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REVIEW

Scaling of avian bipedal locomotion reveals independent effects of body mass and leg posture on gait

Monica A. Daley[1,*] and Aleksandra Birn-Jeffery[2]

ABSTRACT

Birds provide an interesting opportunity to study the relationships between body size, limb morphology and bipedal locomotor function. Birds are ecologically diverse and span a large range of body size and limb proportions, yet all use their hindlimbs for bipedal terrestrial locomotion, for at least some part of their life history. Here, we review the scaling of avian striding bipedal gaits to explore how body mass and leg morphology influence walking and running. We collate literature data from 21 species, spanning a 2500× range in body mass from painted quail to ostriches. Using dynamic similarity theory to interpret scaling trends, we find evidence for independent effects of body mass, leg length and leg posture on gait. We find no evidence for scaling of duty factor with body size, suggesting that vertical forces scale with dynamic similarity. However, at dynamically similar speeds, large birds use relatively shorter stride lengths and higher stride frequencies compared with small birds. We also find that birds with long legs for their mass, such as the white stork and red-legged seriema, use longer strides and lower swing frequencies, consistent with the influence of high limb inertia on gait. We discuss the observed scaling of avian bipedal gait in relation to mechanical demands for force, work and power relative to muscle actuator capacity, muscle activation costs related to leg cycling frequency, and considerations of stability and agility. Many opportunities remain for future work to investigate how morphology influences gait dynamics among birds specialized for different habitats and locomotor behaviors.

KEY WORDS: Bird, Walking, Running, Dynamic similarity, Biomechanics, Energetics, Leg morphology, Stability, Systematic review, Meta-analysis

Introduction: comparative biomechanics of striding bipedalism

Humans walk and run bipedally (see Glossary), with two legs moving in an alternating pattern, a half-cycle out of phase (Alexander, 2004). Such gaits are sometimes called striding gaits (see Glossary) to distinguish them from hopping gaits, in which the two legs move in synchrony, and skipping gaits, in which the two legs are neither perfectly in synchrony nor exactly 50% out of phase (Gatesy and Biewener, 1991; Alexander, 2004). Habitual use of striding bipedal gaits (walking and running; see Glossary) as the primary mode of transport has evolved independently several times among vertebrates, in primates (including humans), lizards and theropod dinosaurs (including modern birds) (Gatesy and Dial, 1996; Hutchinson, 2006; Hutchinson and Allen, 2009; Snyder, 1962).

Birds are a diverse lineage of bipedal animals with exceptional locomotor agility and ecological range, inhabiting nearly every terrestrial habitat on Earth, including deserts, coastal wetlands, polar regions, high alpine and human urban settings. Extant birds span a >2500-fold range in body mass and exhibit vast diversity in length proportions of the hindlimb bones (Gatesy and Middleton, 1997; Zeffer et al., 2003). Yet, birds have a consistent avian body plan, with discrete use of wings for propulsion in air or water, and legs for terrestrial movement (Abourachid and Höfling, 2012; Gatesy and Dial, 1996; Heers and Dial, 2015). This discrete specialization of wings and legs likely facilitates functional plasticity by allowing independent function, yet cooperative use of wings, legs and tail (Gatesy and Dial, 1996; Heers and Dial, 2015; Provini et al., 2014). All birds use bipedal terrestrial locomotion for at least part of their life history (Heers and Dial, 2015), although some of the least-terrestrial species, such as swifts, may only do so before they learn to fly. Interestingly, the basic arrangement of the hindlimb bones (Fig. 1) and the movement patterns of the joints are consistent across bird species, despite variation in skeletal proportions (Gatesy and Biewener, 1991; Gatesy and Middleton, 1997; Stoessel and Fischer, 2012). Thus, birds provide a valuable opportunity to study functional morphology, biomechanics and scaling of bipedal gaits.

Here, we review the scaling of avian bipedal gaits from the available literature data, to explore how body mass, limb length and limb posture influence the dynamics of walking and running. For simplicity, we focus only on walking and running (striding) gaits, not hopping or skipping. It is important to acknowledge that this only scratches the surface of bipedal diversity, because many birds, especially passerines, regularly use hopping and skipping gaits (e.g. Verstappen and Aerts, 2000; Verstappen et al., 2000). However, hopping and skipping gaits have been relatively less well studied, so little information exists to inform a comprehensive review.

Striding bipedal gaits share many similar characteristics across species. Striding bipeds transition from walking to running with increasing speed, and show characteristic ground reaction force patterns and body center of mass (CoM) energy fluctuations within each gait (Alexander, 2004; Daley et al., 2016; Gatesy and Biewener, 1991; Gatesy, 1999; Heglund et al., 1982; Rubenson et al., 2004) (Fig. 2). These features of walking and running can be described by the spring-loaded-inverted pendulum (SLIP) model, with walking characterized as vaulting over relatively stiff legs, and running as bouncing on more compliant legs (Fig. 2A) (Alexander, 2004, 1992; Daley et al., 2016; McGeer, 1990, 1992; Seyfarth et al., 2002). Walking is typically characterized by out-of-phase fluctuations in kinetic energy (E_k) and gravitational potential energy (E_g), whereas running is characterized by in-phase fluctuations of E_k and E_g. Fast running typically includes an aerial phase, when no legs are in contact with the ground.

[1]Structure and Motion Lab, Royal Veterinary College, Hawkshead Campus, Hawkshead Lane, North Mymms, Hertfordshire AL9 7TA, UK. [2]School of Engineering and Materials Science, Queen Mary University of London, London E1 4NS, UK.

*Author for correspondence (mdaley@rvc.ac.uk)

M.A.D., 0000-0001-8584-2052; A.B., 0000-0003-2633-006X

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Journal of Experimental Biology (2018) 221, jeb152538. doi:10.1242/jeb.152538

Glossary

Bipedal
Moving on two legs, including walking, running, hopping and skipping gaits.
Cursorial
An animal well adapted for high-speed terrestrial locomotion.
Dimensionless speed
Square root of Froude number, also called 'relative speed'.
Duty factor
Fraction of a stride that the foot is in ground contact: stance duration divided by stride duration.
Dynamic similarity
Constant motions and forces with changes in body size.
Froude number
A key dimensionless quantity based on the ratio of inertial forces to gravitational forces in an inverted pendulum.
Gait
A pattern of leg movement during terrestrial locomotion with repeating, rhythmic motions.
Geometric similarity
Maintenance of the same shape with changes in body size.
Grounded running
Running gaits with a duty factor >0.5 (no aerial phase; see Fig. 2).
Isometric scaling
Synonymous with geometric similarity (constant shape with increasing size).
Running
Gait with kinetic energy and gravitational potential energy fluctuating in phase.
Stance period
Duration of foot contact of single leg within a stride cycle.
Stride cycle
A complete cycle of leg movements, from contact of one foot until the next contact of the same foot.
Stride frequency
Number of strides taken per unit time.
Stride length
Distance traveled during a single stride.
Striding gaits
Bipedal gaits with out-of-phase oscillations of the legs (e.g. walking and running).
Swing period
Time required to move the leg forward in preparation for the next foot contact.
Walking
Gait with kinetic energy and gravitational potential energy fluctuating out of phase.
Walk–run transition speed
Typical speed at which an animal switches from walking to running.

This corresponds to a duty factor (DF; see Glossary) of <0.5, where the DF is the fraction of the stride cycle (see Glossary) that an individual foot is in ground contact (Fig. 2). However, unlike humans, both small and large birds also use 'grounded running' (see Glossary) at intermediate speeds, and show a more gradual transition between walking and running dynamics (Gatesy and Biewener, 1991; Rubenson et al., 2004; Hancock et al., 2007; Daley et al., 2016; Bishop et al., 2018). In grounded running, the footfall patterns resemble a walk, with double support phases (DF>0.5), but energy fluctuations resemble a bouncing run, with in-phase fluctuations of E_k and E_g (Alexander, 2004; Daley et al., 2016; Gatesy and Biewener, 1991; Hancock et al., 2007; Rubenson et al., 2004) (Fig. 1B, middle panel).

Although bipedal gaits are qualitatively similar across avian species, previous work has revealed differences among species in the stride length and stride frequency (see Glossary) characteristics

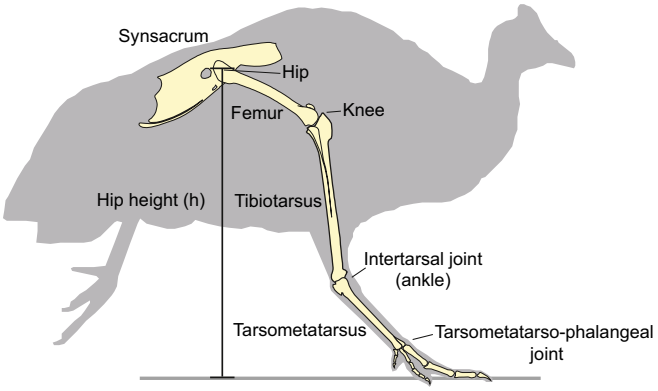

Fig. 1. Schematic illustration of guinea fowl hindlimb bones and joints, representative of a typical avian hindlimb anatomy.

as a function of speed (Abourachid, 2001; Alexander, 2004, 1984; Gatesy and Biewener, 1991; Heglund et al., 1982; Maloiy et al., 1979). It remains uncertain how body size and limb morphology each influence the specific stride length and stride–frequency combinations used by individual bipedal species.

In recent years, data have been published for an increasing diversity of striding avian bipeds, with gait–speed data now covering numerous species with diverse body mass, hindlimb proportions, leg posture and locomotor ecology (Table 1). Considering the sparse sampling of species in previous scaling studies on bipedal gait, ranging from four to eight species (Gatesy and Biewener, 1991; Heglund et al., 1982; Maloiy et al., 1979), a single outlier could substantially skew scaling trends. Consequently, we consider it timely to review the literature evidence for body mass scaling and leg postural factors in avian bipedal gaits. In the sections that follow, we first review the principles of dynamic similarity (see Glossary) as a framework for comparing gait across species, and then examine the existing literature data on striding gaits of birds, providing our own meta-analysis of the scaling trends. Finally, we discuss possible functional interpretations of the observed scaling trends with respect to mechanical demands, energy economy, stability and agility of bipedal locomotion. We hope our review highlights interesting open questions, inspires further scaling studies and underscores the continuing potential for comparative biomechanics to provide insight into the relationships between morphology and locomotor function. Although our focus here is on bipedal gaits of birds, our findings are useful in revealing general scaling rules that could inform the design and control of legged robots and human assistive and rehabilitation technology.

Dynamic similarity as a framework for comparative gait analysis

Classic work by Alexander introduced 'dynamic similarity' as a useful concept for comparing gait across species of varying body size (Alexander, 2004, 1984; Alexander and Jayes, 1983). Two animals move in a dynamically similar manner if all motions and forces appear identical once data are converted to dimensionless quantities based on characteristic physical parameters (Alexander and Jayes, 1983; Alexander, 1984). Here, we follow the conventions of McMahon and Cheng (1990) and McGeer (1990) using body mass (M), leg length (L) and gravitational acceleration ($\boldsymbol{g}$) as the base physical parameters to obtain dimensionless quantities. Dimensional analysis can be used to derive appropriate scaling factors to convert all physical quantities to dimensionless values from these base units (Table 2).

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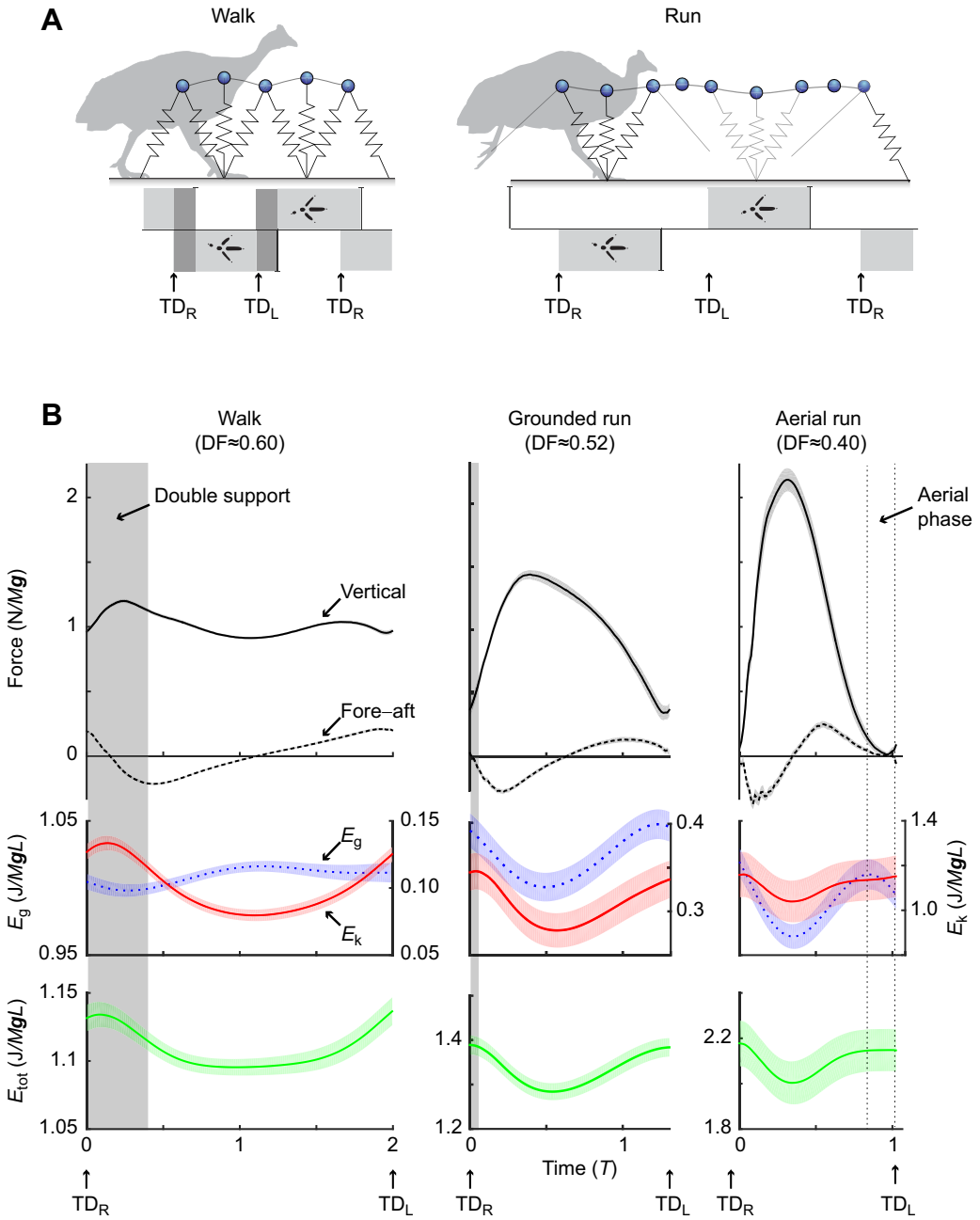

Fig. 2. Walking and running gaits in birds. (A) Schematic illustration of a walking and running guinea fowl, with gaits approximated by a spring-loaded-inverted pendulum (SLIP) model. TD_R is touch-down of the right foot, TD_L is touchdown of the left foot. Walking is characterized by vaulting over a relatively stiff leg, with the body highest at mid-stance. Running is characterized by bouncing on a compliant leg, with the body lowest at mid-stance. (B) Measured ground reaction forces (top) and energy fluctuations (middle, bottom) of guinea fowl moving at slow ($0<V'<0.6$, average 0.44), intermediate ($0.6<V'<0.9$, average 0.77) and fast ($1.2<V'<2.1$, average 1.5) speeds. As speed increases, stance period and duty factor (DF) decrease, double-support periods decrease, and aerial phases occur. Walking and running gaits are distinguished by relative phasing of kinetic energy (E_k, red solid line) and gravitational potential energy (E_g, blue dashed line). Birds use grounded running at intermediate speeds, with run-like energy fluctuations and walk-like presence of double-support (DF>0.5).

Dynamic similarity is expected only for systems that involve the same fundamental movement mechanisms and forces, and guaranteed only for systems that are both dynamically and geometrically similar – that is, both function and shape must be constant with increasing size to exactly meet the requirements of dynamic similarity. Although animals are unlikely to perfectly meet these requirements, the theoretical predictions provide a useful reference for interpretation of empirical scaling trends (Alexander and Jayes, 1983). Any deviations from dynamic similarity predictions should highlight functional differences between species.

Dynamic similarity analysis is often used in combination with model-based analysis of gait (e.g. inverted pendulum, SLIP or other simple models) to allow consideration of the fundamental forces involved (Alexander, 1992; Birn-Jeffery et al., 2014; Bullimore and Donelan, 2008; Farley et al., 1993; McGeer, 1990; McMahon and Cheng, 1990). In his classic work on dynamic similarity, Alexander used reasoning based on the gravitational forces acting on an

Table 1. Literature sources for bird species included in this Review

Common name	Species	Classification	ID	Body mass (kg)	Hip height (m)	Reference
Painted quail	*Excalfactoria chinensis*	Galliformes	pq	0.045	0.052	Gatesy and Biewener, 1991
Common quail	*Coturnix coturnix*	Galliformes	qu	0.150	0.060	Abourachid, 2001
Northern lapwing	*Vanellus vanellus*	Charadriiformes	lw	0.170	0.135	Kilbourne et al., 2016
Bobwhite	*Colinus virginianus*	Galliformes	bw	0.186	0.085	Birn-Jeffery et al., 2014
Magpie	*Pica pica*	Passeriformes	mp	0.240	0.150	Verstappen and Aerts, 2000
Pied avocet	*Recurvirostra avosetta*	Charadriiformes	av	0.334	0.154	Kilbourne et al., 2016
Eurasian oystercatcher	*Haematopus ostralegus*	Charadriiformes	oy	0.457	0.126	Kilbourne et al., 2016
Brown tinamou	*Crypturellus obsoletus*	Tinaniformes	bt	0.500	0.140	Abourachid et al., 2005
Svalbard rockptarmigan	*Lagopus muta hyperborea*	Galliformes	rp	0.501	0.120	Nudds et al., 2011
Elegant crested tinamou	*Eudromia elegans*	Tinaniformes	et	0.744	0.170	Hancock et al., 2007
Red-wing tinamou	*Rhynchotus rusfescens*	Tinaniformes	rt	0.800	0.170	Abourachid et al., 2005
Common pheasant	*Phasianus colchicus*	Galliformes	ph	1.03	0.190	Birn-Jeffery et al., 2014
Black-legged seriema	*Chunga burmeisteri*	Cariamiformes	bs	1.30	0.420	Abourachid et al., 2005
Guinea fowl	*Numida meleagris*	Galliformes	gf	1.38	0.180	Birn-Jeffery et al., 2014
Red-legged seriema	*Cariama cristata*	Cariamiformes	rs	1.50	0.530	Abourachid et al., 2005
Guinea fowl	*Numida meleagris*	Galliformes	gf	1.70	0.190	Birn-Jeffery et al., 2014
Mallard duck	*Anas platyrhynchos*	Anseriformes	ma	1.81	0.165	Usherwood et al., 2008
Wild turkey	*Meleagris gallopavo*	Galliformes	wt	3.03	0.293	Birn-Jeffery et al., 2014
White stork	*Ciconia ciconia*	Ciconiiformes	ws	3.50	0.459	van Coppenolle and Aerts, 2004
Wild turkey	*Meleagris gallopavo*	Galliformes	wt	5.69	0.395	Gatesy and Biewener, 1991
Rhea	*Rhea americana*	Ratites	rh	18.0	0.810	Abourachid, 2001
Rhea	*Rhea americana*	Ratites	rh	20.0	0.820	Gatesy and Biewener, 1991
Emu	*Dromaius novaehollandiae*	Ratites	em	37.0	0.900	Abourachid, 2000
Ostrich	*Struthio camelus*	Ratites	os	90.0	1.190	Gatesy and Biewener, 1991
Ostrich	*Struthio camelus*	Ratites	os	111.0	1.260	Daley et al., 2016
Ostrich	*Struthio camelus*	Ratites	os	116.8	1.260	Birn-Jeffery et al., 2014

inverted pendulum model to propose Froude number [$\mathrm{Fr}=V^2/(\boldsymbol{g}L)$; see Glossary] as a key dimensionless quantity for terrestrial locomotion (Alexander and Jayes, 1983; Alexander, 1984). Froude number is derived from the ratio of inertial forces to gravitational forces in an inverted pendulum, where V is average forward speed, $\boldsymbol{g}$ is gravitational acceleration and L is leg length (Alexander and Jayes, 1983; Alexander, 1984). Froude number can also be derived as the ratio of a moving animal's average kinetic energy (MV^2) to gravitational potential energy ($M\boldsymbol{g}L$) (Biewener, 2003). In turn, the square root of Fr is dimensionless speed [$V'=V/(\boldsymbol{g}L)^{0.5}$; see Glossary] (McGeer, 1990; McMahon and Cheng, 1990) (Table 2). If Froude number accurately captures all essential forces governing gait dynamics, animals are expected to use the same gaits, DF, gait transition speeds and force patterns when compared at equal Fr or V' (Alexander and Jayes, 1983; Alexander, 1984).

Alexander's original dynamic similarity analysis successfully predicted gait transition speeds and DF based on Froude number (Alexander, 1983, 1984). However, the analysis was less successful at predicting relative stride length, which varied considerably among species. Alexander suggested that the variation in stride length at dynamically similar speeds might relate to differences between 'cursorial' (see Glossary) and 'non-cursorial' species (Alexander and Jayes, 1983; Alexander, 1984). For example, quadrupedal primates were found to take strides 1.5 times as long those of 'cursorial' mammals (Alexander and Jayes, 1983). Such deviations from dynamic similarity might suggest differences between species in fundamental movement strategies, mechanical demands or sources of energy cost influencing gait, which could relate to specialization for different locomotor ecologies, habitats and non-locomotor behaviors including feeding and courtship.

Do striding birds maintain dynamically similar gaits with variation in body size?

Literature search and meta-analysis of scaling of avian bipedal gaits

Here, we review literature data on avian walking and running to test the dynamic similarity hypothesis. We included avian species for which the available literature data spanned at least five speeds, including a dimensionless speed [$V'=V/(\boldsymbol{g}L)^{0.5}$] of 0.75. This reference speed is near the walk–run transition speed (see Glossary) across species (Daley et al., 2016; Gatesy and Biewener, 1991; Hancock et al., 2007; Rubenson et al., 2004), and was selected to provide a consistent dimensionless speed for the scaling analysis while including the maximum number of species.

Table 2. Dimensional analysis and scaling predictions for dynamic similarity

Quantity	Dimensions	Scaling factor	DS and GS scaling
Length (m)	L	L	$cM^{1/3}$
Time (s)	T	$(L\,\boldsymbol{g}^{-1})^{1/2}=\boldsymbol{g}^{-1/2}L^{1/2}$	$(cM^{1/3})^{1/2}=cM^{1/6}$
Force (N)	F	$\boldsymbol{g}M^1$	cM^1
Frequency (Hz)	T^{-1}	$(L\,\boldsymbol{g}^{-1})^{-1/2}=\boldsymbol{g}^{1/2}L^{-1/2}$	$(cM^{1/3})^{-1/2}=cM^{-1/6}$
Speed (m s^{-1})	LT^{-1}	$(L\boldsymbol{g})^{1/2}=\boldsymbol{g}^{1/2}L^{1/2}$	$(cM^{1/3})^{1/2}=cM^{1/6}$
Work (N×m=J)	FL	$\boldsymbol{g}M^1L$	$cM^1M^{1/3}=M^{4/3}$
Impulse (Ns)	FT	$\boldsymbol{g}M^1(L^{1/2}\boldsymbol{g}^{-1/2})=\boldsymbol{g}^{1/2}M^1L^{1/2}$	$cM^1(M^{1/3})^{1/2}=M^{1.167}$
Power (J s^{-1}=W)	FLT^{-1}	$\boldsymbol{g}M^1L(\boldsymbol{g}^{1/2}L^{-1/2})=\boldsymbol{g}^{3/2}M^1L^{1/2}$	$cM^1(M^{1/3})^{1/2}=M^{1.167}$
Leg stiffness (N m^{-1})	FL^{-1}	$\boldsymbol{g}M^1L^{-1}$	$cM^1M^{-1/3}=M^{2/3}$

L, length; T, time; F, force. Scaling factors are derived using the base units of mass (M), leg length (L) and gravitational acceleration ($\boldsymbol{g}$). The corresponding body-mass scaling prediction ($y=cM^b$) assumes both dynamic similarity (DS) and geometric similarity (GS).

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The most useful data sets were those reporting all gait timing parameters as a function of speed, plus body mass (M), hindlimb bone lengths (femur, tibiotarsus and tarsometatarsus) and standing hip height (H) for the study species (Fig. 1). A stride period (t_{stride}) consists of one full locomotor cycle for an individual limb, including a swing period (t_{swing}; see Glossary) and stance period (t_{stance}; see Glossary), so $t_{stride}=t_{stance}+t_{swing}$. From these, we calculated DF ($=t_{stance}/t_{stride}$), stride length ($L_{stride}=V\times t_{stride}$) and stride frequency ($f_{stride}=1/t_{stride}$). For studies reporting only stride length and stride frequency, the variables t_{stance}, t_{swing} and DF were not available for analysis. For studies without reported hip height or segment lengths, we used published species-averaged values (Gatesy and Middleton, 1997; Zeffer et al., 2003).

For the scaling analysis, we converted all gait data to dimensionless quantities according to the dimensional scaling factors shown in Table 2. After fitting curves to the gait–speed data for each species (Fig. 3), we took the gait data at a reference dimensionless speed of 0.75 for each species in the scaling analysis. This allowed the scaling trends to be considered at a consistent dimensionless speed across species. Nonetheless, the overall size-related trends are consistent across the speed range, with larger birds using relatively shorter stride lengths and higher stride frequencies compared with small birds, after normalizing all data to dimensionless quantities (Fig. 3). To confirm that choice of reference speed did not influence the scaling trends, we calculated scaling factors at reference speeds of 0.5 and 1.0, and found that the scaling factors remained within 0.005. The scaling trends are considered in more detail in the next section.

We considered three possible measures of nominal leg length for scaling comparisons across species: (1) standing hip height (H), (2) the sum of femur, tibiotarsus and tarsometatarsus bone segment lengths (ΣL_{seg}) and (3) a reference length calculated as $L_{iso}=0.2M^{0.33}$, which corresponds to isometric (geometrically similar) leg length scaling with a posture typical of a 1 kg bird (Birn-Jeffery et al., 2014). Hip height is often used as a convenient measure of the functional limb length; however, it is challenging to measure accurately in birds, because both the hip and the knee are typically hidden under body plumage of birds, with only the ankle and foot joints externally visible (Fig. 1). Additionally, the hip height of birds is known to vary considerably with speed (Gatesy and Biewener, 1991; van Coppenolle and Aerts, 2004). By contrast, using the sum of bone segment lengths (ΣL_{seg}) as a leg length measure provides a more consistently measurable quantity, using museum skeletal specimens. However, ΣL_{seg} confounds the effects of body size and leg posture, because small animals use relatively crouched postures with short effective leg length relative to bone segment lengths (Birn-Jeffery et al., 2014; Gatesy and Biewener, 1991). Nonetheless, the sum of bone segment lengths may represent a reasonable functional limit of leg length, representing a fully extended, straight leg. Based on this, we suggest that if only a single leg length measure is used, ΣL_{seg} may be the most parsimonious length scaling value.

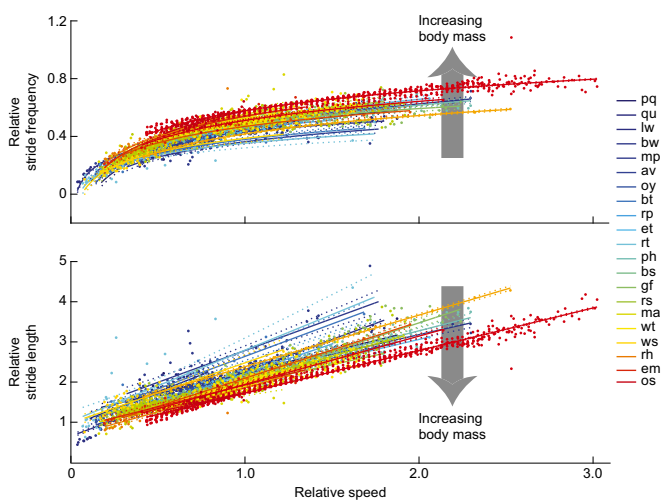

Fig. 3. Dimensionless stride length and stride frequency as a function of dimensionless speed for 21 bird species. Published avian gait data for 21 species, color-coded from smallest (dark blue, painted quail) to largest (red, ostrich). See Table 1 for species abbreviations. Large animals tend to use relatively higher stride frequencies and shorter stride lengths compared with small animals at the same dimensionless speed.

Here, we want to consider the independent effects of body mass scaling and leg morphological variation on bipedal gait. We used the isometric scaling (see Glossary) reference length (L_{iso}) to convert gait data to dimensionless quantities for the statistical analysis to avoid confounding body size and limb morphology. For measures of leg morphology, we calculated leg length index ($L_{idx}=\Sigma L_{seg}/L_{iso}$) as a measure of leg length relative to body size, and posture index ($P_{idx}=H/\Sigma L_{seg}$) as a measure of crouched versus upright leg posture. We used linear mixed effects (LME) models in the MATLAB statistical toolbox (v2015b, MathWorks, Natick, MA, USA) with continuous factors body mass (M), leg length index, posture index and a random effect based on phylogenetic classification at the order or infraclass level (Table 1) (Prum et al., 2015). All data were $\log_{10}$ transformed for LME analysis, resulting in a linear prediction equation in the form:

$$\log(y) = \log(a) + b(\log(M)) + c(\log(L_{idx})) + d(\log(P_{idx})). \quad (1)$$

After taking the base-10 exponential of both sides, this becomes:

$$y = aM^{b}(L_{idx})^{c}(P_{idx})^{d}, \quad (2)$$

where the LME coefficient estimates correspond to scaling exponents applied to body mass (M), leg length index (L_{idx}) and posture index (P_{idx}). For scaling of dimensionless gait measures, dynamic similarity theory predicts a body mass scaling exponent $b=0$. We consider the null hypothesis that animals move with dynamic similarity against the alternative hypotheses that locomotor dynamics vary with (1) body mass ($b\neq0$), (2) leg length index ($c\neq0$), posture index ($d\neq0$) and (4) phylogenetic differences. Phylogenetic non-independence was included as a random effect because the sparse sampling of a diverse and ancient clade leads to high uncertainty in evolutionary divergence times.

Empirical scaling trends

Scaling of leg morphology with body mass

It is well established that larger birds have relatively longer hindlimb segment lengths and a relatively straighter leg posture compared with those of small birds (Fig. 4) (Gatesy and Biewener, 1991; Gatesy and Middleton, 1997; Maloiy et al., 1979; Stoessel et al., 2013; Zeffer et al., 2003). Consistent with previous studies, we found positive allometric scaling of total anatomical leg length (ΣL_{seg}) and posture index ($H/\Sigma L_{seg}$) with body mass (Fig. 4, Table 3). These two effects of longer and straighter legs each contribute to the relatively higher hip height of large animals; however, there is high variance among species in limb posture index (Fig. 4). Although the scaling of leg length and posture is consistent across studies, the functional relationships between leg posture and gait have remained unclear (Biewener, 1989; Birn-Jeffery et al.,

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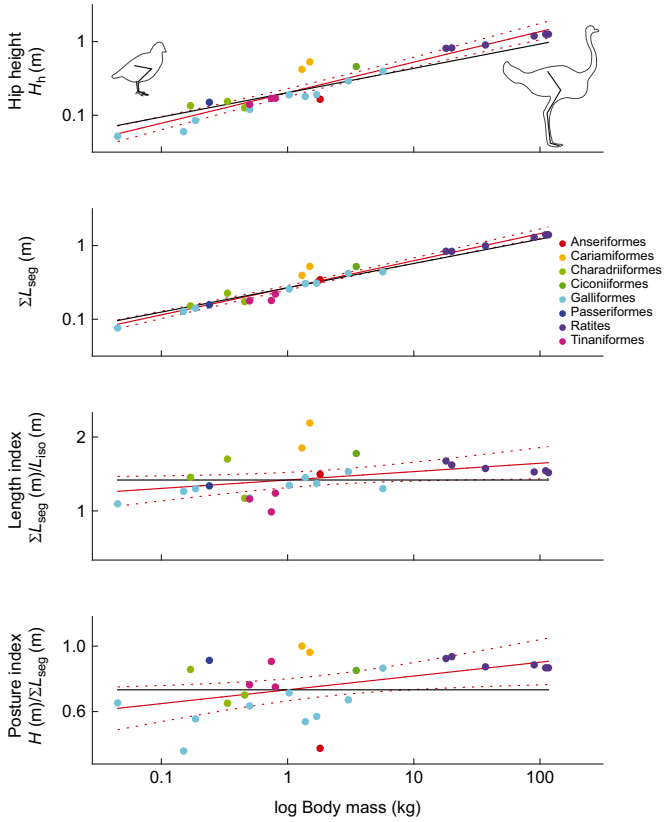


Fig. 4. Scaling of hindlimb length and posture among striding birds. Large animals have relatively longer legs owing to positive allometry of hindlimb bone lengths and a straighter, more vertically oriented leg posture. Body mass scaling trends are shown for hip height (H), anatomical leg length (ΣL_{seg}), leg length index ($\Sigma L_{seg}/L_{iso}$) and leg posture index ($H/\Sigma L_{seg}$). Anatomical leg length is based on the sum of femur, tibiotarsus and tarsometatarsus bone lengths (Fig. 1). Black lines indicate the prediction for geometrically similarity (no change in shape with increased size). Empirical scaling trends are shown in red (fit and 95% confidence interval, Table 3). Marker colors correspond to species classification at order or infraclass level (see Table 1).

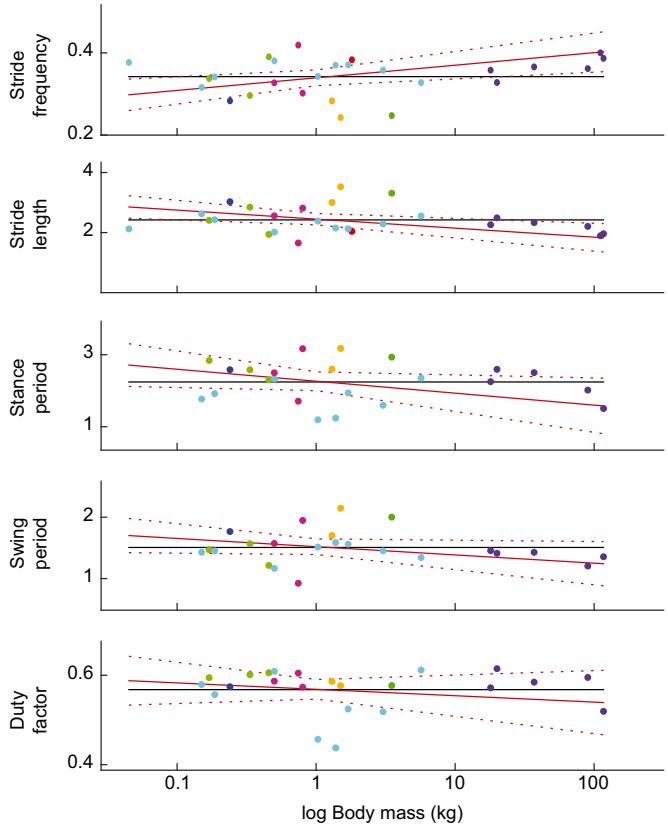


Fig. 5. Scaling of gait measures as a function of body size among striding birds. Large birds use relatively shorter stride lengths and higher stride frequencies than smaller birds when moving at a dynamically similar speed (0.75). Large birds achieve higher frequencies with shorter stance and swing periods (see Table 4). Duty factor does not scale consistently with body size. Birds of intermediate body mass show considerable scatter in gait, and the outliers tend to also be outliers in leg length index (see Fig. 6). Black lines indicate the slope expected for geometrically and dynamically similar animals (no change in shape or dynamics with increased size; see Table 2). Empirical scaling trends are shown in red (fit and 95% confidence interval). For marker color code, see Fig. 4.

2014; Daley and Usherwood, 2010; Gatesy and Biewener, 1991). Below, we discuss how our current analysis of the literature data suggests independent effects of body mass, leg length and leg posture on bipedal gait.

Scaling of gait relative to dynamic similarity predictions

Striding birds do not move in a dynamically similar manner across the size range from painted quail to ostrich. The empirical scaling trends from our analysis across 21 species and a >2500-fold range in body mass reveals that large animals consistently use relatively higher stride frequencies and shorter stride lengths compared with small animals at equivalent dimensionless running speeds (Fig. 5, Table 4). Larger animals achieve higher stride frequencies using relatively shorter stance and swing periods (Fig. 5, Table 4). Stance period shows a stronger scaling effect than swing period, but both contribute to the shift in stride frequency with body size.

The observed positive allometry of stride frequency, with exponent b=0.05 in dimensionless units (Table 4), corresponds to a scaling exponent of −0.12 in SI units (Table 5). This is higher than the prediction of −0.17 for dynamic and geometric similarity (see Glossary), and −0.21 for dynamic similarity based on empirical hip height scaling (Table 5). Stride length shows a negative allometry of −0.05 in dimensionless units, which corresponds to a scaling exponent of 0.28 in SI units. This is slightly lower than the predicted exponent of 0.33 of dynamic and geometric similarity, and considerably less than the predicted exponent of 0.41 based on empirical scaling of hip height (Table 5). Thus, larger animals take shorter strides for their body mass, and especially short considering that they have longer legs for their body mass.

Gatesy and Biewener (1991) reported a scaling exponent of 0.38 for stride length, suggesting positive allometry with body mass. However, Gatesy and Biewener's (1991) analysis was based on the fastest measured treadmill running speeds, and the larger animals were moving at faster dimensionless speeds. The authors also

Table 3. Body-mass scaling exponents calculated for leg length and leg posture variables.

Quantity	b	Lower	Upper	R^2
Hip height (m)	0.41	0.36	0.47	0.90
ΣL_{seg}	0.37	0.33	0.40	0.96
$L_{idx}=\Sigma L_{seg}/L_{iso}$	0.10	−0.01	0.22	0.12
$P_{idx}=H/\Sigma L_{seg}$	0.08	0.01	0.14	0.21

ΣL_{seg}, sum of bone segment lengths; L_{idx}, leg length index; L_{iso}, isometric scaling reference length; P_{idx}, posture index; H, hip height. Data are shown in Fig. 4.

Table 4. Statistical models for effect of body mass, posture index and length index on gait

Variable	Factor	*F*	*P*	Estimate	Lower	Upper	R^2	d.f.
Stride frequency	Constant	309.3	<0.0001	0.37	0.32	0.41	0.62	1,22
	Body mass	19.9	0.0002	0.05	0.02	0.07		
	Posture index	3.4	0.0799	−0.18	−0.39	0.02		
	Length index	28.0	<0.0001	−0.63	−0.87	−0.38		
Stride length	Constant	174.6	<0.0001	2.06	1.84	2.31	0.64	1,22
	Body mass	20.9	0.0001	−0.05	−0.07	−0.02		
	Posture index	3.7	0.0673	0.18	−0.01	0.38		
	Length index	32.1	<0.0001	0.64	0.41	0.88		
Stance period	Constant	29.3	<0.0001	2.25	1.64	3.08	0.45	1,19
	Body mass	7.9	0.0111	−0.08	−0.14	−0.02		
	Posture index	9.4	0.0063	0.84	0.27	1.42		
	Length index	3.2	0.0880	0.52	−0.09	1.13		
Swing period	Constant	2.5	0.1311	1.15	0.96	1.37	0.52	1,19
	Body mass	6.2	0.0220	−0.04	−0.07	−0.01		
	Posture index	0.0	0.9267	0.01	−0.32	0.34		
	Length index	21.3	0.0002	0.77	0.42	1.12		
Duty factor	Constant	72.7	<0.0001	0.63	0.56	0.70	0.23	1,19
	Body mass	1.5	0.2332	−0.01	−0.03	0.01		
	Posture index	6.7	0.0180	0.26	0.05	0.47		
	Length index	0.7	0.4032	−0.09	−0.31	0.13		

All species were compared at a relative speed of 0.75. For summary of scaling exponents in SI units, see Table 5. *F*-statistics and *P*-values are shown for the LME statistical model, with 'estimate' corresponding to dimensionless scaling exponents, with lower and upper 95% confidence intervals.

reported that large birds used relatively shorter strides and higher frequencies than small birds when compared at similar relative speeds (Gatesy and Biewener, 1991), consistent with our current analysis. Previous analyses of mammalian gait have also reported a scaling exponent of 0.38 for stride length, based on comparisons at gait transition speeds and maximum speed, suggested to be 'physiologically equivalent' speeds (Heglund et al., 1974). However, neither gait transition speed nor maximum speed results in comparisons at equal Froude number (or dimensionless speed) across species. Larger animals were consistently moving at faster relative speeds in previous scaling comparisons. In laboratory settings, it can be very challenging to measure the true maximum speed an animal might achieve in its natural environment. Considering the challenges and uncertainties of identifying maximum speeds or physiologically equivalent speeds, comparison at equal dimensionless speeds seems a more parsimonious approach. According to our current analysis, at dynamically similar speeds, small birds move with relatively longer strides and lower frequencies for their body size than large birds.

Table 5. Summary of predicted and observed scaling exponents in SI units

	Prediction		Observed	Difference	
Gait measure	DS_M	DS_H	*b*	(*b*–DS_M)	(*b*–DS_H)
Stride frequency	−0.17	−0.21	−0.12	0.05	0.09
Stride length	0.33	0.41	0.28	−0.05	−0.13
Stance period	0.17	0.21	0.09	−0.08	−0.12
Swing period	0.17	0.21	0.13	−0.04	−0.08
Predictions based on dimensional analysis (see Table 2)					
Mechanical work	1.33	1.41	1.28	−0.05	−0.13
Force impulse	1.17	1.21	1.09	−0.08	−0.12
Mechanical power	1.17	1.20	1.19	0.02	−0.01
Leg stiffness	0.67	0.59	0.72	0.05	0.13

Table shows observed scaling exponents (*b*) in SI units, compared with dynamic similarity predictions, assuming geometric scaling of leg length with body mass (DS_M), and empirical scaling of hip height with body mass (DS_H).

Does duty factor scale with body size?

Duty factor is considered a functionally important feature of gait because it can accurately predict peak and average vertical ground reaction forces (Alexander, 1984, 1992). Our current analysis suggests that DF does not show consistent body-mass scaling among birds, but is highly variable across species (Fig. 5, Table 4). Gatesy and Biewener (1991) found slightly higher DF for small birds, but primarily based on the bobwhite quail showing higher DF than the other species studied. In a study of five flightless ratite species, Abourachid and Renous (2000) found that a single small species, the brown kiwi, stood out from the other birds in using high DF. Previous studies have suggested a tendency for small birds with crouched postures to move with a relatively higher DF, maintaining DF >0.5 over more of their speed range (Abourachid, 2001; Gatesy and Biewener, 1991; Hancock et al., 2007). Although our current analysis suggests a potential posture effect on DF, the trend suggests that crouched animals use lower DF (opposite to the trend previously suggested; Table 4). This may be an artifact of the overrepresentation of ground-feeding galliforms within the dataset. Many galliforms have relatively more crouched postures than other birds, and yet use shorter stance periods and lower DF compared with those of other similarly sized species (Figs 4 and 5).

The observation that birds generally maintain similar DF across the >2500-fold mass range suggests that peak vertical ground reaction forces scale with dynamic similarity. This is further supported by recent findings that ground birds from quail to ostrich maintain similar peak vertical forces in both steady and non-steady locomotion (Birn-Jeffery et al., 2014). The maintenance of consistent DF, and therefore vertical forces, across the range of body size might reflect consistent safety factors of musculoskeletal tissues among terrestrial vertebrates, and similar peak bone and muscle stresses (Biewener, 1983, 1989, 2005). Nonetheless, there is high interspecific variance in DF, especially at intermediate body size (Fig. 5), suggesting that DF and peak vertical forces during

bipedal gaits probably do vary considerably with morphological, behavioral and ecological factors not considered here.

Functional relationships between leg morphology and gait

Despite some apparent clustering of leg morphology and gait features within avian clades, the addition of phylogenetic classification as a random effect in the statistical analysis did not improve the fit of the model (likelihood ratio tests, P=0.7–1.0). This could suggest that other factors such as habitat specialization play a larger role in the observed clustering of morphology and gait. We find high variance at intermediate sizes, but larger body sizes are represented only by ratites, and intermediate sizes are overrepresented by galliforms. In future studies, more comprehensive and systematic sampling of gait dynamics across the avian clade could provide further insight into the interactions between evolutionary history and habitat specialization on bipedal locomotion.

Despite the limitations of sparse sampling, the available data do suggest that morphological specialization for different locomotor ecology is associated with functional shifts in gait. Outliers in gait are also outliers in leg length relative to body mass (L_{idx}), indicating that gait varies with leg morphology (Fig. 5). Animals with long legs for their mass use relatively longer strides, lower stride frequencies and longer swing periods (Table 4, Fig. 6). These findings are consistent with the increased limb inertia of relatively long legs. For example, the pied avocet (Charadriiformes), black and red-legged seriema (Cariamiformes) and white stork (Ciconiiformes) all have long, straight legs for their mass, and run with relatively low stride frequencies, long stride lengths and long swing periods (Fig. 5) (Abourachid et al., 2005; Kilbourne et al., 2016; van Coppenolle and Aerts, 2004). Conversely, the elegant crested tinamou (Tinaniformes), painted quail (Galliformes) and Eurasian oystercatcher (Charadriiformes) have short legs for their mass, and run with relatively high stride frequencies, short strides and short swing period (Fig. 6) (Gatesy and Biewener, 1991; Hancock et al., 2007; Kilbourne et al., 2016). These variations in gait with leg length index are consistent with trade-offs in cost between stance and swing phases, with longer legs resulting in higher limb inertia and tendency to prolong swing period to mitigate swing costs.

Although gait does vary with leg morphology, the effect of leg length on gait does not directly correspond to predictions of dynamic similarity. The red-legged seriema has legs more than twice as long for its mass compared with those of the elegant crested tinamou (Fig. 6), but takes strides only $0.4L_{iso}$ longer. Long-legged species take long strides relative to their body mass, but short strides relative to their anatomical leg length. One possible explanation for this is that long-legged birds may be underpowered for their leg length because muscle mass scales geometrically with body mass (Maloiy et al., 1979). Although they have long legs, they may not have sufficient extra muscle mass required to power long strides. Whatever the explanation for the specific gait patterns, the outliers highlight that gait dynamics are strongly influenced by variation in limb morphology, which appears to be associated with adaptation for different locomotor ecology.

It is also worth noting that the effects of leg length and leg posture on gait oppose the general scaling trends with body mass (Table 4). For example, relative stride frequency increases with body mass, but decreases with leg length index. These findings suggest that the

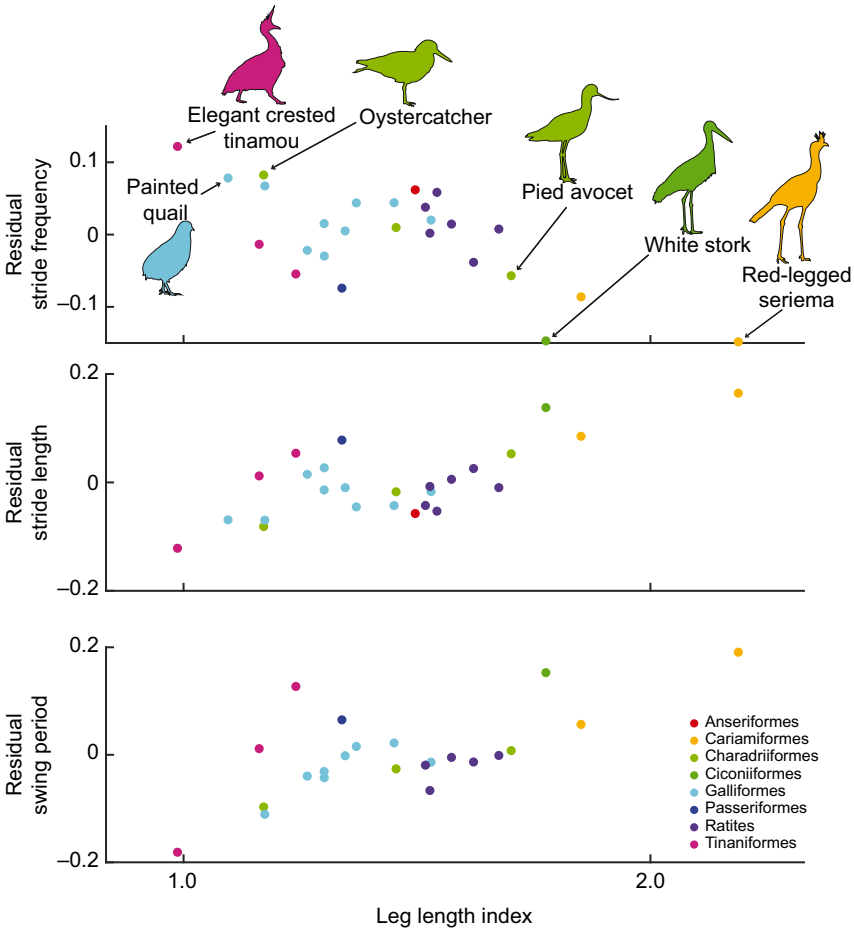


Fig. 6. Leg length relative to body mass significantly influences gait dynamics. Scaling residuals are plotted against leg length index. Birds with long legs for their mass run with lower stride frequency, longer stride length and longer swing periods. Most ground birds (galliforms and ratites) have relatively small deviations from the general body mass scaling trends (Fig. 5). Some birds with especially low and high leg length index are highlighted.

deviations from dynamic similarity with body mass are not directly related to allometric scaling of leg length. The increase in leg length with body size tends to ameliorate the effects of body mass scaling, allowing animals of different size to more closely approximate dynamic similarity. It is also interesting to note that there are no scaling outliers among species larger than 10 kg, possibly suggesting that larger animals might be more heavily constrained by the functional demands to support body weight with increasing size.

Functional interpretation of observed scaling trends

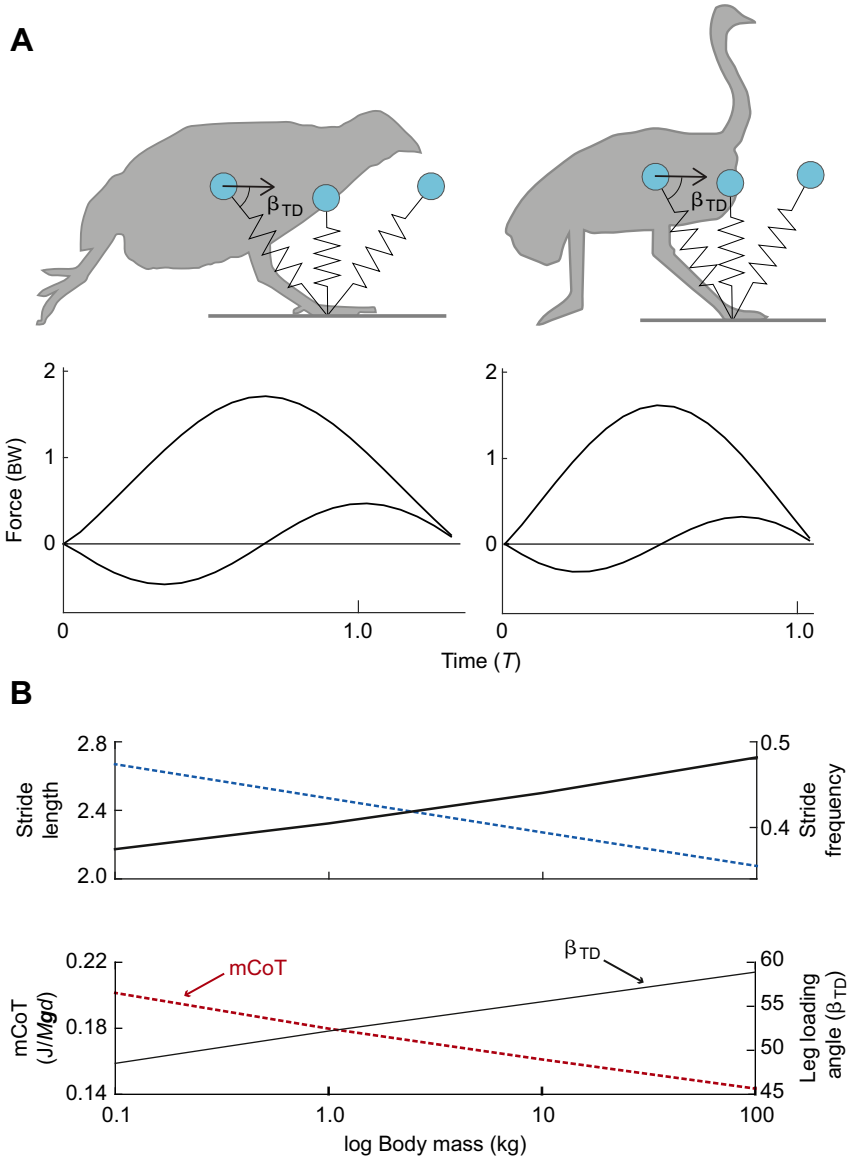
Based on our scaling analysis, we suggest that the striding gaits of birds are influenced by functional trade-offs in the mechanical demands for force, work and power relative to muscle capacity versus activation costs related to leg cycling frequency. Understanding these trade-offs requires consideration of the mechanical demands relative to available muscle capacity and the scaling of metabolic energy costs with body size. It is well established that mass-specific metabolic cost of transport (joules required per kilogram body mass to travel a given distance) decreases with increasing body mass, scaling as $M^{-0.32}$ (e.g. Fedak et al., 1974; Taylor et al., 1982). Yet, the energetic cost to generate ground reaction force in J N^{-1} is relatively constant with increasing body mass (Kram and Taylor, 1990; Roberts et al., 1998). Large animals operate their muscles at absolutely lower frequencies and travel an absolutely greater distance per stride, therefore requiring fewer muscle activation–contraction cycles to travel a given distance. Thus, the main reason large animals have lower energetic cost of transport is that they use absolutely lower stride frequencies, and therefore lower muscle activation frequencies (Kram and Taylor, 1990; Taylor et al., 1982; Roberts et al., 1998; Pontzer, 2016).

Although large animals have lower energetic cost of transport, they face relatively higher mechanical demands for muscle force, work and power relative to their available muscle capacity. Large birds face challenges in supporting their body mass against gravity, because vertical ground reaction force demands scale as M^1 (Table 2), but force capacity (proportional to muscle fiber cross-sectional area) scales with only slight positive allometry as $M^{0.73–0.78}$ (Bennett, 1996; Maloiy et al., 1979), suggesting that muscle stress (force/area) should increase as $M^{0.22–0.27}$. However, the scaling of force demands can be partially overcome through shifts in limb effective mechanical advantage with increasing body size, so that muscle stress actually scales nearly independently of size, as $M^{0.06}$ (Biewener, 1989). Nonetheless, shifts in limb mechanical advantage cannot alter work and power demands. Dynamic similarity predicts that mechanical work demand will increase with body mass as $M^{4/3}$ and power demand as $M^{7/6}$ (Table 2). Maximum mass-specific work and power output of muscle is relatively constant across vertebrates (Askew et al., 2001; Nelson et al., 2004; Zajac, 1989). Consequently, total capacity to produce work and power relate to muscle mass, which scales geometrically with body mass (M^1) (Maloiy et al., 1979). Dividing demands for work and power by the available muscle capacity, mass-specific work demand is predicted to scale as $M^{1/3}$, and mass-specific power demand as $M^{1/6}$. Based on this, a 100 kg bird would have 10-fold higher mass-specific work demand and threefold higher mass-specific power demand than a 0.1 kg bird, when moving at a dynamically similar speed. These considerations suggest that large birds must activate a larger fraction of their available muscle capacity to meet the demands for force, work and power during stance, operating nearer to muscle actuator limits compared with small animals.

The relatively shorter stride lengths of large birds may help mitigate the risks and costs of operating near muscle actuator limits by maintaining more vertical leg loading, which minimizes fore–aft forces and muscle work (Fig. 7). A SLIP model of gait dynamics predicts that gaits with relatively shorter strides demand lower fore–aft forces, total force impulse and stance phase work (Fig. 7). However, shorter strides also necessitate correspondingly higher stride frequencies, which are likely to increase swing-phase muscle activation costs. Based on this, we suggest that the gaits of large birds are consistent with pressure to mitigate scaling of force, work and power demands relative to available muscle capacity, but at a cost of requiring relatively higher leg cycling frequencies (Fig. 7). Many large cursorial animals have especially well-developed elasticity in the distal limb, which can help facilitate rapid leg swing through an elastic recoil 'catapult' mechanism (McGuigan and Wilson, 2003; Schaller et al., 2009; Smith et al., 2006; Wilson et al., 2003). However, it remains unknown whether these mechanisms reduce the muscle activation costs associated with the swing phase. It is also worth noting that limb moment of inertia increases as $M^{2.1}$ among birds (Kilbourne, 2013), suggesting that large birds should incur higher muscle torque demands for leg swing, and therefore higher muscle activation costs in swing. Nonetheless, larger birds opt for gaits with relatively shorter strides and higher leg cycling frequency than the gaits of small birds, suggesting that, on balance, large animals face greater priority to mitigate stance-phase mechanical demands, despite the likely associated increase in swing-related costs.

In contrast, the gaits of small birds likely reflect higher priority to mitigate frequency-related costs in both the stance and swing phases of locomotion because they must operate their muscles at absolutely higher contraction frequencies. A 0.1 kg bird must cycle its legs threefold faster than a 100 kg bird at a dynamically similar speed. High-frequency contractions incur relatively higher ATP activation costs (Rome and Lindstedt, 1997, 1998). Adaptation for exceptionally fast contraction is possible; for example, hummingbird flight muscles operate at ∼40 Hz (Rome and Lindstedt, 1998). However, protein isoforms that allow especially fast contractions require high operating temperatures, and are associated with high aerobic metabolic rates (Rome and Lindstedt, 1997, 1998). Consequently, although frequency of muscle contraction is unlikely to be a hard constraint on gait dynamics, it is an important factor in the metabolic energy cost of gait (Kram and Taylor, 1990; Roberts et al., 1998). The relatively longer strides of small birds likely incur relatively higher stance-phase mechanical work demands (Fig. 7), but allow longer stance and swing periods, implying relatively lower muscle contraction frequencies for both stance and swing phases (Fig. 5, Table 4). These considerations suggest greater priority for small birds to minimize the absolute frequency of muscle contractions.

Stability and agility are also likely to be important factors in scaling of avian bipedal gait relative to body mass. Small birds are likely to move through relatively 'rougher' terrain environments, frequently encountering bumps, holes and obstacles that are large relative to their leg length. Consequently, the gaits of small birds might reflect a necessity to maintain robust stability and agility in relatively rough terrain, even at the cost of incurring relatively higher mechanical work demands. Small birds use gaits with longer stance period and leg angular sweep during stance, which increases the intrinsic mechanical stability and robustness to variation in terrain height (Daley and Usherwood, 2010) (Fig. 7). Small animals also have relatively faster neural response time compared with that



Functional trade-offs	Small	Large
Fore–aft forces	High	Low
Force impulse	High	Low
Swing frequency	Low	High
Stance work	High	Low
Terrain robustness	High	Low
Neural responsiveness	High	Low

Fig. 7. Functional trade-offs inferred from model-based analysis of observed shifts in stride length and stride frequency between small and large birds. (A) A SLIP model is used to predict the vertical and fore–aft ground reaction forces required for gaits typical of a 0.1 kg bird (left) and a 100 kg bird (right). (B) Small birds use relatively longer strides (blue dashed line) and lower stride frequency (black line) compared with large birds. This requires a shift in leg loading angle during stance (β_{TD}, black line in bottom panel). Larger animals use shorter strides that keep the leg loading angle (β_{TD}) and ground reaction forces closer to vertical, reducing fore–aft forces and mechanical cost of transport (mCoT, red dashed line) during stance. However, shorter strides at the same speed demands higher swing frequency. The longer strides of smaller birds also have potential stability and agility benefits, for increased robustness in uneven terrain and higher neural responsiveness, because stance period is longer relative to fall times and neural feedback delay times.

of large animals, owing to absolutely shorter nerve transmission distances (More et al., 2010). Sensorimotor loop delays increase in proportion to nerve transmission distance, and therefore leg length, which scales as $M^{0.41}$; yet, stance period scales as $M^{0.09}$ (Table 5). These findings suggest that smaller animals have faster sensorimotor response times in both absolute and relative terms, with delay as a fraction of stance predicted to scale with $M^{0.32}$. This is qualitatively similar to the scaling trend found by More and colleagues (2010) for mammals, but we find that birds show a more pronounced increase in delay relative to stance with increasing body mass, owing to the positive allometry of leg length and negative allometry of stance period (Table 5). We suggest that the gaits of smaller birds, with relatively longer stance periods, might reflect functional demands to make frequent within-stance adjustments to achieve stability and maneuverability in relatively rough terrain. Thus, scaling of stance period could reflect differences in the scaling of terrains typically encountered by small versus large birds, and therefore differences in the relative fraction of locomotion spent in relatively steady versus non-steady movement. However, a direct link between natural terrain roughness and preferred gait dynamics among striding birds has not yet been conclusively shown.

Future directions

Current scaling analyses do not account for the vast diversity of avian ecology, life history and locomotor behaviors. In this Review, we have focused on the well-studied striding bipedal gaits of walking and running, but birds use their legs for a diverse range of behaviors, including hopping and skipping, jumping for flight take-off, arboreal locomotion, swimming, water running and scratch preening (Abourachid and Höfling, 2012; Biewener and Corning, 2001; Heers and Dial, 2015; Portugal et al., 2016; Provini et al., 2012a,b, 2014). Although most birds use striding gaits during some part of their life history, other behaviors are undoubtedly ecologically important. Many arboreal passerine species must move through complex three-dimensional environments with highly varied surface compliance and stability (Abourachid and Höfling, 2012). For these animals, perching balance in the face of perturbations is likely to be especially important. The leg and foot morphology of ducks likely reflects adaptations that enable them to effectively paddle through water and move on land (Biewener and Corning, 2001). Long-legged wading birds spend a large fraction of their time balancing on one leg in water, and the demands of standing balance have likely shaped morphological adaptations of the leg (Chang and Ting, 2017). Yet, we still have relatively little insight into how different locomotor behaviors and musculoskeletal demands have shaped the evolution of locomotor morphology among diverse avian species.

Foot morphology and function is one particularly under-explored aspect of avian gait dynamics. Bird foot morphology is diverse, and control of foot–substrate interactions is likely to be crucial in effective movement and balance (Abourachid et al., 2017; Backus et al., 2015). Yet, the relationship between foot form and function remains poorly understood. Foot shapes range from the relatively basal and common anisodactyl foot (with digit 1 backward, digits 2–4 forward) to the next most frequent arrangements of heterodactyl and zygodactyl feet, which both have two toes facing forwards and two toes backwards (Bock and Miller, 1959), and the more derived pamprodactyl foot (Collins, 1983), with two inner toes forward and two outer toes that can rotate forward and backwards (Abourachid et al., 2017; Botelho et al., 2014; Livesey and Zusi, 2006). Foot morphology appears to be a relatively plastic developmental structure across the avian lineage, which may have facilitated the observed diversity in foot anatomy (Botelho et al., 2015a,b). Although it is clear that birds exhibit a wide diversity of foot form and function, it remains unclear how the specific foot morphologies influence foot–substrate interactions to shape gait dynamics. The foot plays a crucial role in control of gait, because small shifts in foot contact dynamics have the potential to rapidly change the direction and magnitude of ground forces, and may determine the difference between a slip and fall or a successful foot contact. It will be very interesting for future work to investigate the diversity of foot morphology and biomechanics among birds adapted to different substrate conditions.

The field of comparative biomechanics is increasingly multidisciplinary, gaining insight from many fields and approaches including theoretical mechanics, musculoskeletal modeling, optimization theory, robotics, experimental physiology, functional anatomy and movement ecology, among others. A single review cannot hope to integrate all of the perspectives that have contributed to current knowledge. Yet, we hope we have highlighted the continuing utility of dynamic similarity and scaling principles for interpreting shifts in functional demands among animals of different size and morphology. Advances in technology have enabled measurement of locomotor dynamics over an increasingly broad range of conditions, including free-ranging and wild animals during foraging, predator–prey interactions and migration (Dewhirst et al., 2017; Hubel et al., 2016). Studies of non-steady locomotor dynamics can help reveal how animals balance multiple functional demands, including energetic costs, stability, injury avoidance, speed and maneuverability (e.g. Tan and Wilson, 2011; Birn-Jeffery et al., 2014). The potential for functional demands to limit performance and lead to direct trade-offs is most acute during maneuvering at high speeds, such as predator–prey interactions (Wilson et al., 2018). Consequently, it will become increasingly important to consider locomotor dynamics during ecologically relevant ranges of behavior. Recent work has also highlighted the need to fully consider three-dimensional motions during maneuvering behaviors (Kambic et al., 2014), which have often been neglected in studies of bird gait. As we continue to explore an increasingly rich range of animal locomotor behaviors, we suggest that the findings will be most informative when interpreted based on fundamental physical principles and mechanical demands that underlie gait.

Acknowledgements

We thank David Lee and Christian Hubicki for useful discussions, two anonymous reviewers for constructive feedback, Jade Hall for digitizing literature data and Jim Usherwood for providing the raw data on mallard ducks from Usherwood et al. (2008).

Competing interests

The authors declare no competing or financial interests.

Author contributions

M.A.D. and A.B.-J. conceived of the paper topic and reviewed the literature. M.A.D. performed the data analysis and developed scaling equations. A.B.-J. provided raw data on several species of birds from Birn-Jeffery et al. (2014). M.A.D. and A.B.-J. wrote and edited the paper.

Funding

This work was supported by a grant ('Mechanics and energetics of stable bipedal locomotion in uneven terrain: Does a trade-off exist between economy and stability?', BB/H005838/1) to M.A.D. from the Biotechnology and Biological Sciences Research Council (BBSRC).

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