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Hind Limb Skeleton of the Orange Rumped Agouti (Dasyprocta leporina Linnaeus, 1758): Structural and Functional Perspective

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Authors' contributions

This work was carried out in collaboration between all authors. Author VS defined the theme of the study, performed the statistical analysis, wrote the protocol, and wrote the first draft of the manuscript. Author KAL participated in collection and preparation of the specimen and editing the manuscript. Authors SR and AA participated in the literature review and review of the manuscript. All authors read and approved the final manuscript.

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ABSTRACT

The present study was aimed to document the anatomy of the hind limb skeleton from a structural and functional perspective for the better understanding of locomotor behavior of the orange rumped agouti *(Dasyprocta leporina)*, a caviomorph rodent on the verge of domestication in Trinidad and Tobago. The study was carried out by collecting bones from 6 adult male and 6 adult female animals. The results showed that several features were indicative of emphasized parasagittal movements and stabilized joints. The well-developed ischial tuber, long and strongly built ilium with wide wing and close grouping of greater and lesser trochanter near the proximal tuberosity of the

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femur imply that the animal possesses a well developed flexor-extensor muscle set adapted to quick movements (reaction). The rather elongated body of the calcaneus strengthened the good jumping ability of *D. leporina*. These features along with elongation of the shank and foot indicate that *D. leporina* exhibits a well-developed cursorial ability with high jumping potential.

Keywords: Dasyprocta leporina; agouti; functional morphology; hind limb anatomy.

1. INTRODUCTION

Rodents are the most diversified mammalian order and live in a variety of terrestrial habitats due to the amazing adaptation of the appendicular skeleton with regard to limb use and behaviour [1,2,3]. The orange rumped agouti (Dasyprocta leporina) belong to the caviomorph rodents native to northeastern South America as well as Trinidad and Tobago and are found in a wide range of forests including the rain forests [4,5,6]. The D. leporina is a fast running animal with great ability to trot, gallop, jump vertically and move with remarkable speed and agility, resembling a small ungulate in its locomotor behaviour [7,8]. It often builds burrows in riverbanks or under the roots of trees [1] and caches excess food in shallow pits [7,9].



Fig. 1. The orange rumped Agouti. (Dasyprocta leporina)

The *D.leporina* is very popular exotic meat in Trinidad and Tobago from October to February of every year. An average of 90,000 animals is harvested from the forest during each hunting season [10, 11, 12]. These large extractions together with the depletion of habitat may result in the survival of this species being threatened. In recent years, there are a growing number of wildlife farmers [11] in Trinidad and Tobago venturing to domesticate this animal through breeding to meet the dietary demand for meat. The process of domestication also inspired the idea of using them as laboratory models [13].

The domestication of *D. leporina* in Trinidad and Tobago evoked an interest in the

musculoskeletal system due to their wide functional spectrum like fast running, leaping, digging and shoveling [1,7,8,9]. The terrestrial quadrupeds rely on speed and acceleration to escape from predators [7,14]. Since the hind limbs are the source of most of the propulsive force during locomotion, the functional adaptations are better reflected in the hind limb. So the study of anatomy of the hind limb anatomy will be more appropriate in understanding locomotor behaviour of this animal.

Though few studies on the appendicular system of caviomorph [14,15,16,17,18,19] were done, the musculoskeletal system of the *D. leporina* has not yet been studied. Considering the greater anatomical diversity of the caviomorph rodents, it would be inappropriate to extrapolate the information from other caviomorph rodents to the *D. leporina*. In addition, the study of the locomotor behaviour in the *D. leporina* is considered to be very important in the domestication process of this animal. So it is necessary to carry out an independent work on the hind limb skeleton of *D. leporina* from a structural and functional point of view.

A detailed study on the morphology of the hind limb skeleton of the *Dasyprocta leporina* was carried out in the present work. The main hind limb traits of the *D. leporina* were also analyzed from a structural and functional perspective. It is expected that this study will be useful in future ecomorphologic, evolutionary and domestication studies on these rodents.

2. MATERIALS AND METHODS

A total of 12 adult orange rumped agoutis (6 male and 6 female) of more than 2 years old were purchased from the wild life farmers in Trinidad. The animals were euthanized by the use of a mixture of ketamine (35 mg/kg body weight) and xylazine (5 mg/ kg body weight). The Institutional Ethical Committee, Faculty of Medical Sciences, The University of the West Indies, Trinidad and Tobago, approved the research project. The hind limb was dissected

out from the trunk. The muscles of the hind limb were carefully dissected and teased from the bones to leave the bones with minimal soft tissue attachments, then submerged into different plastic cups containing 3% sodium hydroxide. The plastic cups were then covered and placed under the sun and checked for complete detachment of muscle from the bone for every 30 minutes [20]. The bones were completely detached from the muscles in 3 hours time. The bones were then rinsed in running water and then air-dried. The bones were studied for the structural features and functional correlations were drawn. The various morphometrical measurements of the major long bones were measured with the help of a vernier caliper.

3. RESULTS

3.1 Os Coxae

The os coxae was robustly built and the ilium and ischium were oriented parallel to the vertebral column.

3.1.1 Ilium

The ilium was elongated and consisted of a wide wing and a narrow shaft. The shaft of the Ilium measured 10.0 \pm 0.2 cm in length, 1.2 \pm 0.08 cm width and the width of the wing measured 2.4 ±0.12 cm. The wing presented a tuber sacrale dorsally and robust tuber coxae ventrolaterally. The dorsal iliac crest was thick and convex, ran caudally from the tuber sacrale until it terminated in a hook-like muscular projection. The dorsal iliac crest was cut away at its junction with the muscular projection, forming the greater ischiatic notch. The tuber coxae were grooved medially. The dorsolateral surface was wide and showed the gluteal fossa, which was divided by gluteal crest into dorsal and ventral portions. The ventromedial surface bore a wide, distinct, auricular articular surface forming an irregular semilunar shape dorsally for the sacrum. The shaft was short, robust and columnar and contributed to the acetabulum caudally. The shaft presented an indistinct iliopubic eminence and psoas tubercle on its ventral border (Fig. 2).



Fig. 2. Dorsal (A), Ventral (B) and Lateral(C) views of the pelvis of *D.leporina* 1. Ilium 2. Ischium 3. Pubis 4. Iliac crest 5.Greater ischiatic notch 6.Lesser ischiatic notch 7.Tuber sacrale 8.Tuber coxae 9.Tuber ischii 10.Pelvic arch 11. Obturator foramen 12. Obturator notch 13. Psoas tubercle 14.Gluteal crest 15. Dorsal gluteal fossa 16. Ventral gluteal fossa

3.1.2 Ischium

The ischium was elongated, and consisted of a extended horizontal plate cranially hv symphyseal (1.98 ± 0.09 cm in length) and acetabular/body (3.5 ±0.13 cm in length) parts on either side of the obturator foramen. The acetabular part surmounted by ischial spine which extended onto the caudal part of ilium and formed the greater ischiatic notch. The ischial spine was indented to form a lesser ischiatic notch caudally. The ischial tuber was prominent and had two processes. There was a small notch on the caudal side of ischial tuber. The ischial arch was broader. The pelvic symphysis was fused (Fig. 2).

3.1.3 Pubis

The pubis was L -shaped with cranial or acetabular $(3.0 \pm 0.08 \text{ cm} \text{ in length})$ and caudal or symphyseal $(2.1 \pm 0.07 \text{ cm} \text{ in length})$ parts. The caudal border of the pubis accounted for about half the circumference of the large, oval shaped obturator foramen. A round notch was present on the obturator foramen close to the acetabulum.

The acetabulum was deep, round and limited by well-extended walls. It was located dorsally relative to the level of the spine and oriented laterally (Fig. 2).The pelvic symphysis was present in both sexes. It was longer in males (3.1 \pm 0.09 cm in length) than the females (2.9 \pm 0.08 cm in length) and terminated cranially at the level of sacral 3-4 (5-6 in females). The male pelvis also measured larger with 4.1 \pm 0.12 cm conjugal diameter and 3.2 \pm 0.09 cm in transverse diameter than the females 3.8 \pm 0.09 cm in transverse diameter.

3.2 Femur

The femur was relatively slender and oriented parallel to the vertebral column. The shaft of the femur was measured 8.5 ± 0.07 cm in length and 0.8 ± 0.03 cm in width. The femoral head had a spheroid articular surface and supported by a well-developed, elongated neck. The fovea capitis was reduced to an indistinct depression. The greater trochanter was very well developed and placed higher than the femoral head. The lesser trochanter was strongly marked and formed an eminent tubercle, placed on the caudal aspect of the proximal extremity of the femur. The trochanteric fossa was wide and very deep. The trochanteric ridge connected the greater and lesser trochanters. The third

trochanter was evident in the mid-shaft and connected to the great trochanter by a solid crest. The distal extremity was more extended mediolaterally in relation to the width of the shaft and the total length of the bone. The intercondyloid fossa was significantly wider whereas the patellar groove on the trochlea was narrower. The condyles presented an ellipsoidal articular surface and epicondyles were prominent. There were two sesamoid bones (febellae) embedded in the tendons of the origin of the gastrocnemius muscle (Fig. 3A-F).

3.3 Patella

The patella was comma shaped with a rough and convex cranial surface as opposed to the caudal surface, which formed a smooth plane for the articulation at the patellar groove. The length, width (at the base) and thickness (at the base) of the patella was measured as 2.0 ± 0.02 cm, 0.8 ± 0.01 cm and 0.7 ± 0.01 cm respectively. The base of the patella, the point of attachment for the quadriceps muscle was gently flattened. The pointed, elongated apex was directed caudally creating space for the attachment of the middle and lateral patellar ligaments (Fig. 3G).

3.4 Tibia and Fibula

The tibia and fibula were long and separated bones, placed vertical to the vertebral column. The tibia was robust and very long whereas fibula was very thin and rod like. The tibia was measured 9.2 \pm 0.05 cm length and 0.6 \pm 0.01 cm width at mid shaft. The fibula was measured 8.0 ± 0.02 cm in length and 0.25 ± 0.01 cm width at the mid shaft. The proximal extremity of the tibia presented a more concave lateral articular surface than the medial condule. The intercondylar eminence had a deep central groove. The lateral intercondyloid tubercle was larger than the medial one. The articular fibular projection was distinct and broad for the attachment with the tibia. The tibial tuberosity was a well-developed crest extended parallel to the shaft and terminated in a small tubercle, the attachment of the semimembranosus muscle. The distal tibia had a deep, concave articular surface and presented a medial malleolus on the medial side. The fibular head and articular fibular projection of the tibia were of same width. The fibula was separated from tibia by an interosseous space that ran the whole length of the leg. The proximal end was flattened. The shaft was slender and the distal fibula ended on the lateral malleolus. The distal fibula articulated with the tibia (Fig. 4)

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Fig. 3. Cranial (A), Caudal (B), Medial (C) and Lateral (D) views, Proximal (E) and distal extremity (F) of the left femur and the lateral surface (G) of the patella of the *D. leporina* 1. Femoral head 2.Femoral neck 3.Fovea capitis 4.Greater trochanter 5. Lesser trochanter 6.Trochanteric ridge 7.Trochateric fossa 8.Third trochanter 9.Shaft 10.Trochlea 11. Condyles 12.Intercondylar fossa 13.Medial epicondyles 14. Lateral epicondyles



Fig. 4. Cranial (A), Caudal (B), Medial (C) and Lateral (D) views, Proximal extremity (E) and Distal distal extremity (G) of the left tibia and fibula of *D. leporina*

1. Tibia 2. Fibula 3.Medial condyle 4.Lateral condyle 5.Caudal intercondyloid fossa 6.Tibial tuberosity 7.Medial malleolus 8. Lateral malleolus 9.Fibular articular projection 10.Fibular head 11. Interosseous space.

3.5 Tarsal Bones

There were 8 tarsal bones arranged in three rows. The proximal row consisted of the talus. calcaneus and tibial tarsal bones. The tibial tarsal bone was small and disposed medially to the talus and calcaneus. The trochlear groove of the talus ran diagonally from medial to lateral and shaped to fit the tibia. The talus articulated with the central tarsal bone distally and calcaneus caudolaterally. The calcaneus presented a relatively elongated body and well developed tuber calcis and articulated with the fibula medially. The body of the calcaneus had three oval surfaces for the connection with the talus. The central tarsal bone (os naviculare) was placed in the middle row. The central tarsal was placed between the talus on and the cuneiform bones. It consisted of a body and extended plantar process and contacted with first three cuneiform bones distally. The plantar process was very long and ended like a hook. The distal tarsal bones were the first, second, third and fourth. The comparative sizes of the distal tarsal bones were I > II > IV> III. The fourth tarsal bone (os cuboid) articulated with calcaneus dorsally and distally with the fourth metatarsal and the vestigeal fifth metatarsal bone. The first and second tarsal bones were articulated with the second metatarsal bone and the third tarsal bone was articulated with the third metatarsal bone (Fig. 5).

3.6 Metatarsal Bones

The pedis consisted of three well developed metatarsal bones, second, third and fourth. The first was absent whereas the fifth was rudimentary. The comparative lengths of the metatarsal bones were IV>II> III. The proximal extremities created a base, which articulated with the tarsals and joined the neighboring metatarsals together in a row. The shaft or body was elongated. The distal extremities formed a head with a trochlea for the connection with the phalanges. There were two plantar sesamoid bones located in pairs at each of the metatarsophalangeal joints (Fig-6).

3.7 Digits

There were three digits with three phalanges. The sesamoid bone was placed between the middle phalange and distal phalange on each digit. The distal phalanges had shallow articular surface proximally and tapered distally to form a sharp tip with a notch. The distal phalanges formed the bony cores for the claws (Fig. 6).

4. DISCUSSION

The pelvis is long and well developed in the D. leporina unlike in the burrowing rodents [21] where the pelvis is greatly reduced presumably in response to their need to turn within the narrow confines of a burrow. The division of gluteal fossa into dorsal and ventral portions indicates that the gluteus medius partly originates from the dorsal gluteal fossa, whereas gluteus profundus arises from the ventral gluteal fossa as stated in Dasyprocta azarae [19]. However, gluteus profundus takes origin from a distinct fossa of the ilium in other cavioids and other rodents [19]. This musculoskeletal arrangement is difficult to evaluate from a functional perspective. The wide iliac wing creates the expanded surface for the attachment of the gluteus medius muscle, one of the most powerful thigh extensors. [22,23]. The wide iliac wing in D. leporina is considered one of the hallmarks of cursoriality as well as the ability to perform powerful leaps as observed in many terrestrial mammals [22,24].

A proximally projected greater trochanter in *D. leporina* increases the lever arm of gluteus medius and profundus muscles and their mechanical advantage in cursorial species [25, 26]. Therefore, the high mechanical advantage of the gluteus medius and profundus in *D. leporina* is compatible with a powerful extension of the thigh during the propulsive phase of locomotion, a characteristic feature of cursorial species (22, 25, 27, 28].

The second set of extensors of the thigh are semitendinosus, semimembranosus, and biceps femoris which are large and long muscles attached to the ischial tuberosity and the lateral process of the ischium [29]. These muscles are adjusted primarily for excursion but also able to generate large forces [30]. The prominent ischiatic tuberosity in D. leporina suggests an extensive area of origin for these muscles. The relative elongation of the ischium with respect to total pelvic length, situates the areas of origin of these muscles far from the hip joint, thus improving their mechanical advantage, a condition required for powerful extension of the hip at the beginning of propulsion, and for the flexion of the knee during the recovery stroke [23,25].

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Fig. 5. The tarsal bones (A-E) of *D. leporina*

1. Talus 2. Calcaneus 3. Tibial tarsal bone 4. Central tarsal bone 5. I tarsal bone 6. Il tarsal bone 7. III tarsal bone 8. IV tarsal bone 9. Tuber calcis 10.Planatr extensor process 11.Body of the calcaneous 12. Trochlea of talus



Fig. 6. The dorsal (A) Plantar (B) and lateral(C) views of the pes of *D. leporina* 1.1 metatarsal bone 2. II metatarsal bone 3. III metatarsal bone 4.1V metatarsal bone 5.V metatarsal bone 6. Proximal phalange 7. Middle phalange 8. Distal phalange 9. Proximal sesamoid 10. Distal sesamoid

A relatively elevated acetabulum in D. leporina stabilizes the flexion/extension movements at the joint and accentuates parasagittal hip movements of the femur as in other caviomorph rodents [26]. The lateral orientation of the acetabulum in the D. leporina may decrease the compressive forces at the pubic symphysis and enhances the ability to walk or brace with splayed legs. The deep acetabular cavity is limited by well-extended walls in D. leporina and likely to partially restrict rotational movements. The proximally projected greater trochanter could also restrict the mobility of the hip joint, limiting the movements of abduction of the femur, a condition observed in other terrestrial mammals [22,23,24,27,28].

The reduced pelvic symphysis, a typical burrowing modification [31] is not observed in the *D. leporina* where the pelvis symphysis is fully developed and persists in both sexes. The obturator foramen is almost oval in both sexes and the presence of a round notch on the obturator foramen is not reported on other rodents like African giant rat [32], African giant pouched rats [33], rats [34] and rabbits [35].

In highly cursorial and saltatorial mammals, the femur is generally slim and the trochanters are concentrated closer to the proximal end of the bone. It shortens the lever arms over which muscle forces acts and produces swifter responses to the contraction of muscles, yielding quicker but less powerful flexion (iliopsoas muscle) and extension (the gluteus superficialis, tensor fasciae femoris and gluteus medius muscles) of the thigh at the hip joint [36,37]. In D. leporina, the femur is relatively slim and the greater and lesser trochanters are concentrated closer to the proximal end of the bone, implying a relatively high degree of cursoriality. The proximally extended greater trochanter in the D. leporina is considered as an adaptation to terrestrial locomotion, because it restricts the action of the gluteus medius in abduction of the femur at the hip joint and makes the para sagittal action of the limb more efficient as interpreted in small carnivores [22]. The lesser trochanter is an insertion for the iliopsoas muscle; located caudally close to the proximal end of femur. A more proximal location allows the iliopsoas to rapidly flex the thigh [36]. Rapid flexion of the thigh would be advantageous during fast running as well as moving dirt while burrowing. The caudal location of the lesser trochanter would improve the function of iliopsoas as a protractor rather than as a rotator of the femur [23,26,27,

28]. However, the third trochanter in D. leporina is placed at midshaft level which may act as a reinforcement mechanism for the proximal femoral diaphysis in response to increased ground reaction force and to increase the attachment surface area for the gluteal musculature and thereby providing greater efficiency of contracture. A well-defined articular surface of the femoral head with sharp, pronounced margins and well developed, distinct femoral neck in D. leporina increase the mechanical advantage of the gluteal muscles by lengthening their lever arm. This may counteract the increased stress on the hip joint while also allowing greater mobility in a transverse plane which may be related to the ability of burrowing. The high cursorial ability of D. leporina is emphasized also by the relatively high craniocaudal thickness of the distal extremity of the femur, even exceeding its width and a distinctly narrow patellar groove. The deeper condyles, one of hallmarks of cursoriality [37], allow more powerful extension of the knee by the action of the quadriceps femoris.

The fused tibia and fibula are considered to be a digging adaptation in majority of the rodents like hedgehogs [38], Squirrels [39] and rats [34] wheras in *D. leporina*, the fibula is attached with the tibia proximally and articulates distally as in caviomorph rodents Cuniculus paca and Hvdrochoerus hvdrochaeris [40], which indicate their limited capacity in digging. The robustness of the tibia in the D. leporina reflects the importance of the tibia in support and propulsion of the body mass during locomotion as in caviomorph rodents [15]. The tibia and fibula along with the metatarsal segment of *D. leporina* are the main bones responsible for the elongation of the leg as in highly cursorial species [7, 36]. The general design expressed more strongly in cursorial species is that the most powerful hind limb musculature occupies the upper regions of the leg, reaching about one third of the proximal part of the tibia, while the distal end of the bone and the foot forms the attachments for ligaments. So the shortening of the muscle arms quickens the responses of the limb bones to their action [36]. In the present study also it is observed that the tibia is the most distal bone having large muscle attachments. The tibial tuberosity serves as the attachment area for shank flexors and the patellar ligament of the quadriceps femoris and sartorius muscle. The relative length of the tibial tuberosity is short and extending only in the proximal one third in D. leporina which reflects the tendency to group the

muscle attachments near the bone ends as observed in highly cursorial mammals [36].

The proportions of the proximal and distal extremities of the tibia in the *D. leporina* reflect the tibial aspect of "deepening of the knee" (observed also in the distal end of the femur) by increasing relative cranio-caudal depth of the proximal extremity. The distal tibial articular surface is deep and concave, in congruence with symmetrical crests of the trochlea of the talus. These features indicate that the ankle joint in *D. leporina* restricts the movements mainly to plantar flexion-dorsiflexion, typical of cursorial locomotion [27, 35].

The foot in terrestrial mammals is another anatomical region (along with the shank) of the hind limb in which significant cursorial and saltatorial adaptations are apparent [7,36]. The metatarsals are the bones that most fully reflect cursoriality, being relatively elongated in fast running mammals [36]. On the other hand, the tarsal elements in cursorial animals serve to stabilize the ankle joint by creating large and deep surfaces for the articulation with the tibia and fibula. Therefore tarsal bones generally are not elongated. However, in some small arboreal primates, such as tarsiers and galagos, probably the best leapers among the mammals, tarsals can be lengthened significantly, reflecting some particular saltatorial adaptations [36.37]. In D. leporina the basic ankle joint structure followed the general pattern in rodents [41] with some differences in the proportions of the tarsal bones. The main differences in the foot morphology can be seen in elongation of the metatarsals and phalanges.

The most powerful muscle of the hind limb, the gastrocnemius, is attached to the tuber calcis. The well-developed tuber calcis is considered as a cursorial adaptation whereas the elongation of the body of the calcaneus seems to be closely related to saltatorial adaptation. During saltatorial locomotion, strength of the gastrocnemius muscle must act against the force of gravity [36]. In the *D. leporina* well developed tuber calcis and the relatively elongated body of the calcaneus indicates the capability of both cursorial and saltatorial locomotion.

The tarsal bones were typical in *D. leporina* as reported in Wister rats [41] whereas the medial tibial tarsal bone was not reported in the hedgehog [38]. The central tarsal and fourth tarsal bones are relatively elongated in species with greater cursorial adaptations. On the other hand, the plantar process of the central tarsal bone is found to be longest in the less cursorial species [36,42]. In *D. leporina*, central tarsal and fourth tarsal bones are moderately elongated and the former presented a long plantar process. This long plantar process may stabilize the ankle during digging.

The observation of three metatarsals and three digits in the *D. leporina* is similar to that in the guinea pig [43], whereas five metatarsals and five digits were reported in in other burrowing animals like Wistar rat [41], laboratory rat [44], Rabbit [45], Mink [46], Porcupine [47] and Mole rat [34]. However, the pedis comprises four digits in some species of the Ernaceidae family [48]. The reduction in the number of metatarsals and digits reflect the cursorial adaptation of *D. leporina*.

The elongation of the foot relative to the rest of the limb is observed in all efficient runners (7, 36). A "gear ratio" concept is used to illustrate [36] the dependence of the speed and the general foot proportions. Higher gear ratios are indicative of greater running ability. The gear ratio for the gastrocnemius was calculated herein. It is defined as the proportion of the length of the portion of the foot placed prior to the point of support for tibia to the length of the foot skeleton placed caudally to the tibia junction. The longer metatarsal and phalangeal segments of *D. leporina* have an increased gear ratio that probably contributes to the increase in cursoriality.

5. CONCLUSION

The morphological analysis of the hind limb skeleton allowed recognition of particular adaptations and the estimation of possible style of locomotion. The wide ischial tuber, strongly built long ilium with wide iliac wing and marked closer grouping of the greater and lesser trochanter near the proximal tuberosity of the femur imply that the animal possessed the relatively well developed flexor-extensor muscle set adapted to quick movements (reaction). These features along with relative elongation of the shank and foot indicate that D. leporina exhibited well-developed cursorial ability with high jumping potential. The foot proportions are influenced by habitat, and the relatively longer feet are found in forest species where the conditions enhance the jumping potential i.e., the ability to perform powerful jumps of high steepness. Animals, living in more closed, bushy habitats, are characterized by a greater angle of jump departure. However, the topic needs further investigation, because, *D. leporina* has adapted to live in more open, savannah-like environments in Trinidad and Tobago. The good jumping ability in *D.leporina* is strengthened by the morphology of the calcaneus, which has a relatively elongated body, a feature connected with high jumping performance.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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