第六单元改写任务的全文背景

Abstract

Background

Birds share many traits with their dinosaur ancestors, making them the best living group to reconstruct certain aspects of non-avian theropod biology.

Living birds, however, maintain an unusually crouched hindlimb posture and locomotion powered by knee flexion, in contrast to the inferred primitive condition of non-avian theropods: more upright posture and limb movement powered by femur retraction【注：股骨收缩】.

Problem

Such functional differences, which are associated with a gradual, anterior shift of the centre of mass in theropods along the bird line, make the use of extant birds to study non-avian theropod locomotion problematic.

Results

Here we show that, by experimentally manipulating the location of the centre of mass in living birds, it is possible to recreate limb posture and kinematics inferred for extinct bipedal dinosaurs. Chickens raised wearing artificial tails, and consequently with more posteriorly located centre of mass, showed a more vertical orientation of the femur during standing and increased femoral displacement【注：股骨位移】 during locomotion. Our results support the hypothesis that gradual changes in the location of the centre of mass resulted in more crouched hindlimb postures and a shift from hip-driven to knee-driven limb movements through theropod evolution.

Conclusion

This study suggests that, through careful experimental manipulations during the growth phase of ontogeny, extant birds can potentially be used to gain important insights into previously unexplored aspects of bipedal non-avian theropod locomotion【注：两足、非鸟类、兽脚亚目动物的运动】.

Introduction

Based on multiple lines of evidence, it is now widely accepted that birds evolved from bipedal theropod dinosaurs. Birds have inherited numerous locomotory traits from their dinosaur ancestors, including bipedalism【注：用两足运动，二足性】, fully erect posture, and parasagittal hindlimb movement, which are not shared with the other extant group of archosaurs, the crocodilians.

Therefore, it is appealing to think of birds as a model system to gain insights into aspects of non-avian dinosaur biology that are hard to study directly from fossil material, such as the relationship between limb morphology, posture, and locomotion. However, non-avian theropods differ from birds in other traits, cautioning the direct use of extant birds to study non-avian theropod locomotion. Some of these differences are related to the evolutionary shift in the location of the centre of mass (CoM) through theropod evolution, from a posteriorly located CoM in non-avian theropods to a more anterior CoM in birds, due to the progressive enlargement of the pectoral limb. For a biped to balance at mid-stance, the feet must be placed directly underneath the CoM, so the location of the CoM is a major factor influencing limb orientation at mid-stance. Consequently, birds have unusually flexed postures at mid-stance, with a highly flexed hip and horizontal femur, and feet placed cranial【注：颅骨的】 to the hip. In addition, bird bipedalism is often characterized as ‘knee driven’, where most of the hindlimb movement is achieved by knee flexion powered by strong ‘hamstring’ muscles. In contrast, it has been hypothesized that non-avian bipedal dinosaurs had more vertical femora due to the more posteriorly located CoM, and that their hindlimb movement was ‘hip-driven’, powered mainly by the caudofemoralis longus muscle (CFL). The CFL is a large muscle that extends from the tail to the proximal femur and knee, powerfully retracting the femur, and it is expected to have produced larger femoral range of motion in extinct dinosaurs than in birds.

(第六单元改写段落) But, although some researches/literatures look like they see a huge correlation between changes in morphology and postural and locomotor traits in birds, while researchers from all over the world didn’t get any direct experimental evidence for that until now. Actually, only one experimental study, to the knowledge of all of us, has tried really hard to figure out about the relationship between CoM and postural and kinematic changes in birds. In an integrative analysis of posture, limb kinematics, bone loading patterns and so on, Carrano and Biewener stuck artificial tails to chickens. In that way, the CoM went a bit more caudally【注：向后地，向尾部或身体后端】. Doing this, they hoped to kind of imitate theropod-like limb posture, locomotion and other such things.Amazingly, their study got totally unexpected results: birds with tails stuck to them had even more horizontally oriented femora. Though they didn’t get qualitative changes in kinematics during locomotion compared to chickens that hadn’t been manipulated.

Here we present a modified study, based on Carrano and Biewener's experiments, in which we attached more realistic artificial tail to chickens shortly after hatching, and allowed proper exercise during ontogeny. We expected adult chickens with added tails to show a more vertical femur in standing position and increased femoral excursion during locomotion as postulated for non-avian theropod dinosaurs.

Results

In standing position, experimental subjects showed a limb posture with a more vertically oriented femur and a more horizontally oriented tibiotarsus, due to a more flexed ankle joint. During slow walking, significant differences in kinematics were observed among treatments. At the end of the stance phase, the knee joint was more extended in the experimental group (102.0±2.1 deg) than in the control group (83.3±6.0 deg). This resulted in reduced range of knee flexion during the stance phase in the experimental subjects compared to the control group (E: 30.1±3.4 deg; C: 41.3±3.1 deg). The ankle joint of experimental subjects was also more extended than that of the control group at both the onset (E: 138.7±2.1 deg; C: 128.8±2.6 deg) and offset of the stance phase (E: 152.4±1.9 deg; C: 136.0±4.9 deg). Limb segmental angles also showed differences among treatments. Of all the limb segments, the femur showed the largest difference between control and experimental conditions. In experimental subjects, the femur was more protracted【注：伸展】 at the beginning of the stance phase and more retracted at the end of the stance phase than subjects in the control group. As a consequence, the femoral range of motion of experimental subjects during the stance phase was almost three times larger than that of control subjects (E: 43.7±0.8 deg; C: 15.4±0.5 deg).

It is possible that postural and kinematic changes observed in experimental subjects were the result of increased weight and not change in CoM location. However, no postural changes were observed between the control-weight group and the control group during standing. During slow walking, the results are a bit more complex. At the beginning of stance phase, knee angle and femur orientation were significantly different in both the control-weight and experimental groups with respect to the control group, suggesting that the added mass of tail was responsible for the kinematic changes. For all other joint and segmental angles, the control-weight group showed either no changes with respect to the control group (e.g., knee angle) or the changes were opposite to the changes observed in the experimental group. For example, femur orientation in the control-weight group was consistently more horizontal than in the control group through the stance phase, but with similar amount of range of motion (C: 15.4±0.5 deg; CW: 15.2±1.5 deg).

No differences among groups were found in neither antero-posterior (AP) nor medio-lateral (ML) femoral cross-sectional geometry. Femoral length, however, tended to be larger in the experimental group than in the control groups, but this difference was only marginally significant (p=0.057).

Discussion

We have shown that the addition of an artificial tail during ontogeny can produce postural and locomotory changes in chickens, consistent with the posture and kinematics inferred for non-avian dinosaurs. The posterior displacement of the CoM produced a more vertically oriented femur during standing (femur in experimental animals was 40% more vertical than control subjects), and increased femoral retraction and decreased knee flexion during walking. These results indicate a shift from the standard bird, knee-driven bipedal locomotion to a more hip-driven locomotion, typical of crocodilians (the only other extant archosaur group), mammals, and hypothetically, bipedal non-avian dinosaurs.

These postural and kinematics changes cannot be attributed to an increased weight as subjects of the control-weight group did not show the same changes as the experimental group. In fact, the control-weight subjects showed a more horizontally oriented femur during walking with respect to the control group, similar to that observed in Carrano and Biewener's experimental subjects. Therefore, we conclude that the location of the CoM can be a key factor in defining limb posture and kinematics. It has been proposed that the relative mass of the CFL can be used as a proxy to estimate the relative importance of femoral retraction during locomotion in extinct bipedal dinosaurs. Our data show that for a given CFL mass, femoral retraction can be greatly affected by the location of the CoM and limb postures.

Differences in limb orientation can produce substantial differences in loading regimes on limb bones. The orientation of each limb element to the ground reaction force (GRF) indicates the relative contribution of axial and bending forces to external bone loading: a bone perpendicular to the GRF is expected experience greater bending forces than one parallel to the GRF. Because bone adapts to its loading environment, geometric information from limb bones, such as lengths and cross-sectional geometry, are expected to reflect differences in loading regimes and consequently in behavior and locomotor patterns. In this framework, scaling differences in femoral geometry between non-avian theropods and birds have been suggested to be the result of postural differences between these groups. Birds have relatively shorter, stouter femora than non-avian theropods, presumed to be associated with more horizontal orientation. Experimental manipulations of femoral orientation in chickens suggest that torsional loads【注：扭转负荷】 increase as the femur becomes more horizontal supporting the idea that postural differences could be reflected in differences in limb cross-sectional geometry. To test if the postural differences observed in this study produced changes in limb morphology, we measured the length and mid-shaft cross-sectional properties of the femur in all our individuals. However, we found no differences in cross-sectional femoral geometry among groups. Maybe this is not surprising considering that a recent study analyzing the relationship between posture and femur cross-sectional properties failed to find differences between birds and non-avian theropods, suggesting that simple morphological correlates of limb posture should be used with caution. Interestingly, femur length tended to be greater in the experimental group than in both the control-weight and the control group (by 4 and 7%, respectively), although not signifcant. Longer limbs are expected to experience larger bending and torsional moments, so the fact that experimental animals had longer femora suggests that limb verticalization reduces these moments by orienting the bone more parallel to the GRF line of action. If this were the case, it would support the idea that non-avian theropods have relatively thinner femora than extant birds because of postural differences.

Due to the phylogenetic【注：系统发育】 relatedness, extant birds have been used to inform functional aspects of non-avian dinosaur locomotion. However, substantial differences in hindlimb morphology between these groups make difficult to assess the validity of inferences obtained from such studies. It has even been proposed that, due to functional convergence, mammals might be a better system to study bipedal dinosaur locomotion, but the results reported here show that important aspects of non-avian theropod locomotion can be experimentally recreated in modern birds. One caveat, however, is that our approach uses tail reduction as the mechanism for CoM displacement despite it has been recently shown that the evolutionary change in CoM position was driven instead by forelimb enlargement.

We argue that our experimental approach, although not perfect, was effective in displacing the CoM and recreating locomotor patterns expected in non-avian theropods. Thus, we expect that careful phenotypic manipulation of extant birds can open new avenues of experimental investigation into unexplored facets of dinosaur locomotor mechanics and energetics, providing a more nuanced understanding of the relationship between form and function in dinosaur evolution.