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Photogrammetry Disclosed Gibbons' Arboreal Bipedal Walking and Its Characteristic in Canopies

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ABSTRACT

Before our terrestrial bipedal ancestors, our ancestors lived in canopies. The behavior of these arboreal primates was unknown, because leaves in canopies hide the arboreal primates, especially Asian gibbons, our related species. Differing from tropical rain forests, in temperate zones deciduous trees spontaneously drops leaves in autumn and winter, then the primates in canopies become visible. Here I show that white handed gibbons Hylobates lar, used not only suspension (brachiation) but also arboreal bipedal walking besides quadrupedal moving in canopies. Using a photogrammetry Software, 3DF zephyr which makes reliable measurements, the vertical angles of moving varied among their arboreal moving three styles. Less than 50 degrees of vertical angles, the gibbons progressed by brachiation or by bipedal walking. More than 50 degrees of vertical angles, the gibbons progressed by quadrupedal moving. The gibbons did not progress horizontally in quadrupedal moving like knuckle-walking by African chimpanzees and gorillas. The gibbons appeared to keep their torsos erect in all the three arboreal moving styles. In Asian rainforests, tigers, Panthera tigris, the large terrestrial predators might prevent gibbons from terrestrial bipedal walking.

INTRODUCTION

Our bipedal ancestor, Ardipithecus ramidus, 4.4 million years ago reveals facultative terrestrial bipedality with retained arboreal capabilities White et al. (2009). Carbon isotopic evidence from the teeth of five Ar. ramidus individuals suggests that Ardipithecus appears to have exploited a wider range of woodland resources than do chimpanzees, but without relying on the open biotope foods consumed by later Australopithecus White et al. (2009). Thus, the elucidation of arboreal common ancestor before the terrestrial bipedalism is required to understanding the human evolution. The locomotion pattern of the other living arboreal apes in woodland, Asian gibbons is an evolutionary model for the arboreal common ancestors. This locomotion pattern, however, is obscure because leaves in canopies hid gibbons Gittins (1983). The locomotion pattern of gibbons was considered as specialization for suspension (brachiation) by the analysis of skeletons Gebo (1996). Even physical aspects of this swinging locomotion were hidden by leaves and unknown in wild tropical rain forest. Outside canopy with leaves, the locomotion of gibbons were analyzed, for example leaping Channon et al. (2010). In review Vereecke et al. (2006) gibbons employ a wide variety of other locomotor modes, such as diving, leaping, bridging, bipedal walking, running, quadrupedal climbing, and scrambling which were only observed occasionally on the ground in the wild (when crossing roads or gaps in fragmented forests). Therefore, the behaviors of gibbons outside canopies might be exceptional because gibbons mainly live in canopies Gittins (1983). Althogh outside canopies, the locomotion on the ground, flat surfaces, were observed and experimented on Vereecke et al. (2006), in canopies branches expand in various vertical angles which affect the ecology of animals Lowman et al. (1993) differing from only erect plant trunks under canopies. At least the elevation angle of arboreal movement alters gravity action in locomotion Preuschoft (2004). Under canopies, these upright shafts appear to restrict gibbons' locomotion to quadrupedal climbing which was easily observed even in tropical rain forests. In deciduous trees leaves fall by themselves in autumn and winter, then gibbons become completely visible for observation in the trees. Although solar backlight also prevented observers on the ground from filming to analyze their locomotion, shooting above bare trees from a tower and by flying drones appears to overcome this difficulty. The ecology of deciduous trees would disclose the hidden behavior of gibbons in canopies where gibbons mainly live. The development of three-dimensional (hereafter called "3D") mapping enables reliable measurements including vertical angles of branches for the analysis of locomotion in video recorded observation. Although 3D mapping was formerly created by laser scanning, Laser measurement for trees, however, was imperfect because thin branches rarely reflect laser and are lack in 3D model and mapping Kumazaki et al. (2017).

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Photogrammetry for bare deciduous trees overcome these difficulties and produce the objective data of gibbons' locomotion in trees. The purpose of this report is to disclose gibbons' locomotion in canopies for understanding human ancestors' arboreal locomotion before terrestrial bipedal walking using a photogrammetry software, 3DF zephyr which makes reliable measurements for the absolute coordinates in arboreal locomotion.

MATERIALS AND METHODS

Subjects

The gibbons consist of a 32-year-old mother, a 23-year-old father and their three offspring: 8-year-old male, 5-year-old-male and 2-year-old female. The weight of the 33-year-old mother was 10.1kg in February 2020.

Video Observation

The behavior of five white-handed gibbons in planted natural trees on an island at Tokiwa zoo in Ube city, Yamaguchi prefecture, Japan was recorded by video cameras with resolution1080 progressive to create still images on 10 November 2018 for an hour (from 9:44 to 10:48: 64 minutes) and on 7 November 2016 preliminary research, Figure 1 when the leaves of the deciduous trees fell, from the tower (37 meters high) of Sekitan Kinen-kan neighboring the zoo under the permission of the zoo and Sekitan Kinen-kan. In video observation the five gibbons remained in canopies and did not go down to the ground. Because video cameras distorted vertical angles, angles of moving direction on video screens were not used. on a large branch on 7 November 2016. This branch was lopped off before 2018.

Figure 1: Arboreal bipedal walking by a gibbon

Photogrammetry

A photogrammetry Software, 3DF zephyr makes reliable measurements by the use of photographs and especially aerial photographs about the bare deciduous trees on the island. A drone flied around the island and took one thousand and six hundred overlapping photographs from various perspectives on the island on 25 May 2022. Based on the parallactic images of these overlapping photographs, the 3DF zephyr generated a stereo image of the trees on the island Figure 2.

Figure 2: Screenshot of 3D model by 3DF Zephyr.

Identification in 3D Map

On 10 November 2018, a high-angle view was recorded by video camera. Then, in the playback on large monitors, the movements of gibbons was detected and their still images was created Figure 3a.

Figure 3a: A still image of gibbon's bipedal walking cut from a overlooking image.

The 3DF zephyr can rotate and scale up or down the stereo image keeping absolute value of the coordinates. Therefore, the 3DF zephyr can generate a screen image Figure 3b which matches a still screen image from the video record Figure 3c. screen image Figure 3c from the video record. In the video playback, the distant branch overlapped as if the gibbon would step on the distant branch. However, the model and mapping by 3DF Zephyr excluded this distant branch. Using these matched images by the video and photogrammetry, the locations of gibbons' touches on the trees in video records were identified based on the kept absolute coordinates of photogrammetry images.

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Then the 3DF Zephyr calculated their vertical angles based on the water surface as the horizon.

Figure 3b: A rotated and scaled up image generated by 3DF Zephyr which matches a still

Figure 3c: a still screen image from the video record.

Definition of Locomotion

Brachiation is progress by swinging from hold to hold only by the arms, forelimbs. Bipedal walking is progress with only hind limbs. Hereafter the bipedal walking more than three steps was measured. Quadrupedal moving is progress with both forelimbs and hind limbs. Each sample size of locomotion was more than 50 for large size comparison. The detecting time for brachiation by five gibbons was nine minutes and that of quadrupedal walking by five gibbons was 57 minutes from an hour video observation on 10 November 2018.

Definition of Angles of Location

Brachiation: The angle of brachiation is the vertical angle from the location where the previous forelimb touched to the location where the following forelimb touched. Bipedal walking: The angle of bipedal walking is the vertical angle from the location where the previous hind limb touched to the location where the following hind limb touched. Quadrupedal moving: The angle of quadrupedal moving is the vertical angle from the location where the previous forelimb or hind limb touched to the location where the following forelimb or hind limb touched. Although, because the forelimbs are longer than hind limbs in gibbons, the location where the following hind limb touched was sometimes below the location where the previous forelimb touched, the progress was upward. Then this vertical angle was not measured as the negative but positive value.

Data Analysis

Means and standard errors of means (mean ± SEM) were calculated. Before comparisons, I used Kolmogorov-Smirnov tests for the normal distribution of data and Levene tests for equal variances of groups. If the data were not distributed normally and if the variances of groups were not equal, I used non-parametric tests: Mann-Whitney U tests and Kruskal-Wallis tests. Statistical tests (two-tailed) were done on IBM SPSS Statistics version 26.

Data Availability

All data generated and analyzed during this study are included in this manuscript.

RESULTS

The Frequency of Arboreal Locomotion

In video observation, the five gibbons remained in canopies and did not go down to the ground. The data of bipedal walking included three times of bipedal walking on 7 November 2016, but the data of bipedal walking on the lopped off branch were excluded because this branch did not exist in the 3D map. Therefore, the sample size of bipedal walking steps on 10 November 2018 during an hour observation is 52. The detecting time for 50 strokes of brachiation by five gibbons was nine minutes and 58 steps of quadrupedal walking by five gibbons was 57 minutes in an hour video observation on 10 November 2018. On 10 November 2018, the frequency per hour of brachiation was 333.3 and that of quadrupedal walking was 61.1 and that of bipedal walking was 48.8 in canopies.

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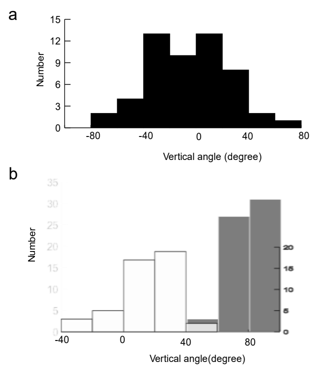
The distribution of the vertical angles in brachiation (mean ± standard error of mean, -9.1±4.6 degrees, N = 50) has two peaks Figure 4a but was not different from the normal distribution (Kolmogorov-Smirnov tests, Dmax = 0.088, P = 0.20). However, the distribution of vertical angles in bipedal walking (16.2±2.5 degrees, N = 55 Fig. 4b) and that in quadrupedal moving (68.0±2.1 degrees, N = 58, Fig. 4b) were not normal distributions (Kolmogorov-Smirnov tests, bipedal walking Dmax = 0.175, P < 0.01; quadrupedal moving: Dmax = -0.193, P < 0.01). The vertical angles of bipedal walking (16.2±2.5 degrees, N = 55), those of quadrupedal moving (68.0±2.1 degrees, N = 58) and those of brachiation (-9.1±4.6 degrees, N = 50) varied (Kruskal-Wallis test, $\chi 2$ = 118.14, N = 163, df = 2, P < 0.01, effect size: ε2 = 0.733, Fig. 4a and 4b). The vertical angles of bipedal walking were smaller than those of quadrupedal moving (Mann-Whitney U tests, U = 0.0, N = 113, Z = -9.177, P < 0.01, effect size: r = 0.863) and the distribution of vertical angles in bipedal walking from -30 to 50 degrees and those in quadrupedal moving from 53 to 87 degrees were divided by 50 degrees Figure 4b.

Figure 4 a: The distribution of vertical angles in brachiation; b: The distribution of vertical angles in bipedal walking (white bars) and quadrupedal moving (gray bars).



DISCUSSION

Although statistical tests were impossible because of a single observation, the frequency of bipedal walking was almost equal to that of quadrupedal walking in canopies where gibbons mainly live. In 64 minutes, 52 steps of arboreal bipedal walking by 5 gibbons were observed. This indicated that arboreal bipedal walking by gibbons was not rare but ordinary in canopies. Because even in tropical rainforests, under canopies, there are naked and vertical trunks, quadrupedal climbing is easily detected differing from hidden bipedal walking in canopies. Although the leaves in canopies hide gibbons' arboreal bipedal walking, the gibbons are not the specialists of brachiation, but use three arboreal locomotion patterns: brachiation, bipedal walking and quadrupedal moving. This agrees with the experiments of gibbons indicating their versatility for various locomotive patterns and their capability for "terrestrial" bipedal walking Vereecke et al. (2006). However, in wild, gibbons restricted themselves to forest canopies, arboreal habitats Gittins (1983). In Asian rainforests, tigers, Panthera tigris, the large terrestrial predators Kitchnener et al. (2010) might prevent gibbons from terrestrial bipedal walking. In Africa, around 8 million years ago machairodont cats, the felid genera Dinofelis and Machairodus appeared and the former ambushing (incapable of a high-speed chase in open grassland) large predators, hyaenondontids, Hyainailouros suluzeri and H. napakensis, diminished Turner et al. (2004). the large sabre-toothed cats (Machairdonitnae) seemed to prefer open grassy habitat to dense forest Salesa et al. (2006). This absence of large predators in African forest floors might enable terrestrial bipedal walking in forest before leopards, Panthera pardus, were present around 3.5 million years ago in eastern Africa Turner et al. (2004). Our bipedal ancestor, Ardipithecus ramidus, 4.4 million years ago White et al. (2009) corresponds to this absence period of large terrestrial predators. The gibbons' styles of locomotion in trees were varied based on the vertical angles. Although in canopies trees expand their branches horizontally, in quadrupedal moving, the progress of gibbons was not horizontal. Spool-shaped humeral trochlea which can hyperextension of fore-arms and brachiation Gebo (1996) and combined with hanging by only fore arms make torsos erect. These postures appear to remain in quadrupedal moving (vertical angle: 68.0±2.1 degrees) and bipedal walking (vertical angle: 16.2±2.5 degrees) on horizontally expanding branches in canopies. If their relative long arms would reach branches and stems from their erect trunks, the gibbons appear to move quadrupedally. Therefore, gibbons mainly hang these branches and use brachiation. If they use hind limbs in locomotion, they appear to keep erect postures. In quadrupedal moving, their progress was not horizontal. This disagrees with chimpanzees and gorillas who sometimes go horizontally in quadrupedal moving, arboreal knuckle walking in chimpanzees Kivell et al. (2009) and terrestrial knuckle walking in gorillas Simpson et al. (2018). In brachiation, gibbons sometimes progressed upward. The accumulated kinetic energy after a series of brachiations could make gibbons to swing against gravity. Because a monkey (Japanese macaque) modified the momentum of throwing stones Tokida et al. (1994), gibbons appear to appreciate kinetic energy. Without accumulated kinetic energy like the first brachiation from quiescence, gibbons appear to progress only downward. These two types of brachiation appear to result in the two peaks in the distribution of vertical angles of brachiation Figure 4a. The wide range of vertical angles in brachiation suggests that the main locomotive pattern of gibbons is brachiation.

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Under 50 degrees of vertical angles, gibbon used only forelimbs in brachiation, or only hind limbs in bipedal walking in canopies. If their relative long arms would not reach branches and stems from their erect trunks, the gibbons appear not to move quadrupedally but to walk bipedally. The gibbons in canopies of bare deciduous trees with photogrammetry would show other aspects of the ecology of gibbons.

DECLARATIONS

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Ethic Declarations

All observations were in compliance with the United States Animal Welfare Act. This study was approved by Tokiwa Zoo.

Competing Interests

The author declares no competing financial interests.

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