DISCUSSION

Food is a critical biological factor responsible for a wide range of adaptive radiations in the animal kingdom; between the different groups as well as animals within the same group. Adaptive radiation in birds has oriented mainly in two directions - feeding and locomotion - and this is found to be at its peak in the order Passeriformes. The present day passerines have taken to almost every conceivable food niche available to them.

A review of the literature on feeding behaviour of the passerine birds has shown that the birds with diverse feeding habits and ways have been selected by the previous workers and attempts have been made to correlate the structural variations with the diversity in behaviour. Except for the studies in the intrafamiliial or phylogenetic relationships no emphasis has been laid by the functional anatomists on such studies in the birds belonging to the same family and with similar feeding behaviour.

Both the birds selected for the present investigation belong to the subfamily Sturninae. Of these, the Common Myna is strictly resident while the Rosy Pastor is a migratory one and they show more or less similar feeding behaviour. Both
are omnivorous in diet. However, the observations noted here reveal that these birds show some variations with regard to the epidermal structure, the bony elements and the musculature of the feeding apparatus. In the present discussion, an attempt has been made to explain the structural diversities studied and how far these reflect upon their food and feeding behaviour.

Implications of the findings made during the present investigations in the functional anatomy of these birds may be discussed under the following headings:

1. The Feeding Apparatus,
2. The Hind Limb Locomotor Apparatus, and
3. The Histochemical Studies.

1. The Feeding Apparatus

It is generally known that the basic stock of the passerine birds was a group of insectivorous birds with a short thin bill like that of the present day old-world Warblers. (Beecher, 1953 and Storer, 1960) which in due course of time adapted themselves to live in various habitats and most of them took to more than one food niche. The beak of an omnivorous bird is a moderate one which can deal with many different kinds of plant and animal diet. Further, it does not exhibit any special characteristics as such, it is too
weak for crushing seeds and too coarse for picking up small insects (Hess, 1951). The two starlings studied here are essentially ground feeders but like true aristocrats of the omnivorous feeders they do not only forage about after insects and worms but they hunt flying insects in the air occasionally and feast on fruits and seeds also.

Adaptive Features in the Epidermal Structures of the Bill and the Tongue

As mentioned earlier, the epidermal structures of the bill and the tongue play an equally important role in the feeding mechanism. According to Goodman and Fisher (1962) "the epidermal structures, which actually come in contact with food, demonstrate seemingly obvious adaptations for a particular food habit". In response to a particular food niche, the birds put these structural diversities to the most efficient use for the capture, transport and other mechanical preliminaries to the digestion of food. "Functionally, the method of feeding is of even greater importance than the kind of food taken" (Beecher, 1951).

The bill in both the starlings is moderate in length and height with its upper arm slightly longer than the lower one. The small un-notched wedge of the upper bill is of a
great advantage, in picking off insects and other food particles from the ground as well as grains, seeds and berries from the plants. The anterior part of the bill with its sharp maxillary and mandibular tomia is used like a pair of forceps. The lateral grooves along the maxillary tomia serve to house the mandibular tomia, so that the food particles do not fall out while feeding.

The hard palate has blunt ridges which are useful in holding, but not in breaking or crushing the food such as the grains, seeds and berries. The backwardly directed spines and horny projections facilitate transport of food towards the gullet by preventing it from escape. The large spines along the choanal slit, directly slightly inwards and backwards, do not permit the food to enter the choanal slit. The palatal boss just anterior to the choanal slit is useful in orientation of the food on the palate before it is gulped. Three such structures are present in these starlings but they are prominent in the Rosy Pastor than in the Common Myna. The median ridge of the rhinotheca forming the hard palate is also very prominent in the former. The epidermal structure of the bill is relatively homogeneous in the Common Myna in which insects form the major bulk of the diet. Malhotra (1967) has also observed that the epidermal structure
of the bill is conspicuously homogeneous in the insectivore than in the seed eater.

The tongue is a lanceolate structure and exhibits variation only in the degree of fraying at the tip in the two birds. The bifid tip of the tongue is much more lacerate, brush-like structure in the Rosy Pastor and is more useful in sucking nectar, on which it feeds gluttonously. The Common Myna also feeds on nectar occasionally but compared to that of the Rosy Pastor its nectar diet is very low. Similar variations in the degree of fraying of the tongue have also been observed by Gardner (1926). The present observations on the food and the feeding habits of the birds studied thus reveal that they respond to the same food niches but at different levels. The Rosy Pastor is more a grain and fruit eater whereas the Common Myna prefers insect diet and this is very well reflected in the epidermal structures of the bill and the tongue.

Osteology

While the fundamental plan of the skull structure is the same in birds, particularly so in the passerines, variations manifest themselves in dimensions of the skulls and the dimension ratios between the different components of the skull.
Very large orbits with a narrow supraorbital isthmus and thin interorbital septum found in both the starlings facilitate a forward vision for ground feeding and indicate the lack of force at the bill tip that is distributed to the cranial elements in the wood-pecking and carnivorous feeding habits. Since these birds do not break or crush their plant and animal diet they do not require highly ossified, sturdy bone structure. None the less the bony elements are not so delicate like those found in Sunbirds and Honeycreepers which are specialised as the nectar feeders. The palate is composed of thin and long bones without any palatal keel. The palatal keel found in the seed eaters and nut crackers, viz., Crackles and Hawfinches is not present in these birds. This structure is not required in these birds as they simply swallow their food. The mandible is also not very high as observed in the exclusively seed eating passeriforms.

Though an overall picture of the cranium in these birds show a homogeneity in the structure of its skeletal components, a detailed study reveals some interesting features which throw light upon the adaptations met with in these birds. The skull of the Common Myna is slightly larger than the Rosy Pastor, but the ratios of different bony elements are important for the functional efficiency of the jaw apparatus in adapting to a particular food niche.
The ratios for the bill length and the post-bill width are slightly higher in the Rosy Pastor which feeds mainly on grains and seeds. In view of the fact that the short, broad and high bill is an adaptation to the seed eating habit in birds (Beecher, 1951, 1953, 1962; Sims, 1955), the greater ratio for the bill length in the Rosy Pastor is not very clearly understood. It may, however, be explained on the fact that the Rosy Pastor feeds more frequently on nectar and a longer beak is better suited for reaching the honey of flowers. The ratio for the posterior articular process length, on the other hand, is greater in the Common Myna which can be correlated with its higher consumption of insects. While gaping, the Common Myna has to encounter an additional resistance offered by the soil. A massive muscle is therefore required for gaping action and a longer posterior articular process provides larger surface area for the attachment of this massive muscle. No doubt, the Rosy Pastor is also a gaper, but its consumption of insects is low. Besides, when feeding on fruit pulp or reaching for nectar its beak is subjected to a weaker resistance. Likewise, the ratio for the quadrate length indicates their preference for insect and plant diet. The higher ratio for the quadrate length is associated with the higher mechanical advantage and low kinesis of the bill in seed eating birds while the reverse is true for the insectivores.
which require speed at the bill tip (Beecher, 1962). The present observations of the ratios for the quadrate length are in good agreement with the study of the kinetics and mechanical advantage in the two birds and support this contention. With comparatively longer quadrate bone the Rosy Pastor has a greater mechanical advantage and hence a greater power at the bill tip that is required for its higher gramnivorous habit. On the other hand, the Common Myna, having a relatively more kinetic cranium gets an increased speed at the bill tip for its insect eating habit. Apart from the differences in the length ratios, the structural variations in the posterior articular process and the quadrate bone are also very conspicuous in the two birds. The tip of the orbital process of the quadrate in the Rosy Pastor is much more broader than that in the Common Myna, the former has a highly massive muscle originating from that tip. The articular processes are more prominent and broad-tipped in the Common Myna than in the Rosy Pastor. Such an arrangement, in the absence of a medial brace (Bock, 1960), minimises the chances of disarticulation during the feeding operation. Besides, the ventro-lateral surface between the inner and posterior articular process for the attachment of the highly massive muscle is quite evident in the former. Variations in the ratios of different bony elements thus can be correlated with their preference for different kinds of food.
Ligaments of the Skull

Ligaments of the skull are associated with the jaw articulation and serve three major functions (Bock, 1964). The external and the internal jugo-mandibular ligaments hold the quadrate-articular joint in its place and protect it from being disarticulated. The occipito-mandibular, the orbital, the vomeral and the lacrymo-jugal ligaments do not permit excessive movements of the upper jaw (Fisher, 1955). Though this function is more important in the degree of cranial kinesis, they do not influence the basic mechanism of kinesis. On the other hand the post-orbital and the lacrymo-mandibular ligaments play an important role in governing the kinetic movements of the cranium.

Of the ligaments present in the birds studied here, the post-orbital ligament is well developed. This ligament, spanning the gap between the lateral wall of the cranium and the mandible is responsible for coupled kinesis observed in these birds. In this phenomenon the distance between the points of attachments remains constant which results in forward swing of the quadrate during the depression of mandible. This in turn pushes on the palatal complex and brings about the protractory movement of the upper beak. The occipito-mandibular ligament is moderately developed and acts as a stop to prevent the
excessive protraction of the upper beak. The orbital, the vomeral and the lacrymo-jugal as well as lacrymo-mandibular ligaments are not detectable in these birds. However, a white sheet of connective tissue is present which exhibits tensile movements. Presumably, as Bock (1964) has suggested, this patch of connective tissue represents one of these ligaments. The external and the internal jugo-mandibular ligaments are small ribbon-like structures and help the quadrate-articular hinge to maintain the position of the jaw articulation with the cranium.

Kinesis, Lever Systems and Mechanical Advantage

As already mentioned the primary advantage of the cranial kinesis is that it provides increased diversities of jaw manipulation and this makes the avian beak an efficient prehensor. It has been pointed out by Bock (1964) that the two basically different kinetic mechanisms are observed depending upon the presence or absence of the postorbital and/or the lacrymo-mandibular ligaments and upon the structure and nature of the quadrate-articular hinge. Though the movements of the bony elements are the same, the movements of the jaws differ. These two types designated as coupled and uncoupled kinesis signify a mechanical linkage of the two jaws.
The prokinetic skull of the starlings show coupled cranial kinesis achieved through the postorbital ligament. As explained earlier, this flexible but inextensible band brings about the concomitant movements of the two jaws, setting in motion more than two lever systems.

Bock (1964) has discussed six possible functions of the cranial kinesis in birds and these have been critically reviewed by Zusi (1969). The role of kinesis in gaping mechanism is well established and its significance in the avian feeding behaviour is well known. Beecher (1962) examined kinetic properties and calculated the mechanical advantage at the bill tip in several closely related genera of passerine families. He found that a good correlation exists between the kinetic properties and the mechanical advantage in the seed and insect eating birds. The birds with a high per cent of insect diet had increased mobility and speed at the bill tip but less mechanical advantage; while the birds taking high per cent of seed food had lesser kinetic movements but high mechanical advantage. Further, he also noted that the longer orbital process of the quadrate seemed to be correlated with the power and with reduced kinetic movement.

The present observations in the two genera of the
family Sturnidae show a high degree of kinetic movements, the Common Myna having slightly more cranial kinesis than the Rosy Pastor. The mechanical advantage calculated in these birds and the ratios for the quadrate length are all in fine correlation with their preference for insect or seed diet. Although both the genera are omnivorous, the Common Myna which prefers insect food has higher cranial kinesis (36.2°) and low mechanical advantage (0.28°) whereas the Rosy Pastor feeding more on seeds and grains have slightly less kinetic beak (35°) and greater mechanical advantage (0.31°).

Myology

The influence of muscles on the configuration of the bony elements is so pronounced that the variations found in the skeletal elements reflect the functional capacity of the muscles attached to them. Structural diversities and the relative development of the jaw muscles have been often explained as adaptations to meet the functional demands of animal to its particular food niche. As mentioned earlier, several authors working on the myology of the feeding apparatus have observed striking correlations existing between the form and functions of various muscles and the specific feeding habits.
Adductors of the Lower Jaw

Adduction of the lower jaw is accomplished mainly by the M. Add.mandib.ext.supf., M. Add.mandib.ext.medialis, M. Add.mandib.prof., M. Add.mandib.medius and the M. Pseudotemporalis. Along with these muscles M. Add.mandib.int. and M. Add.mandib.post. also contribute to the adduction of the lower jaw.

The major adductor muscles mentioned in these birds are massive and exhibit a tendency towards the pinnate type of fiber arrangement. The most superficial muscles, viz., the M. Add.mandib.ext.supf.pars dorsalis is however very broad muscle, and unipinnate in nature. The pinnate region towards the supramedaatal ridge is very small. Some muscle fibers are fused below with the inner slip of the M. Add.mandib.ext.medialis; towards the postorbital process. The pars ventralis of the M. Add.mandib.ext.supf. and the M. Add.mandib.prof. are long and massive pinnate muscles. The action of such muscle is a bit slow but gives a more grasping power to the birds for holding the food which here consists among other things fruits, seeds and grains. The power of adduction is increased by a very large and massive M. Add.mandib.ext.medialis. Along with the large M. Pseudotemporalis, both the slips of the M. Add.mandib.ext.medialis cover a large portion of the both outer
and medial surfaces of the mandible. Such an arrangement of the muscles confer a greater strength upon the bill. The M. Add, mandib. medius is a highly tendinous multipinnate muscle almost vertical in disposition which creates an upward pull at the posterior region of the mandible and keeps its cranial attachment tight against the abduction force. The M. Add, mandib. post. is a small parallel muscle acting as a weak adductor of the lower jaw. The M. Add, mandib. internus, the most compact muscle also acts as an adductor but due to its origin on the palate it also brings about retraction of the upper jaw.

The starlings studied here are primarily insectivores. As they have taken to an omnivorous feeding habit, they eat grains and seeds in large quantity. Besides, they even show a carnivorous mode of feeding occasionally. So with a moderate bill typically suited for insects and seed eating habit, these birds, with pinnate type of fibre arrangement in the adductor muscles, have better grasping power. Because of this they are able to feed on flesh also. It is significant to note that they are not able to tear the flesh but pinch it away in small bits.

**Abductor of the Lower Jaw**

The Depressor mandibulae practically the only muscle responsible for the powerful abduction of the lower jaw, is a
conspicuously massive muscle in the whole jaw musculature in these starlings. It spreads its origin over the entire posterior wall of the skull. Its strong and tendinous insertion covering the entire ventro-lateral extension of the posterior articular process gives it a great leverage and force necessary for the gaping habit of these birds.

Zusi (1959, 1967), has stated that the M. Depressor mandibulae in the family Sturnidae and particularly in *Sturnus vulgaris* has no effect on the upper jaw. But during the present study it was observed that this muscle did bring about a slight protraction of the upper beak as well. This is accomplished through the post-orbital ligament. Since this ligament does not permit the backward displacement of the lower jaw during depression, the quadrate is displaced forward which pushes on the palatal complex and the upper jaw is raised a little from its normal position. As the postorbital ligament is attached near the quadrate-articular joint, it "reduces the amount of protraction" (Zusi, 1967) obtained in these birds through this ligament.

**Protractor of the Upper Beak**

The M. Sphenop-térygo-quadratus, responsible for the cranial kinesis is very well developed in these birds. This is another adaptive feature for the gaping habit and involves
an enormous forward spread of the muscle. The origin of the 
M. Spheno-pterigo-quadratus in these birds covers almost the 
entire surface of the laterosphenoid and extends over the 
orbito-sphenoid as well as the antero-lateral margin of the 
basisphenoid. This forward spread of the origin facilitates 
a powerful elevation of the upper beak during the feeding 
mechanism.

Besides the powerful protraction, depression of the 
lower jaw is also effected by this muscle. In performing the 
latter function the same chain of movements are set by the 
upward pull of the quadrates.

Retractors of the Upper Beak

Retraction of the upper beak is accomplished by the 
M. Add.mandib.int., M. Pseudotemporalis and M. Add.mandib.post. 
The internus series brings about the retraction by directly 
pulling the palatines backwards. The M. Pseudotemporalis and 
M. Add.mandib.post. pull the orbital process of the quadrates 
downwards so that the whole sequence of movements becomes 
reversed from that found during protraction.

Muscles of the internus series and the M. Pseudotempo-
ralis are highly massive muscles with a pinnate type of 
arrangement whereas the M. Add.mandib.post. is a small parallel
type of muscle. The M. Add, mandib, int, dor, anterior and posterior parts are small unipinnate muscles while the M. Add, mandib, int, vent, anterior is bipinnate and the posterior part is the most compact muscle with a multipinnate fiber arrangement. All the four parts make a complex system extending between the two movable entities - the palate and the mandible; because of this type of arrangement they work together bringing about the concomitant movements of the two jaws. Of the four parts the vent, posterior has a powerful hold over the mandible due to its insertion spreading on the outer side of the mandible. The M. Pseudotemporalis is also a highly massive muscle extending from the tip of the orbital process to the medial surface of the mandible. By virtue of its origin and insertion on the movable elements of the jaw apparatus this muscle also brings about adduction of the lower jaw as well as the retraction of the upper beak. Since its attachment on the mandible spreads over a large portion of the ramus, the adduction of the lower jaw is more powerful action than the retraction of the upper beak. The M. Add, mandib, post. being a small parallel muscle, situated more posterior and vertical in position than the other adductors, it acts as a very weak adductor. Because of its origin from the quadrate it assists in the retractive function of the internus series more effectively than in the adduction of the lower jaw.
It is thus evident from the foregoing account of the jaw musculature that these birds are very well adapted for the gaping mechanism during their feeding behaviour. The highly massive Mm. Depressor mandibulae and Sphenopterygo-quadratus evince a very powerful abduction of the lower jaw and a marked protraction of the upper beak necessary for the efficient gaping mechanism.

Muscles operating the Tongue

The main function of the tongue in these birds is the transportation of food towards the gullet and this mainly involves its protraction, retraction and depression.

Protraction of the tongue is brought about by the M. Branchio-mandibularis which pulls the entire hyoid apparatus forwards. The retraction of the tongue is effected mainly by the M. Gularis anterior which extends between the ventral surface of the articular and the basibranchial of the hyoid apparatus. Withdrawal of the tongue by this muscle is assisted by the M. Gularis posterior which helps in pulling the hyoid apparatus backwards. The tongue is depressed as a result of the combined action of several muscles, the most important among them are the M. Hyoglossus and the M. Hypoglossus, the former is a strong depressor of the tongue and the latter helps in this action. The other muscles are the M. Sterno-hyoideus,
the M. Grico-hyoides and the M. Tracheohyoides. The latter muscle also helps in the withdrawal of the tongue.

Quantitative Analysis of the Jaw Muscles

The effective force exerted by the bill of a bird during its feeding operations depends upon several factors. Among the various structural components of the lever system that operate the jaw apparatus, muscles which supply the power for their operation are the deciding factors in different movements of the jaws.

The potential strength of the force exerted varies inversely with the length of the work arm whereas the tongue varies directly with the length of the force arm. This is highly dependent on the morphological setup of the individual muscle while the effective force depends on the muscle power-relative development and the physiological setup of the muscle. The total mass of a muscle is generally taken as an index of the muscle power. The same practice is followed here also. The angle of the muscle which it makes with the force arm is equally an important factor. The effective force of adduction, abduction, protrusion and retraction involving all these factors, which an individual muscle can exert on its movable attachment are significant in understanding its functional capacity.
Though the effective force of adduction by individual muscles, viz., the M.A.M.E. supf., M.A.M.E. medialis, M.A.M. prof., M.A.M. medius and M.A.M. post., are greater in the Common Myna, the effective force of adduction by the M. Pseudotemporals in the Rosy Pastor is the highest of all the adductor forces. (Table XI). The higher value for the total effective force of adduction exerted by all the adductor muscles together in the Rosy Pastor (0.022454) than in the Common Myna (0.016112) accounts for the higher value of the force of adduction by the M. Pseudotemporals in the former. The effective forces of abduction, protraction and retraction are higher in the Common Myna (0.009532, 0.02761 and 0.021265) than in the Rosy Pastor (0.002454, 0.000496 and 0.011057).

These results can be correlated with the differences found in the food consumption by these birds. The higher effective force of adduction observed here in the Rosy Pastor can be accounted for the relatively high consumption of grains and seeds. The Common Myna which feeds mainly on insects does not require an adductive force to the same extent. Instead, it requires a higher gaping power and greater effective forces of abduction and protraction as well as retraction for its frequent probing action into the grass mat and soil. The Rosy Pastor which also gapes but more frequently on the fruits and flowers does not encounter a strong resistance as that in the Common Myna.
2. The Locomotor Apparatus

It is a well known fact that in the avian feeding behaviour locomotor apparatus play an equally important role as the jaw apparatus itself and in the terrestrial habitat the legs are the main organs involved in it. Successful feeding behaviour on the ground necessitates a good mobility over the surface. For a good mobility the most required adaptation in avifauna is an efficient bipedalism. In the two birds studied here, feeding as a rule, is mainly done on the ground and the weight of the body while standing, perching or walking is balanced on two legs.

Adaptive Features in the Skeletal Elements

Though the absolute sizes of the bony elements differ slightly, except for the pelvic width, other ratios of relative development exhibit no significant variations in these birds. The figures for the bony elements other than the pelvic width mentioned here refer to the Common Myna.

The Pelvic Girdle

Shape of the synsacrum is a good indicator of the build of the entire body - greater width of pelvis reflects a heavy, broad structure (Fisher, 1946). Besides, according to the same author, "wide pelvis provides better support which may
be termed as an adaptation correlated with more extensive use of the hind limb, whether that use is in predation as in hawks or in terrestrial locomotion as in coragyps and vultures."
The relatively larger build of the body of the Common Myna is reflected in its greater pelvic width ratio (67.42%) compared to that of the Rosy Pastor (62.70%). Further, it is evident from such a wide pelvis that these birds are very well adapted for their terrestrial habitat.

The ratios of the pre-and post-acetabular ilium show that the former (41.02%) is slightly longer than the latter (37.09%) while the ischium is considerably longer (50.58%) in these birds. Though the postacetabular ilium is comparatively short, the ischium extends farther caudal thereby permitting more posterior origin of many postfemoral muscles. This gives therefore, an increased vector of their effective pull and thus a more force is exerted upon the femur in walking.

The Femur

The femur which has a poorly developed trochanteric ridge, comprises 26.87 per cent of the total leg length. It is nearly as long as the tarsometatarsus (27.72%). This means femur is not reduced in length as is found in the aquatic forms. Owre (1967) has observed an increased length of the femur in Anhinga (22.2%) than in Cormorant (19.3%) where the
form former is more arboreal than the latter though both of them are primarily aquatic birds. A decrease in length and increase in the size of trochanteric crest are adaptations for swimming (Dabelow, 1925). Of the two condyles the external condyle has a deep groove on its posterior side. This facilitates smooth sliding of the fibular head while these birds perch on the roost.

The Tibiotarsus

The tibiotalarsus with its broad condyles is elongated and forms nearly half the length (45.41%) of the leg. The former characteristic according to Owre (1967) is important as a weight bearing adaptation while the greater length gives speed to the bird in locomotion. The cnemial crests are also very prominent and acutely deflected from the shaft. The inner cnemial crest is better developed and broad plate-like while the outer one has a narrow spine-like tip. This provides larger surface area for the origin of the internus head of Gastrocnemius and other muscles in this area, characteristically well developed for the wide range of rapid movements for the cursorial type of existence. Similar characters are also observed earlier by Miller (1937) who considered these features as adaptations to non-aquatic life and which serve to straighten the limb and provide firm support.
The Tarsometatarsus

Elongation of this element in the birds adds one more joint to the hind limb for the provision of increased speed in locomotion. The long shallow groove, extending the tarsal length, is present for the passage of the stout tendons of the muscles of the shank region especially the flexors and extensors of the toes. The trochlea for the hallux is broad which indicates a better development of the hallux. Similarly the trochlea for the digit III is also well developed.

Digits

The feet of these birds show anisodactyl type of arrangement of the digits - three widely apart anterior toes and a strong posteriorly directed hallux. The feet of this type are adapted for two purposes; efficient walking as well as perching. The long hallux with a strong and curved nail acts as a prop while walking on the ground and in perching it provides a firm grip over the branch of a roost. The free anteriorly directed toes spread over a relatively larger surface area and thus form a broader base whereby the point of gravity comes to lie between the feet and balance the body while walking or running.
Myology

Shapes and placement of the leg muscles in a bird are as important factors as their relative development to the body weight. It is very well known that in the birds which dwell the terrestrial habitat, the leg muscles - especially those of the shank region have short-bellies and long tendons. Further, they are situated more proximally and thus eliminate weight at the distal end which is swung in a wide arc during locomotion. Such an arrangement has little mechanical advantage but gives speed to the bird at the expense of strength.

The shapes of muscles of shank region in the birds under investigation, indicate the greater bulk of the musculature is situated more or less proximally. Functional analysis of the major muscle groups are considered here according to the movements of different parts of legs they bring about.

Muscles moving the Femur

A very slight flexion of the femur is brought about by the Mm. Iliotrochantericus posterior and Iliotrochantericus anterior. The angle at which they are inserted suggests rotation rather than flexion but their action opposed by the Mm. Ischiofemoralis and obturator internus causes flexion and by their group action femur is held fixed with regard to
rotation thereby bracing the base of the leg in action and in maintaining posture. The short and broad bellies of these muscles indicate short range of action providing power for their movements.

The Mm. Ischiofemoralis and Obturator internus are antagonistic to the two iliobrachialis muscles but not very powerful extensors of the limb which is indicated by their more proximal situation than the other extensor muscles and less bipinnate nature of this muscle.

The Mm. Adductor longus et brevis anterior and posterior are serving as the main extensors of the limb. They cannot adduct the leg in normal position because of their origin just posterior and dorsal to their insertions. The posterior part which runs up to the femur more horizontally can use all its power in effective movement while the anterior part acts to thrust the head of the femur upward in the acetabulum. This thrust increases remarkably when the femur is flexed and hence this part is more effective in maintaining the posture. The anterior part operates through a wide range of movement in femoral extension whereas the posterior part through a short range but with good speed.

The M. Piriformis pars caudofemoralis functions to move the tail sideward, more or less independent of leg
movements. Unlike in the swimming birds, (Miller, 1937) heads of the two sides of this muscles work alternately and do not depress the tail.

The M. Obturator externus serves mainly in posture. It is an adductor, but is able to rotate the trochanteric region slightly posterior.

Muscles moving the Femur and Tibia

The M. Sartorius is a flexor of the femur and extensor of the tibiotarsus, the latter action is the result of its active contraction accompanied by the 'tendon action'; while the former action is effected only when tibial extension is opposed by the tibial flexors. In walking and running it serves in the recovery stroke bringing both the femur and tibiotarsus forward as well as in jumping and climbing it contributes to the power drive of the M. Femorotibialis. Thus, it plays an important role both in recovery and power drive whereas this same muscle in aquatic birds serves only in recovery stroke in swimming (Miller, 1937).

The M. Iliotibialis is the only important abductor of the leg but it can cause this movement only when tibial extension is opposed by the biceps femoris and semitendinosus. Its extensor function is just an auxiliary to the M. Femorotibialis.
The Mn. Biceps femoris and Semitendinosus are chief power source in tibial flexion. When tibial flexion is opposed they serve as femoral extensors also. The biceps acts in the final stage of tibial flexion because of the biceps loop which acts as a pulley only in the later stage of this action and brings about extreme flexion. In running this muscle serves, along with the M. Femoro tibialis, to swing the entire leg backwardly.

The M. Semitendinosus acts differently than the M. Biceps femoris in that it pulls the tibiotarsus from femur when the tibial flexion has gone past 90 degrees. This is counterbalanced by the biceps. In tibial rotation also these muscles balance each other because of their insertions; the biceps inserts on fibula while the semitendinosus on the tibia at the same level. M. Semimembranosus acts as an auxiliary to the latter because of their common insertions.

Muscles moving the Tibiotarsus

The M. Femorotibialis is the largest muscle of the thigh region; but is the simplest muscle in its action and the only function it performs is the extension of tibiotarsus. It contributes to the action of biceps and semitendinosus in swinging the entire leg backward in walking. Of the three parts, the externus and medius are fused and act as one part.
This with the internus part aids in this manner, without other complications such as femoral flexion (sartorius) or abduction (iliotibialis). Since the internus part is inserted at the tibial head its leverage is much less powerful than that of the other functional unit which is inserted on patella. The internus part does not show modifications found in the medius part so it does not appear to be an important adaptation with regard to power of tibial extension (Miller, 1937).

**Muscles moving the Tarsometatarsus**

Both the M. Gastrocnemius and M. Tibialis anterior originate in part from the femur and in part from either patella or cnemial crest. They are antagonistic to each other, the tibialis anterior serving mainly as a tarsal flexor while the gastrocnemius is chiefly an extensor of the tarsus.

The tibial head (lateral head) of M. Tibialis anterior can also cause tibial extension to balance the tibial flexion; but it is not important in major extension of the tibiotalarsus. Since the tibialis anterior is the only direct tarsal flexor it acts in the recovery strokes in walking and running.

The M. Gastrocnemius is the largest among the whole
leg musculature. Its extensor function is of great importance in every kind of locomotion - walking, running, climbing and swimming. Though this muscle is divisible in three distinct parts, they work in two functional units, the small medial head is of less importance in major power movements.

The external part arising from the femur exerts a force contributing to tibial flexion which is held in check by the M. Femorotibialis. The internal part, very well developed in these birds is solely an extensor of the tarsus because it has no connection with the femur. As it does not cause tibial flexion, it is the most efficient part for the running movements.

The M. Peroneus brevis as an accessory to the M. Gastrocnemius in tarsal extension acts on the lateral side of the tarsus. It is extremely weak but due to its strong tendon serves as a brace, preventing tarsal rotation that might otherwise result from the action of gastrocnemius on the medial side of the hypotarsus.

Muscles moving Tarsometatarsus and Toes

a. Toe Flexors and Tarsal Extensors

The Mm. Flexor perforatus digiti II and Flexor perforatus digiti III are similar in action on their respective digits serving to flex the toes as a whole. Since the tendons
of these flexors run over the heel, they also extend the tarsus when the toe flexion is opposed. The M. Flexor perforatus digiti IV is attached to the first, second and third phalanges of the fourth digit and hence brings both flexion as well as curvature of that digit. The latter action is prevented in standing and propulsive stroke of running. Thus muscle has the same influence upon the tibial flexion and tarsal extension as the other flexors of the digits. The M. Flexor perforans et perforatus digiti III brings about tarsal extension besides its digital function. The M.F.P.et P.III acts to curve the third digit at its first joint. It can bring about toe curvature without flexion, but as it perforates tendon of F.P.d.III a slight flexion of the entire digit is effected.

The M. Flexor hallucis longus and the M. Flexor digitorum longus function as a unit because the former supplies a small tendon slip to the first digit. This makes its function mainly that of curvature of the three toes. As in the other flexors, these muscles also cause flexion of toe from the base when the foot is on the ground and bearing the weight of the bird.

The M. Plantaris and M. Peroneus longus are closely associated with the toe flexors but are primarily tarsal extensors. The plantaris is a weak extensor as it is connected
to the ligamentous and cartilaginous sheaths. The peroneus longus brings about both tarsal extension and flexion of the third digit, the former is more important. Because of the peroneus tendons on the posterolateral surface it can balance even more than the peroneus brevis can balance the force of the M.G.ext. on the medial side of the hypotarsus. This can thus contribute to the toeing-in.

b. Toe Extensor and Tarsal Flexor

The M. Extensor digitorum longus is slightly less developed than the M. Flexor digitorum longus and M. Flexor hallucis longus. This muscle acts as a toe extensor and when opposed by the toe flexors, as a tarsal flexor. It works along with another interacting group of muscles, which are the gastrocnemius, the tibialis anterior and the toe flexors. The important movements to produce an intricate balance of actions include the synergist action, the tendon effect and the relaxation of tonus.

c. Toe Extensors and Abductors

Extension and abduction of the hallux is effected by the M. Extensor hallucis brevis. The M. Abductor digitii IV is also present in these birds which brings about the abduction of that digit. In abducting they act only at their bases and have no effect on the distal joints of the digits.
Other toe extensors as well as toe flexors are not detectable in the birds studied.

Quantitative Comparison of Muscles

Relative development of leg musculature - expressed as a percentage - to the body weight and the total leg weight gives a good indication of its locomotory behaviour. The birds under investigation exhibit similar locomotory behaviour and this is reflected in their almost equal ratios (Table XXI) of the musculature to the body and the total leg weight. Volumes of the individual muscles in relation to the total volume of the leg muscles (Table XXII) are more significant in that they indicate their work capacities in this particular walking and short running mode of locomotion.

The M. Gastrocnemius, the extensor of the tarsus, is the largest muscle in the leg musculature comprising 17.55 per cent of the total weight of the leg muscles. This is because of the great importance of tarsal extension in locomotion. Similarly the M. Femorotibialis which acts directly against the body weight while extending the tibiotarsus is also a highly bulky muscle (13.60%). The M. Tibialis anterior (9.64%), an antagonist of the gastrocnemius also indicates its power in the recovery stroke as it is the only direct tarsal flexor. Likewise, the M. Adductor longus et brevis,
chiefly responsible for the power applied in the femoral extension, has greater bulk (8.03\%) than the other muscles contributing in this action. Among the other muscles of the thigh region, bulk of the M. Iliotibialis (5.08\%) is greater in these birds because of its function as an auxiliary to the M. Femorotibialis. Of the two tibial flexors, the M. Semitendinosus (5.12\%) is better developed than the M. Biceps femoris (4.55\%). According to Miller (1937) the latter muscle shows relatively great work capacity in the swimming forms than in the terrestrial birds. Among the rest of the muscles, high bulk ratios for the toe flexors indicate adaptation for the perching habit of these birds. Of all the toe flexors, a strikingly high bulk ratio for the M. Flexor digitorum longus can be accounted for the better development of hallux, which has important functions in perching as well as in walking. It gives more powerful grip during perching action and acts as a prop while walking and running.

**Histochemical Studies**

Various histochemical techniques applied to the study of skeletal muscles have revealed two fiber types and as mentioned earlier, they have been generally classified on the basis of diameter and intensity of the staining reaction.

It has been claimed that there exists a "reciprocal
relationship" between the activities of the enzymes of aerobic and anaerobic metabolisms (Dubowitz and Pearse, 1960a, b; Jinnai, 1960; Ergel, 1962, 1965, 1970; George and his collaborators, 1966; and Jasmin et al, 1971). However, a number of histochemists including Stein and Padykula (1962), Romanul (1964), Bocek and Beatty (1966), Edgerton and Simpson (1969), Ashmore and Doerr (1971) have shown that this contention does not hold good for all skeletal muscles. This has confounded the simple division of muscle fibers into two histochemical types. Moreover, in histochemical studies it is often difficult to relate the staining intensity for an enzyme to its activity or its concentration (James, 1972). Davis and Gunn (1972) have also demonstrated that the fibers may have a high activity of enzymes for both aerobic and anaerobic metabolisms. Further, they have shown that the absolute levels of activities were not indicated thereby and their relationship in muscle fibers were not necessarily the simple "reciprocal" one as suggested by earlier workers.

In the present investigation localization of the two metabolites and their related enzymes revealed that the jaw and leg muscles of the starlings studied here are of "mixed" type. Besides, it is evident (Table XXIV) that there
is no predominance of either type of fiber; their per cent
distribution is more or less equal. This may be explained in
view of the fact that these omnivorous birds require neither
a sustained muscular power as is found in the carnivores nor
a quick action as is evident in the insectivores. Their
muscles, therefore, do not exhibit either predominant
aerobic or predominant anaerobic metabolic activities.

With regard to the histochemical profiles of the
muscle fibers, it has been observed during the present study
that the relationship of the fiber type to the fiber diameter
and the speed of contraction is not constant and their
"reciprocal relationship" is not very evident. Further, the
presence of both AChE and BuChE at every end plate regardless
of the fiber type confirms the results reported earlier by
Klinar and Zupancic (1962). The results presented in the
Table XXVI indicate that in the Common Myna, the muscles of
the thigh region as a whole show only medium levels of enzymic
activity whereas in tibiotarsal region, AChE is at its
maximum. However, the activity of BuChE is same in both the
regions. Besides, the two parts of Gastrocnemius muscle also
show the same levels of enzymic activities, though the
externus part has a higher percentage of type I fibers and
the internus part has a higher percentage of type II fibers
From these observations it appears that there is no correlation between the fiber types and the activities of these enzymes in the leg muscles of Common Myna, as was reported by Chinoy and George (1965) in the pectoralis muscles of certain groups of birds. As the two regions of the leg show a clear distinction in the levels of enzymic activity, this may be correlated with the extent of activity characteristic of the groups of muscles. A higher level of activity of these enzymes can be attributed to a greater activity of the muscles of the tibiotarsal region. However, strikingly low levels of activity of these same enzymes in the leg muscles of the Rosy Pastor as well as in the jaw muscles of both the birds are not clearly understood. The 'en-plaque' type of motor end plates were observed in all the muscles studied here. Chinoy and George (1965) also obtained similar results in certain vertebrate muscles and they have suggested that the occurrence of 'en-plaque' type of motor end plates is a characteristic feature of the vertebrate skeletal muscles.

The present study of different histochemical attributes provides further evidence that the muscle fiber is a very dynamic cell and that it changes in its physiological and metabolic properties (Guth and Wells, 1972). It has been reported by Goldspink (1969) recently that the activity of enzyme within an individual muscle fiber depends not on the
state of development and growth but also on the physiological conditions that are imposed on the muscle. Many workers including Gordon et al (1957), while studying the effect of exercise on the skeletal muscles; Guth and Samaha (1969), and Guth and Wells (1972) while studying the trophic effect of nerve have shown in mammalian skeletal muscles that physiological and metabolic properties can be altered either in response to exercise or an interaction between neural and muscular factors. Further, Guth and Yellin (1971) and Yellin (1972) have reported that "the classification of mammalian muscle fibers into three types is a misleading oversimplification". They have objected to the current approach in characterizing the muscle fibers and have pointed out that the term "fiber type" tends to mislead one into believing that they are stable characteristics of a muscle. In characterizing the mammalian diaphragm Davis and Gunn (1972) have concluded that two types of fibers - according to their capacity for aerobic and anaerobic metabolism and intrinsic speed of contraction - can be demonstrated histochemically. "Fast-twitch" fibers use either aerobic or anaerobic or combined aerobic and anaerobic metabolisms, while "slow-twitch" fibers use either aerobic or combined aerobic and anaerobic metabolism.

Insofar as the birds during the present investigation are concerned, the muscle fibers exhibit their capacity to
use both aerobic and anaerobic metabolism in response to a functional demand of birds. This "mixed type" of histochemical nature of their muscles can be justified in view of the fact that their omnivorous feeding behaviour involves slow as well as fast actions depending upon the nature of food. When feeding on insects they have to be quick in action whereas graminivorous and occasional carnivorous feeding behaviours demand slow but sustained activity of the jaw muscles. Likewise, when feeding on ground the leg muscles are put to use in walking and short running which involves rather quick action of the hind limb muscles; on the other hand, their perching habit demands sustained activity from these muscles. For these demands they do not require specialized muscular activity. Instead, they need muscles that are capable of performing various functions; and "mixed" muscles are physiologically best suited for such a functional demand. So in this respect also, along with other structural adaptations, these birds are very well adapted to their feeding, perching as well as locomotor behaviour.