2005

Negotiating a three-dimensional environment: limb kinematics of terrestrial birds during sloped ascents

Heather D. Davis

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Negotiating a three-dimensional environment:
Limb kinematics of terrestrial birds during sloped ascents.

By
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Presented in partial fulfillment of the requirements for the degree of
Master of Science
University of Montana
May, 2005

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Flight capable and flightless ground birds routinely negotiate terrestrial environments that are not simply flat, but rather consist of three-dimensional sloped terrain (e.g. gullies, cliffs) and obstacles (e.g. rocks and trees). Recently it was discovered that galliform birds exhibit a novel locomotor behavior that involves simultaneous use of legs and wings on inclines in order to increase hindlimb traction and performance (Dial 2003, Bundle and Dial 2003). I surveyed the limb kinematics of juveniles and adults from basal avian groups (ratites and tinamous) as they ascended steep substrates and compared them to the chukar, a model species. Emus, Ostriches, Rheas, Chilean Tinamous, Elegant Crested Tinamous, and Chukars were trained to ascend as steep an incline as possible (from 0° to 90°) and their limb kinematics (hindlimb joint angles, wingstroke and excursion angles, and forelimb angle of attack) were studied using high-speed video (125-250 fps). Beginning shortly after hatching, locomotor performance of young ratites on inclines improved steadily. Performance differences among species were positively correlated with forelimb use. Ostriches and rheas were capable of ascending inclines up to 65°, while emus, with their extremely reduced wings, were only capable of 45° slopes. Forelimb recruitment may be dictated by the excursion potential of the shoulder joint of each species. Ratites have reduced wings, secondarily reduced shoulder skeletal morphologies, and they exhibit a laterally oriented glenoid fossa, which restricts their movement to a dorso-ventral plane. These birds recruit their forelimbs for stability, using sprawling, contra-lateral limb forelimb movements in order to shift their center of mass forward on the slope. Tinamous have fully functional wings, a transitional pectoral skeletal morphology and exhibit an intermediate locomotor pattern. At shallower inclines, their wings were recruited asymmetrically, perhaps to increase balance, while at steeper slopes (up to 70°) they shifted to a symmetrical wing beat resembling those of chukars. Chukars performed wing assisted incline running (WAIR) at inclines ≥60°-100°, and have the derived pectoral skeletal morphology common to volant birds. There appears to be a threshold at approximately 60°, above which wings must be recruited in order to increase both traction and stability on an incline.
TABLE OF CONTENTS

| Abstract .......................................................................................................................... ii |
| List of Tables ................................................................................................................... v |
| List of Figures ................................................................................................................... vi |
| Chapter 1: On the Origin of Flight in Birds ................................................................... 1 |
| Avian fossils and the origin of flight .............................................................................. 1 |
| New directions in the origin of avian flight ................................................................. 3 |
| What can extant animal locomotion tell us about the locomotion of extinct forms? .... 4 |
| Morphology of the shoulder and forelimb movement .................................................... 5 |
| Current research on avian forelimb function during incline running ......................... 7 |
| Figure Legend ................................................................................................................. 8 |
| Figure 1.1 ....................................................................................................................... 9 |
| Chapter 2: How do terrestrial birds negotiate inclines bipedally? .............................. 10 |
| Introduction ..................................................................................................................... 10 |
| Materials and Methods ................................................................................................. 13 |
| Experimental Design .................................................................................................... 13 |
| Animal Care .................................................................................................................. 16 |
| Inclines: Adjustable Ramps ......................................................................................... 17 |
| Training ......................................................................................................................... 17 |
| Filming and Kinematic Markers .................................................................................... 18 |
| Analysis ......................................................................................................................... 19 |
| Results ............................................................................................................................ 21 |
| Comparative Limb Kinematics and Performance on Maximum Inclines ..................... 21 |
| Ratite ontogeny of performance .................................................................................... 24 |
| Forelimb Kinematics of Tinamous and Chukars on Maximum Inclines ....................... 25 |
| Discussion and Conclusions ......................................................................................... 28 |

iii
## List of Tables

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Table 2.1</td>
<td>Study species and filming parameters.</td>
<td>42</td>
</tr>
<tr>
<td>Table A1.1</td>
<td>Description of Kinematic Variables</td>
<td>52</td>
</tr>
<tr>
<td>Table A2.1</td>
<td>Hindlimb Protraction and Retraction Angles on Horizontal and Maximal Inclines</td>
<td>55</td>
</tr>
</tbody>
</table>
### List of Figures

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Figure 1.1</td>
<td>Avian phylogeny and the transition in pectoral morphology which accompanies the transition from terrestrial forms to flighted forms.</td>
<td>9</td>
</tr>
<tr>
<td>Figure 2.1</td>
<td>Ratite Phylogeny and Shoulder Morphology.</td>
<td>47</td>
</tr>
</tbody>
</table>
| Figure 2.2 | Comparative Hindlimb Kinematics on Maximum Inclines  
A. Duty Factor on Maximum Inclines  
B. Interspecific Average Relative Stride Lengths on Maximum Inclines  
C. Interspecific Average Relative Step Lengths on Maximum Inclines  
D. Relative Stride Frequency | 48 |
| Figure 2.3 | A. Mean Body Angle in Relation to Substrate and Wing Excursion in Ostrich and Rhea  
B. Differential Incline Performance and Wing Use | 49 |
| Figure 2.4 | Ratite Ontogeny of Performance  
A. Age specific performance of emus, rheas, and ostrich  
B. Wing Excursion Angles on Maximum Inclines | 50 |
| Figure 2.5 | Forelimb Kinematics of Chukars and Tinamous on Inclines | 51 |
| Figure A1.1 | Illustration of Kinematic Variables | 54 |
| Figure A2.1 | Representative Hindlimb Protraction and Retraction Angles during the Stance Phase of Horizontal and Inclined Running. | 57 |
Chapter 1: On the Origin of Flight in Birds

Avian fossils and the origin of flight

Modern birds are among the best known vertebrates in terms of their physiology, behavior, and ecology, but our understanding of even basic aspects of ancestral avian locomotor affinities or abilities remain contentious or at least ambiguous. Much of the problem can be attributed to the inherent limitations of inferring function from preserved skeletal material, which is exacerbated by a fossil record that is grossly incomplete. Despite a long history of this practice (Huxley, 1870; Horner 1979, McNeill Alexander, 1985, Gatesy, 1990, Hutchinson et al. 2002), we have only a superficial understanding of the limb kinematics during bipedal locomotion of extant birds. Extrapolating these tenuous functional relationships to protobirds, which may have used their anatomy and morphology in ways that have only begun to be appreciated, is particularly troublesome for our understanding of the origin of avian flight.

For more than a century, discussions focused on the evolution of avian flight have necessarily revolved around the exquisite fossil specimens of Archaeopteryx lithographica found in Europe in the mid 1800’s (Meyer, 1860; Hecht et al., 1985). However, recent fossil discoveries from the Jehol deposits of Liaoning Province, China, as well as Spain, Argentina, and Germany have significantly broadened our understanding of proto-bird skeletal anatomy and evolution. Archaeopteryx, the first true flying bird in the clade Aviale, is now believed to have been preceded by several non-volant, feathered, bipedal, dinosaurian taxa: Sinosauropteryx, Protarchaeopteryx, and Caudipteryx (Fig. 1) (Qiang et al., 1998; Norell et al., 2002). These basal members of Avifilopluma (feathered dinosaurs), have prompted the re-examination of synapomorphic
character traits once thought to be exclusively avian, such as the furcula (fused clavicles), a laterally flexing wrist and, especially, feathers. These traits are now thought to have evolved in non-avian theropods well before the origin of flight, solidifying the link between modern birds and their theropod ancestors (Padian and Chiappe, 1998). In fact, a recently described basal tyrannosauroid possessed what are portrayed as proto-feathers (Xu et al., 2004). This consilience between the fossil record and cladistic information has established modern birds (Aves) phylogenetically as feathered, bipedal, theropod dinosaurs (Gauthier, 1986; Gauthier and de Queiroz, 2001; Padian and Chiappe, 1998).

The capacity for flapping flight remains central to understanding the success (i.e., current diversity and distribution) of living birds (Norberg, 1990), yet the evolutionary origin of bird flight remains even more controversial than bird ancestry (Padian, 2001b, 2001c). The nature of the debate surrounding the origin of powered flight in birds has historically been polemic and divisive (for a review see: Padian, 2001c, Witmer, 2002). Since the days of Darwin and Mivart, the question of transitional forms has been at the forefront of the evolutionary discussion. It is generally accepted that a plausible theory of the evolution of flight in birds must adequately address the adaptive potential of incipient wings in the stages of aerodynamic forelimb development (Bock, 1965). Despite this agreement, researchers have tended to align themselves with one of two popular hypotheses, resulting in two polarized schools of thought that rely heavily on limited fossil materials and volumes of anecdotal functional interpretations. The cursorial hypotheses propose that ancestral birds were specialized runners and, therefore, must have evolved powered flight from the ground up (Williston, 1879; Nopsca, 1907; Caple
et al., 1983; Ostrom, 1986, and many others). The arboreal school contend that proto-birds were scansorial climbers that took to the air from the trees by passing through a gliding or flap-gliding phase (Marsh, 1880; Bock, 1965, 1986; Norberg, 1985; Feduccia, 1996; Geist and Feduccia, 2000; Xu et al., 2003 and others). None of these hypotheses adequately explain the absence of functional transitional forms in the evolution of avian flight, and both are ultimately untestable given the limits inherent in the interpretation of the fossil data and the absence of extant forms exhibiting intermediate stages (e.g. parachuting, Padian, 2001b).

**New directions in the origin of avian flight**

More recently, the trend has been to move away from the cursorial-arboreal dichotomy, and toward an understanding of the evolution of the flight stroke itself using aerodynamic modeling (Burgers and Chiappe, 1999; Burgers and Padian, 2001; Hedenström, 2002; Padian, 2001a, 2001c; Padian and Horner, 2002; Rayner, 2001). Padian and colleagues have proposed that since theropods were predatory bipeds, they may have employed lateral slashing movements by the manus and forelimb during prey pursuit. Such kinematics may have been similar to the movements ultimately required for flapping flight and thus preadapted the forelimbs for this functional transition (Burgers and Chiappe, 1999; Gishlick, 2001; Padian and Chiappe, 1998). However, there is no comparable behavior in extant bipedal animals to lend support to this hypothesis. What appears certain is that there should have been a shift from the primitive, antero-posterior movement of quadrupedal reptilian ancestors, to a dorso-ventral movement in derived bipedal proto-birds leading to flapping, aerodynamic flight.
The locomotor patterns of bipedal theropods apparently differed in overall function from their tetrapod ancestors in that the former decoupled their forelimbs from associated movement with the rest of the body (Farlow et al., 2000; Gatesy, 1990; 2001; Middleton and Gatesy, 2000). Gatesy and Dial (1996) coined the term “locomotor module” to draw attention to the distinct morphological and functional groupings of musculoskeletal regions of the body. As such, theropods exhibited a single locomotor module comprised of the hindlimbs and the tail as an integrated functional group (Gatesy and Dial, 1996). Modern birds are also considered bipeds, but have decoupled their hindlimbs from the tail module and now are described as having three separate locomotor modules (tail, hindlimb, and forelimb) (Gatesy and Dial, 1996; Dial, 2003b). What remains poorly understood is the locomotor character of the forelimb module among extinct cursorial bipeds and what might have been the transitional stages leading to the development and utility of forelimbs in the modern forms (Middleton and Gatesy, 2000). Protobirds (*Avifilopluma*) were bipedal, cursorial dinosaurs whose feathered forelimbs were employed in unknown ways, and as such, careful reconstruction of their forelimb movement may be relevant to the study of the origin of avialan flight (Gauthier and de Queiroz, 2001; Padian, 2001b; Padian and Chiappe, 1998; Sereno, 1999).

What can extant animal locomotion tell us about the locomotion of extinct forms?

Until we can clearly understand form and corresponding function in living species, we will be unable to interpret even simple locomotory functions of extinct forms. Models based on studies of extant animal locomotion provide the best analogs from which to extrapolate information to extinct forms. Therefore, if we can study
comparative functional morphology and biomechanics in order to quantify and explain extant limb design, evolution, and function, we might be able to provide a link to the locomotor patterns of extinct forms. This approach has recently generated a novel hypothesis that addresses the adaptive value of proto-wings and transitional wings using extant precocial species as models of basal forms. (Bundle and Dial, 2003; Dial, 2003a). The wing-assisted incline running (WAIR) hypothesis posits that the forces generated by flapping wings during inclined ascents are directed towards the substrate, and thereby increase the animal’s hindlimb traction as it escapes to elevated refuges (e.g. boulders, cliffs, trees) (Bundle and Dial, 2003; Dial, 2003a). Proto-wings could have been adaptive for animals during anti-predator avoidance behavior, if they realized increased escape performance from the increased hindlimb traction. Further research into the scope and ubiquity of WAIR, linked to the anatomy and kinematics of the forelimb, will augment our understanding of the adaptive role of WAIR and other non-traditional forelimb locomotion, as well as its applicability to extinct forms.

**Morphology of the shoulder and forelimb movement**

The morphology of the shoulder joint has been proposed as an important indicator of forelimb locomotion (Jenkins Jr., 1993). In particular, the orientation and shape of the glenoid fossa may provide insight into the range of motion permitted at the joint among various extinct and extant taxa. The transition from feathered, non-avialan theropods (e.g., *Deinonychus antirrhopus*, a dromaeosaurid) to the volant members of the clade *Aviale* documents a concurrent transition from a ventrally positioned glenoid to an intermediate, laterally positioned joint, to a saddle shaped, dorsally oriented glenoid.
fossa. This transition is hypothesized to reflect a shift in forelimb function from one of limited elevation and, thus, restricted limb excursion along the dorso-ventral plane, to the more derived dorso-ventral limb excursion (where the forearms meet during upstroke and downstroke), a condition apparently necessary for flight (Jenkins Jr., 1993).

*Archaeopteryx* (a basal member of *Avialae*) exhibits a more laterally oriented glenoid, which has prompted speculation of its flight capability, yet it clearly shows the transition in the shoulder and forelimb from the non-flying ancestral state to the more derived condition (Jenkins Jr., 1993 as modified in Figure I).

By comparing the static joint morphologies to the corresponding kinematics of the limb and locomotor behaviors among extant animals, one may gain insight into the locomotor style of extinct forms (Gatesy et al., 1999; Alexander 1976, 1983, 1985). There are numerous studies of hindlimb kinematics in vertebrates that range across taxa and include humans, birds, horses, lizards, and other tetrapods (Carlson-Khuta et al., 1998; Gatesy and Biewener, 1991; Hoyt et al., 2000; Irschick and Jayne, 1998, 1999; Iversen and McMahon, 1992; Jayne and Irschick, 1999; Vilensky et al., 1994). Some of these studies have examined the effect of shallow inclines on quadrupeds, but very little information is available on inclined bipedal kinematics (but see: Irschick and Jayne, 1998, 1999; Jayne and Irschick, 1999 for studies on lizards running on shallow inclines). Even less has been done to examine the behavior and possible function of the forelimb in non-human bipedal animals. In particular, the kinematics of the avian forelimb during inclined locomotion have been left unexamined with the exception of WAIR (Dial et al., in press).

6
Current research on avian forelimb function during incline running

Wing assisted inclined running has been demonstrated in several galliform species and is proposed to assist in predator avoidance. However, galliforms are powerful burst fliers and possess the neuromuscular physiology and skeletal morphology necessary for flapping flight. Theropod dinosaurs do not appear to have had the appropriate range of limb excursion necessary for flight, as evidenced by their primitive shoulder morphology. Thus, an interesting extant analog to theropod locomotion would be the cursorial, flightless birds known as ratites, as they are most similar to extinct forms in terms of their shoulder morphology and locomotion. In order to determine the ubiquity of WAIR, I examined a range of basal avian taxa with a range of shoulder skeletal morphology and flight ability and measured their performance and locomotor kinematics on inclines. In order to better understand how winged bipeds negotiate a three-dimensional terrestrial environment, I focused on a comparison of basal taxa on inclines, and on a comparison of locomotor performance on inclines during ontogeny.
**Figure Legend**

Phylogeny of bird-line archosaurs as adapted from Gauthier and de Quieroz (2001) with illustrations of the evolutionary transition of the glenoid fossa (where the humerus articulates with the pectoral girdle of the shoulder) from Jenkins (1993). *Deinonychus antirrhopus* (A) shows a ventrally oriented glenoid, while *Archaeopteryx lithographica* (B) exhibits a more laterally oriented glenoid, and modern flighted birds (C) show the derived, dorso-lateral orientation which permits wing excursion along the dorso-ventral as well as the antero-posterior plane. Arrows indicate the probable range of motion permitted at each joint given the articular morphology.
Figure 1.1

Maniraptora

Avifilopluma (Feathered Dinosaurs)

Dinosauria

Archosauria

Archosauromorpha

Ornithischia

Pseudosuchia

Theropoda

Avialae (Flying Dinosaurs)
Chapter 2: How do terrestrial birds negotiate inclines bipedally?

Introduction

The contentious debate surrounding the origin of avian flight has persisted for well over a century (Darwin, 1859; Williston, 1879; Marsh, 1880; Nopsca, 1907; Bock, 1965, 1986; Caple et al., 1983; Norberg, 1985; Ostrom, 1986; Feduccia, 1996; Geist and Feduccia, 2000; Xu et al., 2003). Historically, research efforts have focused on evaluating the ecological setting in which avian flight was thought to have evolved, whether on the ground from cursorial bipedal animals, or in the trees from quadrupedal or scansorial climbers. Discourse centered on issues such as the feasibility of using gravity to establish airflow around the wing from an arboreal takeoff location, or whether cursors could achieve a velocity that would allow them to overcome drag effectively during a terrestrial takeoff. However, recent research has shifted away from questions centered on the functional role of milieu and towards understanding the expected transitional forms in the origin of the flight stroke itself (Burgers and Chiappe, 1999; Burgers and Padian, 2001; Hedenström, 2002; Padian, 2001a, 2001c; Padian and Horner, 2002; Rayner, 2001).

The importance of transitional adaptive stages to the evolution of avian flight is paramount to understanding of the trajectory of the process. The recent work of Dial and Bundle (Dial, 2003; Bundle and Dial, 2003) proposes a functional explanation based on experimental data that address a potential adaptive stage in the transition from a bipedal, feathered cursor to a flighted bird. This hypothesis suggests that the adaptive value for proto-wings lies with an anti-predator behavior, described as wing assisted incline
running (WAIR) (Dial, 2003; Bundle and Dial 2003). Young ground birds, while still unable to fly, use their incipient wings during bouts of flap-running in order to increase their traction while ascending steep inclines (Dial, 2003). It has recently been confirmed that this behavior (which might increase the potential for predator avoidance, increase dispersal ability, or perhaps increase foraging success) redirects aerodynamic forces towards the substrate, much like the spoiler of a race car (Bundle and Dial, 2003). WAIR provides an example of a possible transitional stage in the development of a flight capable, flapping wing, in that it illustrates the utility of an incipient wing to a completely terrestrial animal (young Chukar chicks are unable to fly).

This hypothesis uses locomotion of extant animals as the functional basis to infer the locomotor styles of extinct forms. Studies of comparative functional morphology and biomechanics are considered integral components of paleobiology, particularly in regard to reconstructing aspects of locomotion. However, in order to be able to extrapolate information from extant forms into the past, we must first thoroughly understand current locomotor patterns. Birds are bipeds, along with humans, yet little progress has been made toward elucidating the function of the avian forelimb in non-volant locomotion. In fact, WAIR was the first research protocol to examine the locomotor role of the forelimb during bipedal terrestrial avian locomotion, inclined or otherwise (Dial, 2003, Bundle and Dial, 2003). A closer study of the avian forelimb during non-traditional (non-volant) locomotion is necessary in order to flesh out the ubiquity of WAIR, and its usefulness as an overarching evolutionary explanation for the origin of avian flight. If WAIR provides a functional adaptive trajectory for the evolution of avian flight, there may be extant functional intermediaries. Phylogenetically basal birds, such as ratites and tinamous,
have locomotor habits that are similar to those thought to have been exhibited by extinct theropods, in that they are terrestrial, bipedal, precocial, cursors. They also exhibit a shoulder morphology which mirrors the primitive condition of a laterally oriented joint articular surface. They should be considered good models of transitional forms because they may have retained basal functional locomotor characteristics in the same way they exhibit basal anatomical characteristics. If we use an extant behavior to understand the evolution of avian flight, one might expect that behavior to be pleisiomorphic, and to observe it in basal animals.

There are several questions which are pertinent to understanding the role of the forelimb in the evolution of transitional stages on the trajectory towards flapping flight using extant birds as models. Most importantly is how bipedal cursors negotiate a three dimensional environment. Little attention has been paid to the fact that although extant avian cursors primarily live in open environments, the real world is three-dimensional and these animals encounter slopes and inclines in their natural habitats. We know that some galliforms use their wings to increase performance in a terrestrial setting (Bundle and Dial 2003, Dial 2003). That being the case, it is unknown whether non-galliform terrestrial birds use their forelimbs during inclined running. If they are using them, we need to understand when and how they deploy them and to what purpose. Do they experience an increase in locomotor performance by utilizing their forelimbs, and if so, how might that translate into an adaptive advantage for the animal in the real world?

In an effort to evaluate how bipedal, cursorial birds utilize their hindlimbs, and the potential function of their forelimbs, during terrestrial level and inclined locomotion, I provide a kinematic survey of representative cursorial avian bipeds. I examined several
species of basal avian clades (Fig. 2.1) in order to quantify limb use during steeply inclined ascents, by focusing on kinematics in an effort to describe non-traditional avian forelimb use. I examined the utility of their forelimbs in relation to how and when they were employed during incline running, as well as the relationship between steepness of slope and limb excursion. Is locomotor performance in a three dimensional environment correlated with trends in forelimb use, shoulder morphology, and wing size in basal birds during steep ascents? Do birds that use their forelimbs while making incline running outperform those that do not? Does an observed trend from a more primitive to a more derived shoulder morphology track with an increase in locomotor performance? If birds use their forelimbs to increase performance up inclined slopes, then species with larger wings will be able to ascend steeper inclines than those with smaller or less developed wings. Among birds that do recruit their wings on inclines, the range of motion at the shoulder joint, as inferred from the orientation of the glenoid fossa, should correlate with wing excursion and be a useful predictor of locomotor performance on inclines in that birds with more derived shoulder morphologies will be better performers on inclines.

Materials and Methods

Experimental Design

One of WAIR’s strengths as an evolutionary hypothesis is that it can be observed in extant animals. Since it has been so recently described, its ubiquity is unknown, however, it would make intuitive sense to be quite prevalent should it actually be as adaptive a behavior as has been proposed, particularly during ontogeny. If WAIR is a plausible transitional evolutionary locomotor behavior, we might expect to be able to
observe some form of it in one of two places, either in chicks during vulnerable life stages, or in basal birds which morphologically resemble early bird ancestors. I chose five species of basal birds in order to study the kinematics of both limbs during inclined locomotion, based on a suite of phylogenetic and morphological characters. The species I chose represent the basal avian taxa, and were observed during their development to determine whether WAIR is specific to any ontogenetical stage.

Ratites (e.g. emu, kiwi) are large bodied, secondarily flightless birds that are arguably good models for proto-avialan locomotion because they are cursorial bipeds and demonstrate a superprecocial life history. They are phylogenetically the most basal of the extant avian taxa, but are descended from flight capable forms, so their inability to fly is considered secondarily derived. While no one would expect a full grown ratite to use its wings aerodynamically during flapping flight, it has been previously undocumented as to whether they may be using their forelimbs in ways not yet understood in order to increase overall locomotor performance. Ratites also posses shoulder anatomies that have been considered to be representative of a more primitive condition, in terms of the orientation and shape of the glenoid fossa, similar in morphology and in aspect to the early theropod dinosaurs (Feduccia, 1985). Based on the WAIR hypothesis, even incipient proto-wing structures could conceivably augment locomotor performance by assisting hindlimb efficiency. As such, these secondarily flightless birds may also depend on their non-aerodynamic forelimbs for locomotion early in development.

I chose three species of ratites (*Dromaius novaehollandiae, Rhea americanus, Struthio camelus*) to represent a range of variation of both forelimb size and shoulder anatomies. The ratites all have a laterally oriented glenoid, with restrictive bony labia on
both the dorsal and ventral aspects. Emus are large bodied and have vestigial forelimbs (Table I). Their shoulder joint is characterized by a fused scapulocoracoid, there are no defined attachment points for the pectoralis (the major flight muscle in flighted species), meaning that they have no sternal keel (carina) and lack a delto-pectoral crest, and exhibit cartilaginous clavicles with no fusion (absence of a furcula). I chose to use emus as a baseline indicator of performance, since their lack of a functional forelimb makes them a good control against which to compare the performance of other birds. Rheas are smaller bodied than emus, yet have a much larger forelimb (Table I). They also lack a keel and defined deltopectoral crest, and show a similar degree of fusion at the scapulocoracoid. Ostriches are the largest bodied birds, and while they are flightless, they have large feathered, forelimbs (Table I). Their shoulder morphology and muscle attachments mirror those of the rhea.

Tinamous (Tinamiformes) are closely related to ratites, yet they have completely developed wings and the capacity for short, burst flight. What is most compelling about Tinamiformes as study species is that they share similar life history traits to the more derived galliforms, are comparable in body size to chukars, and have what can be described as intermediate shoulder morphologies (Table I). The two species of tinamou (Notoprocta perdicaria and Eudromia elegans), used in this study are found in semi-arid habitats and are primarily terrestrial (Davies, 2002). The tinamous have a more dorso-laterally oriented glenoid than ratites, however the scapular and coracoid facets which make up the glenoid are relatively equal in terms of their contribution to the cavity as compared to those of more derived birds (Galliformes, Passeriformes). I was particularly interested in whether these basal birds with similar habitats and life history
strategies would show locomotor patterns similar to those described by Dial and Bundle (2003). Both species of tinamou were purchased as adults at the beginning of the study, so no ontogenetic information was collected for these species. Detailed skeletal anatomy was examined from museum specimens on loan from the American Museum of Natural History (AMNH), as well as from expired study animals.

Finally, Chukar partridges (Alectoris chukar) were also used in this study in order to compare a well described WAIR performer to the other avian species described above. Chukars preferentially use WAIR to ascend inclines, and while the mechanics of WAIR have been well described in adult birds, a more detailed study of the kinematics of WAIR is presented here. Chukars have the strongly dorso-laterally oriented glenoid characteristic of most modern birds. The coracoid facet is larger and more pronounced than that of the scapula, which creates a more dorsal orientation. Museum specimens were used to describe pectoral morphology, on loan from the University of Montana Phil Wright Zoological Museum (UMZ).

Animal Care

Six species of ground dwelling birds spanning two orders of magnitude (0.5kg – 100.0kg) were studied during bouts of horizontal and inclined running. Three species of ratites: Emu (N = 2), Rhea (N = 2), and Ostrich (N = 2), two species of tinamou: Chilean tinamous (N = 2) and Elegant crested tinamous (N = 2), and Chukar partridges (N = 3) were housed at the University of Montana Flight Lab in Missoula, MT for the duration of the study. Birds were obtained from various gamebird farms within the Northwestern United States. During the experimental period, from May 2002 to January 2004, birds
were cared for daily, provided water and food *ad libitum*, and housed in large outdoor aviaries (15.2 m (length) x 6.2 m (width) x 3.9 (height)). Young birds were housed indoors until deemed hardy enough to be released into the outdoor facilities. During the course of this study, any animal that expired was prepared as a museum specimen and used as an anatomical reference.

**Inclines: Adjustable Ramps**

Both indoor and outdoor runways were used during the study. Due to their large size, the ratites were filmed primarily on a large, adjustable incline outdoor ramp (2.4 m (length) x 0.86 m (width) x 0.04 m (height)). The ramp was covered with coarse-grained sandpaper and short pieces of lathing to increase foot traction. Once the animals had ascended the incline, a downhill ramp provided them access to an unconfined area.

The indoor ramp (2.0 m (length) x 0.3 m (width) x 0.04 m (height)) was also adjustable and covered with thin foam netting (0.005 m x 0.005 m) in order to increase traction. The animals were corralled at the top of the incline, as their presence at the top served to motivate the study animal to climb the incline in order to rejoin the group.

**Training**

To insure maximal and repeatable locomotor performance, all birds required substantial training upon the inclined runways. Each study animal was trained for a period of two weeks prior to filming for kinematic analysis. Each training bout consisted of 20 minute sessions of incline running, and each session was repeated for each study
animal 5 times weekly. As part of this training regime, a treadmill was also used when possible to condition the animals. Both species of tinamou required extensive conditioning on the treadmill, and they took the longest to habituate to their human handlers, being the only birds in the study not to be hand-reared by humans. All birds were motivated to run on both horizontal runways and inclined ramp angles. For the ontogenetic portion of this study, the birds were encouraged to attempt the inclines from the day they arrived and their success was measured in terms of the steepest incline they could manage on a daily basis. The ramp was gradually increased in increments of 5° and the incline angle was considered to be too steep once the bird had attempted and failed twice to successfully climb the ramp. Foam padding and a full size mattress were placed underneath the ramps in order to prevent any animal injuries. No animals were injured during filming and data collection.

Filming and Kinematic Markers

The ratites were filmed using a high speed digital camera system (125 fps, Redlakes Masd. Inc., Motion Scope) linked to a digital video recorder (Sony). The events were filmed from two perspectives as the birds ascended variously inclined runways, ranging from 0° to 70°. A camera mounted orthogonally to the ramp surface was synched to a laterally positioned camera via an LED cue. The hindlimb was marked at the hip, knee, ankle, and metatarsophalangeal joint, while the forelimb was marked at the shoulder, elbow and wrist with reflective adhesive tape (3M 8850).
Tinamous and chukars were filmed at 250 fps ascending the indoor ramp. I used a high speed camera system, (Redlakes Masd. Inc., PCI 500), comprised of two internally synched cameras in dorsal and lateral positions. In order to better visualize the shoulder and hip joint locations, I sutured small reflective balls to the ligaments integral to both joints. Other markers (at the wrist, wingtip, division between the primary and secondary feathers, knee, ankle and metatarsalphalangeal joints) consisted of reflective tape adhered to the animal’s body or feathers. Contour feathers were plucked at the hip, shoulder, and knee in order to have a clear view of the joint marker.

Analysis

Ratite video was transferred to a computer with video editing software (Pinnacle DV 500). Tinamou and chukar films were recorded directly on Redlakes digital PCI cameras. All the video was digitized using Videopoint software (Lennox Softworks, 1997) or Ariel Performance Analysis Software (APAS, Ariel Dynamics, San Diego, CA) which allow the pixel position of the marker to be converted into a two dimensional coordinate system. The $x$ axis is defined as being parallel to the substrate, the $y$ axis is vertically perpendicular to the $x$ axis, and the $z$ axis is perpendicular to the $x,y$ plane. The dorsal camera allows description of movement along the $(x,z)$ plane and the lateral camera captures dorsal/ventral movement along a $(x,y)$ plane.

The space was calibrated by filming a calibration cube with marked locations separated by known distances to determine an equation which I could use to account for the effect of parallax from the camera lenses and allow me to convert the coordinates
from pixels to meters. I used Excel (Microsoft 2000) to calculate the average velocities of the animals during each run and to calculate the angle between the ramp and the ground to determine the ramp’s slope angle. In order to facilitate comparison between the two ramps used in the study, I rounded the ramp angles to the nearest 5 degrees. Time was measured directly from the film by dividing the frame numbers by the film speed of the camera system (i.e. 5 frames at 250Hz = 0.02s).

To reduce the influence of size and because it was not possible to standardize velocity, I normalized the runs by calculating the Froude numbers (\(Fr\), a ratio of inertial force exerted on an object to the weight of the object),

\[
Fr = \frac{v^2}{gh}
\]

where \(v\) is forward velocity, \(g\) is the acceleration due to gravity (9.8 m\(^2\)), and \(h\) is the hip height of the animal, in order to compare runs at dynamically similar relative velocities (Alexander, 1977). This allows for comparison between animals of different body sizes, moving at different speeds, because the mechanics of movement are thought to be similar at equivalent \(Fr\) values (e.g. gait transitions usually occur within a specific \(Fr\) range) (Alexander, 1977; Mochon and McMahon, 1980).

Limb kinematic variables were measured as per the following descriptions, a concise list of definitions is presented as Table A1.1 in Appendix 1. Wing stroke plane is defined as the plane of travel made by the wingtip during the majority of the downstroke of the wing. The wingstroke angle is the angle created by the wingstroke plane and the substrate (ramp or ground surface). The body angle is defined as the average angle
between the line created by the line connecting the shoulder and the hip of the animal, and the substrate. The wing excursion angle is located between the line connecting the shoulder and hip of the animal and the line connecting the shoulder and wrist of the forelimb. The angle of attack was calculated as the angle formed by the intersection of a line connecting the leading and trailing edges of the wing at mid-downstroke and the slope of the ramp itself. The angle of incidence is the angle formed by the intersection of the wing stroke plane and the plane of the angle of attack. These angles are illustrated in Figure A1.1 of Appendix 1. I measured the kinematics of all the limbs, but only report selected hindlimb kinematic results in addition to forelimb kinematics here. The majority of hindlimb kinematic data are included as Appendix 2. All non-angular hindlimb measurements needed to be normalized across species in order to account for body size and were converted to dimensionless variables following Gatesy and Biewener (1991). Stride period and frequency were used to determine the stride length, and from that the relative stride length was calculated by dividing the original length by the hip height of the animal. Step length was calculated as a distance between the two hip markers located in the beginning frame of the stance phase of the stride (toe on) and the end frame of the stance phase (toe off). The relative step length was then taken by dividing the step length by the hip height of the animal (Appendix 1).

**Results**

**Comparative Limb Kinematics and Performance on Maximum Inclines**

The hindlimb kinematics of all the birds on their maximum inclines showed similar patterns when compared to each other. Duty factors were relatively similar on
inclines, with the larger bodied animals spending slightly more time in the stance phase of a stride (Figure 2.2a). The relative measures of the animal’s strides, including relative step length, relative stride length, and relative frequencies, also indicated that the birds were using their hindlimbs to ascend the inclines in a rather stereotypic fashion (Figure 2.2b, c, d). Gatesy and Biewener (1990) have suggested that hindlimb kinematics, specifically during protraction, may be the result of a central pattern generator and be the result of a fixed movement pattern that has evolved as an adaptation to running over heterogeneous substrates. It may be the case that the similarities between species are suggestive of a shared inability to modify a fixed pattern on a treacherous sloped incline.

While the leg kinematics tended to be somewhat stereotypic, the body angles on maximum inclines showed a great deal of interspecific variation. Ratites, in general, did not pitch their bodies into the substrate as they ascended the inclines (Figure 3A). Perhaps due to their large body size, these animals did not have the natural inclination to ascend the ramps that was apparent in the other birds. When ostriches and rheas did successfully climb the steep slopes, they tended to pitch their bodies forward only slightly, maxing their body angles around 20° on their maximum slopes. Crested tinamou had a mean body angle of 25° (± 7°). Crested tinamou had a mean body angle of 23° (± 12°). Chukars showed the greatest average body angle, in addition to being capable of ascending the steepest slopes, at 65° (± 8°). This means that the chukars are pitching their bodies much further forward than either species of tinamou as well as the ratites (Figure 2.3A).

The basal taxa exhibited a range of locomotor performance on inclines. Overall, the ratites exhibited the poorest performance on inclines when compared to the smaller
bodied animals (Figure 2.3B). However, the ratite species with larger wings (ostrich and rhea) were able to ascend steeper inclines, and when doing so, used their forelimbs asymmetrically (one protracted while the other was retracted along the antero-posterior plane).

Tinamous were better performers on the inclines than the ratites, as they were able to consistently ascend steeper inclines and recruited their wings both asymmetrically and symmetrically (both forelimbs exhibiting extension and flexion in tandem in the dorso-ventral plane). Both Chilean and Elegant crested tinamous were able to ascend inclines of up to and including 70 degrees, and recruited their forelimbs symmetrically when faced with their maximum incline steepness (Figure 2.3B).

Chukars were capable of ascending inclines greater than 100 degrees while performing WAIR (Figure 2.3B). Chukars begin to use their forelimbs at inclines greater than 60°. Chukars have been shown to be capable of incline running from a very early age, 2-3 days post hatching (Dial 2003). Chukars preferentially performed WAIR rather than flying, even when ascending inclines of more than 100 degrees.

All three bird groups have a different style of locomoting up inclines. It was clear that using the forelimbs during steep ascents gave the animals a performance advantage, however all three groups used somewhat different styles of forelimb locomotion. Ratites recruited their forelimbs when possible, but did not move their forelimbs in the antero-posterior flapping pattern characteristic of WAIR. Tinamous facultatively recruited their forelimb on steep inclines, switching from an asymmetrical, sprawling pattern typical of ratites to the symmetrical flapping motion described in WAIR. The chukars were the
most capable of ascending steep inclines, and used their forelimb module concurrently with their powerful hindlimbs in order to climb inverted slopes.

**Ratite ontogeny of performance**

Ratites showed a variable capacity for incline running across age classes and species (Fig. 2.4A). All ratites were able to ascend inclines of 30 degrees at one month of age. Young emus improved their performance by 15 degrees in the next nine months, and yet were never able to ascend inclines steeper than 45 degrees. Both rheas and ostriches greatly improved their performance as they aged. Young rheas could ascend inclines of up to 65 degrees by the time they reached 6 months, when their performance appeared to plateau. Ostriches were successful on inclines of up to 60 degrees during the study. Ostriches grow extremely quickly, and are the largest extant members of the class Aves (Davies, 2002). Ostriches were only tested on the inclines until they were 5 months of age, after which they became too dangerous to maneuver onto the ramps, and their large body size prevented us from maintaining the level of safety required for both the human handlers and the study animals. Both young ostriches and young rheas consistently utilized their wings on inclines, which served to increase performance.

While ratites showed a varied degree of incline performance ability, it was clear that the larger winged species were more successful in climbing the ramps. Both Ostriches and Rheas have much larger wings than emus, and were thus better able to recruit those wings during their ascents. The emu’s forelimbs are considered to be vestigial, and are of little to no use during locomotion for these animals. Both rheas and ostriches were able to utilize their forelimbs during incline running, however, they did
not use the anterior-posterior directed flap-running which is characteristic of WAIR.
Ratites showed forelimb movements that were similar to the sprawling pattern found in
quadrupedal reptiles, in that their forelimb movements were asymmetrical, side to side
movements along the x, z plane (Figure 2.4B). While they did not show the characteristic
WAIR behavior, they did use their forelimb module in concert with their hindlimb
module in order to increase their performance on inclines.

Perhaps in order to compensate for an inability to effectively pitch their bodies
forward and by doing so, shift the location of their center of mass (COM) to become
more stable on the incline, both bird species extended their wings asymmetrically on
steep slopes (Figure 2.4B). This behavior is common in other bipeds on inclined slopes,
such as humans. It may serve to move the COM forward and thus closer to the substrate
to give the animals better balance. Ratites have a generally upright posture as compared
to the more crouched posture of the tinamous and chukars.

Forelimb Kinematics of Tinamous and Chukars on Maximum Inclines

*Angle of Attack*

Angle of attack is an important gauge of the potential aerodynamic function of an
airfoil, in this case a wing. Angles of attack that are too high, or too low will cause air to
be disrupted and prevent laminar flow over the surface of the airfoil, creating an inability
to generate lift and/or thrust. Both tinamous and chukars increased their angles of attack
as incline steepness increased. Both taxa showed the greatest angle of attack on their
maximum inclines (Figure 2.5A), indicating an aerodynamic utility to the forelimb on
steep inclines.
Wingstroke Angles

Wingstroke angles from the maximum incline ascended by each species varied within both phylogenetic groups (Figure 2.5B). Wingstroke angle measures movement of the wing along the dorso-ventral and/or antero-posterior planes by the wings, as seen from the lateral camera. It thus describes movement of the forelimb in the $x,y$ plane. The tinamou species had similar average wingstroke angles, with Chilean tinamous at $45^\circ$ (± $14^\circ$) and Crested tinamous at $57^\circ$ (± $9^\circ$). However, both species of tinamou used WAIR intermittently, interspersed with a flap-bounding gait which relied on a more asymmetrical forelimb use pattern similar to that of ratites. While this behavior is effective in terms of allowing the animals to ascend inclines while recruiting their wings, it should be considered a less coordinated version of the WAIR described in chukars and other galliforms. The tinamous on the whole have a more dorso-ventrally oriented wingstroke plane during bouts of WAIR, similar to the wingstroke plane necessary for flight. WAIR was performed by the tinamous at the transition between terrestrial running and flight. It occurred at near the limits of the incline ability, and seems to suggest that after a certain steepness threshold, they prefer to fly to reach elevated refuges than perform incline running.

This is in contrast to chukars, which will perform incline running preferentially at angles exceeding vertical (> $105^\circ$) (Figure 2.5B). Chukars showed an average wingstroke angle that was similar to those shown by the tinamou species, at $19^\circ$ (± $2^\circ$). The average wingstroke angles of the chukars on their maximum inclines are much more acute than their tinamou counterparts, reflecting a more antero-posterior wingstroke plane due in part to the extreme pitching forward of their bodies during WAIR. Chukars show a
dorso-ventral oriented wingstroke plane when in flight, and then shift their wingstroke plane during WAIR bouts. This allows them to direct the accelerative forces created by their wings into the substrate (Bundle and Dial 2003). The tinamous on the whole have a more dorso-ventrally oriented wingstroke plane during bouts of WAIR, similar to the wingstroke plane necessary for flight.

Angle of Incidence

The angle of incidence is a reflection of the airflow around the wing during incline running. It is a measure of how much the wing itself has been pitched forward (angle of attack) with the wing stroke plane relative to the substrate. Ideally, the incident angle would be conserved across all inclines by some alteration of either body angle, wingstroke angle or attack angle. This seems to be the case on steep angles in chukars, but not so in tinamous (Figure 2.5C). As previously stated, tinamous show a variable propensity to use WAIR, and are best described as intermittent WAIR performers. The highly variable nature of their forelimb use reflects in part their propensity to startle and flush very easily, which constantly keeps them on the cusp of flight while running or flap-bounding. Chukars appear to modulate both their incident angles carefully across inclines, either by changing their angle of attack, or their wingstroke angles, or both, as the slope becomes progressively steeper. This serves to guarantee the flow of air over the wing will be sufficient to generate the substrate directed aerodynamic forces necessary to increase hindlimb traction.


Discussion and Conclusions

Bipeds on Inclines

Birds have a range of incline motor performance that is correlated with changes in posture and forelimb utilization. There appears to be a 60° threshold above which wings must be recruited in order to ascend steep inclines. In order to traverse inclines, the center of mass must be lowered vertically, as well as moved towards the substrate, much like humans climbing steep slopes. A recent study by Roberts and Belliveau (1995) showed that humans alter the work done by their joints on inclines, and the primary mechanism for doing this is by increasing the joint moment, rather than the excursion of the joint itself. This can be accomplished in a variety of ways, specifically by bending the joints more acutely, effectively assuming a crouching position, also by pitching their body forward into the substrate, as well as by recruiting the wings asymmetrically in tandem with the hindlimb module, much like human forelimb use during running or incline climbing. This ability to change postures on inclines reflects the potential for incline running across taxa.

Species which have high centers of mass, and are large bodied, such as the ratites, are less able to climb steep slopes. This is because the ground reaction forces generated during incline running are shifted forward, away from the alignment of the joints in the hindlimb, effectively increasing the out-moment arm and resulting in more work being done at each joint (Roberts and Belliveau 2005). Their large body size, coupled with the long limbs and lower effective limb lengths (Biewener 1991), make it difficult for them to assume a crouching position while on a slope. In addition, they do not pitch their
bodies forward into the substrate while making the ascent. The smaller bodied rheas were the best performers of the ratites on inclines, and that seems to be due to their greater ability to pitch their body into the substrate, assume a more crouched hindlimb posture, and utilize their wings to shift their center of mass.

Both tinamou species and the chukars are smaller bodied and better able to change postures while running up inclines. They were able to lower their center of mass and use their wings to generate forces which helped stick them to the substrate. Tinamous were less able to pitch their bodies forward, yet showed postural changes in the hindlimb which reflect a high degree of bending, thus serving to lower the center of mass. They were able to ascend inclines greater than 60° when they recruited their wings symmetrically. Chukars were better able to pitch their bodies forward, perhaps owing to the greater traction provided by their powerful wing-strokes. Chukars often do not recruit their wings until they are forced to ascend slopes that are greater than 60°, and yet on steep slopes will preferentially use WAIR instead of flying. Their ability to both change their body posture, as well as utilize their forelimbs is positively correlated with their performance.

**Forelimb Utilization and Kinematics on Inclines**

In general, birds that utilized their forelimbs during inclined locomotion exhibited greater performance ability. The emus, with their reduced, vestigial wings were never able to ascend inclines greater than 45°, even as young chicks. Both rhea and ostrich, while not performing WAIR, did show an increase in performance as they recruited their forelimbs asymmetrically on steeper inclines and used their wings to help them climb the
inclines throughout development. In a study on penguin waddling, which could be considered an asymmetrical gait, lateral movements were shown to increase the kinetic energy available to be converted into potential energy (Griffin and Kram 2000). These types of movements in the forelimbs could serve not only to increase balance and lower the center of mass, but also to make uphill running more efficient.

Both species of tinamou used WAIR when faced with steep slopes, and used a more intermittent, asymmetrical pattern of forelimb use when on shallower inclines. Chukars preferentially used WAIR (symmetrical flapping) to ascend inclines well past 90°. Symmetrical wing recruitment appears to be necessary in order to ascend inclines above 60°, although any forelimb use increases performance.

Tinamous and Chukars both altered their wingstroke angles and angles of attack as the slope of the incline increased. The ability to generate aerodynamic forces with the wings during incline running appears to be related to the synergistic relationship between the hindlimb and forelimb modules. Careful modulation of the flight-stroke in relation to the substrate, as well as the same attention to the orientation of the wing itself is necessary for the extreme performances shown by the Chukars. Tinamous, which show much more variability in their wingstroke kinematics, may be unable to coordinate the two locomotor modules to the same degree, thus decreasing their performance.

Shoulder Morphology and WAIR

The shoulder morphology of these birds mirrors the transition of the glenoid as described by Jenkins (1993), going from a laterally oriented glenoid which constrains movement in the D/V plane, to a more dorso-ventrally oriented glenoid in both tinamous
and chukars. In tinamous however, the absence of the larger coracoidal facet seen in chukars creates a slightly more lateral orientation to the shoulder cavity. This may be related to the more dorso-ventral wingstroke angle seen during WAIR in this species. However, because the tinamous also use a sprawling forelimb movement during ascents, movement along the antero-posterior plane doesn’t seem to be restricted. What may be limited however, is movement along the A/P plane while the forelimb is extended. The enlarged coracoidal facet in the chukar shoulder may allow for a slightly more rotational movement, allowing for a wingbeat in the antero-posterior plane. Experiments examining the range of motion permitted at the shoulder joint in living animals could shed light on the issue of mobility constraints at the shoulder. In addition, the development of the glenoid cavity during the ontogeny of young animals and its relationship to incline performance needs to be evaluated.

**Extant Models and Biological Uniformitarianism**

The best analogs for understanding extinct forms are modern analogs. Dial (in prep) has recently suggested the concept of “biological uniformitarianism”, which encourages paleobiologists to prioritize hypotheses of the behavior and locomotion of extinct forms by the principle of uniformitarianism (processes that are occurring now are assumed to be the same processes that existed in the past). This gives more weight to hypotheses that examine extant forms for information that can be extrapolated into the past. Since transitional forms are key to an understanding of evolutionary history and relationships, the examination of extant basal species should provide clues to extinct transitional forms.
WAIR has been proposed to be a transitional form in the evolutionary history of avialan flight. However, while WAIR is certainly effective in the species that utilize it, it is hypothesized to be one of many potential incremental stages in the trajectory towards flight. This study has shown that basal avian species show a range of non-traditional forelimb locomotion when running on inclines. By looking at non-traditional uses of the forelimb in the context of predator avoidance in extant animals, we may be getting closer to an earlier transitional stage which may, in fact, have been transitional to WAIR. Bipedal feathered dinosaurs could have gained an advantage by using sprawling forelimb motions on inclines to escape predators, thus gaining an adaptive advantage. The gradual shift from sprawling to a more synchronous movement of the forelimb could have led towards the development of the wingstroke. From there, WAIR could have evolved, and transitioned into flapping flight. By looking at the evolution of flight in terms of incremental adaptive stages and predator avoidance, quantifying extant examples of those hypothesized transitional stages in extant birds by focusing on the wingstroke, we can develop a more detailed picture of non-traditional wing use and its impact on the evolution of flight.
Acknowledgements

I am extremely grateful to Ken Dial for his unwavering support in all phases of this project. I also am deeply indebted to Matt Bundle, as he provided invaluable assistance and advice, as well as commentary on a previous version of this manuscript. Many thanks go to Paolo Segre and Brandon Jackson, who assisted with data analysis and compilation and provided useful comments on this manuscript. Richard Hutto and Charles Leonard have been supportive committee members and provided comments on this and on a previous version of this manuscript. Terry Dial, Ross Randall, Jessica Sherburne, and Loryn Zerr assisted with animal handling, filming, and care. Erin Bohman provided excellent illustrations of the skeletal material. Dan Whaley and Matt Bestram provided much needed technical support that is greatly appreciated. The American Museum of Natural History, and the Phil Wright Zoological Museum provided generous specimen loans.
References


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Table 2.1

<table>
<thead>
<tr>
<th>Species</th>
<th>Mass</th>
<th>N</th>
<th>Average Hip Height (m)</th>
<th>Wing Length (m)</th>
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<tr>
<td>Emu (<em>Dromaius novaehollandiae</em>)</td>
<td>31.2kg</td>
<td>2</td>
<td>0.77</td>
<td>0.08</td>
</tr>
<tr>
<td>Rhea (<em>Rhea americana</em>)</td>
<td>23kg</td>
<td>2</td>
<td>0.62</td>
<td>0.58</td>
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<tr>
<td>Ostrich (<em>Struthio camelus</em>)</td>
<td>100kg</td>
<td>2</td>
<td>1.12</td>
<td>0.65</td>
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<tr>
<td>Chilean Tinamou (<em>Nothoprocta perdicaria</em>)</td>
<td>458g</td>
<td>2</td>
<td>0.12</td>
<td>0.19</td>
</tr>
<tr>
<td>Crested Tinamou (<em>Eudromia elegans</em>)</td>
<td>660g</td>
<td>2</td>
<td>0.16</td>
<td>0.22</td>
</tr>
<tr>
<td>Chukar (<em>Alectoris chukar</em>)</td>
<td>673g</td>
<td>3</td>
<td>0.15</td>
<td>0.21</td>
</tr>
</tbody>
</table>
Figure Legend

Figure 2.1

Modern avian phylogeny as adapted from Sibley and Ahlquist (1990). Ratites (a clade that includes ostrich, emu, rhea, cassowary and kiwi) are secondarily flightless terrestrial birds that have primitive shoulder morphologies and reduced pectoral musculature. The orientation of their glenoid cavity (the point of articulation between the humerus and scapulocoracoid) is lateral. Restrictive bony labia, coupled with potential neuromuscular limitations, prevent excursion along the dorso-ventral plane. Tinamous, which are capable of weak bouts of short flight have a dorso-laterally oriented glenoid. Both the scapula and the coracoid contribute equally to the articular surface of the glenoid cavity. Chukars exhibit a more pronounced dorsal orientation of the glenoid than tinamou due to a reduced scapular facet and proportionally larger coracoidal facet. This transition in glenoid orientation is proposed to mirror the transition from a sprawling, asymmetrical forelimb use the dorso-ventral flapping needed for flight.

Figure 2.2

Hindlimb kinematics of study species on their maximum inclines. (A) Duty factors of species on maximum inclines. Duty factor is the fraction of the stride period that the foot is in contact with the substrate. Generally, the large bodied ratites spent longer with their foot in contact with the ground on their maximum inclines. (B) Average relative stride lengths of the study species on their maximum inclines. Emu and Ostrich took relatively shorter steps on inclines than did the other, smaller bodied species. (C)
Relative step lengths were similar across species on their maximum inclines. (D)

Relative frequency was similar across species on maximum inclines.

Figure 2.3

Comparative incline performance and kinematics. In general, species that showed the greatest performance on inclines were those species that pitched their bodies forward into the substrate to the greatest degree. As show in (A), mean body angle increased as the incline increased, and the chukars, while being able to climb the steepest slopes, also had the greatest mean body angles in relation to substrate. Within each species, the mean body angle increased as the substrate angle increased, indicating a positive correlation between body angle and incline performance. Wing use is also positively correlated with incline performance across species. While both asymmetrical and symmetrical wing recruitment was observed in the study species, symmetrical wing use was seen in those species able to traverse the steepest slopes. Tinamou recruited their wings asymmetrically on inclines except at the upper limits of their performance, when they transitioned to a symmetrical pattern. Chukars used wing assisted incline running (WAIR) on slopes steeper than 60°.

Figure 2.4

Ratite incline performance varied across age classes and was correlated with wing excursion angles and relative wing size. (A) Emu had a maximum incline performance of 45° which was where their performance plateaued at 4 months. Rheas were ultimately capable of ascending inclines of up to 65° at 9 months of age. Ostrich were only used in
this study up to the age of 5 months because their large size created a danger to both the animals and their human handlers. Ostriches develop extremely quickly, and by 5 months they were nearly 5 feet tall. At five months they were able to ascend inclines of 60°. Both wing size and wing use were positively correlated with performance. Both rheas and ostriches recruited their large wings on inclines and the wing excursion angles (B) mirrored their performance capabilities, in that rheas had greater wing excursion and were able to ascend slightly steeper inclines.

Figure 2.5

Comparative wing kinematics in chukars and tinamous across incline angles. Chukars means are indicated by closed boxes, Crested tinamou means are indicated by open boxes. (A) All birds increased their angle of attack as incline angle increased. Chukars are capable of greater angles of attack, due in part to the greater forward pitch of their bodies as they ascend inclines. Tinamous also modulate their attack angle as incline increases. (B) Stroke angles were variable in tinamous across inclines, due in part to their transition from an asymmetrical pattern of forelimb use to a more symmetrical flapping at steeper inclines. On steep inclines their stroke angle was greater than chukars, indicating a more dorso-ventral orientation to their wingstroke. Wingstroke angle was negatively correlated with incline steepness in chukars, meaning that as the incline increased, chukars oriented their symmetrical wingstroke in a more antero-posterior plane, effectively bringing their wings through a wingstroke plane that would orient aerodynamic forces towards the substrate. The incident angle (C) appears to be highly conserved across angles in chukars, while being much more variable in the tinamous.
Figure (D) shows an actual representation of a chukar on a 70° and a 90° incline, with the angles depicted from actual data, and with the angles illustrated as measured.
Average Relative Stride Lengths on Maximum Inclines

Relative Step Length

Relative Frequency

Figure 2.2
Figure 2.3

A. Mean Body Angle in Relation to Substrate

B. Differential Incline Performance
Figure 2.4

A

Ontogeny of Ratite Incline Performance

B

Wing Excursion Angle on Maximum Incline
### Appendix 1

#### Table A1.1

<table>
<thead>
<tr>
<th>Hindlimb Kinematic variables</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stride Period</td>
<td>Length of time that the entire stride cycle takes to complete from initial toe touchdown to following toe touchdown of the same leg.</td>
</tr>
<tr>
<td>Stride Frequency</td>
<td>Number of strides per second</td>
</tr>
<tr>
<td>Duty factor</td>
<td>Fraction of the stride period that the foot is in contact with the ground.</td>
</tr>
<tr>
<td>Stride Length</td>
<td>Velocity divided by the stride frequency</td>
</tr>
<tr>
<td>Step Length</td>
<td>Distance between the hip points at “toe on” and “toe off”</td>
</tr>
<tr>
<td>Relative Stride length</td>
<td>Stride length divided by the animal’s average hip height.</td>
</tr>
<tr>
<td>Relative Step length</td>
<td>Step length divided by the animal’s average hip height.</td>
</tr>
<tr>
<td>Limb Protraction Angle (α)</td>
<td>The angle created between the vertical hip height of the animal, and the hip and metatarsophalangeal joints at the beginning of the stance phase of a stride (toe on).</td>
</tr>
<tr>
<td>Limb Retraction Angle (β)</td>
<td>The angle created between the vertical hip height of the animal, and the hip and metatarsophalangeal joints at the end of the stance phase of a stride (toe off).</td>
</tr>
<tr>
<td>Limb Excursion Angle (θ)</td>
<td>α + β Indicated as a measure of the hindlimb excursion during the stance phase of a stride.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Forelimb Kinematic Variables</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wingstroke Plane</td>
<td>The plane of travel of the wingtip during the downstroke</td>
</tr>
<tr>
<td>Wingstroke Angle</td>
<td>The angle between the wingstroke plane and the substrate</td>
</tr>
<tr>
<td>Body Angle</td>
<td>The average angle created between a line connecting the shoulder and hip of the animal, and the substrate</td>
</tr>
<tr>
<td>Wing Excursion Angle</td>
<td>The angle created between a line connecting the shoulder and hip of the animal, and the shoulder and wrist of the forelimb.</td>
</tr>
</tbody>
</table>
Figure Legend

Figure A1.1
Illustration of angles and distances and measured from dorsal and lateral views.
Figure A1.1

Dorsal View

Lateral View

Theta = Alpha + Beta
### Hindlimb Joint Excursion on a Horizontal Substrate

<table>
<thead>
<tr>
<th>Species</th>
<th>$\alpha$±(SEM)</th>
<th>$\beta$±(SEM)</th>
<th>$\theta$±(SEM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhea</td>
<td>35°±5</td>
<td>32°±12</td>
<td>67°±9</td>
</tr>
<tr>
<td>Ostrich</td>
<td>29°±7</td>
<td>30°±5</td>
<td>59°±4</td>
</tr>
<tr>
<td>Emu</td>
<td>32°±5</td>
<td>28°±8</td>
<td>60°±7</td>
</tr>
<tr>
<td>Tinamou</td>
<td>30°±2</td>
<td>25°±7</td>
<td>55°±5</td>
</tr>
<tr>
<td>Chukar</td>
<td>30°±2</td>
<td>32°±5</td>
<td>62°±5</td>
</tr>
</tbody>
</table>

### Hindlimb Joint Excursion on Maximum Incline

<table>
<thead>
<tr>
<th>Species</th>
<th>$\alpha$±(SEM)</th>
<th>$\beta$±(SEM)</th>
<th>$\theta$±(SEM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhea</td>
<td>18°±7</td>
<td>45°±9</td>
<td>63°±8</td>
</tr>
<tr>
<td>Ostrich</td>
<td>11°±4</td>
<td>32°±3</td>
<td>43°±4</td>
</tr>
<tr>
<td>Emu</td>
<td>14°±5</td>
<td>30°±5</td>
<td>44°±5</td>
</tr>
<tr>
<td>Tinamou</td>
<td>15°±5</td>
<td>42°±3</td>
<td>57°±5</td>
</tr>
<tr>
<td>Chukar</td>
<td>5°±2</td>
<td>45°±7</td>
<td>50°±6</td>
</tr>
</tbody>
</table>
Figure Legend

Figure A2.1

Representative hind limb kinematics graphically represented during the stance phase of horizontal and maximum ascents for ratites, tinamous and chukars. I scaled limb lengths to normalize size differences between limb segments as well as intra- and interspecific size differences. The birds appear to be using their legs in a similar fashion on steep inclines.
Figure A2.1

Emu Horizontal

Rhea Horizontal

Ostrich Horizontal

Tinamou Horizontal

Chukar Horizontal

Emu Inclined 45°

Rhea Inclined 65°

Ostrich Inclined 60°

Tinamou Inclined 75°

Chukar Inclined 90°