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# SOME GENERAL NOTES ON THE AVIAN HINDLIMB BIOMECHANICS[1]

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Hind limbs, like other components of avian locomotor system, play an important role in defining a unique ecological niche, which, in turn, provides ecological segregation of species. Hind limbs make the bird able to move quite effectively and economically on various substrates as well as in the water. Features in the morphology of limbs clearly show specific morphological and ecological peculiarities of particular groups.

Trying to outline the scope of morpho-ecological approach for reconstruction of phylogenesis as a chain of successive adaptations, K.A. Yudin (1965) pointed out, that the perspective of this method strongly depends on the level of our knowledge of comparative anatomy and biomechanics of particular component of locomotor system. Its morphology, biomechanically analyzed, not only can bring an understanding of recent adaptations, but allows to build hypotheses on evolution of this system along with evolution of the entire group. Hind limbs furnish a researcher with a load of morphological facts, which can be interpreted using morpho-ecological approach. The main outcome of such an approach is the reconstruction of phylogeny.

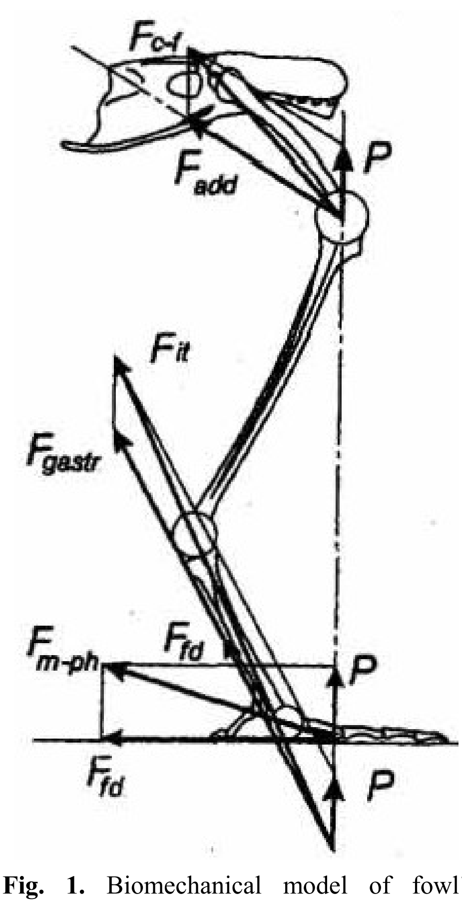


**Fig. 1.** Biomechanical model of fowl's (*Gallus gallus bankiva*) hind limb in the middle of the contact phase. Interaction of muscles' forces with GRF in parasagittal plane. Further explanations see in text.

Hind limbs of birds are brought into parasagittal plane. Important aspects of Z-shaped limbs of birds and mammals during contact phase have recently been discussed by A.N. Kuznetsov (1999). This author paid the main attention to the question of energy consumption during locomotion, although he has also touched a topic of muscles-skeleton interaction. In general, literature on functional morphology is overloaded with controversial and unclear assumptions. One of them is an opinion, that *m. iliotrochantericus caudalis* retracts the femur (Cracraft, 1971), whereas *antitrochanter* prevents breakage of its *collum.* The other is a statement, that *m. fibularis brevis* is powerful flexor (!) of intertarsal joint (Moreno, 1990) despite its strange insertion on tarsometatarsus. All mentioned discrepancies display a strong necessity to build more or less strict biomechanical model of avian hind limb. Present study gives a simplified model of avian hind limb along with biomechanical methods of its analysis.

Hind limbs of the fowl (*Gallus gallus bankiva* L.) have been taken as more or less generalized object. A number of poses during contact period of walking with constant speed have been selected: at the beginning of contact phase, in the middle (center of gravity projects on the point of contact) and at the end. Actual anglular values between elements have been defined by filming the 2-weeks chick (290 frames per sec.).

Statics (the first section of theoretical mechanics) in graphical interpretation has been used for analysis of the model. Such an approach has been used by Kummer (1959) for

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biomechanical analysis of mammalian skeleton. Later, it has been widely used in studying of jaw apparati of birds (Dzerzhinsky, 1972) and mammals (Nikolsky, 1997). Mentioned approach is graphical; forces of skeleton-muscular interactions are drawn as vectors over the picture of apparatus. This allows to combine a clearness of image with real geometry of object. Lengths of vectors are proportional to real values of forces. Interpretation procedure allows a free movement of vectors along lines of their actions.

## MECHANICAL MODEL OF AVIAN HIND LIMBS

A simplified mechanical model of hind limbs should first be build as an object of the functional analysis. Skeletal part of such a model includes four large and several smaller bones. They are pelvis, tibiotarsus, tarsometatarsus and phalanges of third digit. Fibula, metatarsale I and phalanges of other digits, although not utilized in the analysis, are also shown on drawings. Hind limb is treated as flat entity: its elements can rotate only around transverse axes, going through center of corresponding joints. The spherical hip joint has a point of rotation, thus requiring 3-dimensional treatment. This point is also moved medially from the parasagittal plane of the limb.

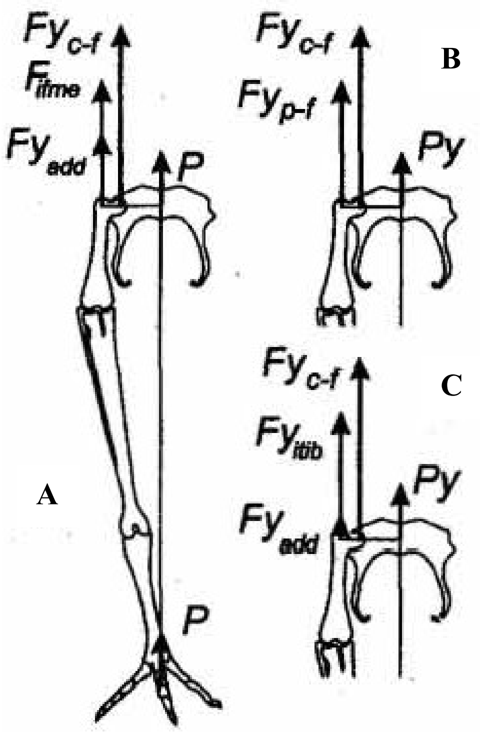


**Fig. 2**. Biomechanical model of fowl’s (*Gallus gallus bankiva*) hind limb in transverse plane in the middle of contact phase (A), at the beginning (B, fragment) and at the end (C, fragment). Control of balance in hip joint. Further explanations see in text.

For simplicity muscles are shown by vectors of forces. Following muscles have been used in the model:

1. Long muscle, posterior to femur, inserting on tibiotarsus (such as *m. flexor cruris lateralis*, or more steeply oriented *m. iliofibularis*).
2. Similarly oriented short muscle, which starts from the pelvis ventrally and inserts to the distal femur, such as *m. puboischiofemoralis*.
3. Short pelvic muscle, which originates on preacetabular ilium and inserts on lateral surface of proximal femur (such as powerful *m. iliotrochantericus caudalis*).
4. Short adductor of the limb, which goes over hip joint from *crista iliaca* to femoral trochanter (such as *m. iliofemoralis externus*).
5. Long extensor of knee – *m. iliotibialis lateralis*, which crosses knee joint, inserts on tibiotarsus and incorporates the patella.
6. Short extensor of knee, such as *m. femorotibialis medius.*
7. Flexor (of ventral extensor) of intertarsal joint, corresponding to medial portion of *m. gastrocnemius*.
8. Long flexor of toes (*m. flexor digitorum longus*), which starts on both bones of the shank, ventrally crosses intertarsal, metatarsophalangeal and interphalangeal joints and inserts variably on phalanges of fore toes.

Patella and joint cartilages increase radii of arcs, by which tendons cross the joints. To show this in the model, we drew circles of corresponding diameter around centers of each joint.

Center of gravity (CG) of fowl, like in other birds, is situated near the knee joint. The direction of ground reaction force (***P*** on drawings) has long been a matter of debates. As has been eventually shown, its angle is variable: it is slightly tilted back at the beginning of contact phase, vertical – at the middle and tilted forward at the end. Jayes and Alexander (1978) introduced so-called “target”, a point to which a ground reaction force is directed during entire contact phase. This point is situated slightly above the knee joint and corresponds to that, experimentally obtained for quail (Clark, Alexander, 1975).

## ANALYSIS OF FORCES DISTRIBUTION IN THE MIDDLE OF CONTACT PHASE

In the middle of the contact phase, ground reaction force (GRF) is vertical and goes trough the center of knee joint. We assume that it crosses the foot in proximal interphalangeal joint of digit III. Our aim is to figure out the position and values of forces necessary to compensate GRF (***P***) to keep the bird in equilibrium.

**Analysis of forces in parasagittal plain.** Let us start the analysis from the foot. Passing in front of metatarsophalangeal joint III, ***P*** tries to overextend the mentioned joint and should be compensated by $F_{fd}$. Vector of this force goes tangentially to the circle of the mentioned joint. Equilibrium is achieved if resultant force goes through the center of the joint. We draw it ($F_{m\text{-}ph}$) through the center of the joint and the point of intersection of two mentioned lines. Two lines and a segment, intersecting in the point, allow to draw parallelogram to determine a necessary force of contraction for long digital flexor.

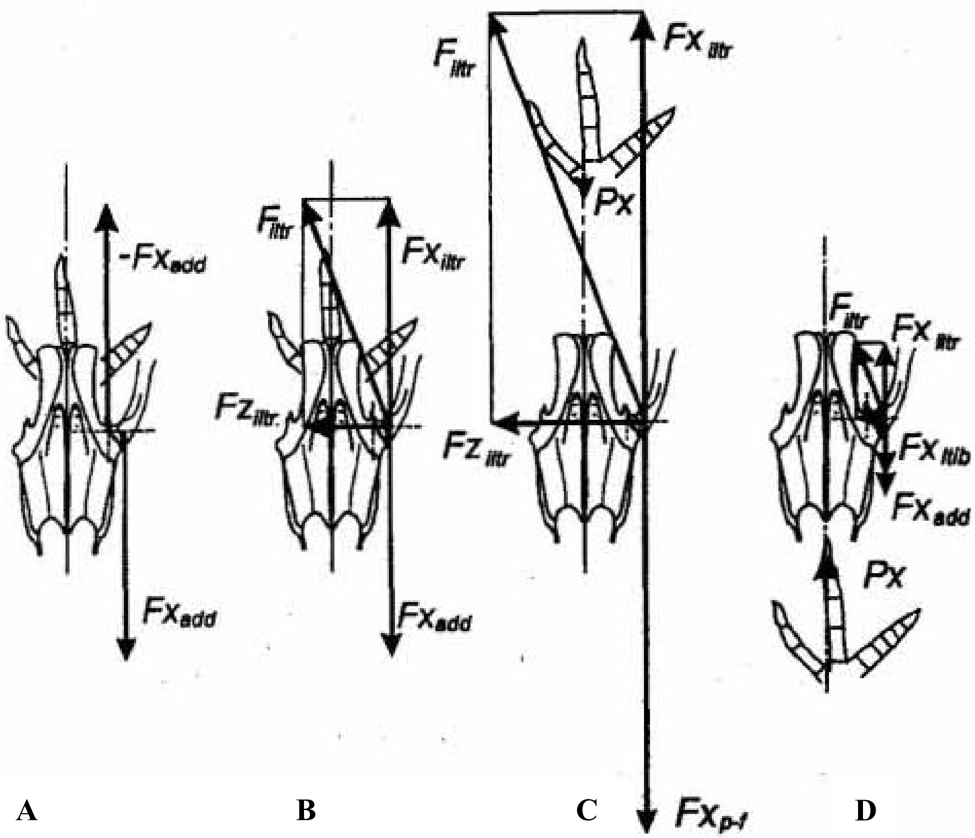


**Fig. 3**. Biomechanical model of fowl's (*Gallus gallus bankiva*) hind limb in frontal plane in the middle (A, B), at the beginning (C) and at the end (D) of contact phase. A – a couple of forces supinating the limb; B – neutralization of this effect by *m. iliotrochantericus*; C,D – control of rotational equilibrium of the limb. Center of hip joint is shown by the intersection of dotted lines. Further explanations see in text.

To determine conditions of equilibrium in intertarsal joint, we should draw a diagonal of future parallelogram ($F_{it}$) through the center of the joint, while muscular vector should correspond to the direction of terminal portion of Achillean tendon. This vector also corresponds to the tendon of long digital flexor if we neglect its closer position to the center of the mentioned joint. To keep an equilibrium, the contraction of gastrocnemius ($F_{gastr}$) is necessary to fill help $F_{fd}$.

Equilibrium in knee joint is achieved by itself, since vector of GRF goes directly through its center. Then the next goal is to balance a hip joint. The force of gravity, which passes forward in front of the mentioned joint, tends to protract it. This tendency should be compensated by the contraction of femoral retractor, such as *m. puboischiofemoralis*. It inserts on the femur, not being involved in the movement of the knee joint. Thus, the knee joint appears as a center of intersection of three vectors – GRF ***(P)***, adductoral force ($F_{add}$) and their resultant force ($F_{c\text{-}f}$).

**The problem of counteracting rotational forces.** We balanced a limb in parasagittal plane. However, force vectors ***P*** and $F_{add}$ lie in different planes. Both miss the center of hip joint. Each of them has a lever, producing a moments of rotation in transversal (fig. 2) and frontal (fig. 3) planes.

In transversal plane (fig. 2, A) the ground reaction force ***P*** goes vertically from the point of contact with the ground. It produces bending moments in all three considered joints of the limb. In knee and intertarsal joints, these forces are balanced by ligaments, which restrict their mobility. Moreover, medial flexion (adduction) in mentioned joints is prevented by laterally positioned muscles (such as *m. femorotibialis, m. fibularis longus*). Spherical hip joint does not have such restrictors. The danger of medial limb turn in relation to the body must me neutralized by force of muscles' contraction. The required force is determined by the combination of parallel forces: resultant force equals a geometrical sum of parallel vectors and is applied to the point, which divide a segment between points of their application inversely to their values. Abducing force $Fy_{add}$ is drawn along the longitudinal axis of femur, whereas the resultant $Fy_{c\text{-}f}$ in the equilibrium should go through the center of the femoral head. Above mentioned conditions allow to define the force $Fy_{add}$ necessary for the equilibrium. Because distances to the center of femoral head from sagittal plane and axis of femur relate to each other as 35 to 15, the value of the force should be about 2,3***P***. Fig. 2, A clearly shows that the value of vertical component of the mentioned force is higher, than that of $Fy_{add}$. Thus, to keep equilibrium an additional abducting force is necessary, which can be applied by external ilio-femoral muscle ($F_{ifme}$). If this muscle is too weak, than the similar effect can be achieved by the cumulative action of several other muscles.

The femoral collum has also a lever in frontal plane (fig. 3, A) for a couple of forces. These are a horizontal component of *m. puboischiofemoralis* ($Fx_{add}$) and an opposite force, exerted by the muscle to pelvis – $Fx_{add}$. These two forced tend to supinate femur and the entire limb.

Limb has a number of powerful pronators to compensate this tendency. First of all, it is a large *m. iliotrochantericus caudalis,* which exerts a force $F_{iltr}$ to the lateral surface of femoral trochanter (fig. 3, *C)*. This force neutralizes the effect of $Fx_{add}$. by its longitudinal component ($Fx_{iltr}$).

## ANALYSIS OF FORCES DISTRIBUTION AT THE BEGINNIGN OF CONTACT PHASE

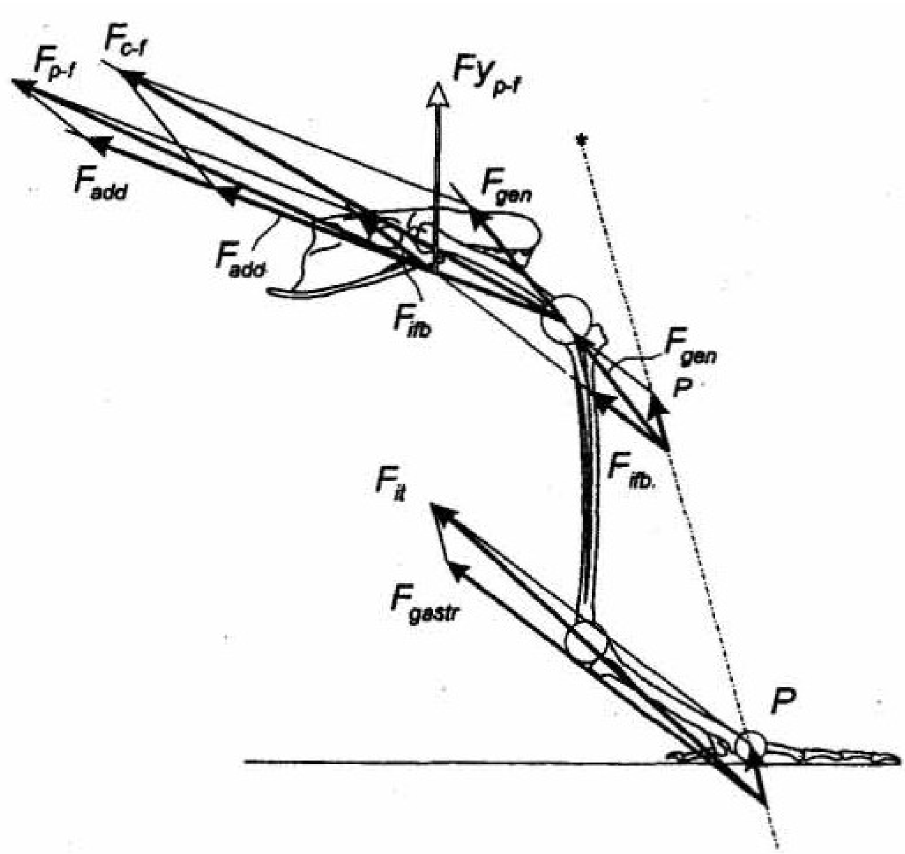


**Fig. 4.** Biomechanical model of fowl's (*Gallus gallus bankiva*) hind limb at thebeginning of contact phase. "Target" is shown by the asterisk. Further explanations see in text.

At the very beginning of the contact phase, the limb is maximally protracted (fig. 4), the knee joint is extended, fulcrum is close to the base of third toe and GRF (***P***) passes in front of the joint. The problem of balance in metatarsophalangeal joint does not exist, since ***P*** is passing through the center of this joint. The force distribution parallelogram for gastrocnemial muscle $F_{gastr}$, that provides a balance in the mentioned joint, is drawn as in the case of fig. 1 (for the combined force $F_{fd}$+$F_{gastr}$). Due to the absence of one-joint knee flexors in birds (like in most terrestrial vertebrates), two-joint flexors are used in balancing the discussed joint. Force vector of relatively steeply oriented *m. iliofibularis* is shown on fig. 4 ($F_{ifb}$), although a medial flexor of the shank can be used for this purpose. Parallelogram is build from the intersection point of muscle vector and GRF with resultant force ($F_{gen}$) going through the center of the knee joint. The next task is to balance this force in relation to the hip joint. A short femoral adductor – *m. puboischiofemoralis* ($F_{add}$) – is the most suitable for this. A resulting effect is regulated by *m. iliofemoralis* (since the lever of this muscle is shorter, it should exert more force to keep the balance). To proceed it is necessary to find a sum force of two (in other case – four) muscles, which retract a limb. We must sum force vectors $F_{ifb}$ and $F_{add}$ at the point of their intersection. Resultant force ($F_{p\text{-}f}$) has a significant vertical component ($Fy_{p\text{-}f}$) to balance a pelvis in transverse plane, thus neutralizing its tilt. A selection of required combination $F_{ifb}$ and $F_{add}$ is possible due to the shifts in their angles. In frontal plane, a horizontal component of the force $F_{p\text{-}f}$ ($Fx_{p\text{-}f}$) is neutralized by the longitudinal exertion of *m. iliotrochantericus caudalis* ($Fx_{iltr}$ on fig. 3, B).

## ANALYSIS OF FORCES DISTRIBUTION AT THE END OF CONTACT PHASE

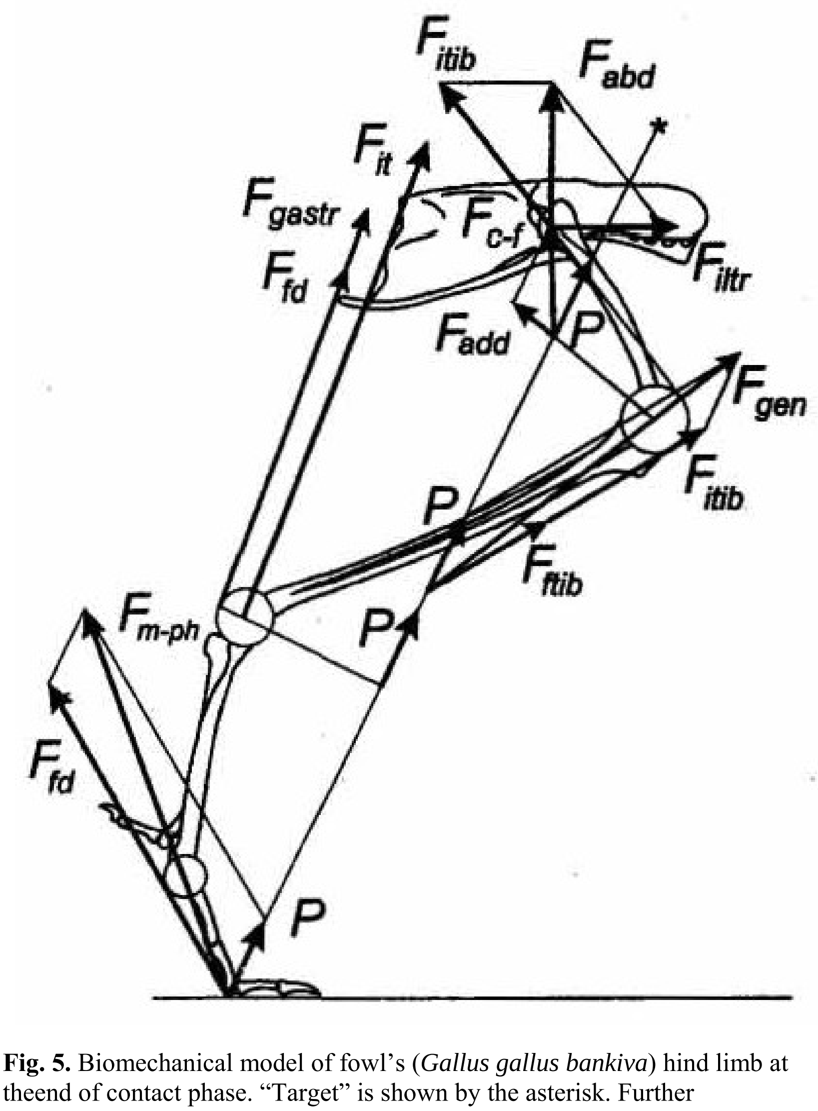


**Fig. 5.** Biomechanical model of fowl's (*Gallus gallus bankiva*) hind limb at theend of contact phase. "Target" is shown by the asterisk. Further explanations see in text.

At the end of contact phase (fig. 5) the push is provided by penultimate phalanx of third toe. That is why the line of ***P*** action is situated outside of the metatarsophalangeal joint, thus requiring for balance a significant effort of long digital flexor ($F_{fd}$). Parallelogram cannot be built to determine balance conditions in the intertarsal joint, because a terminal portion of Achillean tendon is close in the direction to that of ***P*** and does not intersect with it in borders of the drawing. In this case, we should sum the forces by the rule of summing of parallel forces, such as shown on fig. 2. The resultant force ($F_{it}$) goes parallel to the mentioned forces and through the center of the intertarsal joint. Its length equals a sum of ***P*** and $F_{it}$, values of which inversely relate to distances from them to the resultant. The resulting force, necessary for the balance of the discussed joint, exceeds that of long digital flexor ($F_{fd}$). An additional force is exerted by gastrocnemial muscle ($F_{gastr}$).

Passing posterior to the knee joint, ***P*** tends to flex it. To counteract this tendency, the action of one or two shank extensors is necessary. These are *m. femorotibialis medialis*, which does not influence the movement in hip joint and *m. iliotibialis lateralis*, which passes the mentioned joint and able to abduct the limb. Forces of two muscles ($F_{ftib}$, $F_{itib}$) are transmitted to tibiotarsus via patella and patellar tendon. Their resultant force is drawn according to the direction of the terminal portion of patellar tendon (fig. 5). A parallelogram is built from the point of its intersection with the vector of GRF. $F_{gen}$ goes through the center of knee joint. The effect of $P$ on hip joint is lower, than in previous cases, since the force passes closer to its center, thus having a shorter lever. Only a slight contraction of *m. puboischiofemoralis* ($F_{add}$) is necessary to counteract it.

A vertical component of this force, $Fy_{add}$ (fig. 2, *C)*, is not sufficient to abduct the femur (the entire force required to keep the pelvis from tilt is 2,3$P$). An additional adductor is necessary, such *m. iliotibialis lateralis*. Since it starts from pre- and postacetabular ilium, its force vector can be drawn through the center of projection of this joint (fig. 5) tangentially to the knee joint. The vertical component of this vector should be $Fy_{itib}$ = 2,3$P$-$Fy_{add}$ (fig. 2, *C)*. This allows to distribute the force, extending the knee joint, among two original forces.

Vertical component of $F_{itib}$ appears as the resultant force with specialized pronators, *m. iliotrochantericus caudalis* ($F_{iltr}$) (fig. 5). The latter, as in previous cases, neutralizes the supination tendency, arising as a side effect of $F_{itib}$ action.

Force vector $Fx_{iltr}$, a longitudinal component of pronating force $F_{iltr}$, neutralizes supination components of *m. iliotibialis lateralis* ($Fx_{itib}$) and *m. puboischiofemoralis* ($Fx_{add}$) (fig. 3 D). Horizontal component of $Px$ also slightly supinate the limb (fig. 3 D) due to its medial to the center of hip joint position (the same pronating component appears at the beginning of contact phase – fig. 3 C). This effect can be compensated by an additional effort of *m. iliotrochantericus caudalis*. However, to show it we have to rescale vectors.

Described biomechanical model of fowl hind limbs is an attempt to produce logical synthesis of elementary and clear mechanical properties of particular morphological elements of limb (parts of skeleton, joints and muscles) into certain system, which would reveal functional peculiarities and potential of locomotor apparatus. Using more or less precise drawing of the object, it applies to it carcass force vectors. This, in turn, allows to build a functioning model, which can decipher certain morphological prerequisites of the limb, that can be later tested in lab and field experiments.

Described method is sensitive to geometrical peculiarities of a researched system. Changing geometry on the course of the locomotor act changes values and direction of force vectors, necessary to keep the limb in equilibrium. Fig. 3, for example, shows a significant drop of rotational forces, necessary to keep the limb balanced. This determines a number and a shape of muscles, necessary to move the limb. The proposed model, thus, can serve as a valuable support in revealing specific morpho-functional connections inside of particular locomotor apparatus. It also explains the presence of many separate muscles, differing by orientation and attachments to the elements of skeleton.

Understanding of *mm. iliotrochanterici* function as limb pronators is an important outcome of the model. Most of the previous authors mentioned their ability to pronate the femur (Watson, 1883; Stolpe, 1932; Wilcox, 1952; Allen, 1962; Dzerzhinsky, 1992) along with its protraction (Hudson, 1937; Miller, 1937; Fisher, 1946; Berger, 1952; Stallcup, 1954; Kurochkin, 1968; Klemm, 1969; Patterson, 1983). However, they failed to explain the necessity of limb pronation, giving a preference to protraction and even retraction (Cracraft, 1971; Nickel et all., 1977) despite the minute lever or its absence to produce the mention action. The real matter is a medial shift of femoral head in relation to its shaft. Adaptive role of this change is clear – pelvic muscles acquired the ability of abduct the femur, thus controlling the hip joint in transverse plane. At the same time, due to the caudal tilt of most of the mentioned muscles, a rotational (supination) moment appears, which can not be prevented by the spherical hip joint. This problem is partially solved by the extension of the articulation onto antitrochanter, making the joint conical with clear transverse axis. To make this axis more stable the muscular control is necessary. This control is provided by *mm. iliotrochanterici.*

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## ABBREVIATIONS

Force vectors: $\boldsymbol{F_{abd}}$ – resultant force, abducting the femur; $\boldsymbol{F_{add}}$– force vector of *m. puboischiofemoralis*; $\boldsymbol{F_{c\text{-}f}}$– resultant of forces applied to the distal femur, which passes through the projection of the center of hip joint onto sagittal plane; $\boldsymbol{F_{fd}}$– force vector of *m. flexor digitorum longus*; $\boldsymbol{F_{ftib}}$,– force vector of *m. femorotibialis medius*; $\boldsymbol{F_{gastr}}$– force vector of *m. gastrocnemius intermedius*; $\boldsymbol{F_{gen}}$– resultant force of shank extensors, passing through the center of the knee joint; $\boldsymbol{F_{ifb}}$– force vector of *m. iliofibularis*; $\boldsymbol{F_{fme}}$– force vector of *m. iliofemoralis externus*; $\boldsymbol{F_{iltr}}$– force vector of *m. iliotrochantericus caudalis*; $\boldsymbol{F_{it}}$– resultant of the force, applied to the foot and passing through the center of intertarsal joint; $\boldsymbol{F_{itib}}$– force vector of *m. iliotibialis lateralis*; $\boldsymbol{F_{p\text{-}f}}$– resultant force of posterofemoral muscles; $\boldsymbol{F_{m\text{-}ph}}$– resultant of the forces applied to third toe, passing through the center of metatarsophalangeal joint; ***P***– ground reaction force; *– "target", to which the ground reaction force is directed. Horizontal components of forces marked with ***x***, vertical – with ***y***. Empty arrow shows the force, treated in other plane.

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**SOME GENERAL NOTES ON THE AVIAN HINDLIMB BIOMECHANICS**

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**Summary**

Since the hind limbs carry out mechanical functions, their functional morphology is biomechanics. To interpret the morphofunctional peculiarities of the avian hindlimbs the biomechanical model *(Gallus gallus bankiva* was taken as an object) has been built using statics in graphic interpretation. The analysis of the three poses of the contact stage (very beginning, middle, very end) revealed the great sensitivity of the chosen graphic method to the geometrical traits of studied system. It has been shown that the vertical component of the femoral retractor's force acquired the ability to counteract the force of gravity tending to adduct the leg. Supination (outward rotation) of the femur as a result of collateral action of the mentioned muscles is neutralized partially by antitrochanter but mainly by *mm. iliotrochanterici.*