Avian bipedal locomotion

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Abstract: Birds represent the vast majority of bipedal species. The avian bipedal locomotion project aims to characterize the functional morphology and biomechanics of small birds in order to distinguish common principles of avian bipedalism in contrast to 'the other bipedal species' (humans). The paper introduces the project and ongoing experiments.

Keywords: Locomotion, birds, x-ray motion analysis, force plate, biomechanics, inverse dynamics analysis

1. INTRODUCTION

Not only humans are able to move bipedally. Most of the approximately 10.000 species of bird are able to efficiently locomote on the ground by their hindlimbs. They do so although the hindlimbs display a surprisingly variable array of specializations. These include highly variant limb element proportions, and the presence or absence of swimming, climbing or cursorial specializations to differing habitats. Moreover, birds vary from less than 10g to 150.000g in body weight. Therefore, birds represent an ideal testbed to study the morphological and biomechanical characteristics of bipedal terrestrial locomotion.

However, some obvious differences to the bipedal gait of humans exist. Due to a cranially shifted center of mass (CoM), the thigh is oriented sub-horizontally to position the feet beneath the CoM [1]. Evolutionary changes of the distal hindlimb likely related to the adoption of active flight have lead to further modifications of the hindlimb elements. The hindlimb of modern birds comprises of the thigh, tibiotarsus (TT), tarsometatarsus (TMT), and the phalanges. In contrast to humans, the heel and middle foot, i.e., the TMT, do not contact the ground during locomotion. The knee acts as the main fulcrum of limb retraction [2]. In birds, movements in the knee contribute to progression more than the hip [3]. Whereas the ankle joint contributes to step length in humans, it is doing so only at very high speeds in birds [3]. Moreover, in humans the transition from walking to running is reflected by a change of the kinetics of the CoM and the footfall pattern [4]. In contrast, birds transition from kinetic walking to running without a change of the footfall pattern [5]. Only at very high speeds an aerial phase is adopted [3]. Thus, three basic avian gaits can be defined: (i) walking, (ii) grounded running with a double support phase, and (iii) running without a double support phase.

Data for avian bipedalism is limited to ground dwelling, terrestrially adapted birds. Therefore the high variability of the group and especially smaller, less terrestrial species are chronically underrepresented.

In the avian bipedal locomotion project we aim to characterize the terrestrial locomotion of small birds from the perspectives of functional morphology and biomechanics in a comparative approach. We designed experiments that will help us to scrutinize body-mass and hindlimb proportions related effects on the characteristics of avian terrestrial locomotion to better reflect the variability of birds. Moreover, we study aspects of the movements of the CoM and self-stability. Additionally, we plan to conduct perturbation experiments in order to gain an understanding of the adaptability of avian bipedal locomotion.

2. APPROACH AND METHODS

In birds, proximal hindlimb elements are covered by feathers, wings, and musculature (Fig. 1). Therefore, we use x-ray motion analysis for a detailed three-dimensional (3D) kinematic description *via* direct observation of bone movements *in vivo*. To this end, we record synchronized high-speed x-ray movies in the latero-lateral and ventro-dorsal projections in two experimental situations: (i) during steady-state locomotion on a treadmill that allows us to record a great range of speeds, and (ii) while traversing two custom-built force plates positioned in front of the image intensifiers (Fig. 1). The latter setup allows us to simultaneously record six degrees of freedom (6dof) substrate reaction forces (SRFs) and torques produced by individual limbs. The dataset will subsequently be used to analyze 3D inverse dynamics and aspects of self stability. In the experiments both x-ray projections are 3D calibrated to assess *x*-, *y*-, *z*- coordinates of skeletal landmarks. Coordinates of the skeletal landmarks are used to obtain kinematic data of hindlimb elements and joints.

To establish our experimental setup and protocol we chose to use a well studied, easily available and terrestrially adapted small bird: the quail. Subsequently, a broad range of small bird species will be acquired from private breeders and trained to perform in our experiments.

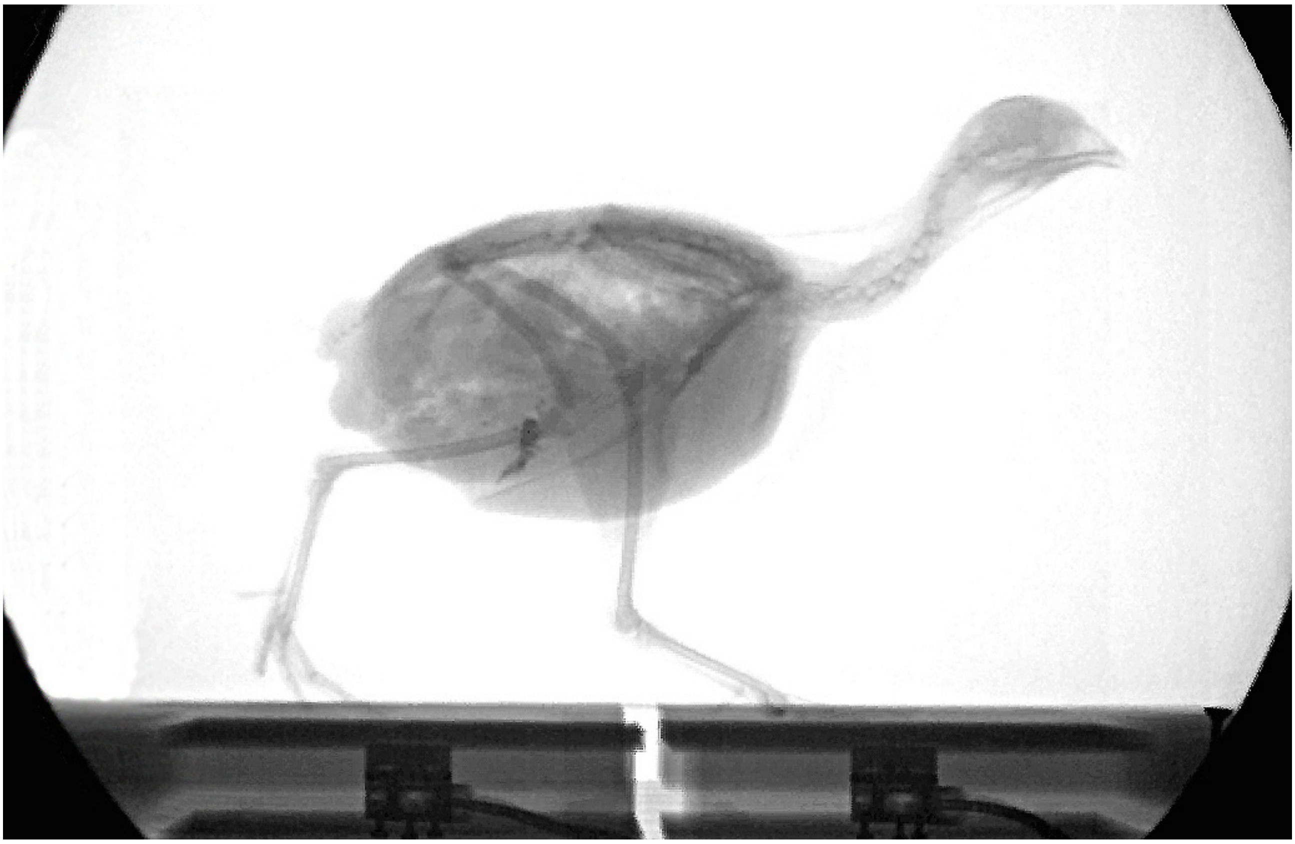

Fig. 1: Latero-lateral x-ray projection of a quail traversing two custom-built force plates. The experiment integrates kinematic and kinetic data.

Body-mass related effects are studied using a ‘domestic scaling system’ – different breeds of chicken. Chicken can be considered as geometrically similar. At the same time, the smallest breeds weigh 10 times less than the heaviest. Thus, in a comparative study the effects of body-mass can be studied while minimizing other influences.

The effects of differing hindlimb proportions are studied within waders which exhibit extremely variant hindlimb proportions, despite close phylogenetic relationship as well as similar body size and weight. We already started experiments with relatively long-limbed Northern lapwing. In contrast, we will also study oyster catchers that have a relatively short TMT and stilts that have an extremely elongated TMT.

3. EARLY RESULTS AND OUTLOOK

The need for the usage of x-ray motion analysis is illustrated by the recording of considerable movements of the thigh during our experiments. On the treadmill a tenfold speed range is easily achieved in all species tested so far. The combination of SRF measurement and kinematics allows us to reconstruct center of pressure paths beneath the feet and movements of the CoM. These data are currently used for a three-dimensional inverse dynamics analysis. Moreover, the effect of speed-dependent head movements (“head-bopping”) on the movement of the CoM is determined.

The comparative approach will help to formulate common principles of bird bipedalism and lead to a better understanding of functional and biomechanical differences and similarities between birds and humans. Future experiments will include perturbations to provoke compensating movements in order to gain an understanding of the adaptivity of avian bipedalism.

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