



Mobility of the forearm in the raccoon (*Procyon lotor*), raccoon dog (*Nyctereutes procyonoides*) and red panda (*Ailurus fulgens*)

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ABSTRACT. The ranges of pronation/supination of forearms in raccoons, raccoon dogs and red pandas were nondestructively examined. Three carcasses of each species were used for CT analysis, and the left forearms were scanned with a CT scanner in two positions: maximal supination and maximal pronation. Scanning data were reconstructed into three-dimensional images, cross-sectional images were extracted at the position that shows the largest area in the distal part of ulna, and then, the centroids of each cross section of the radius and ulna were detected. CT images of two positions were superimposed, by overlapping the outlines of each ulna, and then, the centroids were connected by lines to measure the angle of rotation, as an index of range of mobility. The measurements in each animal were analyzed, using the Tukey–Kramer method. The average angle of rotation was largest in raccoons and smallest in raccoon dogs, and the difference was significant. In the maximally pronated forearm of all species, the posture was almost equal to the usual grounding position with palms touching the ground. Therefore, the present results demonstrate that the forearms of raccoons can supinate to a greater degree from the grounding position with palms on the ground, as compared with those of raccoon dogs and red pandas.

KEY WORDS: forearm, raccoon, raccoon dog, red panda, rotation

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Raccoons (*Procyon lotor*), belonging to the order Carnivora, superfamily Musteroidea and family Procyonidae [5], are excellent tree-climbers (they show ground-dwelling basically, while arboreal in some cases), swimmers and generally known to have highly dexterous forelimbs [6, 11, 16]. They usually inhabit the forest and bush area near aquatic habitats and are omnivorous, eating various kinds of food, such as fishes, arthropods, frogs, nuts, seeds, acorns and berries, using their forepaws skillfully [11, 17]. Raccoon dogs (*Nyctereutes procyonoides*), of the order Carnivora, superfamily Canoidea and family Canidae [3, 18], are also omnivorous [8, 11], but they cannot use their forelimbs skillfully for feeding (i.e., they do not put food in their mouth with their paws) and are not good tree-climbers, although they possess some scansorial abilities (non-arboreal in life style). On the other hand, red (lesser) pandas (*Ailurus fulgens*), classified into the order Carnivora, superfamily Musteroidea and family Ailuridae [5], are arboreal and basically herbivorous mammals that eat bamboo, sprouts, grasses and acorns, although they occasionally capture insects, small birds and rodents [11]. Red pandas have developed special gripping mechanism using a large radial sesamoid bone with passive mobility and the digits, unlike raccoons [1, 2, 4].

It is well known that the large degree of rotation (pronation/supination) of the forearm is one of the factors necessary to acquiring dexterous forelimbs. In several primates, the rotation angle of forearms was examined [10, 12]. In carnivores, however,

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Table 1. The carcasses used in this study

Species	Sex	Donor or Location	Storage place of specimens
Raccoon	Male	OZ	OU
Raccoon	Male	HBMC	OU
Raccoon	Male	HBMC	OU
Raccoon dog	Male	RK	OU
Raccoon dog	Male	RK	OU
Raccoon dog	Male	RK	OU
Red panda	Female	UZ	NSM
Red panda	Female	UZ	NSM
Red panda	Male	UZ	NSM

HBMC, harmful birds and mammals controlled in Hokkaido, Japan; NSM, National Science Museum, Tokyo, Japan; OU, Obihiro University of Agriculture and Veterinary Medicine, Hokkaido, Japan; OZ, Obihiro Zoo, Hokkaido, Japan; RK, roadkill in Hokkaido, Japan; UZ, Ueno Zoological Park, Tokyo, Japan.

the range of mobility of the bones of the forearms has not been nondestructively investigated. Therefore, as a preliminary study, we examined the rotation (pronation/supination) of the forearm bones, using a x-ray computed tomography (CT) scanner, in three carnivore species (raccoons, raccoon dogs and red pandas), which have different behaviors in feeding and life styles (case-arboreal, non-arboreal and arboreal, respectively), although they are similar in the body proportion and size.

MATERIALS AND METHODS

In the present study, three carcasses each of raccoon, raccoon dog and red panda were used for the range of motion (ROM) analyses in the forearm pronation/supination (Table 1). Specimens were refrigerated at -15°C until examinations were performed. The left forearm of each animal carcass whose elbow joint was kept in a right angle was scanned, using a CT scanner (Asteion Super 4, Toshiba, Tokyo, Japan; scanning conditions, 120 kV, 150 mA and 0.5 mm slice thickness), in two positions: maximal supination and maximal pronation. We defined the rotation (supination/pronation) axis as a line connecting the proximal and distal ends of the ulna, and then, the specimen was CT-scanned along the axis. CT-scanned data were visualized as CT images and furthermore reconstructed into three-dimensional images, using an image processing workstation (Virtual Place Advance PLUS, AZE, Tokyo, Japan). To detect the range of rotation (supination/pronation) angle of the radius about the axis, we used the cross-sectional image of the distal forearm. The centroids of the cross sections of the ulna and the radius on the image were respectively detected by ImageJ 1.49 (National Institute of Health, Bethesda, MD, U.S.A.). The axial CT images of two positions (pronation and supination) were superimposed by overlapping the outlines of each ulna, and then, the centroids were connected by lines. The angle made by the lines connecting the centroids of the distal transverse sections of the ulna and radius was defined as supination/pronation angle and was measured as an index of the range of mobility of the radius about the ulna (Fig. 1). On assumption that the supination/pronation angles for each taxonomic group show normal distribution, we tested whether there are statistical differences of the mean supination/pronation angles among the three studied taxa. We used one-way analysis of variance (ANOVA) for comparison among all three taxa, which was followed by Tukey-Kramer test for a pairwise comparison between two selected taxa. The significant differences of the angles among or between the taxa were supported at $P < 0.05$.

RESULTS

Three-dimensional images of the bones of the forearm in each animal are shown in Figs. 2–4. In the maximal pronation position of all species, the long axes of the radius and ulna crossed each other, and the posture was almost equal to that of the usual grounding position with palms touching the ground (Figs. 2–4). In the maximal supination position, the radius rotated around the ulna (Figs. 1–4), and in raccoons, was almost parallel to the ulna in the view from the flexor side of the forearm (Figs. 1 and 2). The range of the supination/pronation angle was the smallest in raccoon dogs (Fig. 1), and in the view from the flexor side, the radius and ulna were overlapped because of small range of the rotation angle, and thus, the interosseous space of forearm was hardly recognized (B2 in Fig. 3).

The ranges of the radius supination/pronation angles were $88.02 \pm 6.20^{\circ}$, $41.92 \pm 9.85^{\circ}$ and $66.76 \pm 5.98^{\circ}$ in raccoons, raccoon dogs and red pandas, respectively (Fig. 5). A significant difference was found between raccoons and raccoon dogs (one-way ANOVA, $P < 0.05$, $n = 3$; Tukey-Kramer test, $P < 0.05$), while there were no significant differences between the ranges of supination/pronation angles of red pandas and raccoons, and those of red pandas and raccoon dogs (Tukey-Kramer test, $P \geq 0.05$).

DISCUSSION

In the present study, raccoons had the largest angle of forearm supination/pronation, among the three examined carnivores. Because the maximally pronated position of the forearm is almost the same as that in the usual position at the supporting phase of

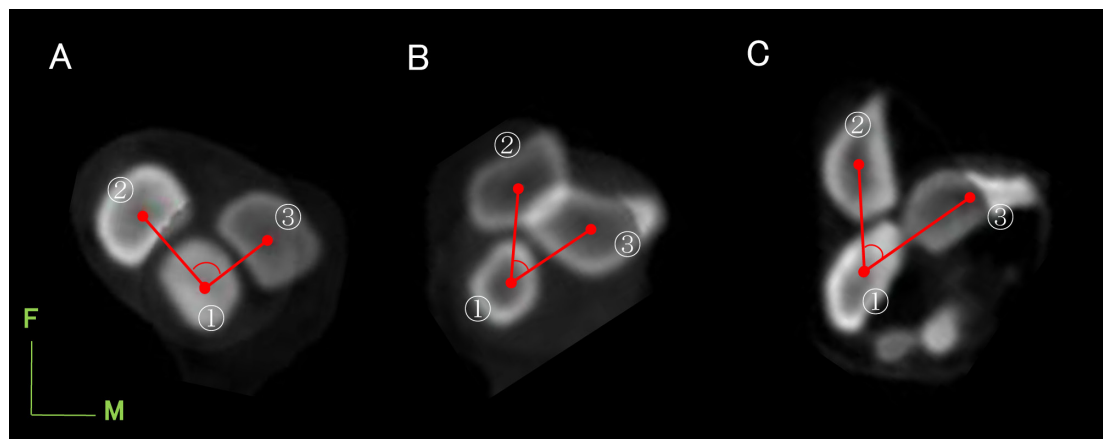


Fig. 1. Axial CT images of left forearms in the raccoon (A), raccoon dog (B) and red panda (C). Centroid of the cross section of ulna (1) and radii in maximal supination (2) and pronation (3). The cross sections were extracted at the position with the largest area in the distal part of ulna. The angle formed by points 1–3 is defined as the range of the pronation/supination angle. Cross bar shows flexor (F) and medial (M) sides.

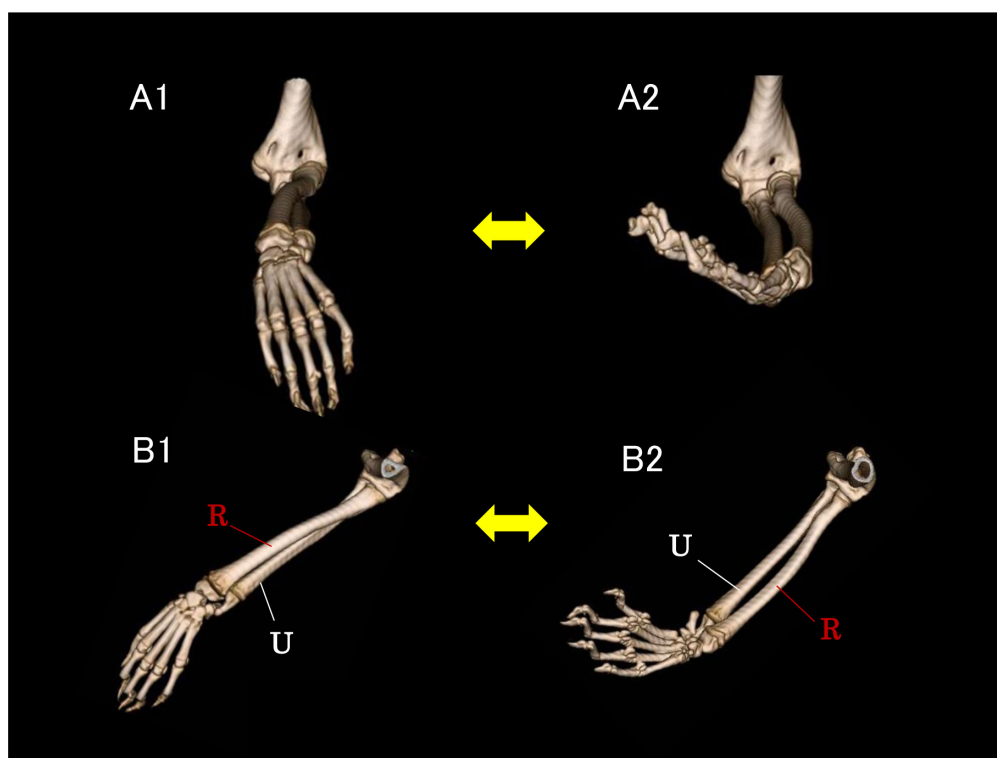


Fig. 2. Distal (A) and flexor side (B) views of three-dimensional CT images of the left forearm of the raccoon. (1) and (2) show maximally pronated and supinated positions, respectively. R: Radius, U: Ulna.

the locomotion for all three species, the largest angle of forearm pronation in raccoons means that raccoons are able to supinate their forearms from the grounding position, to direct their palms more dorsally as compared with other species.

The mobility of limbs has a close relation to various behaviors indispensable for life. The adaptation of manipulation and locomotion varies among species and depends on their habitat. Although, all the animals examined belong to the suborder Caniformia, each has different behaviors for their lives. Taylor [16] classified raccoons and raccoon dogs as ambulatory carnivores, and red pandas as arboreal carnivores. Raccoons and raccoon dogs spend most of their lives on the ground [9, 15, 17], in contrast, red pandas mainly live in trees [11, 14]. In the case of raccoons, however, they possess skillful climbing abilities. They often climb trees to escape from predators when attacked and sometimes employ a tree hollow as their nest [11, 14, 17]. To climb a tree, the raccoon's forelimbs need to be able to grasp the trunk from opposite sides to prevent them from sliding down. Taylor [16]

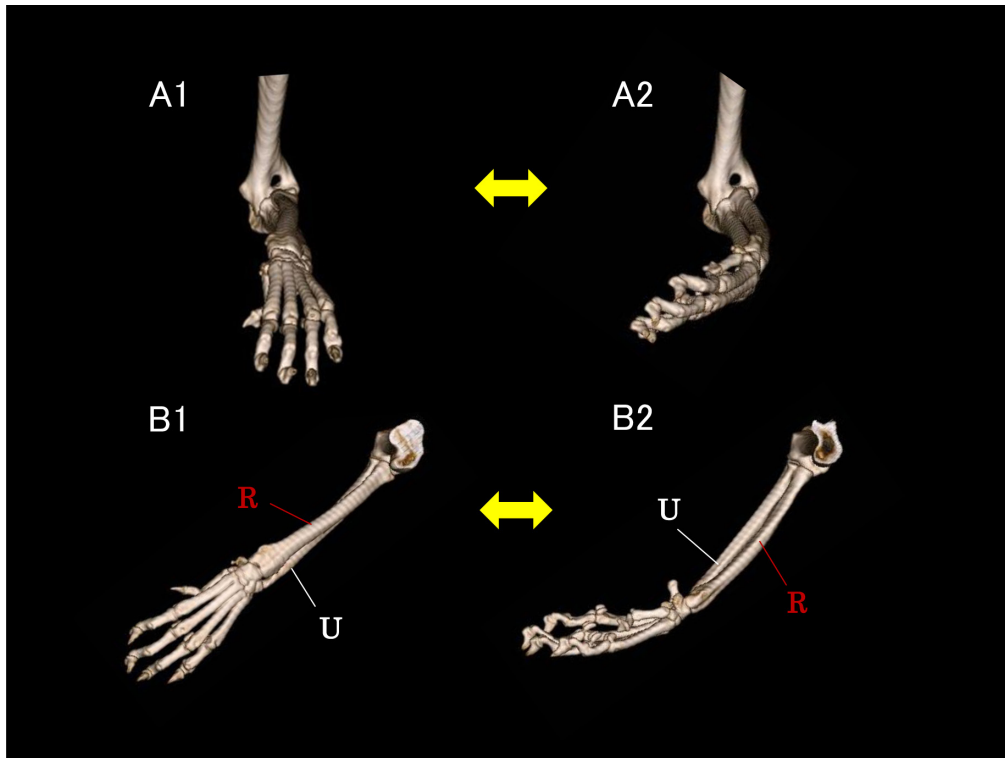


Fig. 3. Distal (A) and flexor side (B) views of three-dimensional CT images of the left forearm of the raccoon dog. (1) and (2) show maximally pronated and supinated positions, respectively. R: Radius, U: Ulna.

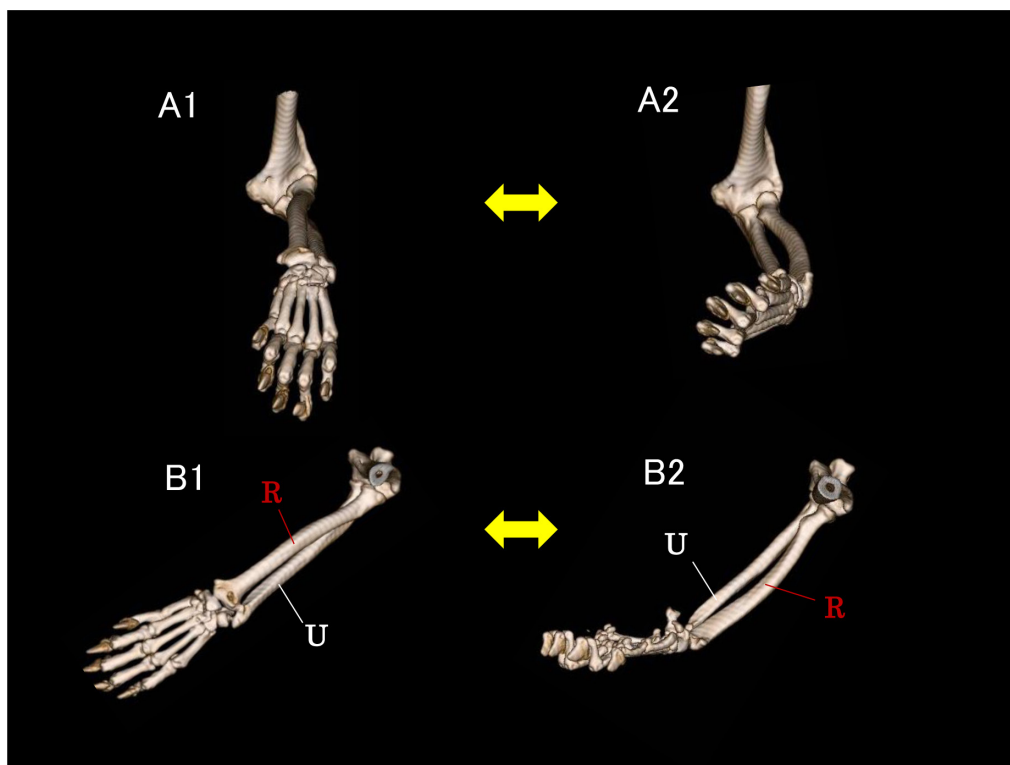


Fig. 4. Distal (A) and flexor side (B) views of three-dimensional CT images of the left forearm of the red panda. (1) and (2) show maximally pronated and supinated positions, respectively. R: Radius, U: Ulna.

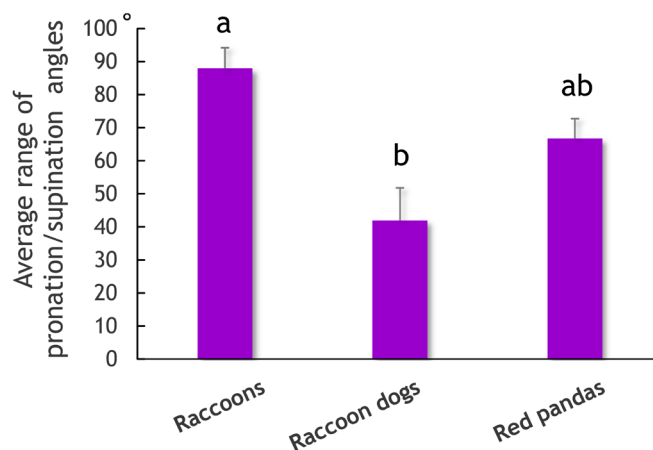


Fig. 5. The average of rotation angles of forearms (mean \pm standard error of mean). There is a significant difference between different symbols (a and b) ($P < 0.05$, Tukey–Kramer test).

reported that larger animals increase surface contact, between their paws and the tree by supinating their feet, in arboreal walking. Therefore, it may be assumed that the large angle of forearm rotation in raccoons endows them with excellent climbing skills.

In the present study, red pandas were shown to have a smaller angle of forearm rotation than raccoons; nevertheless, they are an arboreal species and routinely locomote in trees. It is presumed that their climbing adaptation is more developed than in raccoons. Therefore, many other factors, such as musculature development, body weight and the mobility of upper arms, carpal joints and hindlimbs, as well as the rotation of forearms, may be involved in climbing. It has been reported that, for example, red pandas have well-developed and long claws for clinging to the bark of trees [16]. In further studies, the detection of other factors, involved in climbing, is necessary to reveal the differences in climbing skills between raccoons and red pandas.

With regard to feeding styles, the use of forelimbs in handling food by raccoons differs from the other two species examined in this study. Raccoons generally live near aquatic habitats in forests or marshy bayous, and they have many opportunities to grope for food from the water or muddy areas [17, 21]. To find food in such an environment, raccoons might have acquired several unique forelimb functions. Iwaniuk and Whishaw [6] observed and recorded raccoon forelimb movements during feeding: reaching for and grasping food and bringing it to their mouth. A series of these actions is widely seen in most rodents and primates and regarded as an advanced function of forelimbs [20]. When reaching for food, the forearms would be pronated to direct the palm downwards. Raccoons are capable of finding food depending upon tactile sense only, without visual or olfactory information [7]. When bringing food to the mouth, forelimbs would adduct while supinating the forearms to carry food to the mouth. Moreover, raccoons have slender, hairless, flexible and sensitive digits in their forepaws, with naked palms [6, 11, 13, 19]. Whereas, red pandas have hairy palms and digits; the digits cannot be spread wide and are inflexible, unlike raccoons [11, 16], and gripping food, such as bamboo grasses, is aided by a false-thumb, which is an enlarged radial sesamoid bone [1, 2, 4, 14]. As for raccoon dogs, they use forelimbs only to hold down food and move the mouth toward it.

It is thought that the supination/pronation angle of the forearm is affected by environment and feeding style. In the present study, raccoons, classified as ambulatory carnivores, were shown to have a larger angle of forearm rotation than red pandas, which are arboreal carnivores. It is suggested that the necessity of forearms for feeding in raccoons has a large impact on the rotation angle of forearm as compared with that during climbing in red pandas. This relationship is similar to that of the human (*Homo sapiens*), which utilizes dexterous forelimbs for complicated manipulation and has a larger angle of forearm rotation than arboreal primates [12].

In conclusion, the results of the present study demonstrate that the forearms of raccoons can supinate significantly to a greater degree from grounding with palms, compared with those of raccoon dogs, and may be functionally adapted mainly for feeding and are also used beneficially for climbing, although raccoons are classified as ambulatory carnivores basically. To more comprehensively understand the functional adaptation of forearms in the caniforms, we would need to examine the supination/pronation angle of forearm in other caniform taxa which have different body proportion and size, and/or other special functions of forearm (e.g., fossorial ability) using the same methods.

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