0.981**	−0.763±0.011	−0.723±0.003
Swing duration (s)	97	0.13±0.02	0.10–0.2	0.362**	−0.127±0.017	−0.911±0.005
Frequency (Hz)	101	3±0.87	1.3–4.6	0.969**	0.527±0.01	0.498±0.003
Duty factor (%)	97	63±9	45–80	0.882**	−0.233±0.009	1.776±0.002
Stride length (m)	101	0.3±0.08	0.16–0.51	0.96**	0.471±0.01	−0.498±0.003
Step length (m)	97	0.18±0.03	0.12–0.22	0.833**	0.237±0.011	−0.723±0.003
Swing length (m)	97	0.12±0.06	0.04–0.26	0.964**	0.873±0.017	−0.911±0.005
Protraction angle (deg)	86	47.8±1.9	43.6–51.8	0.015	−0.01±0.009	1.68±0.002
Retraction angle (deg)	90	25.6±5.3	8.2–35.5	0.773	0.479±0.028	1.41±0.006
<i>Coturnix coturnix</i>						
Stride duration (s)	89	0.4±0.1	0.29–0.89	0.850**	−0.519±0.023	−0.519±0.006
Stance duration (s)	89	0.29±0.09	0.16–0.75	0.874**	−0.707±0.029	−0.712±0.008
Swing duration (s)	89	0.11±0.01	0.08–0.15	0.019	−0.049±0.037	−0.959±0.01
Frequency (Hz)	89	2.63±0.47	1.1–3.5	0.849**	0.521±0.023	0.519±0.006
Duty factor (%)	89	70±5	56.4–83.8	0.632**	−0.188±0.015	1.807±0.004
Stride length (m)	89	0.24±0.04	0.14–0.34	0.836**	0.477±0.022	−0.519±0.006
Step length (m)	89	0.18±0.02	0.10–0.23	0.543**	0.293±0.029	−0.712±0.008
Swing length (m)	89	0.08±0.02	0.03–0.14	0.88**	0.949±0.037	−0.958±0.01
Protraction angle (deg)	95	49.7±2.2	43.6–56.3	0.219	0.058±0.011	1.71±0.004
Retraction angle (deg)	86	25.7±7.6	3.8–39.1	0.644	0.868±0.07	1.57±0.021
<i>Corvus monedula</i>						
Stride duration (s)	93	0.45±0.08	0.24–0.7	0.809**	−0.494±0.025	−0.483±0.008
Stance duration (s)	93	0.32±0.08	0.14–0.6	0.852**	−0.717±0.031	−0.701±0.010
Swing duration (s)	93	0.13±0.02	0.09–0.18	0.012	0.041±0.039	−0.872±0.012
Frequency (Hz)	93	2.32±0.45	1.4–4.2	0.81**	0.495±0.025	0.484±0.008
Duty factor (%)	93	70±6.5	56–87	0.73**	−0.227±0.015	1.782±0.004
Stride length (m)	93	0.25±0.05	0.12–0.34	0.817**	0.507±0.025	−0.483±0.008
Step length (m)	93	0.17±0.02	0.10–0.23	0.458**	0.28±0.032	−0.702±0.01
Swing length (m)	93	0.08±0.03	0.02–0.14	0.887**	1.04±0.039	−0.872±0.012
Protraction angle (deg)	64	49 ±2.2	41.8–52	0.308	0.064±0.012	1.7±0.004
Retraction angle (deg)	51	22.9±9.2	−2.4–38.3	0.653	1.43±0.149	1.7±0.049

N, number of trials.

Regression equation: $\ln y = \ln b x + a$, where x is speed; coefficients are presented ± s.e.

* $P < 0.05$; ** $P < 0.01$.