Locomotor Kinematics of Two Semi-Wild Macaque Species (*Macaca assamensis* and *Macaca arctoides*) in Thailand

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Keywords

Quadrupedal walking · Arboreality · Terrestriality · Locomotor adaptation · Assamese macaque · Stump-tailed macaque

Abstract

This project aimed to investigate primate locomotor kinematics noninvasively in the wild. Semi-wild Assamese and stump-tailed macaques were selected for the study, which was performed in Thailand. We investigated their locomotor kinematics and its relationship to habitat use. The macaques' positional behavior was recorded with two video cameras, and kinematic parameters were estimated during terrestrial quadrupedal locomotion, using the markerless method. The data analyzed so far revealed that stump-tailed macaques walk with longer, less frequent strides than Assamese macaques. Although stump-tailed macaques present a smaller angular excursion of the shoulder joint than Assamese macaques, they exhibited a relatively large shoulder girdle motion and anteroposterior translation of the shoulder, which increased their stride length. Additionally, stump-tailed macaques exhibited a digitigrade gait and elbow extension, suggesting a good adaptation to terrestrial locomotion. Assamese macaques, on the other hand, exhibited a gait that did not seem optimized for terrestrial locomotion, using the hands in a palmigrade posture and frequently flexing the fingers at varying degrees. The kinematic characteristics of the two species studied is consistent with previous field observations reporting that Assamese macaques are highly arboreal, whereas stump-tailed macaques are more terrestrial.

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Introduction

Animals move using their body and adapting their motions to the environment in which they live. In particular, locomotion is one of the most basic animal behaviors and reflects the interaction between body structure and natural habitat. Thus, in order to discuss animal adaptation and evolution, information on locomotor behavior, especially quantitative kinematics, is essential. Although a substantial number of studies have focused on animal locomotion using various methods, most have been conducted exclusively in laboratory settings, thus presenting two main limitations: (1) only a few species can be accessed for laboratory experiments; in order to examine animal motions in the laboratory, it is necessary to keep the animals for a relatively long time in good health, and only a few species fill these criteria for such experiments; (2) in a laboratory setting, the motions used by the animal are not necessarily natural. Although these limitations can be overcome through quantitative investigations of the animal's locomotion in its natural habitat, in practice this is rather difficult. To date, most field studies on animal locomotion have focused on the frequency of categorized locomotor repertoires and qualitative body motion descriptions. Despite the unquestionable significance of these studies, they lack information regarding quantitative kinematic and kinetic data of locomotor movements in the field, which prevents a thorough understanding of the animals' locomotor behaviors and, consequently, their morphological adaptation and habitat use. Both morphology and habitat use are closely related to locomotor kinematics, as if locomotion is the center panel of the triptych.

Recently, considerable advances in kinematic apparatuses and techniques have been reported [Blanchard and Crompton, 2011; Cheyne, 2011; McNamara et al., 2018]. The size of video cameras has decreased and their resolution increased, and image distortions can be easily corrected by computer software. Such sophisticated apparatuses and techniques facilitate the measurement of animal motions outside the laboratory. In fact, several kinematic analyses have been conducted at zoos and in captive enclosures [e.g., D'Août et al., 2002, 2004; Isler, 2005; Berillon et al., 2010, 2011; Watson et al., 2011], although kinematic studies on free-ranging wild animals remain limited to a few preliminary reports [Shapiro et al., 2011; Wunderlich et al., 2011; Youlatos and Gasc, 2011; Hanna et al., 2015]. The global objective of our project was to noninvasively study animal locomotor kinematics in a wild environment.

As the first step, the present study aimed to establish the methods for such measurements in a wild environment. The subjects were Assamese macaques (*Macaca assamensis*) and stump-tailed macaques (*Macaca arctoides*) living in a semi-wild environment in Thailand. The term "semi-wild" was selected to describe a living status whereupon the animals remain wild but are provisioned by tourists or village people. One of the reasons for the selection of these particular species was that they live around temples and can be accessed relatively easily. Another more important reason is that knowledge about the locomotor kinematics of wild macaque monkeys is quite limited. Currently, the macaque genus comprises 23 species, among which 22 are widespread across Asia [Groves, 2001; Mittermeier et al., 2013]. In general, these species have a semiterrestrial way of life [Thierry, 2011] being traditionally classified as semiterrestrial quadrupeds, although each taxon shows its own locomotor adaptation. For example, the degree of terrestriality and arboreality differs among taxons. Fooden [1980, 1981, 1982] reported that Assamese macaques are much more arbo-

real than stump-tailed macaques, based on his own and other researchers' observations [McCann, 1933; Bertrand, 1969; Fooden, 1971]. Although the two species broadly overlap geographically and ecologically – they are often observed in the same forest, and their diets are essentially similar – Assamese macaques usually forage high in the canopy, whereas stump-tailed macaques forage on the forest floor. Therefore, classifying all macaque species into the same locomotor category prevents a thorough understanding of each individual group.

The present study aimed to observe how the kinematic characteristics of quadrupedal locomotion differ between Assamese and stump-tailed macaques and how those differences relate to habitat use. We hypothesized that there are significant differences in the locomotor kinematics of these two species that reflect arboreality versus terrestriality, although they have been classified within the same category in terms of locomotor repertoire. In particular, we predicted that Assamese macaques exhibit a stronger arboreal locomotor adaptation. Schmitt [1998, 1999, 2003] argued, on the basis of his own and other researchers' data [e.g., Alexander and Maloiy, 1984; Reynolds, 1987; Larson et al., 2000], that primates walk with larger protraction of the shoulder joint and a more yielding elbow than nonprimate quadrupedal mammals and suggested that compliant gait is part of an initial and fundamental primate adaptation to arboreal locomotion. If so, more arboreally adapted species are expected to have a more compliant gait than less arboreally adapted species. We predicted that Assamese macaques, which are considered highly arboreal [Fooden, 1980, 1981, 1982], display larger forelimb motion and yielding elbow and knee joints whereas stump-tailed macaques, which are considered less arboreal [McCann, 1933; Bertrand, 1969; Fooden, 1971], show relatively strong terrestrial locomotor adaptation, specifically more extended elbow/knee joints. In addition, we predicted that Assamese macaques walk with a palmigrade hand posture whereas stump-tailed macaques use a digitigrade posture, as digitigrade hand postures are reported to offer several biomechanical advantages over plantigrade postures when walking on the ground [Patel, 2008, 2009, 2010a].

Materials and Methods

Subjects

Assamese macaques were filmed at the Wat Tham Pla Temple (20°19'44.4" N, 99°51'45.3" E) in Chiang Rai Province located at the northern end of Thailand, during January 4–9, 2009. In the present study, the Assamese macaques' habitat was located at the western edge of the Shan Plateau, where a series of jagged peaks of weathered limestone abruptly rise from the plain. During the night, Assamese macaques remain in the cracks of the cliffs ensuring their safety, while during the day they stay on the temple's ground to feed. Although this behavior pattern requires the macaques to engage in cliff climbing and descending for a substantial amount of time [Ogawa and Hirasaki, 2009], such complex behavior was not studied in this report. Approximately 130 Assamese macaques from 4 groups live around the Wat Tham Pla Temple [Ogawa and Hirasaki, 2009].

Stump-tailed macaques were filmed at the Khao Krapuk-Khao Tao Mo Wildlife No Hunting Area (12°47'59.0" N, 99°44'24.0" E) in Phetchaburi Province located in central Thailand during May 25–27, 2010. Approximately 180 stump-tailed macaques live there [Maruhashi, 2008] distributed among 4 groups. We filmed one group that was frequently observed around a temple located in the center of the nonhunting area.

Data Collection

Adult individuals that walked quadrupedally in front of two fixed video cameras (Sony, HDR-CX550V) were recorded at 720p60 (resolution of $1,280 \times 720$, 60 fields/s). The animals were never handled in any way, to minimize the influence of our observation. The observations were performed passively, by waiting until the animals walked in front of the cameras. Therefore, it was not possible to select specific individuals as subjects, and instead, inappropriate bouts of locomotion, such as running, galloping, asymmetrical gait and gait performed by nonadult individuals, were excluded. In the present study, only symmetrical gaits with a duty factor above 0.5 were defined as walking gaits and selected for analysis. Data from nonadult individuals were excluded to eliminate the influence of growth and development, although locomotor ontogeny is undoubtedly an important issue [Young and Shapiro, 2018] to be addressed in future studies.

Collection of three-dimensional (3D) kinematic data of symmetrical quadrupedal ground walking was performed by defining a measurement space of approximately $2 \text{ m (w)} \times 1 \text{ m (h)} \times 2 \text{ m (d)}$, at a site frequently crossed by the macaques. Two video cameras were set so that the measurement space was fully within their field of vision. A rectangular calibration grid with eight markers on the corners (1.070 m length, 0.780 m width, 0.780 m height) was placed in the measurement space and filmed before or after data collection. The calibration grid was removed during data collection.

Since the animals were wild and the measurements were noninvasive, no markers were placed on the animals' bodies. Instead, the markerless method was used [e.g., Isler, 2005]. Anatomical landmarks (centers of the fifth metacarpophalangeal, wrist, elbow, shoulder, hip, knee, ankle, and fifth metatarsophalangeal joints) were identified on a subject's body by hand-digitizing on video images using a motion analysis software (Frame-DIAS, DKH, Japan). The digitized landmarks corresponding to the two-dimensional (2D) coordinates of the anatomical landmarks on the subject's body were reconstructed into 3D shape by the software using the direct linear transformation method. This study followed the guidelines for the treatment of animals in behavioral research and guidelines from the Association for the Study of Animal Behavior [2006, 2018] (although at the time of data collection the latest version was that from 2006, the study is fully in accordance with the 2018 version).

Data Analysis

The stride length, cycle duration, walking speed, duty factor, footfall sequence and angles of the shoulder, elbow, hip and knee joints were estimated from the reconstructed data. In the present study, stride length and cycle duration were defined as the distance and duration, respectively, between two successive placements of the same foot. The ankle joint points were used for these estimates. Walking speed was estimated by dividing the stride length by the cycle duration. Duty factor was defined as the fraction of the stride cycle duration for which a foot (hand) was in contact with the ground. Footfall sequence is the touchdown sequence of the hands and feet. Most primates typically walk with a diagonal sequence (DS) gait, in which touchdown of the left hand is followed by touchdown of the left foot. In contrast, other mammals usually display a lateral sequence (LS) gait, in which the touchdown of the left hand is followed by the touchdown of the right foot. Limb joint angles were estimated using 3D coordinates of the shoulder, elbow, wrist, hip, knee and ankle joint landmarks. Since the hand and foot landmarks at the metacarpophalangeal and metatarsophalangeals joints were often invisible during the stance phase due to the presence of grass on the ground, the wrist and ankle joint angles were not estimated in this study. The mean angular position and range of angular excursion were estimated for the shoulder, elbow, hip and knee joints.

Shoulder girdle motion, which contributes significantly to locomotion [Schmidt et al., 2002], was estimated from the reconstructed 3D coordinates. In the present study, the shoulder girdle was defined as the line connecting both sides of the shoulder joint points. Given that only two cameras were available and only one side of the body could be measured, the position of the shoulder joint on the other side of the video cameras was estimated under the assumption that both sides of the limbs and body move symmetrically and with a phase lag of 180° . Motion of the pelvic girdle during locomotion was also estimated using the reconstructed 3D coordinates of the hip joint point.

Table 1. The walking speed, cycle duration, stride length and duty factor during quadrupedal walking in the two macaque species

	<i>Macaca assamensis</i> (<i>n</i> = 14)	<i>Macaca arctoides</i> (<i>n</i> = 12)	Welch's <i>t</i> test
Walking speed, m/s	0.75±0.04	0.77±0.03	ns
Froude number	0.19±0.02	0.20±0.02	ns
Cycle duration, s	0.99±0.04	1.02±0.02	<i>p</i> < 0.05
Relative stride length	2.43±0.08	2.72±0.01	<i>p</i> < 0.001
Duty factor			
Forelimb	0.68±0.04	0.70±0.06	ns
Hind limb	0.65±0.04	0.64±0.05	ns

Values correspond to the mean ± SD. Welch's *t* test (two-tailed) was used to compare the results between the species. ns, no significant difference.

Preferred walking speed ranged from 0.36 to 1.14 m/s for the Assamese macaques and 0.33 to 1.06 m/s for the stump-tailed macaques, which in Froude numbers ($\text{speed}^2/[\text{g} \times \text{hip height}]$) corresponds to 0.04–0.43 (median is 0.20), and 0.04–0.37 (median is 0.19), respectively. Since both duty factor and joint motion are influenced by walking speed, these parameters were estimated only for gaits with Froude numbers between 0.17 and 0.22. Accordingly, results of other parameters obtained from gaits outside this range were also omitted, which reduced the data to 14 bouts of walking gait for Assamese macaques, and 12 bouts for stump-tailed macaques. All parameters were estimated based on this data set except the footfall sequence, for which a larger data set (34 walking bouts for the Assamese and 41 for the stump-tailed macaques) was used, which included gaits unsuitable for other kinematic analyses for various reasons (e.g., accidental movements of the video cameras, too steep an angle of walking direction, walking outside the calibrated space and so on). The results were analyzed through between-species comparisons. The risk of pseudoreplication, often induced by incorrect replication, was minimized by recording as many individuals as possible, which in this case corresponded to 4 individuals from each species. Although this is a limited number of individuals, it was the best compromise, considering the limited duration of data collection, as well as the animal welfare concerns.

Statistical Analysis

Comparisons between Assamese and stump-tailed macaques were performed using Welch's two-sample *t* test (except for the footfall sequence), which addresses small samples better than the Student's *t* test, even when variance homogeneity can be assumed [McDonald, 2014; Derrick et al., 2016]. The number of DS and LS gait occurrences was compared using the χ^2 test.

Results

Stride Length, Cycle Duration and Duty Factor

The mean and standard deviation (SD) of the relative stride length (divided by hip height), cycle duration and duty factor for the selected gaits are shown in Table 1. Given that walking speed was a criterion for selection of gaits for analyses (at Froude numbers of 0.17–0.22), no significant differences were found in walking speed and Froude number between the two species.

Fig. 1. Averaged shoulder and elbow angles during quadrupedal walking at Froude numbers of 0.17–0.22. The waveforms (upper row) start when the hand touches down and end when the same hand touches down again. Short vertical lines represent the time when the foot leaves the ground. Angle definitions are provided in the photographs below. Solid lines, Assamese macaques ($n = 14$ from 4 individuals); broken lines, stump-tailed macaques ($n = 12$ from 4 individuals); stance, stance phase; swing, swing phase.

Significant differences were found between the two species regarding cycle duration and relative stride length, in that both parameters were significantly longer in stump-tailed than in Assamese macaques (two-tailed Welch's t test, $p < 0.05$ for cycle duration and $p < 0.001$ for stride length).

When walking at approximately the same speed, both species exhibited a similar duty factor of both fore- and hind limbs (Table 1).

Footfall Sequence

The diagonal sequence diagonal couplets (DSDC), which is a commonly observed gait in primates, was dominant in both species. However, Assamese macaques sometimes used the lateral sequence diagonal couplets (LSDC), in which touchdown of the left hand is followed by touchdown of the right foot. Three out of 4 individuals were observed using LSDC gaits during level walking on the ground (2/11, 1/8, 1/7 bouts, respectively), which differed significantly from the stump-tailed macaques, which were never observed using the LSDC or lateral sequence lateral couplets (LSLC) during the 41 filmed walking bouts ($p < 0.05$). This result suggests that Assamese macaques exhibit higher gait choice flexibility than stump-tailed macaques.

Joint Angles

Changes in the angles of the shoulder and elbow joints during one stride cycle are shown in Figure 1, where each waveform corresponds to the mean of the collect-

Fig. 2. Averaged hip and knee angles during quadrupedal walking at Froude numbers of 0.17–0.22. Angle definitions are provided in the photographs below, which also show the subjects' posture as their foot leaves the ground. Solid lines, Assamese macaques ($n = 14$ from 4 individuals); broken lines, stump-tailed macaques ($n = 12$ from 4 individuals).

Table 2. Mean angular position of limb joints and amount of limb joint excursion during the stance phase of quadrupedal walking in the two macaque species

	<i>Macaca assamensis</i> ($n = 14$)	<i>Macaca arctoides</i> ($n = 12$)	Welch's t test
Mean angular position, degrees			
Shoulder	61.5±12.7	73.4±14.6	$p < 0.05$
Elbow	141.4±13.2	156.8±15.5	$p < 0.005$
Hip	135.6±15.1	142.9±14.7	ns
Knee	73.5±11.3	80.9±13.5	ns
Amount of joint excursion, degrees			
Shoulder	74.6±11.6	58.4±13.8	$p < 0.01$
Elbow	23.1±6.1	22.0±6.3	ns
Hip	55.7±12.1	66.0±13.4	ns
Knee	24.7±8.5	19.2±6.2	ns

Values correspond to the mean ± SD. Welch's t test (two-tailed) was used to compare the results between the species. ns, no significant difference.

Fig. 3. Contribution of shoulder and pelvic girdle motion to stride length. **a** The maximum distance between the right and left shoulder joints projected on the progression plane was estimated as corresponding to the contribution of the shoulder girdle motion to stride length. The contribution of the pelvic girdle motion was estimated in the same way. **b** Mean and SD of the shoulder girdle contribution of Assamese ($n = 14$ from 4 individuals) and stump-tailed macaques ($n = 12$ from 4 individuals). There was a significant difference ($p < 0.05$) between the two species. **c** Mean and SD of the pelvic girdle contribution of Assamese ($n = 14$) and stump-tailed macaques ($n = 12$).

ed data (14 strides from 4 Assamese macaque individuals and 12 strides from 4 stump-tailed macaque individuals). The angle profiles of the limb joints were similar in both species. Stump-tailed macaques (broken lines), however, appeared to use the forelimbs in more protracted positions (i.e., the shoulder joint was more flexed) than Assamese macaques (solid lines), as indicated by the larger values of the shoulder's mean angular position, estimated for the stance phase (Table 2). For stump-tailed macaques, the mean angular position was also significantly larger for the elbow joint, indicating that this species used the elbow in more extended positions than Assamese macaques did (Table 2). The range of motion at the shoulder was significantly wider in Assamese than stump-tailed macaques (Fig. 1, Table 2).

Similar tendencies were observed for the hind limb joint angles (Fig. 2). At the end of the stance phase, that is, when the foot left the ground, the hip and knee joints of stump-tailed macaques (broken lines) were more extended than those of the Assamese macaques (solid lines). However, this difference was not statistically significant (Table 2).

Contribution of the Shoulder and Pelvic Girdles

Figure 3 shows the estimated contributions of the shoulder and pelvic girdles to the stride length. In the present study, shoulder girdle motion was defined as the maximum distance between the right and left shoulder joints, projected on the plane of progression (Fig. 3a). Larger values indicate that the shoulder girdle largely moved in the horizontal plane. The estimated value was significantly larger in stump-tailed than Assamese macaques ($p < 0.05$; Fig. 3b). The same estimate was conducted for the pelvic girdles (Fig. 3c), with no significant difference between the two species.

Fig. 4. Direction of the hand during quadrupedal walking. **a** Assamese macaques often directed the hands outwards. **b** Stump-tailed macaques directed the hands relatively straight forward.

Hand and Foot Postures

The hand and foot postures during quadrupedal locomotion were difficult to quantify, and comparisons were made on the basis of observations. During walking, Assamese macaques used their hands in more abducted postures than stump-tailed macaques, directing their fingers laterally (Fig. 4a, online suppl. material Video 1; for all online suppl. material, see www.karger.com/doi/10.1159/000496024), whereas stump-tailed macaques directed them straight forward at the sagittal plane (Fig. 4b). Another observed difference was the way in which the hand contacted the ground. Assamese macaques basically used a palmigrade hand posture (Fig. 5a), sometimes showing a “semipalmigrade” gait, in which the forepart of the palm was not in contact with the ground due to finger flexion. Instead, the dorsal aspects of the distal phalanges were in contact with the ground (Fig. 5b, online suppl. material Video 2), clearly showing that the gait of Assamese macaques was by no means digitigrade. In contrast, stump-tailed macaques walked with a digitigrade gait, in which the metacarpal part was elevated, as shown in the photos and palm print (Fig. 5c, d). Regarding the feet, all subjects from both species walked in a semiplantigrade posture, elevating the heel and supporting most of the body weight on the toes and forepart of the foot.

Discussion

The present study revealed substantial differences in the locomotor parameters of Assamese and stump-tailed macaques, even when walking at a similar speed. Stump-tailed macaques walked with longer strides and with longer cycles than Assamese macaques, which indicates that Assamese macaques present a higher stride

Fig. 5. Hand postures during quadrupedal walking. **a** Palmigrade hand posture of Assamese macaques. **b** Occasionally Assamese macaques fully flexed the fingers during locomotion. We call this posture as “semiplantigrade” since the forepart of the palm was not in contact with the ground due to the flexed fingers. **c, d** Stump-tailed macaques walked with a “digitigrade” gait, in which the carpal portions were elevated, as clearly shown in the hand print (**c**).

frequency (Table 1), whereas stump-tailed macaques used longer, less frequent strides to achieve the same speed.

Interestingly, although stump-tailed macaques displayed a longer stride, their shoulder range of motion was narrower than that of Assamese macaques (Fig. 1), which raises the question of how stump-tailed macaques could achieve a longer stride with the forelimb, with narrow shoulder joint motions. We postulate that, in stump-tailed macaques, the motion of the shoulder girdle contributes to increase stride length. As shown in Figure 3a, horizontal rotation of the shoulder girdle leads to a larger anteroposterior movement of the shoulder joint, thus increasing stride length during quadrupedal locomotion. Since, in this study, stump-tailed macaques exhibited a larger anteroposterior translation of the shoulder (Fig. 3b), this suggests that the contribution of shoulder girdle rotation was larger in this species. It is well known that in large-bodied terrestrial mammals, during quadrupedal gait the scapula moves as if it is the most proximal part of the forelimb [Larson, 1993; Preuschoft et al., 2010], limiting the motion of the glenohumeral joint and consequently giving the joint sta-

bility to resist the force generated during locomotion [Larson, 1993]. On the other hand, in primates during arboreal nonpronograde locomotion the glenohumeral joint moves freely [Rose, 1989] and is responsible for a substantial proportion of forelimb progressive motion. This characteristic may reflect the difference between arboreal primates and large-sized terrestrial mammals, regarding the level of scapula motion during quadrupedal walking. The range of cranial rotation of the scapula and that of glenohumeral joint motion during quadrupedal locomotion were reported as approximately 28 and 60° for vervet monkeys [Whitehead and Larson, 1994], and approximately 40 and 35° for cats [English, 1978a, b]. Information regarding scapula motion remains poor, but available data suggest that a limited range of motion of the shoulder (glenohumeral) joint and a large scapular motion during quadrupedal locomotion may be considered as common features in relatively large-sized terrestrial mammals [Preuschoft et al., 2010]. However, it should be noted that small mammals tend to use more scapular than glenohumeral motion during locomotion [Fischer, 1994]; that is, the comparison has to be conducted between similar-sized animals. The larger shoulder girdle motion observed in stump-tailed macaques during quadrupedal walking (Fig. 3b) suggests that this species is more adapted to terrestrial conditions than Assamese macaques.

Another feature that characterizes stump-tailed macaques is the largely extended elbow and knee joints (Fig. 1, 2, Table 2). Most arboreal primate species walk with flexed elbows and knees [Schmitt, 1998, 1999, 2003], which is considered to increase stability during arboreal locomotion on thin and unstable substrates. On the other hand, extension of the elbow and knee joints enables the animals to use inverted pendulum mechanics during terrestrial quadrupedal locomotion, increasing the efficiency of mechanical energy [Griffin et al., 2004]. Therefore, the higher elbow and knee extension observed in stump-tailed macaques suggests that this species displays a terrestrially adapted gait. This is further supported by the digitigrade hand postures (Fig. 5) observed in stump-tailed macaques during terrestrial locomotion. When traveling on the ground, digitigrade postures offer several biomechanical advantages, including a more effective forelimb length and attenuation of wrist joint movements [Patel, 2008, 2009, 2010a]. In contrast, the gait of Assamese macaques does not seem to be optimized for terrestrial locomotion. This species displays smaller shoulder girdle movements (Fig. 3b), and the elbow and knee joints were relatively flexed (Fig. 1, 2, Table 2) compared with those of stump-tailed macaques. The hand posture was very different from the terrestrially adapted digitigrade posture, with the proximal parts of the hand kept in contact with the ground during the stance phase (Fig. 5a, b). A hand posture with flexed fingers during locomotion is often observed in highly arboreal species, such as the spider monkey (*Ateles geoffroyi*) and is considered an arboreal adaptation [Okada, 1985; Patel, 2010b].

The question arises as to why primates – especially arboreal species – use a compliant gait even during terrestrial locomotion. Gaits on arboreal substrates impose compliant quadrupedalism [Schmitt, 1998], whereas gaits on the ground do not. The advantages of compliant gaits are not necessarily important on the ground. In a study on the kinematics and kinetics of quadrupedal locomotion in 5 primate species, Schmitt [1998, 1999] found that gaits were less compliant on the ground than on a simulated arboreal substrate in all subjects. However, primates are generally reported to walk in a compliant fashion even when on the ground [e.g., Alexander and Maloiy, 1984; Reynolds, 1987]. The morphology of highly mobile forelimbs in primates [e.g.,

Ashton et al., 1968; Manaster, 1979; Morbeck, 1979; Rodman, 1979; Schaffler and Burr, 1984; Schaffler et al., 1985; Rose, 1988] could partly explain this observation, although the anatomical features that impose a compliant gait on the ground have not been well identified. However, this does not explain why the hind limbs are also used in a compliant way on the ground. A supplemental explanation relates to the strategy of locomotor control. Ishida et al. [1974] revealed that hind limb muscles are activated in a similar manner during bipedal and quadrupedal walking. Goto and Nakano [2018] reported similar results based on their muscle synergy analysis [Ivanenko et al., 2004]. Hirasaki and Matano [1996] revealed that joint kinematics of the hind limbs of Japanese macaques are conserved between quadrupedal level walking and vertical climbing. Goslow et al. [1989] insisted that the motor patterns of homologous muscles have been maintained during evolution. Thus, control of limb motion may be conserved between different modes of locomotion at least in macaque monkeys; such patterns are not maintained in chimpanzees [R. Goto, pers. commun.] or spider monkeys [Hirasaki and Matano, 1996]. Although Larson [1998] demonstrated that the forelimb activity of primates does not follow the neuromuscular conservation hypothesis [Goslow et al., 1989], she suggested that the hypothesis may apply to primate hind limbs. If this is indeed the case, there is a motor control strategy for compliant hind limb motion, which is well tuned for arboreal locomotion, and the strategy is also used during terrestrial locomotion with small adjustments, as shown in studies by Schmitt [1998, 1999], to generate a compliant gait. However, without further investigation, this is just speculation.

Several results observed in this study, such as the duty factor, footfall sequence and the laterally directed hand posture, suggest that the locomotion of Assamese macaques is tuned for cliff climbing. To ensure safety, Assamese macaques sleep in the cracks of cliffs. Timmins and Duckworth [2013, p. 108] reported that “Karts’s expanses of bare rock may themselves be important to Assamese macaque,” based on their own observations and on previous reports that they reviewed. Although Fooden [1986] speculated that Assamese macaques slept in trees, subsequent studies revealed that most members of the species use steep cliffs as sleeping sites, engaging in cliff climbing and descending for a substantial amount of time [Ogawa and Hirasaki, 2009]. Workman and Schmitt [2012] argue that rock (and cliff) travel differs considerably from terrestrial and arboreal travel. As such, they proposed the use of the term “petrous” to indicate the substrate and incorporate the implications of its precise sharpness and verticality that lead to the complexities and risk of locomotion on rock surfaces. Given that arboreal adaptation influences terrestrially moving monkeys, petrous adaptation may impose similar constraints on arboreal and/or terrestrial locomotion. For example, the more flexible footfall sequence observed in Assamese macaques may be related to an unstable petrous locomotor repertoire. Assamese macaques walked mostly with a DS gait, although LS was also observed (approx. 11.8%). In cliff climbing, hands and feet must reach out for the next available hold wherever it is located. The limb motion sequence varies according to the cliff conditions. LS gaits are usually favored during quadrupedal walking on a descending slope, probably due to the alternating role of fore- and hind limbs according to the weight shift. However, our data were collected during ground level walking. Therefore, we postulate that the need for flexible limb use in cliff climbing may have some relation to the relatively flexible footfall sequence during level quadrupedal locomotion observed in Assamese macaques. The laterally directed (abducted) hand posture (Fig. 4a) is also

considered as an adaptation for hand holds during cliff and tree climbing, as an abducted hand posture enables the monkeys to power grip the substrate. If animals hook the long and flexed fingers on a horizontal branch, the hand does not need to remain abducted, in which case, the thumb does not play an important role. However, abducted hand postures allow the animals to efficiently hold the grip with their fingers and the thumb during climbing.

Presently, further comparisons with other macaque species are difficult since kinematic studies in other species are scarce, and the available data are mostly generated from laboratory experiments. Our previous studies [Hirasaki and Matano, 1996; Hirasaki et al., 2010] revealed that Japanese macaques walk with a more flexed elbow and knee than both Assamese and stump-tailed macaques, suggesting that this species is more adapted to arboreal conditions. This idea is supported by their shorter, more frequent strides. However, it must be kept in mind that observed locomotor parameters differ between field and laboratory measurements [Shapiro et al., 2011].

On the basis of the limited data analyzed so far, we postulate that the quadrupedal gait of stump-tailed macaques is well adapted to terrestrial conditions, whereas the quadrupedal gait of Assamese macaques is influenced by their unique cliff-climbing behavior. These results support the hypothesis formulated in the Introduction that there are significant differences in the locomotor kinematics of these two species that reflect arboreality/terrestriality. However, we must keep in mind that the present results were obtained solely from quadrupedal walking on the ground, which is only one part of the locomotor repertoires of Assamese and stump-tailed macaques, and are thus not robust enough for solid conclusions about the relationship between locomotor kinematics and habitat use. Future studies are needed, including data on additional terrestrially or arboreally adapted primate species, comparisons between wild and zoo- or laboratory-born individuals of the same species, and analyses on 3D kinematics of cliff climbing, and using more accurate methodologies.

The present study had some limitation related to the 3D kinematics: not only is its accuracy relatively low compared to laboratory studies, as the calibration was sometimes difficult when the target animal was far from the video cameras. The low accuracy was partly due to the markerless analysis, since the estimated landmark positions were digitized by hand on 2D images, and the 3D coordinates were reconstructed from these digitized data. As such, 2D digitization errors, which are supposed to be larger than those in marker analysis, are magnified during reconstruction for 3D coordinates. Sellers and Hirasaki [2014] have recently developed a new method for kinematic measurements of free-ranging animals, which is based on a 3D photogrammetric reconstruction. This method uses the Structure from Motion algorithm, allowing full calibration based on the separation of the individual cameras, thus potentially providing more accurate results. The recent, rapid development of deep learning techniques, such as R-CNN (region-based convolution neural network) [Girshick et al., 2014] or OpenPose algorithm [Cao et al., 2017], may also offer new possibilities for markerless methods. As the hardware and software improve, these new methods will overcome the accuracy issues of 3D motion capture calibration for free-ranging animals and resolve the inherent time constraints. We believe that kinematic analysis in a wild environment is a promising, future direction in the field of primate locomotion studies, given its tremendous potential.

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Statement of Ethics

This study was designed following the guidelines for the treatment of animals in behavioural research and teaching (Association for the Study of Animal Behaviour), was approved by the Institutional Animal Care and Use Committee of Kyoto University Primate Research Institute, and was permitted by the National Research Council of Thailand (Permission No. 0002.3/6481 on 17 November BE 2551).

Disclosure Statement

The authors declare that they have no conflict of interests.

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Author Contributions

E.H. and Y.H. conceived and designed the research, with advice from S.M. E.H., S.M. and Y.H. performed the observations in the field. E.H. analyzed the data and wrote the manuscript with editorial advice from S.M. and Y.H.

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