Locomotor Adaptations in the Hindlimbs of Owls: the Burrowing Owl (*Athene cunicularia*), compared to the Little Owl (*Athene noctua*)

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ABSTRACT - The present study provides an attempt to evaluate some morphological adaptations for terrestrial locomotion in the Burrowing Owl (*Athene cunicularia*). The Little Owl (*Athene noctua*), which is commonly considered a relatively generalised member of the genus, has also been examined for comparisons. Morphological features of the hind limb of the Burrowing Owl revealed by this analysis are interpreted as a consequence of adaptations for high-speed terrestrial locomotion and probably for digging. These adaptations are expressed, for example, in the elongation and thinning of the distal limb elements, promotion of the rotational expanse of the shank and foot, and shifting of muscle bellies in a proximal direction. However, level of the morphological modifications is greatly limited by a necessity to retain basic functional morphological specificity of the hind limb in these taxa. These adaptations, at least in owls, appear to be effective "tools" for prey capture. Some results of the current study can be partly extrapolated to other avian groups because of the fact, that some adaptations of hind limb morphology, associated with a terrestrial life-style, are universal.

Key words *- Strigidae, functional morphology, terrestrial locomotion, hind limb, myology, osteology.*

Adaptations locomotrices dans le membre postérieur des chouettes : la Chevêche des terriers (*Athene cunicularia*) comparée à la Chouette chevêche (*Athene noctua*) - La présente étude tente d'évaluer certaines adaptations morphologiques à la locomotion terrestre chez la Chevêche des terriers (*Athene cunicularia*). La Chouette chevêche (*Athene noctua)*, généralement considérée comme un membre relativement généralisé du genre, a aussi été examinée pour comparaison. Les caractères morphologiques du membre postérieur de la Chevêche des terriers révélés par cette analyse sont interprétés comme la conséquence d'adaptations à la locomotion terrestre à grande vitesse et probablement au fouissage. Ces adaptations s'expriment par exemple par l'allongement et l'amincissement des éléments distaux du membre, la promotion du champ de rotation du jarret et du pied, et le déplacement des masses musculaires en direction proximale. Cependant, le niveau des modifications morphologiques est fortement limité par la nécessité de conserver la spécificité morphofonctionnelle du membre postérieur chez ces taxons. Ces adaptations, au moins chez les chouettes, paraissent être des « outils » efficaces pour la capture des proies. Certains résultats de cette étude peuvent être partiellement extrapolés à d'autres groupes aviens parce que certaines adaptations de la morphologie du membre postérieur, associées à un mode de vie terrestre, sont universelles.

Mots-clés *– Strigidae, morphologie fonctionnelle, locomotion terrestre, membre postérieur, myologie, ostéologie.*

INTRODUCTION

Morphological modifications of the locomotor apparatus of the hind limb, that accompany the passage to a terrestrial life-style and thus speedy locomotion, have been described for representatives of many orders of birds (e.g., Storer, 1971; Raikow, 1985). Such morphological adaptations can also be used to increase our knowledge of the phylogenetic relationships among groups. Nevertheless, in publications on the hind limb myology and osteology of owls (Shufeldt, 1881, 1889; Hudson, 1937; Hoff, 1966; Ford, 1967; Ward *et al*., 2002), little information regarding the locomotor apparatus itself has appeared. This is surprising because a number of interesting fossil owls, particularly typical owls (Kurochkin & Mayo, 1973; Arredondo, 1976; Weesie, 1982; Mourer-Chauviré & Weesie, 1986; Olson & James, 1991; Arredondo & Olson, 1994; Mourer-Chauviré *et al*, 1999; Pavia & Mourer-Chauviré, 2002) that date to the Pleistocene and Holocene have been found on islands, in the absence of mammalian predators. It is also well known that several different owls lineages evolved gigantism, in most cases proceeding to a terrestrial life-style. It is therefore attractive to highlight some features of the functional morphology of this group in the context of cursorial adaptations. It is worth bearing in mind that it is quite possible for phylogenetic studies to encounter the misleading effects of convergent evolution (i.e., some anatomical features that may not be homologous); it is the opinion of the author that only functional investigations, infallible methods of morphological interpretation, can submit some comprehension

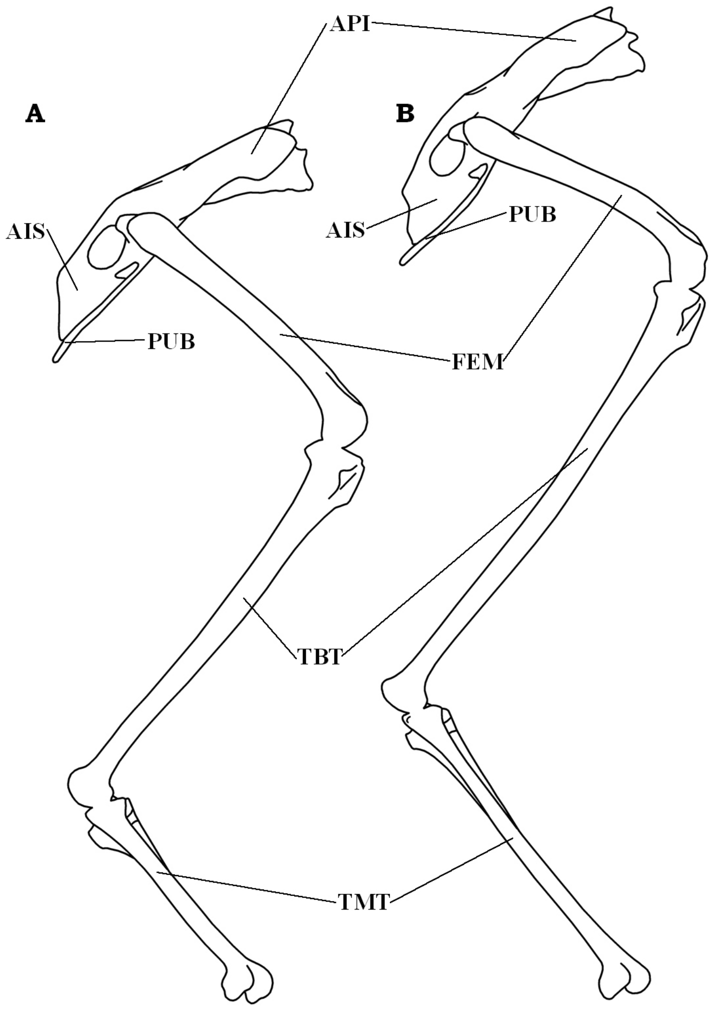

Figure 1 - The hind limb of the Little Owl (A) and Burrowing Owl (B) in lateral view: AIS – ala ischii, API – ala preacetabularis ilii, FEM – femur, PUB – pubis, TBT – tibiotarsus, TMT – tarsometatarsus.

to the phylogeny of these groups.

The purpose of this paper is thus to evaluate the adaptations for terrestrial locomotion that are seen in the hind limb morphology of the Burrowing Owl – *Athene cunicularia* (Molina, 1782), a taxon highly modified to a terrestrial life-style (Del Hoyo *et al*, 1999). Adaptations seen in this owl were then compared to those seen in the Little Owl, *A. noctua* (Scopoli, 1769), considered to be exhibit a more generalized morphology of its hind limbs. Pavia & Mourer-Chauviré (2002), for example, considered little owls to be one possible prototype of various terrestrial insular species, described from Pleistocene of the Mediterranean Islands.

MATERIAL AND METHODS

One carcass each of *Athene cunicularia* and *A. noctua* which were kindly provided by S.L. Olson, J. Dean (Smithsonian Institution) and K.B. Gerasimov (Moscow State University), along with skeletons of both species (from the osteological collection of the Paleontological Institute of the Russian Academy of Sciences) form the material for the present work.

Preparation and drawings of bones, ligaments and muscles were realized by means of binocular *Zeiss, Stemi SV6* with a camera lucida. The mass of each dried muscle was found to the nearest 1 mg with the removal of sesamoid bones. The relative mass of muscle reduces to mass of all muscles of the hind limb.

The present discussion is founded on the use of statics in graphical interpretation, which have produced good results as part of skeletal biomechanics analyses of mammals (Kummer, 1959) as well as in studies of the feeding apparatus of birds (Dzerzhinsky, 1972). All nomenclature follows Baumel *et al*. (1993).

RESULTS AND DISCUSSION

Elongation of the hind limb at the expense of lengthening the distal limb elements (especially the tarsometatarsus), in spite of reduction of the femur, is characteristic of the Burrowing Owl, as opposed to the Little Owl (fig.1). This relative elongation promotes an increase in step length

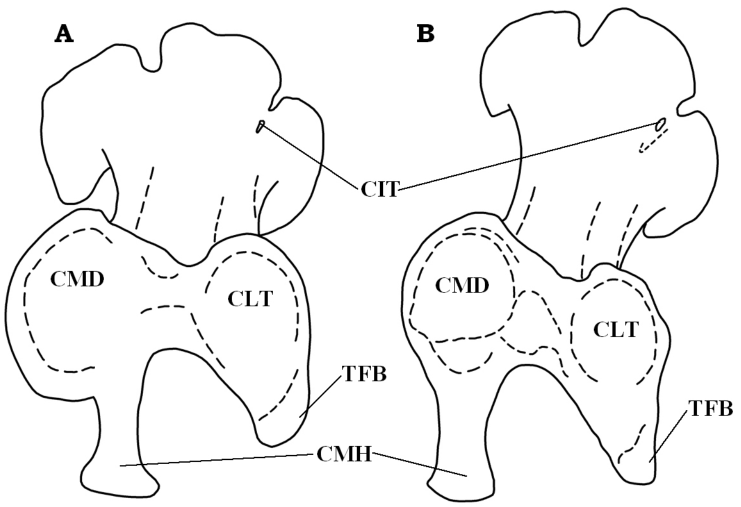

Figure 2 - Tarsomatatarsus of the Little Owl (A) and Burrowing Owl (B) in proximal view: CIT – canalis interosseus tendineus, CLT – cotyla lateralis, CMD – cotyla medialis, CMH – crista medialis hypotarsi, TFB – tuberositas m. fibularis brevis.

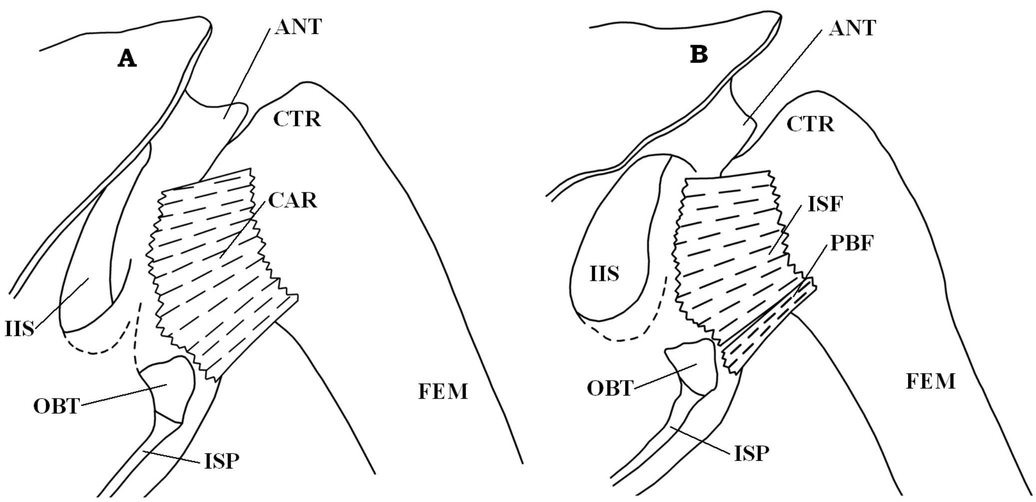

Figure 3 - The hip joint of the Little Owl (A) and Burrowing Owl (B) in caudal view: ANT – antitrochanter, CAR – capsula articularis, CTR – crista trochanteris, FEM – femur, IIS – foramen ilioischiadicum, ISF – lig. ischiofemoralis, ISP – membrane ischiopubica, OBT – foramen obturatum, PBF – lig. pubofemoralis.

in cursorial birds based on an assumption of the preservation of the same angles between skeletal elements;

Pavia & Mourer-Chauviré (2002) described an apparent tendency in the lengthening of the distal hindlimb elements in members of the genus *Athene* and correlated this with a transition to a terrestrial life-style. However, lengthening of the hind limb is just a precondition for increasing step length, not velocity of locomotion (Bennett, 1996).

On the other hand, the thinning of the skeletal limb elements (fig.1) and shifting of the muscle bellies of the shank in a proximal direction, characteristic of the Burrowing Owl as opposed to the Little Owl, is evidently connected with decreasing the moments of inertia in the limb during rapid back-and-forth movement. This trend then can be inferred as a contribution to increasing the velocity of locomotion.

The dorsally curved femur that is seen in the Burrowing Owl is characteristic of the majority of cursorial and swimming birds (Kurochkin, 1968; Raikow, 1985); this shaped bone is produced as a result of the counteracting femoral retractors and femorotibiales muscles that tend to bend the shaft ventrally. According to Kummer (1959), the shaft of the femur follows the trajectory of the sum vector of the forces affecting this bone.

Furthermore, a shift in the *linea intermuscularis cranialis* in a medial direction is also characteristic to the Burrowing Owl (the cranial intermuscular line originates from the lateral part of *crista trochanteris* in the Little Owl). This difference is a clear consequence of the increase in size (more that in 1.3 times) of the *m. femorotibialis medialis* in the Burrowing Owl, in comparison with the Little Owl.

The Burrowing Owl can also be characterized by a more ventrally bended and outwardly twisted tarsometatarsus (fig.2), again in comparison to the Little Owl. This ventrally curved tarsometatarsus is related to its resistance to the powerful *m. flexor digitorum longus* (the ratio of the weight of this muscle for the Burrowing Owl is 14.4%, as compared to 10.6% for the Little Owl). It's difficult to clarify the degree of outward torsion of the tarsometatarsus in these taxa, but probably these are produced as a result of counteraction in opposition to the above-mentioned muscle's force. Caribbean and West American populations of Burrowing Owls, in the absence of burrowing mammals, quite often excavate a

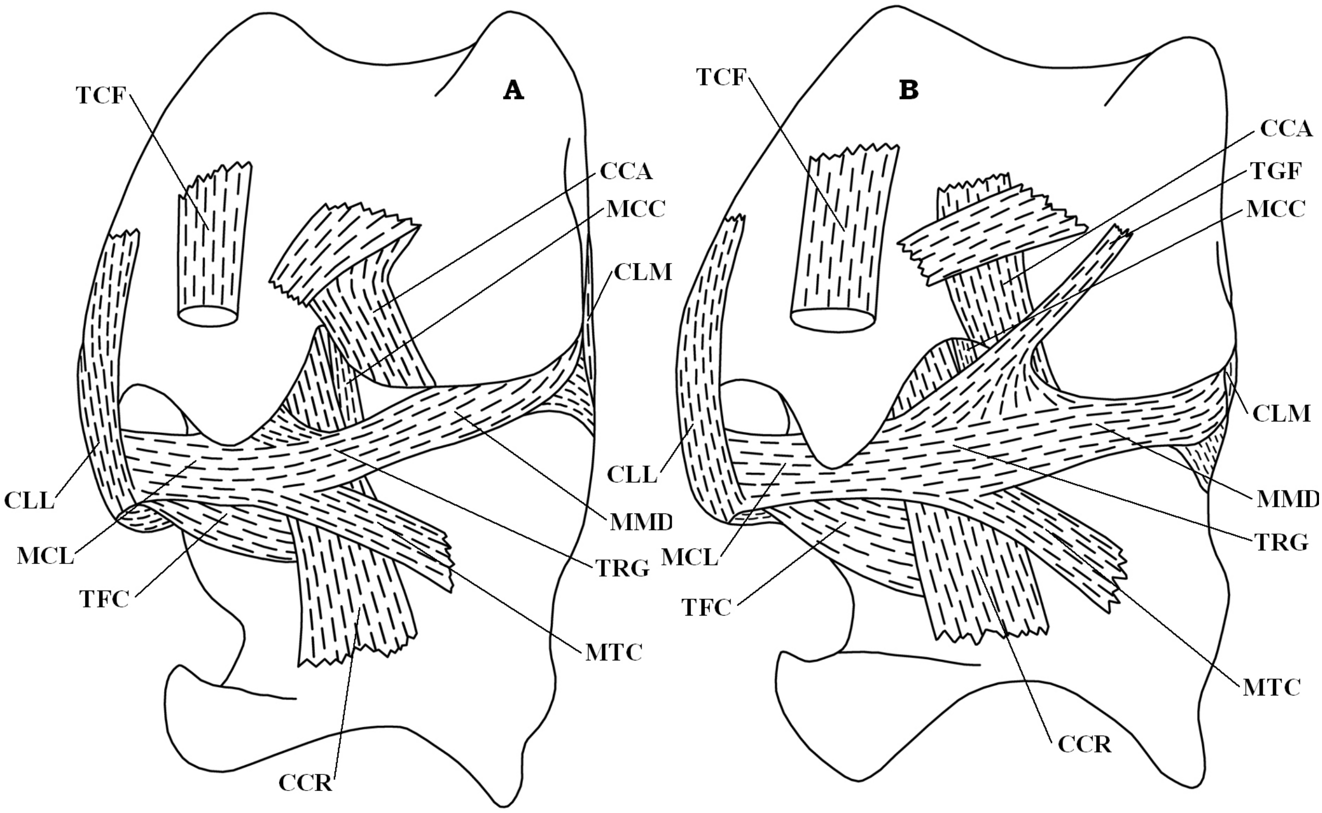

Figure 4 - Flexed ankle joint of the Little Owl (A) and the Burrowing Owl (B) in frontal view: CCA – lig. cruciatum caudale, CCR – lig. cruciatum craniale, CLL – lig. collateralle laterale, CLM – lig. collaterale mediale, MCC – meniscus medialis: cornu caudale, MCL – lig. meniscus collaterlalis, MTC – lig. meniscotibiale craniale, MMD – meniscus medialis, TCF – m. tibialis cranialis p. femoralis, TFC – lig. tibiofibulare craniale, TGF – lig. transv. genus: cornu femorale, TRG – lig. transversum genus.

burrow using their beak and limb (Thomsen, 1971), providing a mechanism to produce torsion. Similar design features of the tarsometatarsus have been noted for galliform birds, which are adapted for shoveling soil and vegetation (Sych, 1999).

Development of ossifications (sesamoids) in the long terminal tendons of *m. fibularis brevis, m. tibialis cranialis, m. extensor digitorum longus,* and *m. flexor digitorum longus* in the Burrowing Owl is due to a relative increase in jerky movements of these tendons as their negative extensibility is eliminated. During the trajectory of the run – for instance while hunting – accumulation of potential energy in extended tendons is a disadvantage (Alexander, 1984) because extra work is required to reduce the swinging of the emerging "pendulum motion". Bennett & Stafford (1988) showed that stiff regions of the tendon are less liable to deformation on stretching; such regions are thinner and lighter, when compared with unstiff regions of similar length. Overall, this functions to slightly lessen of the weight of the limb.

In addition, the horizontal orientation of the preacetabular ilium seen in the Burrowing Owl moves the *m. iliotrochantericus caudalis* ventrolaterally and thus places it in a more effective position for inward rotation of the hind limb. This is in spite of the side effects produced by the outward rotation of the femoral retractors during locomotory jerks.

Reduction in size of the antitrochanter and differentiation of the caudal part of the joint capsule (*capsula articularis*) into two ligaments (fig.3) – *lig. ischiofemoralis* and *lig. pubofemoralis*, is seen in the Burrowing Owl, as compared with the Little Owl (the caudal part of the joint capsule in this taxon is undivided). On the one hand, such reorganization acts to strongly abduct the femur and the whole leg; on the other its principal role is to limitfemoral abduction (especially in the protracted position). Abduction is transferred from the antitrochanter to the ligaments of the joint capsule; it is this differentiation that probably allows the Burrowing Owl to spread loads uniformly between the ligaments.

The *M. popliteus* of the Burrowing Owl is characterized by a lower level of maturity of the aponeurotic skeleton and by lengthening of fibers (in the Little Owl this muscle has a pinnate arrangement). This allows it to increase the amplitude of contractions and inwardly rotate the tibiotarsus more effectively (this muscle rotates the tibiotarsus in contractions inwardly rotating it respectively to the head of the fibula positioned on the lateral condyle of the femur (Gurtovoi & Dzerzhinsky, 1992)). The Burrowing Owl differs from the Little Owl in this respect in the possession of more asymmetrical distal condyles of the femur. This is evidently connected with the greater inward rotation of the shank during terrestrial locomotion enabling it to make abrupt turns of the body on one leg while running. The transverse ligament (*lig. transversum genus*) has a branch beginning from the medial condyle of the femur and in extended position of knee joint it limits the inward movement of the tibiotarsus. In the Little Owl this ligament branch is absent (fig.4).

Powerful development of *m. gastrocnemius* – the chief intertarsal extensor – should be taken into consideration. It accounts for 12.2% in the Burrowing Owl against 9.6% in the Little Owl.

Noted for the Burrowing Owl, shortening of *lig. transversum* (the ligament on the distal end of the tibiotarsus holding the terminal tendon of *m. tibialis cranialis*) reduces the arm of force of the muscle, thus enables to flex the intertarsal joint with greater angular velocity, but it is accompanied by reduction of the moment of force on the foot. Therefore the bulk of *m. tibialis cranialis* grows up to 10.2% for the Burrowing Owl vs. 9.3% for the Little Owl, thereby compensate for mentioned privation. Consequently, condition of this system in the Burrowing Owl becomes unusual, as compared with other typical owls (*lig. transversum* of within family Strigidae elongated in comparison with the same of the majority of other orders).

The lateral process of the hypotarsus in the Burrowing Owl projects in the lateroproximal direction and brings terminal tendon of *m. fibularis brevis* (fig.2) to a more advantageous position for inward rotation of the tarsometatarsus and stabilization of the intertarsal joint (ligament tension in it increases the jerkiness of movements). The terminal tendon of this muscle is ossified. These features undoubtedly are due to counteraction to outwardly rotation of the foot, what can be important during digging, and what is more this considerable extends rotational power of the foot as means of prey capturing.

A curious mode of hunting of the Little Owl was described by Schtegman (1960), when the bird caught the Great Gerbils (*Rhombomys opimus*) in their holes. This universality determined opportunity for further morphological experiments in new conditions: either in the absence of terrestrial predators and rivals (i.e. on islands) or with abundance of prey. In the latter case, restructuring leading, as a rule, to loss of some morphological features is justified (Dzerzhinsky & Korzun 1977). It can be observed in the example of the Burrowing Owl, whose cursorial adaptations gave it an access to considerable food resources and allows occupying new niche.

Some results of the current study might be extrapolated to other avian groups because of the fact, that some adaptations of limb morphology, associated with a terrestrial life-style, are universal.

CONCLUSION

Hind limb morphological features of the Burrowing Owl showed a deep adaptation to terrestrial locomotion and possible for digging. The first adaptation includes longer step length and potentially faster limb movements due to lengthening and thinning of the distal limb elements and shifting of the muscle bellies of the tibiotarsus in a proximal direction, as well as promotion of rotational expanse of the shank and increase of jerky movements at the expense of changing of level ratios and development of ossifications in tendons.

Adaptations for digging are possibly related to an increase in jerkiness of movements in the intertarsal joint (due to bringing the terminal tendon of *m. fibularis brevis* to a more advantageous position), and recreation of tarsometatarsus morphology, which allows to resist inward rotation of the foot more effectively. At the same time, some changes in morphological features characteristic for the majority of typical owls take place. This is expressed in the shortening of *lig. transversum* and the shifting in a proximal direction of the attachment point of *m. tibialis cranialis*.

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