The Condor 100:574–579

INTRASPECIFIC VARIATION IN THE HINDLIMB MUSCULATURE OF THE NORTHERN FLICKER[1]

SUSAN BERMAN, JILL ADDESA, ROBERT HANNIGAN, VINCENT RESTIVO AND JOSEPH RODRIGUES
Department of Biology, College of the Holy Cross, Worcester, MA 01610,
e-mail: sberman@holycross.edu

Abstract. We carried our bilateral dissections of the hindlimb musculature of 51 preserved specimens of the Northern Flicker (*Colaptes auratus*) in order to assess the degree of anatomical variation in a non-passeriform taxon. We found three variations. M. iliofibularis, described as typically single-headed in the Piciformes, had two distinct heads in 18 of the 51 specimens (unilateral in 11 and bilateral in 7). M. pubo-ischio-femoralis is described as single-headed in *Colaptes,* but in 23 of our specimens there were two distinct bellies; in 9 this condition was unilateral and in 14 it was bilateral. In 35 of the 51 specimens, M. flexor perforatus digiti IV consisted of two heads. In 16 specimens the muscle had three heads, a condition only described in some procellariiform and galliform birds. This condition was bilateral in all 16 specimens. As possible explanations for these variants we consider atavism, adaptive variation, and random variation. We urge caution in characterizing picid species on the basis of these three muscles.

Key words: Colaptes auratus, *hindlimb musculature, intraspecific variation, morphology, Northern Flicker, random variation.*

In recent decades, comparison of avian appendicular musculature has been one method employed in elucidating phylogenetic relationships (see McKitrick 1991 for a review). Although there has been a long-standing awareness of anatomical variation among individuals of a species (Berger 1956), the implications of such variation for phylogenetic studies, specifically those involving avian appendicular musculature, have only recently been investigated (Berman et al. 1990, Raikow et al. 1990, Raikow 1993). Time constraints and lack of available specimens generally preclude the use of large sample sizes in anatomical studies. Hence, most species are characterized on the basis of a unilateral condition in only a few specimens, giving rise to the possibility that the species has been represented by an anomalous or atypical individual. Raikow et al. (1990) conclude that in most passerine birds, the rate of error in characterizing the typical condition for a species averages about 2.0%. However, Bledsoe et al. (1997) have found that at least one species of woodcreeper (*Dencrocincla anabatina*) is highly variable with respect to ossification of hindlimb tendons.

The present research is a first attempt at assessment of the degree of intraspecific variation in the hindlimb musculature of a non-passeriform taxon.

METHODS

We carried out bilateral dissections of the hindlimb musculature of 51 preserved specimens of Northern Flicker (*Colaptes auratus*) borrowed from the Carnegie Museum of Natural History (CM), the Museum of Vertebrate Zoology, University of California, Berkeley (UCB), University of Connecticut (UCT), and the Museum of Natural History, University of Kansas (UK). Specimen numbers are as follows: CM 1541,1692, 1712,1820, 2551, 3365, 3366, 3529, 3567, 3574, 3575, 4795, 5854, 5968, 5969; UCB 2151, 2389, 2390, 2473, 3543; UCT 13 uncatalogued specimens referred to here as numbers 1-13; UK 39627, 40341, 42003, 45178, 45538, 47943, 53028, 53030, 66976, 66977, 67376, 67377, 67378, 67379, 67380, 67381, 67382, 67383.

Dissections were carried out under stereomicroscopes with magnifications from 6 to 25×. Iodine stain (Bock and Shear 1972) was used to enhance the orientation of muscle fibers. Preliminary drawings were made with the aid of a camera lucida. Anatomical nomenclature follows Baumel et al. (1972), and abbreviations are as given in Zusi and Bentz (1984). The condition described as typical is that given in George and Berger (1966).

RESULTS

Only 3 of the 35 hindlimb muscles were found to be variable, as described below.

M. ILIOFIBULARIS

This muscle arises by fleshy and tendinous fibers from the caudalmost part of the dorsal iliac crest and from the cranial two-thirds of the dorsolateral iliac crest. In most specimens (Fig. 1A) there is a single belly that extends distally along the caudal surface of the thigh deep to Mm. iliotibialis lateralis and femorotibialis externus, and superficial to Mm. caudofemoralis, ischiofemoralis, and pubo-ischio-femoralis.

In 18 of the 51 specimens (35.3%), the muscle is divided into two distinct heads (Fig. 1B). Pars superficialis arises from the dorsal iliac crest and from the cranial one-third of the dorsolateral iliac crest. Pars profundus arises from the entire dorsolateral iliac crest,

[1] Received 5 August 1997. Accepted 27 January 1998.

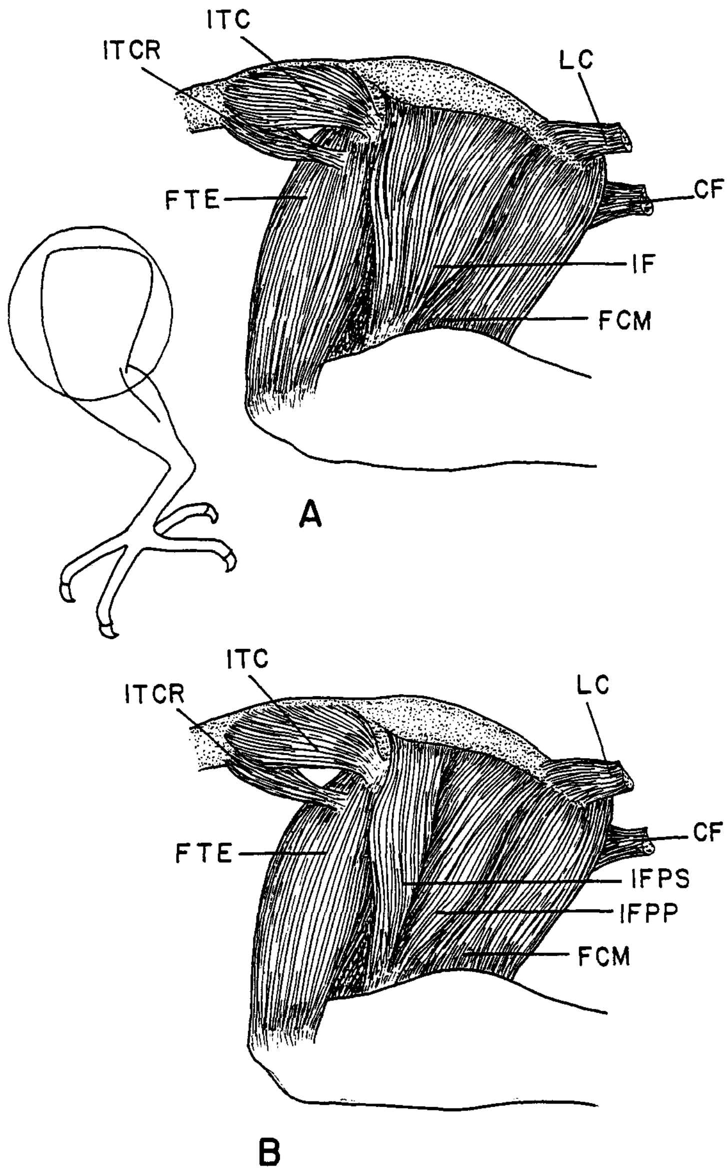

FIGURE 1. Left lateral upper thigh of *Colaptes auratus*. (A) Typical condition in piciform birds with M. iliofibularis as a single head. (B) Condition found in 18 of the 51 specimens with the muscle divided into two distinct heads, pars superficialis and pars profundus. Abbreviations: CF, M. caudofemoralis; FCM, M. flexor cruris medialis; FTE, M. femorotibialis externus; IF, M. iliofibularis; IFPP, M. iliofibularis pars profundus; IFPS, M. iliofibularis pars superficialis; ITC, M. iliotrochantericus caudalis; ITCR, M. iliotrochantericus cranialis; LC, M. levator caudae.

the cranialmost part of its origin being deep to that of pars superficialis. In 11 specimens this condition is unilateral and in 7 it is bilateral.

In both single- and double-headed conditions the single tendon of insertion passes through the ansa iliofibularis and inserts on the caudal surface of the fibula.

M. PUBO-ISCHIO-FEMORALIS

George and Berger (1966) and Hudson (1937) describe this muscle as variable in appearance among species as well as within at least one species, the Rock Dove (*Columba livia*). It may be a single mass or consist of two independent bellies. *Colaptes* is listed as among those birds with a single belly, and this is the condition

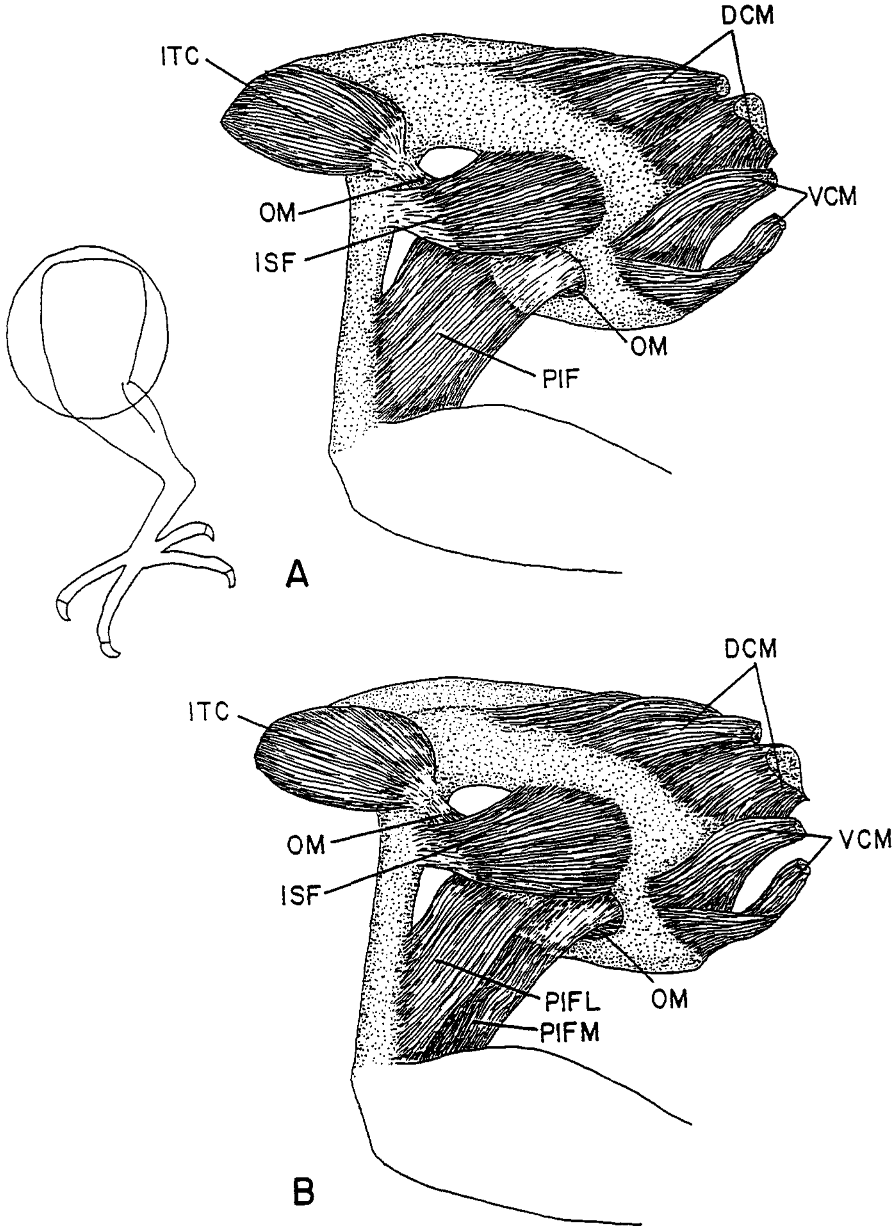

FIGURE 2. Left lateral upper thigh of *Colaptes auratus.* (A) Typical condition in this species with M. pubo-ischio-femoralis as a single head. (B) Condition found in 23 of the 51 specimens with the muscle divided into two distinct heads, pars lateralis and pars medialis. Abbreviations: DCM, dorsal caudal muscles; ISF, M. ischio-femoralis; OM, M. obturatorius medialis; PIF, M. pubo-ischio-femoralis; PIFL, M. pubo-ischio-femoralis pars lateralis; PIFM, M. pubo-ischio-femoralis pars medialis; VCM, ventral caudal muscles.

in 28 of our 51 specimens (Fig. 2A). However, in 23 specimens (45.1%) there are two distinct bellies, pars lateralis and pars medialis (Fig. 2B). In 9 of these 23 specimens the condition is unilateral, whereas in 14 it is bilateral.

In those specimens with the typical condition, the muscle is as described in George and Berger (1966). In those with two bellies, pars lateralis arises by an aponeurosis from the ventral margin of the ischium extending from just caudal to the obturator foramen to about one-half the length of the ischiopubic fenestra. The flat, parallel-fibered belly extends distally to insert by fleshy fibers on the caudolateral surface of the distal one-half of the femur and on the popliteal fossa. Pars medialis originates in its cranial one-half from tendinous fibers on the deep surface of the aponeurotic origin of pars lateralis. Its caudal one-half originates by tendinous fibers from an aponeurosis that covers the lateral surface of M. obturatorius medialis. The flat, parallel-fibered belly is about 6 mm wide. It extends distally to insert with pars lateralis on the distal end of the femur and the popliteal fossa and by fleshy and tendinous fibers on the medial surface of M. gastrocnemius pars intermedius.

M. FLEXOR PERFORTUS DIGITI IV

This muscle is described by George and Berger (1966) as consisting of either one or two heads. They make no reference to the condition in the Piciformes.

In 35 of our 51 specimens, the muscle consists of two heads of origin (Fig. 3A). The lateral head (pars lateralis) arises by a flat tendon from the caudolateral surface of the lateral femoral condyle. The medial head (pars medialis) arises by fleshy and tendinous fibers from the caudal surface of the femur just proximal to the condyles, and from the intercondylar region. The two heads are separated by the tendon of M. iliofibularis and by M. flexor hallucis longus. The fusiform bellies unite about one-half way down the shank and give rise to a single tendon that crosses the intertarsal joint, passing through the tibial cartilage to insert on the plantar surface of the basal phalanx of digit IV. Contrary to what was reported by Hudson (1937) for the Picidae, the tendon is perforated by that of M. flexor digitorum longus.

In 16 of our specimens (31.4%), the muscle arises by three distinct heads (Fig. 3B). Here, the third head (pars intermedius) appears to be derived from pars medialis. Pars lateralis is the same in origin and appearance as described above. Pars medialis is somewhat smaller in these specimens, but when combined with pars intermedius the size is about the same as pars medialis in those specimens with only two heads. This condition is bilateral in all 16 specimens.

Pars intermedius arises by a wide, flat tendon from the intercondylar region between pars medialis and M. flexor hallucis longus. The three heads unite about one-half way down the shank and give rise to a tendon that inserts as previously described. The overall size and relationships to surrounding muscles are the same in both two- and three-headed conditions.

DISCUSSION

Categories of anatomical variation have been discussed elsewhere (McKitrick 1986, Raikow et al. 1990). As each of the three variant conditions described here are the same in all of the individuals that possess them, there is no evidence that transformation (i.e., rapid, directional selection produces high, but transient, variability; Guthrie 1965, Williamson 1981) is operating. Likewise, the relatively high percentage of each of these variants in our sample argues against random mutation or incongruity. The remaining possibilities, atavism, adaptive variation, and random variation are considered for each variant.

Two heads of origin for M. iliofibularis have been described in several other groups, none of them Piciformes (see McKitrick 1991 for a review), but in each case they are characterized as cranial and caudal, rather than superficial and deep. We therefore believe this variation to be a derived, rather than an ancestral, condition and not attributable to atavism. As there is no noticeable difference in size, relationships, or any other aspect of the appearance of this muscle in the two conditions, it seems unlikely that one has an adaptive value over the other. In addition, the high frequency of bilateral asymmetry argues against the adaptive variation hypothesis. We thus conclude that one or two heads of M. iliofibularis is most likely a random variation or polymorphic trait in this species.

Given the high degree of variability of M. puboischio-femoralis among birds (McKitrick 1986), we would not argue that either condition seen here is an atavistic trait. This is another case in which size, appearance, and relationships of the muscle as a whole do not differ in one- and two-headed conditions. Hence, it is unlikely that either condition is an adaptive variation. It seems most probable that the presence of one or two heads in M. pubo-ischio-femoralis is a random variation in this species. Interestingly, Hudson (1937) characterized this muscle in *Colaptes* as a single mass, this conclusion having been drawn from the dissection of two specimens. He did not state whether both right and left legs were examined.

No reasonable argument can be made for atavism in the case of variations in M. flexor perforatus digiti IV. There are no other piciform birds in which three heads of origin have been observed. Three heads are described in some galliforms (Hudson et al. 1959) and some procellariiforms (Klemm 1969), but there is no evidence to suggest that the Piciformes are a sister group of either. Moreover, in both groups the three heads are significantly different from what we have described here. Again, as the overall size and relationships of the muscle are the same in both two- and three-headed conditions, we do not feel that there is any adaptive value of one over the other. Hence, the most likely hypothesis is random variation.

We know of no other studies of intraspecific variation in a non-passeriform group. Certainly we would not make a generalization on the degree to which it could be expected based upon one species of the Piciformes. It would be desirable to carry out similar studies using large sample sizes on other members of the Picidae as well as other families. However, time constraints and, more importantly, reluctance of museums to loan specimens for destructive dissection will probably preclude such study. At this point we offer two recommendations: (1) given the high degree of variability revealed in this study, the number of heads of these three muscles should not be used in characterizing species, at least from within the Picidae, unless large sample sizes show these conditions to be less variable than in *Colaptes auratus*, and (2) dissections should be carried out bilaterally whenever possible.

We thank the following institutions for providing specimens used in this study: Carnegie Museum of Natural History, Museum of Vertebrate Zoology, University of California, Berkeley, University of Con-

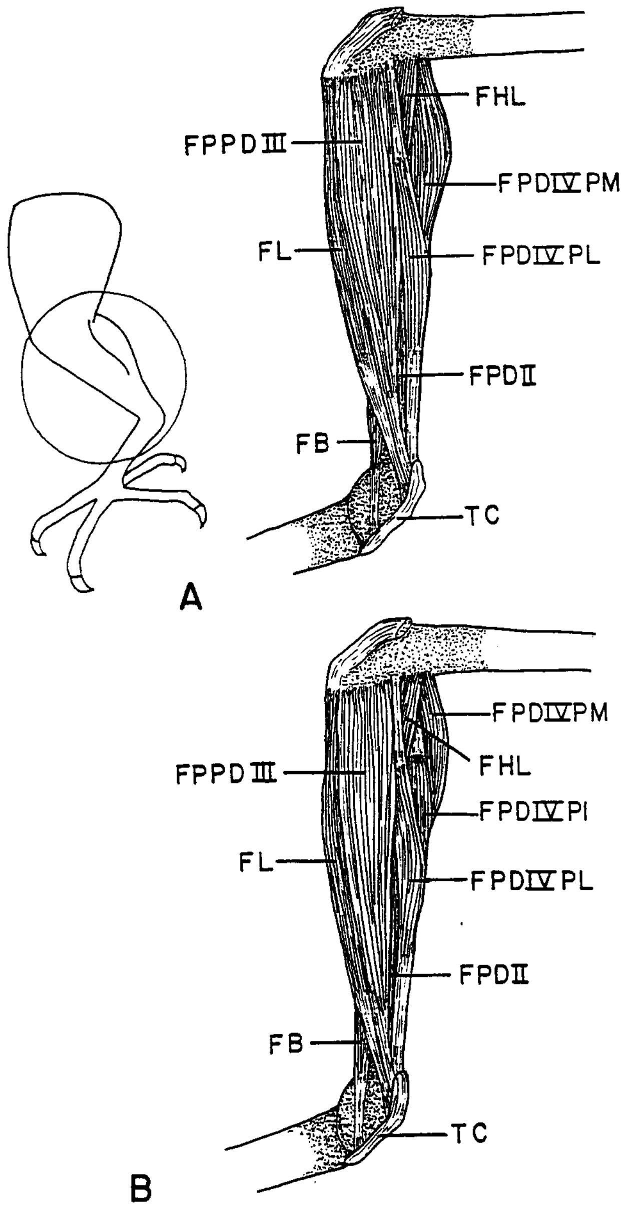

FIGURE 3. Left lateral shank of *Colaptes auratus.* (A) Typical condition found in 35 of the 51 specimens with M. flexor perforatus digiti IV divided into two heads. (B) Condition found in 16 specimens with the muscle divided into three distinct heads, pars lateralis, pars medialis, pars intermedius. Abbreviations: FB, M. fibularis brevis; FL, M. fibularis longus; FHL, M. flexor hallucis longus; FPPD III, M. flexor perforans et perforatus digiti III; FPD II, M. flexor perforatus digiti II; FPD IV PI, M. flexor perforatus digiti IV pars intermedius; FPD IV PL, M. flexor perforatus digiti IV pars lateralis; FPD IV PM, M. flexor perforatus digiti IV pars medialis; TC, tibial cartilage.

necticut, and Museum of Natural History, University of Kansas. We are grateful to D. Morley for his help in preparation of the manuscript.

LITERATURE CITED

BAUMEL, J. J., A. S. KING, A. M. LUCAS, J. E. BREAZILE, AND H. E. EVANS [eds.]. 1979. Nomina anatomica avium. Academic Press, London.

BERGER, A. J. 1956. Anatomical variation and avian anatomy. Condor 58:433–441.

BERMAN, S. L., M. CIBISCHINO, P. DELLARIPA, AND L. MONTREN. 1990. Intraspecific variation in the hindlimb musculature of the House Sparrow. Condor 92:199–204.

BLEDSOE, A. H., R. J. RAIKOW, AND L. S. CROWELL. 1997. Intraspecific variation and evolutionary reduction of tendon ossification in *Dendrocincla* woodcreepers. Condor 99:503–511.

BOCK, W. J., AND C. R. SHEAR. 1972. A staining method for gross dissection of vertebrate muscles. Anat. Anz. 130:222–227.

GEORGE, J. C., AND A. J. BERGER. 1966. Avian myology. Academic Press, New York.

GUTHRIE, R. D. 1965. Variability in characters underlying rapid evolution, an analysis of *Microtus* molars. Evolution 19:214–233.

HUDSON, G. E. 1937. Studies on the muscles of the pelvic appendage in birds. Am. Midl. Nat. 18:1–108.

HUDSON, G. E., P. J. LANZILLOTTI, AND G. D. EDWARDS. 1959. Muscles of the pelvic limb in galliform birds. Am. Midl. Nat. 61:1–67.

KLEMM, R. D. 1969. Comparative myology of the hindlimb of procellariiform birds. Southern Illinois Univ. Monogr. in the Sciences, Social Sciences, and Humanities, Sci. Ser. 2.

MCKITRICK, M. C. 1986. Individual variation in the flexor cruris lateralis muscle of the Tyrannidae (Aves: Passeriformes) and its possible significance. J. Zool. 209:251–270.

MCKITRICK, M. C. 1991. Phylogenetic analysis of avian hindlimb musculature. Misc. Publ. Mus. Zool., Univ. Michigan 179.

RAIKOW, R. J. 1993. Structure and variation in the hindlimb musculature of the woodcreepers (Aves: Passeriformes: Dendrocolaptinae). Zool. J. Linn. Soc. 107:353–399.

RAIKOW, R. J., A. H. BLEDSOE, B. A. MYERS, AND C. J. WELSH. 1990. Individual variation in avian muscles and its significance for the reconstruction of phylogeny. Syst. Zool. 39:362–370.

WILLIAMSON, P. G. 1981. Paleontological documentation of speciation in Cenozoic molluscs from Turkana Basin. Nature 293:437–443.

ZUSI, R. L., AND G. D. BENTZ. 1984. Myology of the Purple-throated Carib (*Eulampis jugularis*) and other hummingbirds (Aves: Trochilidae). Smithson. Contrib. Zool. 385:1–70.

The Condor 100:579–582

AN EVALUATION OF WHOLE BODY POTASSIUM-40 CONTENT FOR ESTIMATING LEAN AND FAT MASS IN PIGEONS[1]

T. G. HINTON
University of Georgia, Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29802, e-mail: hinton@srel.edu

JAMES A. GESSAMAN
Department of Biology and Ecology Center, Utah State University, Logan, UT 84322-5305

ROY D. NAGLE AND JUSTIN D. CONGDON
University of Georgia, Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29802

Abstract. A severe limitation in studies of avian ecological energetics is the lack of an accurate, noninvasive technique for determining whole body fat storage in living birds. We explored a technique of assaying total body potassium as a predictor of lean mass (LM) and then derived fat mass (FM) by subtracting LM from total body mass. Body potassium (K), present in lean tissue but not in fat, was estimated noninvasively from naturally-occurring radioactive ^{40}K, which occurs as a fixed ratio to total body K. We assayed 29 pigeon (*Columba livia*) carcasses for ^{40}K and then measured LM from body composition analyses in which fat mass was extracted using petroleum ether. The ^{40}K results were regressed against LM using five different combinations of independent variables. Regression equations were tested by comparing predicted LM (and FM predictions by subtraction from body mass) to measured LM values obtained from a

[1] Received 15 December 1997. Accepted 3 April 1998.