

FULL PAPER

Anatomy

Mobility of the forearm skeleton in the Asiatic black (*Ursus thibetanus*), brown (*U. arctos*) and polar (*U. maritimus*) bears

Hayato AMAIKE^{1,2)}, Motoki SASAKI²⁾*, Nao TSUZUKI²⁾, Mitsunori KAYANO²⁾, Motoharu OISHI³⁾, Kazutaka YAMADA³⁾, Hideki ENDO⁴⁾, Tomoko ANEZAKI⁵⁾, Naoya MATSUMOTO⁶⁾, Rumiko NAKASHITA⁷⁾, Misako KUROE⁸⁾, Hajime TARU⁹⁾, Gen BANDO¹⁰⁾, Yuko IKETANI¹⁰⁾, Ryohei NAKAMURA¹⁰⁾, Nobutaka SATO¹⁰⁾, Daisuke FUKUI¹¹⁾ and Nobuo KITAMURA¹⁾

¹⁾Hokkaido University School of Veterinary Medicine and Obihiro University of Agriculture and Veterinary Medicine, Cooperative Veterinary Education Program, Hokkaido University, Sapporo, Hokkaido 060-0818, Japan

²⁾Obihiro University of Agriculture and Veterinary Medicine, Obihiro, Hokkaido 080- 8555, Japan

- ⁴⁾The University Museum, The University of Tokyo, Tokyo 113-0033, Japan
- ⁵⁾Gunma Museum of Natural History, Tomioka, Gunma 370-2345, Japan
- ⁶⁾Kamori Kanko Co., Ltd., Sapporo, Hokkaido 060-0004, Japan

⁷⁾Forestry and Forest Products Research Institute, Tsukuba, Ibaraki 305-8687, Japan

- ⁸⁾Nagano Environmental Conservation Research Institute, Nagano, Nagano 381-0075, Japan
- ⁹⁾Kanagawa Prefectural Museum of Natural History, Odawara, Kanagawa 250-0031, Japan

¹⁰⁾Asahiyama Zoo, Asahikawa, Hokkaido 078-8205, Japan

¹¹⁾Iwate University, Morioka, Iwate 020-8555, Japan

ABSTRACT. In several primates and carnivores, pronation/supination angles of the forearm skeleton were examined, and it is thought that a larger angle is useful to acquire dexterous behaviors in feeding and/or life style, including climbing. In this study, the pronation/supination angles in Asiatic black, brown and polar bears were nondestructively examined. These specimens were classified as adult or non-adult. Three or four carcasses of each group of Asiatic black and brown bears were used for CT analysis, whereas only one adult polar bear was used. The forearms were positioned within the gantry of a CT scanner in both maximally supinated and pronated states. Extracted cross-sectional CT images of two positions were superimposed by overlapping the outlines of each ulna. The centroids of the radii were detected, and then the centroid of each radius facing the ulna, were connected by lines to measure the angle of rotation as an index of pronation/supination. In adult brown and polar bears, the angles were smaller as compared with the other groups (Asiatic black and non-adult brown bears and polar bears that the pronation/supination angle is related to arboreal activity in Ursidae.

J. Vet. Med. Sci. 83(8): 1284–1289, 2021 doi: 10.1292/jvms.21-0198

Received: 30 March 2021 Accepted: 6 June 2021 Advanced Epub: 24 June 2021

KEY WORDS: Asiatic black bear, brown bear, forearm, polar bear, rotation

Asiatic black (*Ursus thibetanus*), brown (*U. arctos*) and polar (*U. maritimus*) bears are classified into the order Carnivora, superfamily Ursoidea, family Ursidae. Asiatic black bears usually inhabit moist deciduous forests and brushy areas in Eurasia, and are omnivorous mammals eating fruits, tree nuts, seeds, berries, buds, invertebrates, small vertebrates and carrions [2, 17]. They are capable of skillful climbing to get fruit, tree nuts and honey, and can form tree branches into bird nest-like "bear shelves" in the tops of trees [2, 17, 25]. Brown bears, which live in a broad area of Eurasia and North America, are also omnivorous. Brown bears can climb when young, however, they become unable to climb in the process of growing into an adulthood [6]. Polar bears inhabit the northern part of Eurasia and North America, and Arctic regions, and are almost carnivorous [9]. They mainly hunt seals, but feed on the carcasses of mammals, fish and berries [17]. Polar bears are generally included among marine mammals and can swim

*Correspondence to: Sasaki, M.: sasakim@obihiro.ac.jp

©2021 The Japanese Society of Veterinary Science



This is an open-access article distributed under the terms of the Creative Commons Attribution Non-Commercial No Derivatives (by-nc-nd) License. (CC-BY-NC-ND 4.0: https://creativecommons.org/licenses/by-nc-nd/4.0/)

³⁾Azabu University, Sagamihara, Kanagawa 252-5201, Japan

long distances [2, 19, 21]. On the other hand, they do not have climbing behavior through all developmental stages because there are no trees in their habitat.

In mammalian evolution, Eutheria and Metatheria (marsupials), which are classified in Theria, are descended from arboreal ancestors [13]. Didelphimorphia (opossums) genetically considered as the most primitive groups in exist marsupials [16], indicates an arboreal habit [13]. At present, it is thought that *Juramaia sinensis* is known as one of the oldest eutherian mammals [1, 11], whose scansorial (arboreal) adaptation is suggested. Polly [22] reported that the forelimb shows extensive pronation and supination in almost all scansorial mammals. It has been reported that in rodents such as rats and mice, forearm pronation/supination is skillfully used to take feeds and convey them to their mouth [27].

In several primates and carnivores, the pronation/supination angles of the forearm skeletons were examined, and it has been reported that a larger angle is important to acquire dexterous behaviors in feeding and/or life style, including climbing [10, 14, 18]. The mammals used in the previous studies on the pronation/supination angles were medium in size. However, the rotation in large mammals has not been nondestructively investigated. In large terrestrial mammals, the relationships between the pronation/ supination angles and their life styles are of interest. In this study, therefore, first of all, we examined the mobility of the forearm skeleton using X-ray computed tomography (CT) in three species of genus *Ursus*, Asiatic black, brown and polar bears, which are large mammals with different life styles, considering the phylogenetic confusion among genera and simple understanding.

MATERIALS AND METHODS

In the present study, the carcasses of seven Asiatic black bears (three non-adults and four adults), six brown bears (three nonadults and three adults) and one adult polar bear were used for the range of motion (ROM) analyses of forearm rotation (pronation/ supination) (Table 1). Adults were distinguished from non-adults by closure of the epiphyseal line (arrows in Figs. 1, 3A and 4A). The forelimbs were separated from the trunk and refrigerated at -15° C until examinations. Specimens were positioned within the gantry of the CT scanner (Aquilion LD, Canon, Tokyo, Japan; scanning conditions, 135 kV, 300 mA and 0.5 mm slice thickness) in both maximally pronated and supinated states. At the time of scanning, the ulna and humerus were firmly fixed, thus the location of each bone did not change at pronation and supination, and only the radius was movable (e.g. Fig. 3). CT-scanned data were visualized as CT images and then reconstructed into three-dimensional images on a workstation for image processing (Virtual Place Fujin and AZEWIN, AZE, Tokyo, Japan). The proximal and distal ends of the ulna were connected by a line, and this axis was used for the perpendicular line to obtain the same sectional surface of the ulna at pronation and supination. The sectional surface was created at the most widespread area in the distal part of the ulna. To measure the range of rotation of the radius, the crosssectional image of this part of the forearm was used. The sectional CT images of two positions (pronation and supination) were superimposed by overlapping the outlines of each ulna. The centroids of the cross-sections of the radii on the image were detected by ImageJ 1.51 (National Institute of Health, Bethesda, MD, USA), and the line through the centroid of the radius and the midpoint of the radial facet facing the ulna was drawn for each forearm position. The angle between the lines drawn through the radii on the superimposed cross-sectional images was defined as the rotation angle of the radius in relation to the shaft of the ulna and was adopted as an index of pronation/supination (Fig. 2).

RESULTS

Three-dimensional images of the forearm skeletons in all groups are shown in Figs. 3–5. In the maximally pronated position in each group, the long axes of the radius and ulna are crossed with each other, and the posture was almost the same as that in the usual grounding position with palms facing the ground surface (AD1 and L1 in Figs. 3–5), similar to mid-sized carnivores [10]. In maximally supinated position, the posterior side of the radii of adult brown and polar bears did not clearly appear in the anterodistal view of the forearm, due to their limited supination angles (AD2 in Figs. 4B and 5).

The ranges of the rotation angles of the radius relative to the ulna were Avg., $78.0 \pm 1.9^{\circ}$ (74.3°, 80.6° , 79.3°), Avg., $76.9 \pm 2.1^{\circ}$ (80.0°, 76.7°, 71.0°, 79.7°); Avg., $72.7 \pm 2.9^{\circ}$ (78.5°, 69.6°, 70.0°) and Avg., $45.8 \pm 5.2^{\circ}$ (54.0°, 47.2°, 36.2°) in non-adult Asiatic black, adult Asiatic black, non-adult brown and adult brown bears, respectively, and the pronation/supination angle of one adult polar bear was 39.3° (Fig. 6). In adult brown and polar bears, the angles were smaller as compared with the other groups (Fig. 6). On the other hand, there are no large differences among non-adult Asiatic black, adult Asiatic black and non-adult brown bears (Fig. 6).

DISCUSSION

The present study demonstrated that the forearms of adult brown and polar bears supinate to a lesser degree than those of Asiatic black and non-adult brown bears. The maximally pronated position of the forearm was almost equal to the usual grounding position with palms facing the ground in each group. Therefore, the more largely bears supinate their forearms, the more dorsally they can direct their palms, because the rotation of carpal bone is limited in the radialcarpal joint between the radius and intermedioradial carpal bone, and the carpal bone moves with the radius in pronation/supination of the forearm although this joint allows the extension/flexion and abduction/adduction of the hand [15]. The pronation/supination flexibility is related to behaviors essential for life. In several primates, the pronation/supination angles were examined, and arboreal primates were reported to have larger angles than semi-terrestrial and terrestrial primates, suggesting that pronation/supination flexibility is related to climbing adaptation [18]. However, humans are not arboreal primates and have little climbing ability, although our forearms have greater mobility than those of several arboreal primates.

Species	Maturity*	Sex	SN**	Donor or location	Left/Right
Asiatic black bear	Non-adult	Female	AN-1	HBMC (Gunma, Japan)	Left
Asiatic black bear	Non-adult	Male	AN-2	HBMC (Gunma, Japan)	Left
Asiatic black bear	Non-adult	Male	AN-3	HBMC (Gunma, Japan)	Left
Asiatic black bear	Adult	Male	AA-1	HBMC (Nagano, Japan)	Left
Asiatic black bear	Adult	Female	AA-2	HBMC (Gunma, Japan)	Left
Asiatic black bear	Adult	Female	AA-3	HBMC (Gunma, Japan)	Left
Asiatic black bear	Adult	Male	AA-4	HBMC (Gunma, Japan)	Left
Brown bear	Non-adult	Male	BN-1	HBMC (Hokkaido, Japan)	Left
Brown bear	Non-adult	Male	BN-2	HBMC (Hokkaido, Japan)	Left
Brown bear	Non-adult	Female	BN-3	HBMC (Hokkaido, Japan)	Right
Brown bear	Adult	Female	BA-1	HBMC (Hokkaido, Japan)	Left
Brown bear	Adult	Male	BA-2	Bear Mountain (Hokkaido, Japan)	Left
Brown bear	Adult	Male	BA-3	Bear Mountain (Hokkaido, Japan)	Right
Polar bear	Adult	Female	PA-1	Asahiyama Zoo (Hokkaido, Japan)	Left

 Table 1. The carcasses used in this study

HBMC, harmful birds and mammals control. * Adults were distinguished from non-adults by the closing of epiphyseal line. ** Specimen number.



Fig. 1. The distal end of the forearm skeleton in Asiatic black bears. Adults (B) were distinguished from nonadults (A) by closure of the epiphyseal line (green arrows). R, radius; U, ulna. (Specimens shown in this Figure: A, AN-2; B, AA-2).



Fig. 2. CT cross sectional images of left forearms in a non-adult Asiatic black bear (A1), adult Asiatic black bear (A2), non-adult brown bear (B1), adult brown bear (B2) and adult polar bear (P). Cross section of the ulna (1), and radius in maximal supination (2) and pronation (3) with centroids (dots). The cross sections were extracted at the most widespread area in the distal part of the ulna. The centroid of the radii and the midpoint of a line which connects between both ends of the surface of each radius facing the ulna, were connected by lines, and the rotation angles as an index of pronation/supination were created (specimens shown in this Figure: A1, AN-1; A2, AA-2; B1, BN-1; B2, BA-2; P, PA-1).

Therefore, humans are thought to have evolved to have pronation/supination flexibility to enable complicated manipulations needed for terrestrial life, e.g. the use of instruments [18]. Among carnivores, raccoons exhibit skillful handling and climbing with large pronation/supination angles. Thus, the flexibility may be helpful both for handling and climbing in raccoons [10, 24].

Both Asiatic black and brown bears are omnivorous, and there is no large difference between them in feeding style, i.e., hauling of foods into their mouths by palms or approach of their mouths toward food. However, Asiatic black bears can climb at all ages,



Fig. 3. Antero-dorsal (AD) and lateral (L) views of three-dimensional CT images of the left forearm skeleton of the non-adult (A) and adult (B) Asiatic black bears. (1) and (2) show maximally pronated and supinated positions, respectively. R, radius; U, ulna; Arrow, epiphyseal line. (specimens shown in this Figure: A, AN-2; B, AA-4).



Fig. 5. Antero-dorsal (AD) and lateral (L) views of three-dimensional CT images of the left forearm of the adult polar bear. (1) and (2) show maximally pronated and supinated positions, respectively. R, radius; U, ulna. (specimen shown in this Figure: PA-1).



Fig. 4. Antero-dorsal (AD) and lateral (L) views of three-dimensional CT images of the left forearm skeleton of the non-adult (A) and adult (B) brown bears. (1) and (2) show maximally pronated and supinated positions, respectively. R, radius; U, ulna; Arrow, epiphyseal line. (specimens shown in this Figure: A, BN-1; B, BA-2).



Fig. 6. The pronation/supination angle of the forearms in bears.

and continue a tree climbing for foraging, while making bear shelves, which are the accumulation of broken tree branches after berries or nuts were removed [25]. In brown bears, however, it has been reported that the juvenile has relative good climbing skills, but the subadult comes to loss the abilities [6, 8].

The body size of brown bears markedly increases even after reaching sexual maturity compared with Asiatic black bears, and the brown bears show marked increase in the body size between non-adult and adult stages [17]. This suggests that morphological changes in the musculature, skeleton and/or connective tissues in the forearms of brown bears due to the increase in size may limit the movable range (pronation/supination angle) of the forearm skeleton. It may be assumed that the brown bears have evolved largely in size to survive under cold environments according to Bergmann's rule. With the increase of body size, the bear may have been necessary to alter the features and functions of the musculoskeletal system to support their heavy weight by trade-off with the skills for arboreal life, e.g. limitation of the pronation/supination flexibility of forearms.

Like the brown bear, the polar bear is known to be one of the largest ursids, and indicates remarkable differences in the body size between non-adult and adult stages. The radial rotation angle of the polar bear was much smaller than that of Asiatic black and non-adult brown bears examined in the present study. This result supports the forearms of polar bears being less dexterous than those of other ursids, consistent with the previous report [9]. In this study, the forearm of polar bear was CT-scanned in relatively extended elbow joint angle compared with the other bears. However, the difference in the elbow joint extension/flexion angle is not considered to affect the range of maximum pronation/supination angles in the bears as well as in humans [7]. It is unknown whether the limited mobility of the forearms in the polar bear results from morphological changes due to remarkable growing of the body like seen in adult brown bears or if it is a natural characteristic in this species because the forearms of non-adult polar bears were unable to be examined in this study. In future studies, analyses of the pronation/supination angle in non-adult polar bears are necessary to clarify this. Furthermore, as only one adult polar bear was used in this study, additional examinations with a sufficient number of polar bear specimens should be carried out to confirm the mobility of the forearm skeleton. It is well-known that the polar bear is a long distance swimmer [2, 19, 21], but they swim using a dog-paddle style without pronation/supination flexibility [20]. In addition, the polar bears show maximally pronated position of forearms with palms facing the surface of iceberg when landing from seawater. It is thought that, therefore, the large supination of forearms may be not required for swimming and landing in polar bears, although in vertical tree climbing, arboreal bears need to embrace the trunk of tree from both sides with the palms medially facing by the supination of forearms. Polar bears may more adept at walking than swimming from the point of view of energy expenditure even though they can swim for long distances [3, 5, 19].

In a previous study, the more circular radial head allows the greater movement of pronation/supination in the lower forelimb, and the large rotation shows a positive relationship in arboreal adaptation and manipulative skill [8, 12]. In addition to the roundness of the radial head, VanBuren and Bonnan [26] described that the curvature of the radius is related to active pronation and calculated the angle of curvature of the radius in 189 mammals including the 7 ursid species except *U. thibetanus*. However, each bear species is only one specimen without the consideration of age and sex. In our further studies, it is important that the roundness of the radial head and the angle of curvature would be examined in the radial specimens of genus *Ursus* with enough number, both sexes and different developmental stages.

In the bears, comprehensive changes in other factors, such as the body weight, the mobility of the upper arms, carpal joints and hind limbs, and the related musculature may limit the climbing abilities. In our previous study on adult bears, arboreal bears such as the giant panda and Malayan sun bear develop the fleshy portion of the cranial tibial muscle with a short tendon better and attach the popliteal muscle into more distal area of the tibia as compared with the brown and polar bears with a terrestrial habitat, suggesting that these morphological features offer the strongly fixed supination of the foot and the efficient pronation of the lower leg helpful for holding down the trunk of a tree from both sides in tree climbing [23]. Furthermore, Fujiwara and Hutchinson [4] measured the moment arms of extensor, flexor and adductor muscles in the elbow joint, and reported that the scansorial taxa had a positive correlation in the elbow flexor muscles. In further studies in the ursids, it is worth comparing the physiological cross sectional area (PCSA) and moment arm in the elbow flexor muscles and the supinator and pronator teres muscles with various situations (e.g. non-adult and adult) to understand the arboreal ability.

In conclusion, the present study revealed that adult brown and polar bears have smaller pronation /supination angles of the forearm than Asiatic black bears and non-adult brown bears, and this characteristic may be one of the limitations of arboreal activity. To more precisely confirm the characteristics of forearm rotation in polar bears, a sufficient number of samples with different growth stages is required.

CONFLICT OF INTEREST. The authors have nothing to disclose.

ACKNOWLEDGMENTS. We wish to thank the Nakasatsunai and Shimizu Hunting Clubs for providing the samples.

REFERENCES

- Bi, S., Zheng, X., Wang, X., Cignetti, N. E., Yang, S. and Wible, J. R. 2018. An Early Cretaceous eutherian and the placental-marsupial dichotomy. *Nature* 558: 390–395. [Medline] [CrossRef]
- 2. Craighead, L. 2000. Bears of the World, Voyageur Press, Stillwater.
- 3. Durner, G. M., Whiteman, J. P., Harlow, H. J., Amstrup, S. C., Regehr, E. V. and Ben-David, M. 2011. Consequences of long-distance swimming and travel over deep-water pack ice for a female polar bear during a year of extreme sea ice retreat. *Polar Biol.* **34**: 975–984. [CrossRef]

- 4. Fujiwara, S. and Hutchinson, J. R. 2012. Elbow joint adductor moment arm as an indicator of forelimb posture in extinct quadrupedal tetrapods. *Proc. Biol. Sci.* 279: 2561–2570. [Medline]
- 5. Griffen, B. D. 2018. Modeling the metabolic costs of swimming in polar bears (Ursus maritimus). Polar Biol. 41: 491-503. [CrossRef]
- 6. Herrero, S. 1972. Aspects of evolution and adaptation in American black bears (*Ursus americanus* Pallas) and brown and grizzly bears (*U. arctos* Linné) of North America. pp. 221–231. In: Bears: Their Biology and Management, Vol. 2 (Herrero, S. ed.), IUCN Publ. n.s. 23, Morges.
- 7. Inoue, Y., Yamamoto, Y., Kato, S., Nakazato, T., Echizenya, T. and Yoda, Y. 1995. Relationship between difference in fixed range of the forearm and difficulty in activities of daily living. *Physic. Ther. Jap.* 22: 433–436 (in Japanese).
- 8. Iwaniuk, A. N., Pellis, S. M. and Whishaw, I. Q. 1999. The relationship between forelimb morphology and behavior in North American carnivores (Carnivore). *Can. J. Zool.* **77**: 1064–1074. [CrossRef]
- 9. Iwaniuk, A. N., Pellis, S. M. and Whishaw, I. Q. 2000. The relative importance of body size, phylogeny, locomotion, and diet in the evolution of forelimb dexterity in fissiped carnivores (Carnivora). *Can. J. Zool.* **78**: 1110–1125. [CrossRef]
- Kamioka, M., Sasaki, M., Yamada, K., Endo, H., Oishi, M., Yuhara, K., Tomikawa, S., Sugimoto, M., Oshida, T., Kondoh, D. and Kitamura, N. 2017. Mobility of the forearm in the raccoon (*Procyon lotor*), raccoon dog (*Nyctereutes procyonoides*) and red panda (*Ailurus fulgens*). J. Vet. Med. Sci. 79: 224–229. [Medline] [CrossRef]
- 11. Luo, Z. X., Yuan, C. X., Meng, Q. J. and Ji, Q. 2011. A Jurassic eutherian mammal and divergence of marsupials and placentals. *Nature* **476**: 442–445. [Medline] [CrossRef]
- 12. MacLeod, N. and Rose, K. D. 1993. Inferring locomotor behavior in Paleogene mammals via eigenshape analysis. *Am. J. Sci.* 293: 300–355. [CrossRef]
- 13. Matthew, W. D. 1904. The arboreal ancestry of the Mammalia. Am. Nat. 38: 811-818. [CrossRef]
- 14. Nakamura, T., Yabe, Y., Horiuchi, Y. and Yamazaki, N. 1999. In vivo motion analysis of forearm rotation utilizing magnetic resonance imaging. *Clin. Biomech. (Bristol, Avon)* 14: 315–320. [Medline] [CrossRef]
- 15. Neumann, D. A. 2016. Kinesiology of the Musculoskeletal System: Foundations for Rehabilitation, 3rd ed., Mosby, St. Louis.
- Nilsson, M. A., Churakov, G., Sommer, M., Tran, N. V., Zemann, A., Brosius, J. and Schmitz, J. 2010. Tracking marsupial evolution using archaic genomic retroposon insertions. *PLoS Biol.* 8: e1000436. [Medline] [CrossRef]
- 17. Nowak, R. M. 1999. Walker's Mammals of the World, vol. 1, 6th ed. Johns Hopkins University Press, London.
- 18. O'cconor, B. L. and Rarey, K. E. 1979. Normal amplitudes of radioulnar pronation and supination in several genera of anthropoid primates. *Am. J. Phys. Anthropol.* **51**: 39–44. [CrossRef]
- Pagano, A. M., Carnahan, A. M., Robbins, C. T., Owen, M. A., Batson, T., Wagner, N., Cutting, A., Nicassio-Hiskey, N., Hash, A. and Williams, T. M. 2018. Energetic costs of locomotion in bears: is plantigrade locomotion energetically economical? *J. Exp. Biol.* 221: jeb175372. [Medline] [CrossRef]
- Pagano, A. M., Cutting, A., Nicassio-Hiskey, N., Hash, A. and Williams, T. M. 2019. Energetic costs of aquatic locomotion in a subadult polar bear. Mar. Mamm. Sci. 35: 649–659. [CrossRef]
- 21. Pilfold, N. W., Mccall, A., Derocher, A. E., Lunn, N. J. and Richardson, E. 2017. Migratory response of polar bears to sea ice loss: to swim or not to swim. *Ecography* **40**: 189–199. [CrossRef]
- 22. Polly, P. D. 2007. Limbs in mammalian evolution. pp. 245 268. In: Fins into Limbs: Evolution, Development, and Transformation (Hall, B. K. ed.), University of Chicago Press, Chicago.
- Sasaki, M., Endo, H., Wiig, O., Derocher, A. E., Tsubota, T., Taru, H., Yamamoto, M., Arishima, K., Hayashi, Y., Kitamura, N. and Yamada, J. 2005. Adaptation of the hindlimbs for climbing in bears. *Ann. Anat.* 187: 153–160. [Medline] [CrossRef]
- 24. Taylor, M. E. 1989. Locomotor adaptations by carnivores. pp. 382–409. In: Carnivore Behavior, Ecology, and Evolution, Vol. 1 (Gittleman, J. L. ed.), Cornell University Press, New York.
- 25. Tochigi, K., Masaki, T., Nakajima, A., Yamazaki, K., Inagaki, A. and Koike, S. 2018. Detection of arboreal feeding signs by Asiatic black bears: effects of hard mast production at individual tree and regional scales. *J. Zool. (Lond.)* **305**: 223–231. [CrossRef]
- 26. VanBuren, C. S. and Bonnan, M. 2013. Forearm posture and mobility in quadrupedal dinosaurs. PLoS One 8: e74842. [Medline] [CrossRef]
- 27. Whishaw, I. Q. 1996. An endpoint, descriptive, and kinematic comparison of skilled reaching in mice (*Mus musculus*) with rats (*Rattus norvegicus*). *Behav. Brain Res.* **78**: 101–111. [Medline] [CrossRef]