

# Orangutan Positional Behavior and the Nature of Arboreal Locomotion in Hominoidea

Susannah K.S. Thorpe<sup>1\*</sup> and Robin H. Crompton<sup>2</sup>

<sup>1</sup>*School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK*

<sup>2</sup>*Department of Human Anatomy and Cell Biology, University of Liverpool, Liverpool L69 3GE, UK*

**KEY WORDS** *Pongo pygmaeus*; posture; orthograde clamber; forelimb suspend

**ABSTRACT** The Asian apes, more than any other, are restricted to an arboreal habitat. They are consequently an important model in the interpretation of the morphological commonalities of the apes, which are locomotor features associated with arboreal living. This paper presents a detailed analysis of orangutan positional behavior for all age-sex categories and during a complete range of behavioral contexts, following standardized positional mode descriptions proposed by Hunt et al. ([1996] *Primates* 37:363–387). This paper shows that orangutan positional behavior is highly complex, representing a diverse spectrum of positional modes. Overall, all orthograde and pronograde suspensory postures are exhibited less frequently in the present study than previously reported. Orthograde suspensory locomotion is also exhibited less often, whereas pronograde

and orthograde compressive locomotor modes are observed more frequently. Given the complexity of orangutan positional behavior demonstrated by this study, it is likely that differences in positional behavior between studies reflect differences in the interplay between the complex array of variables, which were shown to influence orangutan positional behavior (Thorpe and Crompton [2005] *Am. J. Phys. Anthropol.* 127:58–78). With the exception of pronograde suspensory posture and locomotion, orangutan positional behavior is similar to that of the African apes, and in particular, lowland gorillas. This study suggests that it is orthograde in general, rather than forelimb suspend specifically, that characterizes the positional behavior of hominoids. *Am J Phys Anthropol* 000: 000–000, 2006. © 2006 Wiley-Liss, Inc.

With the exception of ourselves, the living apes are predominantly tropical forest dwellers (Dohlinow and Fuentes, 1999), and their preferred foods (sensu Wrangham et al., 1998) are predominantly ripe fruits (Pilbeam, 2002), harvested directly from the trees. The morphological commonalities of all apes, such as a broad trunk, dorsally placed scapula, and an ability to raise the arm above the head, are generally accepted as primarily locomotor features and confirm that the hominoids are, in essence, an arboreal clade. Nevertheless, it is the Asian apes that are now most restricted to locomotion in the canopy. Chimpanzees, bonobos, mountain gorillas, and even lowland gorillas spend a relatively large amount of time on the ground, as reflected in their morphological adaptations for quadrupedal knuckle-walking. While orangutans may have further refined their morphological adaptations to arboreal living since their split from the common ancestor, as the only great ape to retain a predominantly arboreal lifestyle, they are an important model in interpreting the shared morphological features of the great apes.

However, orangutan locomotion has so far been only very broadly described. Sugardjito and Van Hooft (1986) provided a broad-ranging description of Sumatran orangutan positional behavior during travel and rest, but grouped 48% of locomotion together under the category “quadrumanous scrambling.” Cant (1987a) refined the classification of locomotion during travel and feeding in Bornean orangutans by distinguishing between modes according to the orientation of the body, and the direction of movement. However, the study by Cant (1987a) was limited to two adult females, and was conducted during an unusual drought, which may be expected to have influenced the ranging and foraging patterns of his subjects. Cant (1987b)

also studied the postures exhibited during feeding in two types of fig trees by Sumatran adult males and females, and found significant differences in positional behavior based on both gender and food type. However, none of these studies provided a comprehensive overview of locomotion and posture during feeding and travel for a single study group. Nor were they detailed enough to allow us to develop an understanding of locomotor anatomy. Recent advances in the standardization of positional mode classifications (Hunt et al., 1996), which advocate approaching locomotion from a biomechanical perspective, have opened the way for a comprehensive and meaningful analysis of primate positional behavior. This is particularly appropriate for orangutans, as they may be expected to exhibit a diverse spectrum of positional modes, due to their large body mass combined with the mechanical constraints imposed on arboreal locomotion by spatial discontinuity in the canopy and the fragility and compliance of arboreal supports (Cant, 1992).

Grant sponsor: European Commission; Grant sponsor: Indonesian Government; Grant sponsor: Leverhulme Trust; Grant sponsor: Royal Society; Grant sponsor: L.S.B. Leakey Foundation; Grant sponsor: Natural Environment Research Council.

\*Correspondence to: Dr. S.K.S. Thorpe, School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK. E-mail: S.K.Thorpe@bham.ac.uk

Received 29 June 2005; accepted 21 December 2005.

DOI 10.1002/ajpa.20422

Published online in Wiley InterScience  
(www.interscience.wiley.com).

TABLE 1. Study subjects

| Age-sex category | Name   | Age (years) | No. focal days | Notes  |
|------------------|--------|-------------|----------------|--|
| Adult male       | Bobby  | Unknown     | 10             | Dominant male  |
|                  | AM2    | Unknown     | 5              | Unidentified young adult male                                |
| Adult female     | Yet    | ca. 34      | 14             | Dominant female, travels with immature son Yossa (see below) |
|                  | Sina   | ca. 29      | 11             | Mid-rank, pregnant, travels with immature son                |
|                  | Ans    | 24          | 11             | Low rank, travels with semidependent infant                  |
| Subadult male    | X      | ca. 31      | 5              |  |
|                  | Yop    | 21          | 3              | Eldest offspring of Yet                                      |
| Immature female  | Chris  | 12          | 12             | Independent daughter of Ans                                  |
| Immature male    | Eibert | 8           | 13             | Independent  |
|                  | Yossa  | 7           | 13             | Son of Yet   |

As argued by Thorpe and Crompton (2005), standard nonparametric tests (such as  $\chi^2$  tests on contingency tables for examining relationships between variable frequencies) are usually fairly robust for two-dimensional analyses. However, such an approach may lead to misleading conclusions, if we attempt to examine multidimensional relationships by analyzing a series of combinations of two-dimensional tables (Gilbert, 1981; Agresti, 1990). A further difficulty arises when cell frequencies are low or zero, as happens very quickly when examining locomotor data, even where the overall data set is numbered in tens of thousands of observations. Thorpe and Crompton (2005) demonstrated that relationships between locomotion and related ecological variables for orangutans in this study group were more complex than could be adequately represented by two-dimensional analysis. They used log-linear modeling to analyze multiple relationships among locomotor and substrate variables. This technique, although sophisticated, does not lend itself to the detailed characterization of positional behavior that is required here. Consequently, the analysis in this paper is restricted to statements of frequency, without recourse to statistical testing. This paper provides the complete positional behavior data set used for the log-linear analysis of orangutan locomotion in Thorpe and Crompton (2005).

While the African apes have, to a greater or lesser extent, forsaken an arboreal lifestyle, it remains a generally accepted hypothesis (e.g., Fleagle, 1988) that the hominoids are characterized primarily by adaptations for forelimb suspension. This study therefore tests the above hypothesis with reference to the most arboreal of great apes, by a detailed qualitative and quantitative description of orangutan positional behavior, for all age-sex categories and during a complete range of behavioral contexts. Our main findings are set in context by comparison with data for other apes and for outgroup comparators.

## METHODS

### Field study

The field study took place in the Ketambe Research Station (3° 41' North, 97° 39' East) in the Gunung Leuser National Park (Leuser Ecosystem, Aceh Tenggara, Sumatra, Indonesia). The area is covered by pristine rain forest on riverine terraces located along the course of the Alas River, and was described in detail by Rijksen (1978) and van Schaik and Mirmanto (1985). The study was carried out between December 1998–December 1999, and all observations were made by a single observer (S.K.S.T.) to ensure consistency. Considerable self-training in esti-

imating height and identification of positional types and support types, angles, and diameters was carried out in the first 6 weeks of the study, and at intervals throughout the study. The majority of data were collected between February–November 1999.

Ten individuals were observed, including adult and immature individuals of both sexes (see Table 1 for subject information). Focal instantaneous sampling on the 1-min mark was employed to enable collection of detailed data on support use and contextual behavior, in addition to a fine-grained classification of positional behavior. Once located, the orangutans were followed for a maximum of 5 consecutive days from when they left their night nest until they built their next night nest, and on at least two separate occasions.

### Positional behavior classification

We obtained 28,797 instantaneous observations of positional behavior, 25,986 being of postural behavior, and 2,811 of locomotion. Great ape positional behavior is highly complex, and it is thus difficult to identify the optimum level of detail at which classification should occur. It is obviously impossible to differentiate every movement, and as Hunt et al. (1996) argued, neither is it desirable, as it is equally impossible to analyze the anatomical implications of each of a near-infinite roster of positional classifications. Nevertheless, the aim of this study was to identify fine-grained differences in orangutan positional behavior, to shed light on some of the key issues surrounding fine-grained similarities and distinctions in great ape morphology, and thus we opted for a detailed classification system that separates *submodes* that are kinematically and mechanically distinct, but pools them into *modes* that may be used for comparative purposes in the future. To enhance clarity in the text and tables, submode labels for the present study are *italicized*, and modes are in **bold**.

The classification of positional behavior follows the theoretical approach detailed by Hunt et al. (1996). The area of the base of support is a key factor in the classification system, and we tried to avoid conflating postures where the area of the base is different, except where accuracy is very limited because of the difficulty of observing orangutans in the canopy (e.g., *sit* and *sit-out*; Hunt et al., 1996). Classifications are defined in terms of the number of weight-bearing body parts (e.g., limbs, or segments such as the ischia), and whether each body part appears to be under predominantly tensile (in suspension under superstrates) or compressive (above the sub-

strate) stress regimes. Body-part positions are included in the definition if they appear to support more than their own mass. Orangutans were frequently observed to combine two or three postural components into hybrid postures to maximize stability or reach. For example, an orangutan might sit, with one forelimb in suspension and one hindlimb in compression, with all parts appearing to support more than their own mass. To reflect these hybrid combinations, the positional component that appeared to bear the most weight ( $>1/2$  body mass where two components were combined, and  $>1/3$  body mass where three components were combined) was recorded first in the definition (component 1). The component that bore the next largest proportion of body mass became component 2, and the third largest became component 3 (Appendix A). An indication of the weight borne by each limb may be drawn from the level of deformation of the supports and the extent to which they rebound when an animal removes its weight; the general position of the body, such as the position of the trunk relative to the limbs and the support; and the appearance of the cheiridia and limbs (Hunt et al., 1996).

In their classification system, Hunt et al. (1996) separated unimanual and bimanual forelimb-suspend and cling in their equivalent of component 1, but they did not separate single and dual use of the hindlimbs in hindlimb suspension, and they recommended that standing on one leg be classified as a bipedal stand. Also, in most cases when there was more than one component in a submode, they did not distinguish single and dual use of the forelimbs in the initial or subsequent components. Here, we separate single and dual use of the forelimbs and hindlimbs in component 1 for suspension and stand, but not other modes, both in an attempt to highlight key kinematic and mechanical information specific to orangutans but to avoid overanalyzing positional behavior, and because the frequency of unaided and hand-assisted bipedalism was of particular interest to us. However, we did not separate single and dual use of hindlimbs or forelimbs in components 2 and 3. Similarly, flexion and extension are recorded for component 1, but not for subsequent components.

We also drew a distinction in component 1 between stand, where the legs are in a vertical and (if both are used) similar kinematic position to each other, and compression, where the legs may be angled in any position below horizontal and may be positioned on substrates at different levels, with different degrees of abduction/adduction and flexion/extension to each other. This distinction is necessary for orangutan posture because of the complexity of the environment and their capacity for supporting body mass using multiple limbs and multiple supports anywhere in their sphere of reach.

Distinction is not made on the basis of footfall pattern or hand/foot grip, because foliage often made this difficult to record, and footfall patterns and grips are outside the intended scope of this study. Joints are regarded as extended only when in full extension, or very nearly so. All other joint positions are recorded as flexion.

To prevent the term "climb" being used to describe locomotion in a horizontal direction, Hunt et al. (1996) advocated that "climb" be used to describe locomotion within  $45^\circ$  of true vertical. Thorpe and Crompton (2005) showed that the mechanics of orangutan climbing between  $20$ – $45^\circ$  of true vertical were fundamentally different from climbing within  $20^\circ$  of true vertical. Their log-linear analysis of the relationships between orangu-

TABLE 2. Comparison of percentages of postural modes in full data set and 25% sample

|                                 | Total data set | 25% sample |
|---------------------------------|----------------|------------|
| Sit                             | 59.7           | 58.1       |
| Squat                           | 0.0            | 0.4        |
| Cling                           | 0.1            | 0.1        |
| Pronograde stand                | 3.6            | 4.3        |
| Orthograde stand                | 7.4            | 5.8        |
| Cantilever                      | 0.0            | 0.0        |
| Orthograde forelimb-suspend     | 3.5            | 3.3        |
| Orthograde quadrumanous-suspend | 1.5            | 2.1        |
| Forelimb/hindlimb suspend       | 9.6            | 9.1        |
| Pronograde suspend              | 3.7            | 3.7        |
| Hindlimb-suspend                | 0.8            | 0.8        |
| Lie                             | 9.9            | 12.2       |
| Postural bridge                 | 0.1            | 0.1        |
| Total                           | 100.0          | 100.0      |

tan locomotion and associated variables found that locomotion was best understood when angled climb/descent (i.e.,  $20$ – $45^\circ$ ) was included in the torso orthograde suspension mode rather than vertical climb/descent. Consequently, in Appendix B, we followed the recommendations of Hunt et al. (1996) by classifying all climbing activity above  $45^\circ$  as **vertical climb** and **vertical descent**, but we also provided values for angled climb in parentheses.

Overall, 129 biomechanically distinct positional submodes were identified: 82 representing posture, and 47 representing locomotion. These conflate into 13 postural and 14 locomotor modes. Positional behavior definitions and frequencies are presented in Appendix A (posture) and Appendix B (locomotion).

### Statistical analysis

The interdependence of observations is a particular problem in the analysis of positional behavior. Sequential observations using a small time interval are thought to produce results in which assumptions of independence may be violated, so that sampling procedures may be required (Boinski, 1989; Hunt, 1992; Dagosto, 1994; Warren and Crompton, 1997). Of the 28,797 bouts observed in this study, only 2,811 were of locomotion. Poor visibility in this study and the tendency of orangutans to rest frequently during bouts of locomotion meant that sequential observations of locomotion were rarely obtained. Consequently, all locomotor bouts were analyzed. However, sequential observations of postural behavior were frequently obtained. To remove the problems of interdependence, our analysis is simply based on a 25% random sample (SPSS analysis,  $n = 7,155$ ). Table 2 shows that postural mode frequencies in the 25% sample do not differ substantially from those for the complete data set.

## RESULTS

### Posture

Due to the variability of orangutan positional behavior, we found it necessary to distinguish more precisely between orthograde and pronograde postures than did Hunt et al. (1996). Thus, at the mode level, **pronograde stand** subsumes all pronograde compressive postures, including those classified under stand mode by Hunt et al. (1996) and *contralateral* and *ipsilateral compression*, which are submodes novel to orangutans. Similarly, **orthograde stand** subsumes both *bipedal* and *mono-*



TABLE 3. Percentages of commonly observed (&gt;1% overall total) postural modes according to behavioral context in comparison to previous studies

|                                    | Present study |      |        |        |      |       |       | Cant (1987a),<br>feed | Sugardjito and<br>van Hooff<br>(1986) <sup>1</sup> |      |
|------------------------------------|---------------|------|--------|--------|------|-------|-------|-----------------------|--|------|
|                                    | Rest          | Feed | Travel | Social | Look | Other | Total |                       | Travel   | Rest |
| Sit                                | 42            | 63   | 59     | 53     | 45   | 60    | 58    | 49                    | 41   | 59   |
| Pronograde stand                   | 0             | 4    | 14     | 4      | 19   | 11    | 4     | <1                    | 26   | 3    |
| Orthograde stand                   | 0             | 7    | 6      | 4      | 13   | 7     | 6     | 2                     |  |      |
| Orthograde forelimb<br>suspend     | 0             | 4    | 5      | 4      | 4    | 2     | 3     | One arm: <1           |  |      |
| Orthograde quadrumanous<br>suspend | 0             | 3    | 2      | 1      | 1    | 5     | 2     | Other: 11             | 33   | 4    |
| Forelimb/hindlimb<br>suspend       | 0             | 12   | 6      | 4      | 11   | 5     | 9     | Ipsilateral: 30       |  |      |
| Pronograde suspend                 | 0             | 5    | 4      | 5      | 3    | 7     | 4     | Other: 6              |  |      |
| Lie                                | 58            | 1    | 1      | 16     | 4    | 1     | 12    | 0                     | 0  | 34   |

<sup>1</sup> Mean values calculated from Tables 3 (pauses during travel) and 4 (rest) in Sugardjito and van Hoof (1986).

*pedal stand* and *compression* if the trunk is orthograde. Suspensory behavior is classified in the same manner. Thus, **pronograde suspend** subsumes the quadrumanous suspend mode of Hunt et al. (1996) and other pronograde suspensory behavior specific to orangutans. **Orthograde forelimb-suspend** compares well with the forelimb suspend of Hunt et al. (1996). However, orangutans exhibit a number of additional orthograde suspensory postures in which the hindlimbs support an equal or greater body mass than the forelimbs, e.g., *orthograde hindlimb-suspend*. Thus, we named an additional mode: **orthograde quadrumanous suspend**.

At the submode level, most additional classifications reflect hybrid combinations, normally between two postural components. However, a novel submode exhibited relatively often (1.2%) was *pronograde stand/forelimb-suspend*. In this posture, orangutans stand with their trunk and hindlimbs in a pronograde stand position, but one or both forelimbs bear significant body mass in suspension, with the arm abducted to a vertical position above the body. *Forelimb-suspend/pronograde compression* is a similar position, but with the majority of body mass borne by the suspended forelimbs, and is thus within the **pronograde suspend** mode. Orangutans also exhibited a novel form of **squat** whereby the majority of weight was supported by the feet with the hips and knees strongly flexed, but substantial weight was also supported by squatting with the distended tummy propped up on another support, parallel to the main weight-bearing substrate (*stomach squat*). Finally, pronograde bridging behavior was previously documented in orangutans. However, on rare occasions in this study, the only female to have a dependant infant was also observed to use an *orthograde bridge*, in which she held supports on either side of a gap in the canopy together to reduce the size of the gap, so that her accompanying infant could cross independently.

## Locomotion

In general, orangutan locomotion is described well by the standardized positional modes of Hunt et al. (1996), although we separated **vertical descent** from **vertical climb** at the mode rather than the submode level, as the effect of gravity results in very different demands on the body during climbing and descending, and orangutans

exhibit demonstrably different mechanics in the two modes (e.g., *rump-first* and *head-first cascade descent*, and *fire pole slide*) (Appendix B). Two further additions at the mode level were **hindlimb swing** and **forelimb-hindlimb swing**. The latter mode describes suspensory behaviors that are neither exclusively orthograde nor pronograde, and which utilize forelimbs and hindlimbs in any sequence (e.g., *ipsilateral swing* and *cartwheel swing*). These submodes are mostly used as an intermediary form of movement to reorient the body between two longer bouts of very different types of locomotion. *Cartwheel swing* and *cartwheel descent* (under the **vertical descent** mode), although infrequent (<1%), are both submodes novel to orangutans. They are bouts of suspensory locomotion resembling the sequence of limb usage seen in human cartwheels, either on horizontal or negatively inclined supports. Both are exhibited predominantly by adolescent individuals during times when they appear playful.

Tree sway is a mode exemplified by orangutans (Sugardjito and van Hooff, 1986). The definition, however, is unique in that it refers to a technique that may encompass a broad range of other positional behaviors. In this study, tree sway was observed to utilize many different postures, which alter as the center of gravity of the body changes position in relation to the support, during oscillations. *Monopedal*, *bipedal*, and *tripedal stand* accompanied by *forelimb suspend* are common components seen during tree sway, as are *ipsilateral* and *quadrumanous suspend*, and *sit/forelimb suspend*. The animal may sway the tree in such a way that it is on top of the support when it moves to the next tree, or in suspension underneath. In this study, orangutans were also observed to oscillate vertical lianas and vertical branches in a movement reminiscent of a child swinging on the end of a rope, in order to swing to a new support. We therefore renamed the mode **sway**, as it is not reliant on trees.

## DISCUSSION

### Comparisons with other studies

Cant (1987a) and Sugardjito and van Hooff (1986) previously quantified orangutan positional behavior, but there are notable differences between this study and previous results. Table 3 shows frequencies for the most

TABLE 4. Percentages of commonly observed locomotor modes according to behavioral context and in comparison to previous studies<sup>1</sup>

| Mode  | Submode                                | Present study  |                |                | Cant (1987a)   |           | Sugardjito and van Hooft (1986), travel |
|---|--|----------------|----------------|----------------|----------------|-----------|---|
|   |  | Travel         | Feed           | Total          | Travel         | Feed      |   |
| <b>Quadrupedal and tripedal walk</b>          |  | <b>15</b>      | <b>24</b>      | <b>18</b>      | <b>12</b>      | <b>12</b> | <b>12</b>                               |
|   | <i>Walk</i>                            | 7              | 11             | 8              | 12             | 12        | ? <sup>3</sup>                          |
|   | <i>Pronograde scramble</i>             | 8              | 13             | 9              | ?              | ?         | ?                                       |
| <b>Torso-orthograde suspensory locomotion</b> |  | <b>39</b>      | <b>26</b>      | <b>35</b>      | <b>62</b>      | <b>53</b> | ?                                       |
|   | <i>Brachiation and forelimb swing</i>  | 16             | 12             | 15             | 11             | 9         | 19                                      |
|   | <i>Orthograde clamber and transfer</i> | 23             | 14             | 20             | 51             | 44        |   |
| <b>Torso-pronograde suspensory locomotion</b> |  | <b>3</b>       | <b>5</b>       | <b>4</b>       | <b>1</b>       | <b>2</b>  |   |
| <b>Forelimb/hindlimb- swing</b>               |  | <b>0</b>       | <b>1</b>       | <b>0</b>       | ?              | ?         | 46 <sup>2</sup>                         |
| <b>Bipedal walk</b>                           |  | <b>7</b>       | <b>8</b>       | <b>7</b>       | # <sup>4</sup> | #         |   |
|   | <i>Bipedal walk</i>                    | 2              | 2              | 2              | 0              | 0         |   |
|   | <i>Assisted bipedal walk</i>           | 5              | 6              | 6              | #              | #         |   |
| <b>Bridge</b>                                 |  | <b>4</b>       | <b>0</b>       | <b>3</b>       | ?              | ?         |   |
| <b>Vertical climb</b>                         |  | <b>14</b>      | <b>21</b>      | <b>16</b>      | <b>12</b>      | <b>19</b> |   |
|   | <i>Vertical climb</i>                  | 12             | 18             | 14             | 12             | 19        |   |
|   | <i>Angled climb</i>                    | 2 <sup>5</sup> | 3 <sup>5</sup> | 2 <sup>5</sup> | —              | —         |   |
| <b>Vertical descent</b>                       |  | <b>8</b>       | <b>12</b>      | <b>9</b>       | <b>6</b>       | <b>14</b> | <b>11</b>                               |
|   | <i>Vertical descent</i>                | 6              | 10             | 7              | 6              | 14        |   |
|   | <i>Angled descent</i>                  | 2 <sup>5</sup> | 2 <sup>5</sup> | 2 <sup>5</sup> | —              | —         |   |
| <b>Drop</b>                                   |  | <b>2</b>       | <b>2</b>       | <b>2</b>       | ?              | ?         | ?                                       |
| <b>Sway</b>                                   |  | <b>7</b>       | <b>1</b>       | <b>6</b>       | <b>7</b>       | <b>0</b>  | <b>12</b>                               |
| <b>Ride</b>                                   |  | <b>1</b>       | <b>0</b>       | <b>1</b>       | ?              | ?         | ?                                       |

<sup>1</sup> Overall frequencies are shown for locomotor modes (**in bold**) and frequencies for submodes (*in italics*) to allow comparison where classification system of previous authors is different from current study.

<sup>2</sup> Quadumanous suspend of Sugardjito and van Hooft's (1986) appears to include all these modes/submodes.

<sup>3</sup> ?, not clear if mode was not observed, or if it was observed but combined with another mode.

<sup>4</sup> #, Cant (1987a, p. 74) notes that assisted bipedalism was observed but was presumably recorded as orthograde clamber, and frequencies are not provided.

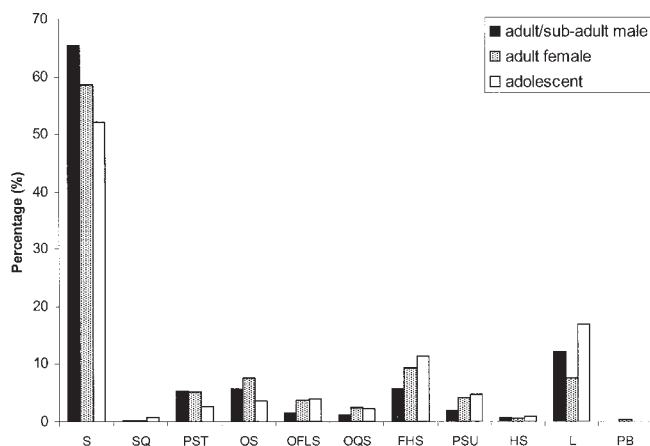
<sup>5</sup> Cant (1987a) defined vertical climbing as locomotion within 22.5° of true vertical. For present study, overall frequencies for **vertical climb** and **descent** are for within 45° of true vertical, but values for true vertical (0–20°) and angled climb (20–45°) are provided separately. Sugardjito and van Hooft (1986) did not provide angular distinction between vertical climb and quadumanous suspend.

commonly occurring postural modes in the most frequently occurring behavioral contexts, and in comparison to the feeding data of Cant (1987a) and the travel and rest data of Sugardjito and van Hooft (1986). **Sit** dominates the postural repertoire of the current subjects in all behaviors except rest, which is dominated by **lie**. Both **pronograde** and **orthograde stand** are most frequently observed during the behavioral context “look,” in which, in response to unfamiliar noises or movements, orangutans will remain stationary and stare in the direction of the unfamiliar sound, often for some time. **Pronograde stand** is also more associated with traveling than with feeding, which suggests that the large disparity between the results of Cant (1987a) and Sugardjito and van Hooft (1986) (Table 3) is a result of differences in behavioral context, although the difference in the present study is rather less than between the other two. Taken as a whole, suspensory modes are more associated with feeding than with other behaviors. However, overall frequencies for suspensory postures in this study are approximately half those of previous studies. Cant (1987a) found that suspensory postures accounted for 47% of positional behavior during feeding, in comparison to 24% here. Mean values calculated from the seven subjects of Sugardjito and van Hooft (1986) for pauses during travel were lower at 33%, but are still twice the 17% frequency recorded in the current study. Cant (1987a) further found

that *ipsilateral suspend* accounted for 30% of observed posture. Here, *ipsilateral suspend* was the most frequently occurring suspensory submode, but accounted for only 7.3% of total bouts, followed by *pronograde quadumanous suspend* at 3.4% (Appendix A). Most forms of suspend were likely to be combined with one or two other submodes.

Quadrupedal locomotion shows a stronger association with feeding than with traveling, whereas **torso-orthograde suspensory locomotion** shows the reverse pattern (Table 4). While frequencies for **quadrupedal** and **tripedal walk** are similar to previous studies for travel, values for feeding are twice those observed by Cant (1987a). This may be partly related to classification, since Cant (1987a) did not record any pronograde scramble, which in this study accounted for 9% of overall locomotion. **Torso-pronograde suspensory locomotion** is also higher in this study than in Cant (1987a), which may suggest that Ketambe orangutans simply exhibited greater levels of pronograde behavior than their Bornean counterparts. This result might also reflect differences in support availability (e.g., density, proportion of pioneer species) between the two sites, related perhaps to regrowth following tree-fall or environmental degradation. Unfortunately, we lack the detailed comparative and three-dimensional data on support availability which would be required to test this proposition.

In this study, **bipedal walk** accounted for 7.3% of overall locomotion, 75% of which (5.5% of total locomotion) was

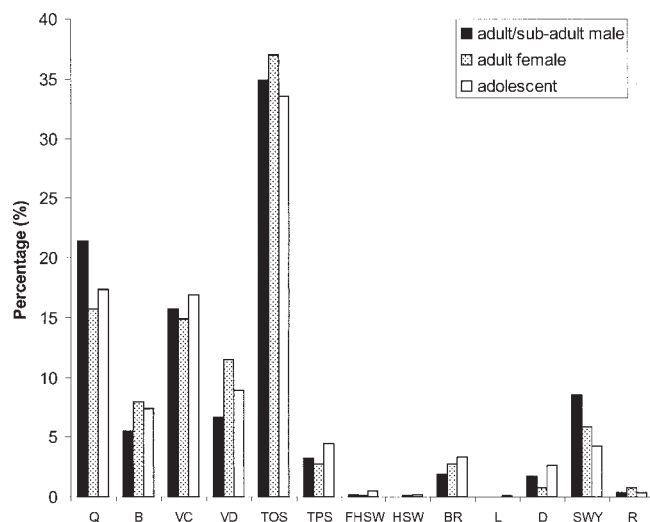


**Fig. 1.** Postural mode percentages according to age-sex category. S, sit; SQ, squat; PST, pronograde stand; OS, orthograde stand; OFLS, orthograde forelimb-suspend; OQS, orthograde quadrumanous suspend; FHS, forelimb-hindlimb suspend; PSU, pronograde suspend; HS, hindlimb suspend; L, lie; PB, postural bridge. Definitions of age-sex categories follow Thorpe and Crompton (2005), who found that relationship between locomotion and related ecological variables for this study group was best understood when subadult and adult males were combined, with adult females and adolescents as separate categories.

hand-assisted. Extended hindlimb positions were exhibited much more frequently than flexed, and *bipedal scramble* was also observed on small, irregularly placed and variously angled supports. In contrast, neither of the previous studies specified any bipedal locomotion. This is probably a matter of classification, as this study employed many of the standardized modes proposed by Hunt et al. (1996), including a distinction between hand-assisted bipedality and hindlimb-assisted orthograde clamber. Cant (1987a) noted that bipedal behavior was observed, but was not recorded as such because it was hand-assisted, and it was therefore presumably classed as orthograde clamber. Similarly, hand-assisted bipedality may have been incorporated into the quadrumanous climb mode of Sugardjito (1982).

While orangutan locomotion is dominated by **torso-orthograde suspensory locomotion**, it is exhibited far less in the current study than in Cant (1987a). This discrepancy is largely related to a reduction in *orthograde clamber* and *transfer*: even when other submodes or types that may have formed the orthograde clamber of Cant (1987a) are included (*assisted bipedalism* and angled climb/descent), frequencies here are still only 32% and 25%, compared to 51% and 44% for traveling and feeding, respectively, in Cant (1987a).

Traditionally, orangutans are renowned as cautious, slow climbers. However, they clearly have the potential for fast and acrobatic locomotion. **Leap**, *inverted quadrupedal run*, **drop** submodes, and *rump-first* and *head-first cascade descents* all imply increased speed at the expense of safety. Some of these behaviors appear to be associated with fleeing aggressive situations (**leap** and *inverted quadrupedal run* were both exhibited only once, and in the context of escape from an aggressive adult during competition for a favored food source). Rijksen (1978) also observed leaping in fleeing subjects, and MacKinnon (1971, 1974) described tumble descents (the equivalent of cascade descents in this study) in the context of escaping aggressive individuals. On the other hand, other fast submodes appear to be part of normal



**Fig. 2.** Locomotor mode percentages according to age-sex category. Q, quadrupedal walk; B, bipedal walk; VC, vertical climb; VD, vertical descent; TOS, torso-orthograde suspensory locomotion; TPS, torso-pronograde suspensory locomotion; FHSW, forelimb-hindlimb swing; HSW, hindlimb swing; BR, bridge; L, leap; D, drop; SWY, sway; R, ride.

travel and feeding behavior: *cartwheel swing*, *cartwheel descent*, and *lunging* and *descending bridge* appear more dramatic than their travel and feeding contexts would necessitate. Notably, most of these bouts were exhibited by adolescents. Figures 1 and 2 show little difference between the positional mode profiles of the different age-sex categories in this study, and Thorpe and Crompton (2005) showed that the age-sex category of an individual has less influence than habitat variables on the observed locomotor profile, when analyzed in a multivariate analysis at the mode-level. However, the comparison by Payne et al. (in press, a and b) of hindlimb muscle dimensions in all the apes found that juvenile orangutans had the largest proportion of total hindlimb muscle volume in the pedal digital flexors, both in comparison to their adult male orangutan and the other apes they studied. They suggested that the difference between the adult and juvenile orangutans may be an artifact of increased levels of terrestriality in captive adult orangutans. However, the locomotor behavior profiles seen here indicate that a secure pedal grip may be more important in wild juveniles than adults, as they exhibit fast and risky locomotion more often than do more mature animals. This suggests that orangutans become more cautious in their locomotion as they age and/or increase body mass. While positional modes are relatively comparable between age-sex categories (Figs. 1, 2), it is possible that the more subtle nuances of locomotion, described by the submodes within each mode, may be found to differ with age. Unfortunately, ape locomotion is a relatively small proportion of their daily positional mode repertoire, and it is difficult in the field to obtain enough locomotor observations to quantify such subtlety.

Overall, this study shows greater levels of pronograde and orthograde compressive locomotion and reduced levels of orthograde suspensory locomotion than in other studies. Furthermore, all suspensory postures were exhibited less frequently in this study. While differences in methodology may certainly account for some differences be-



TABLE 5. Comparison of percentages of food types consumed in Cant (1987a) and present study

| Food type     | Present study | Cant (1987a) |
|---------------|---------------|--------------|
| Fruit         | 64            | 46           |
| Flowers       | 1             | 5            |
| Leaves        | 14            | 16           |
| Bark          | 10            | 31           |
| Ants/termites | 8             | 2            |
| Other         | 2             | 0            |
|               | 4,717 bouts   | 66 hr        |

tween studies (in particular, that we set out to conduct a detailed analysis, whereas previous authors aimed to characterize broad-based trends), the results still indicate large variability across studies. The study by Cant (1987a) was conducted during an “unusual drought,” and it is possible that orangutans were forced to access food resources in less accessible places, such as the fragile and unstable terminal ends of branches, where higher levels of suspensory behavior would be expected. One might then expect that the frequencies for vertical climbing and descent would be greater in Cant (1987a), whereas in fact the results are very similar (Table 4). Unfortunately, Sugardjito and van Hooft (1986) did not present data for food types, but Table 5 shows that comparatively high levels of fruit and ants/termites were consumed in the present study, but considerably more bark was consumed in Cant (1987a). This suggests a rich supply of favored food sources in our study vs. a reduced supply during that of Cant (1987a) (conducted during a drought). However, the implications of this for positional mode frequencies are difficult to predict quantitatively. On the one hand, one might expect that the subjects of Cant (1987a) would need to suspend more to reach the remaining fruit on terminal branches. On the other hand, orangutans use a variety of positional modes to strip bark from trees and lianas, but compression is a necessary component of most of these, as it is a requisite of the leverage necessary to detach bark. As a consequence of this factor alone, “stand” modes would be expected to be higher in Cant (1987a), rather than lower (Table 3). Furthermore, once orangutans have obtained a strip of bark, they generally tend to sit to eat it; this would be expected to skew the results toward *sit*, as the eating of bark tends to be the longest part of the process (personal observations).

Differences may also reflect different subject profiles. The study of Cant (1987a) consisted of two adult females, whereas that of Sugardjito and van Hooft (1986) and the present study report results for both sexes and all age groups. Indeed, Cant (1987b) demonstrated that both food type and gender are important predictors of postural behavior during feeding, as he observed that suspensory behavior for males and females in two types of fig tree ranged from 31% for males in the one fig species to 70% for females in the other. However, Figures 1 and 2 show that although there are slight variations in positional behavior exhibited by adult females for particular positional behaviors in this study, overall adult female positional behavior does not differ substantially from the other age-sex categories. Thorpe and Crompton (2005) also demonstrated that when associations between all behavioral and ecological variables are taken into account, the age-sex category of an individual has limited influence on its observed locomotor repertoire, although results for posture are not yet published.

The log-linear analysis by Thorpe and Crompton (2005) concluded that support type and diameter had the strong-

est influence on observed locomotor repertoire of all the variables they modeled. Height in the canopy and contextual behavior were not found to directly influence locomotion; instead, their effect was modified by support type and diameter, respectively. Therefore, it is possible that the differences between studies simply reflect different patterns of support use and differences in the overall interplay between orangutan positional behavior and the variables that were shown to influence it (Thorpe and Crompton, 2005). The relationship between positional behavior and support use is beyond the scope of this paper, but will be addressed elsewhere. However, the results also suggest that a key mechanism by which orangutans resolve complex habitat problems is substantially decreased stereotypy.

### Implications for ape specializations

Tables 6 and 7 present postural and locomotor frequencies from the present study in comparison to previously published data for other hominoids, cercopithecoids, and atelines, updating the comparison by Hunt (1991a) with new studies on lowland gorillas and mountain gorillas, and expanded data sets on bonobos and orangutans. Carlson (2005) also presented an updated overview of African ape locomotion from studies by Doran (1989); Doran and Hunt (1994); Hunt (1989, 1992); and Remis (1994, 1995, 1998). While differences in some positional behavior classifications preclude his entire data set being used here, we included some values in Table 7 to distinguish between **vertical climb** and **torso-orthograde suspensory locomotion**, which were not separated in Doran (1996). Two outgroup comparators, *Papio* and the atelines, were also included. The inclusion of *Papio* allows us to reassess the analysis by Hunt (1991a) of the distinctiveness of hominoid positional modes in light of our expanded data set. Atelines are included, following the argument by Larson (1998) that postcranial features found in both hominoids and *Ateles* are likely to be features that are highly responsive to function, and consequently likely to be homoplastic characters for hominoids. Unfortunately, only locomotor data are available for the atelines. Frequencies in Tables 6 and 7 are for arboreal behavior only. Differences in methodology mean that only a broad comparison may be made. Nevertheless, Table 6 shows that orangutan postural behavior is more similar to that of the African apes than was previously thought. Hunt (1991a) found that the frequency of arm-hanging was highest in orangutans of all the great apes. In this study it is the presence of **orthograde quadrumanous suspend**, **forelimb-hindlimb suspend**, and **pronograde suspend** that distinguishes the orangutans from the other apes and baboons, but the difference is less pronounced than implied by previous orangutan studies (Tables 3 and 6). Otherwise, orangutans sit, lie, stand (both quadrupedally and bipedally), and forelimb-suspend in very similar frequencies to those exhibited during arboreal behavior by lowland gorillas. Overall, the postural results support the conclusion of Hunt (1991a) that with the exception of gorillas, orthograde suspensions (forelimb and quadrumanous) are the postural behaviors of adaptive significance that are exhibited by the apes in greater frequencies than in *Papio*. However, **orthograde stand** may also prove to be distinctive to apes, if future studies expand data sets on species that currently have small sample sizes, or undetermined frequencies of bipedal posture in Table 6. Furthermore, since bonobos, mountain gorillas, and gibbons all exhibit bipedal walking, it is probable that **orthograde stand** will feature in their postural repertoire.

TABLE 6. Comparison of percentages of arboreal postures in hominoids and Papio

|  | Sit | Squat | Pronograde stand | Orthograde stand | Orthograde forelimb suspend | Orthograde quadrumanous suspend | Forelimb/hindlimb suspend | Pronograde suspend | Lie | Other | N               |
|--|-----|-------|------------------|------------------|-----------------------------|---------------------------------|---------------------------|--------------------|-----|-------|-----------------|
| <i>Pongo pygmaeus</i> <sup>1</sup>           | 49  | 0     | <1               | 2.0              | <1                          | 11                              | 36                        | ? <sup>11</sup>    | 0   | <1    | 1,682 minutes   |
| <i>Pongo pygmaeus</i> <sup>2</sup>           | 58  | 0     | 4                | 6.0              | 3                           | 2                               | 9                         | 4                  | 12  | 1     | 7,155           |
| <i>Pongo pygmaeus</i> <sup>3</sup>           | 61  | 0     | 5                | 7.0              | 3                           | 2                               | 8                         | 3                  | 9   | 1     | 4,560           |
| <i>Pan troglodytes</i>                       | 81  | 2     | 1                | 0.3              | 12                          | 0                               | 0                         | 0                  | 3   | 0     | 2,518           |
| <i>Pan schweinfurthii</i> <sup>4</sup>       |     |       |                  |                  |                             |                                 |                           |                    |     |       |                 |
| <i>Pan paniscus</i> <sup>5</sup>             | 90  | 0     | 2                | 0.0              | 5                           | 0                               | 0                         | 0                  | 3   | 0     | Small           |
| <i>Gorilla gorilla</i>                       | 50  | 29    | 4                | 5.0              | 1                           | 0                               | 0                         | 0                  | 10  | 0     | 473             |
| <i>Gorilla gorilla gorilla</i> <sup>6</sup>  |     |       |                  |                  |                             |                                 |                           |                    |     |       |                 |
| <i>Gorilla gorilla berengei</i> <sup>7</sup> | p   | ?     | p                | ?                | p                           | ?                               | ?                         | ?                  | p   | ?     | Small           |
| <i>Gibbon</i> <sup>8</sup>                   | 64  | 0     | 0                | 0.0              | 36                          | 0                               | 0                         | 0                  | 0   | 0     | Small           |
| <i>Hyllobates</i>                            | 47  | 0     | 0                | 0.0              | 53                          | 0                               | 0                         | 0                  | 0   | 0     | Various studies |
| <i>syndactylus</i> <sup>9</sup>              |     |       |                  |                  |                             |                                 |                           |                    |     |       |                 |
| <i>Papio anubis</i> <sup>10</sup>            | 76  | 1     | 21               | 0.0              | 1                           | 0                               | 0                         | 0                  | 0   | 1     | 580             |

<sup>1</sup> Cant (1987a); Table 8. Bornean adult females only. Frequencies represent proportions of time spent feeding.<sup>2</sup> Present study, all data. Other: hindlimb suspend, cling, splits, cantilever, postural bridge.<sup>3</sup> Present study, juveniles omitted. Other: hindlimb suspend, cling, splits, cantilever, postural bridge.<sup>4</sup> Hunt (1991b); Table 1. Percentage of 2-min instantaneous focal observations for Mahale and Gombe adults while feeding on fruit. Standardized by Hunt (1991b) for time of day.<sup>5</sup> Taken from Hunt (2004), Table 10.1. Percentage of 132 instantaneous time point surveys during arboreal feeding on fruit (Kano and Mulavwa, 1984).<sup>6</sup> Remis (1995); Table 9.<sup>7</sup> Doran (1996), 1-min instantaneous sampling. Modes are noted as P for present, since Doran (1996) did not separate arboreal and terrestrial data.<sup>8</sup> Taken from Hunt (2004), Table 10.1. Average of *H. agilis* and *H. pileatus* from Gittins (1983), 322 bouts sampled by 10-min scan surveys, and Srikosamatara (1984), 655 5-min scan surveys.<sup>9</sup> Taken from Hunt (2004), Table 10.1. Average from Chivers (1972) (percentage of 234 5-sec instantaneous focal surveys) and Fleagle (1976) (percentage of 1,376 postural bouts during feeding).<sup>10</sup> Hunt (1991b), Table 1. Instantaneous focal observations during feeding only.<sup>11</sup>?not clear if this mode was not observed or if it was observed but combined with another mode.



TABLE 7. Comparison of percentages of arboreal locomotion in hominoids, Papio, and atelines

|   | Quadrupedal and tripodal walk | Vertical climb and descent | Bipedal walk | Torso-orthograde suspensory locomotion |                                |  | Drop and leap | Torso-pronograde suspensory locomotion | Sway | Ride            | Bridge | No. bouts |
|---|-------------------------------|----------------------------|--------------|--|--------------------------------|--|---------------|--|------|-----------------|--------|-----------|
|   |                               |                            |              | Orthograde clamber and transfer        | Brachiation and forelimb swing |  |               |  |      |                 |        |           |
| <i>Pongo pygmaeus</i> <sup>1</sup>          | 12                            | 21                         | ?            | 49                                     | 11                             |  | 0             | 1                                      | 6    | ? <sup>14</sup> | ?      | 4,360     |
| <i>Pongo pygmaeus</i> <sup>2</sup>          | 18                            | 25                         | 7            | 21                                     | 14                             |  | 2             | 4                                      | 6    | 1               | 3      | 1,504     |
| <i>Pongo pygmaeus</i> <sup>3</sup>          | 18                            | 26                         | 7            | 22                                     | 13                             |  | 1             | 3                                      | 7    | 1               | 2      | 2,811     |
| <i>Pan troglodytes</i>                      | 36                            | 49                         | 7            | 5                                      | 5                              |  | 0             | ?                                      | ?    | ?               | ?      | 223       |
| <i>schweinfurthii</i> <sup>4</sup>          |                               |                            |              |  |                                |  |               |  |      |                 |        |           |
| <i>Pan troglodytes verus</i> <sup>5</sup>   | 22                            | 68                         | 3            | ? <sup>14</sup>                        | 7                              |  | 1             | ?                                      | 0    | ?               | 0      | 1,417     |
| <i>Pan paniscus</i> <sup>6</sup>            | 32                            | Female, 51/male, 59        | 1            | ?                                      | 9                              |  | 4             | ?                                      | 0    | ?               | 0      | 1,461     |
| <i>Gorilla gorilla gorilla</i> <sup>7</sup> | 19                            | Female, 24/male, 31        | 5            | 17                                     | 3                              |  | ?             | 0                                      | 8    | ?               | ?      | 122       |
| <i>Gorilla gorilla</i>                      | 53                            | 40                         | 2            | ?                                      | 5                              |  | 0             | ?                                      | 0    | ?               | 0      | 153       |
| <i>beringei</i> <sup>8</sup>                |                               |                            |              |  |                                |  |               |  |      |                 |        |           |
| <i>Gibbon</i> <sup>9</sup>                  | 1                             | Female, 33/male, 27        | 2            | 0                                      | 67                             |  | 14            | 0                                      | 0    | 0               | 0      | Small     |
| <i>Hylobates</i>                            | 0                             | 16                         | 8            | 0                                      | 59                             |  | 2             | 0                                      | 0    | 0               | 0      | Small     |
| <i>syndactylus</i> <sup>10</sup>            |                               | 32                         |              |  |                                |  |               |  |      |                 |        |           |
| <i>Lagothrix lagothricha</i> <sup>11</sup>  | 29                            | 14                         | 0            | 30                                     | 9                              |  | 4             | 2                                      | 1    | 0               | 10     | 3,926     |
| <i>Ateles belzebuth</i> <sup>12</sup>       | 21                            | 13                         | 1            | 28                                     | 22                             |  | 2             | 0                                      | 2    | 0               | 11     | 3,760     |
| <i>Papio anubis</i> <sup>13</sup>           | 68                            | 21                         | 0            | 0                                      | 0                              |  | 10            | 0                                      | 0    | 0               | 0      | 26        |

<sup>1</sup> Cant (1987a), calculated from Table 3. Locomotor bout sampling with distance for Bornean adult females only. Frequencies represent proportions of travel distance. Vertical climb/descent values are underestimated, as Cant (1987a) defined vertical climb as climbing within 22.5° of true vertical. Other studies cited here defined it within 45° of true vertical.

<sup>2</sup> Present study; all data.

<sup>3</sup> Present study; juveniles omitted.

<sup>4</sup> Hunt (1991b), Table 3. Percentage of arboreal locomotion in all contexts for Gombe and Mahale subjects. Not standardized.

<sup>5</sup> Doran (1996), calculated from Table 16.5. Locomotor bout sampling. Vertical climb/descent values include orthograde clamber/transfer and pronograde clamber. Individual values for males and females are from Carlson (2005). See text for discussion.

<sup>6</sup> Doran (1996), calculated from Table 16.5, 1-min instantaneous sampling. Vertical climb/descent values include orthograde clamber/transfer and pronograde clamber. Individual values for males and females are from Carlson (2005). See text for discussion.

<sup>7</sup> Remis (1995), Table 11. Wet season data only. Adults only. Data for orthograde clamber may overlap with bipedalism, as Remis (1995) noted that it was difficult to discriminate relative proportions of weight borne by forelimbs and hindlimbs. Drop is included in orthograde suspend. Oscillation equates to "acrobatic behaviors" of Remis (1995), including leap, tree sway, fireslide (equivalent to rump descent-freepole in this study), and bridging.

<sup>8</sup> Doran (1996), calculated from Table 16.5. Instantaneous sampling. Vertical climb/descent values include orthograde clamber/transfer and pronograde clamber. Individual values for males and females are from Carlson (2005). See text for discussion.

<sup>9</sup> Taken from Hunt (2004), Table 10.3. Average of *H. agilis*, *lar*, and *pileatus* from Gittins (1983) (percent of 255 10-min scan surveys), Fleagle (1980) (percent of 211 pooled feeding and travel bouts obtained with continuous focal sampling), and Srikosamatara (1984) (percent of 218 5-min scan surveys).

<sup>10</sup> Taken from Hunt (2004), Table 10.3. Average from Fleagle (1980) (percent of 1,206 pooled feeding and travel bouts obtained with continuous focal sampling) and Gittins (1983) (percent of 208 10-min scan surveys).

<sup>11</sup> Cant et al. (2001, 2003). Adults only. Instantaneous focal animal sampling on 5-min mark. Vertical climb/descent values are slightly underestimated, as Cant et al. (2001, 2003) defined vertical climb as climbing within 22.5° of true vertical.

<sup>12</sup> Cant et al. (2001, 2003). Instantaneous focal animal sampling on 5-min mark. Adults only. Vertical climb/descent values are slightly underestimated, as Cant et al. (2001, 2003) defined vertical climb as climbing within 22.5° of true vertical.

<sup>13</sup> Hunt (1991b), Table 3. Percent of arboreal locomotion in all contexts. Adults only. Not standardized.

<sup>14</sup> ?, not clear if this mode was not observed, or if it was observed, but combined with another mode.

While vertical climbing accounts for a significant proportion of ape arboreal locomotion, and must be energetically highly demanding since it is performed more or less directly against the gravity vector, it is not unique to apes (Table 7). Indeed, it is the single locomotor mode common to all species compared in this paper. The African apes generally show increased frequencies of vertical climbing and descent in comparison to orangutans, which is to be expected, given that they primarily travel on the ground rather than through the canopy, and climb to access arboreal food sources. In contrast, orangutans only climb to access food on different levels in the canopy or to access preferred substrates for locomotion (Thorpe and Crompton, 2005).

Most locomotor frequencies are similar in orangutans and the African apes, with a particular similarity in many modes found between frequencies in orangutans and lowland gorillas. Differences between these species in ride and bridging behaviors are likely to be related to methodology. Thus, **torso-pronograde suspensory locomotion** is probably the only mode that distinguishes orangutans from the other apes studied. If so, the presence of pronograde postural and locomotory suspension in *Pongo* but not the African apes is particularly interesting, given that African ape positional behavior is dominated by compressive pronograde. Might this suggest that adaptations for pronograde evolved in parallel in orangutans and the African apes, with orangutans developing both suspensory and compressive pronograde, and the African apes, due to their largely terrestrial nature, only developing compressive pronograde? This may be viewed as a somewhat heretical concept, since many still regard *Proconsul* as a suitable model for the locomotor morphology of the ancestor of the living great apes (e.g., Larson, 1998). However, in view of more recent reviews by Harrison (2002) and Begun (2002), it may nevertheless be a concept that merits some attention. Clarification of whether the quadrumanous climbing and scrambling classification by Doran (1992a,b, 1993, 1996) for chimps, bonobos, and mountain gorillas includes suspensory pronograde would shed light on this issue.

Similarity in the frequencies of orthograde compressive postures and locomotion between lowland gorillas and orangutans is paralleled by similarities in the hindlimb kinematics of this posture (Hofstetter and Niemitz, 1997), which may be due to the energetic cost of maintaining an upright posture in animals with a top-heavy build (Payne et al., in press, a and b). However, similarities in frequencies and kinematics do not seem to be reflected in clear similarities in hindlimb muscle dimensions and maximum moments of force (Payne et al., in press, a and b), implying that orthograde positional behavior in adult male orangutans and gorillas is not necessarily dynamically similar (Alexander and Jayes, 1983), although it may be functionally similar in terms of kinematics and frequencies. Specifically, we would not expect the hindlimb to be used so much as a rigid strut in gorillas, as it undoubtedly is in orangutans (Buettner-Janusch, 1967; Hamanda, 1985; Tuttle and Cortwright, 1988; Payne, 2001; Payne et al., in press, a and b).

Table 7 shows that *brachiation* and *forelimb swing* and **bipedal walk** are present in all apes, but not in *Papio*. *Orthograde clamber* and *transfer* are present in all great apes, and are similarly absent in *Papio*. While Table 7 indicates that these submodes are also absent in the hylobatids, the samples for these data are very small. Fleagle (1976) noted that climbing in siamangs is

forelimb-dominated, and his Figure 2 seems to depict *orthograde clamber*. Recent work by Collis (2001) also indicates that siamangs exhibit *orthograde clamber*, although the results have not yet been fully published. Gibbons may also be found to exhibit *orthograde clamber*, although Cartmill (1985) argued that their small body size and highly derived brachiating specializations are likely to be derived after the split from the common ancestor of the great apes, and Young (2003) found that gibbon specializations skewed the analysis of hominoid postcranial uniqueness and variability. Therefore, gibbons probably represent a poor model for the common ape postcranial adaptation. Of these submodes, *orthograde clamber* and *transfer* and *brachiation* are also present in the atelines, which, according to the argument of Larson (1998), would suggest that these behaviors may have been acquired in parallel.

Overall, this study suggests that it is in fact orthograde positional behavior in general, rather than forelimb suspend specifically, that distinguishes apes from Old World monkeys, and that may be regarded as characterizing the positional behavior of the living hominoids. This idea is supported by increasing evidence that orthograde also characterized the morphology of a number of Miocene apes, including *Morotopithecus*, the proposed sister taxon of the crown hominoid clade, dating from at least 20 mya (MacLatchy et al., 2000). While *Morotopithecus*'s dentition resembles that of *Proconsul* and *Afropithecus*, its postcranium is distinct from the other Early and Middle Miocene forms in its orthograde adaptations (MacLatchy, 2004). These include features of the vertebrae associated with limited lower back morphology (MacLatchy, 2004); features of the glenoid fossa indicative of loading over a wide range of movements (MacLatchy, 2004); and high cortical area relative to periosteal area of the femur, indicating high axial rigidity (Ruff, 1989; Ruff and Runestad, 1992; Runestad, 1994). MacLatchy et al. (2000) concluded that *Morotopithecus* possessed orthograde and substantial forelimb mobility, and a locomotor repertoire that probably included forelimb suspension, slow brachiation, cautious clambering, vertical climbing, and quadrupedalism (MacLatchy, 2004; Young and MacLatchy, 2004). The later Miocene taxa *Oreopithecus* and *Dryopithecus*, believed to belong to the crown hominoid clade (MacLatchy et al., 2000), also possessed adaptations for suspensory, orthograde behavior similar to those in modern hominoids (Harrison, 1987; Moya-Sola and Kohler, 1996; Harrison and Rook, 1997). Furthermore, Senut (2003) argued that the Late Miocene *Orrorin* was adapted to bipedalism, but was also a climber. For example, the anatomy of the proximal femur in *Orrorin* (some 6 mya; Senut et al., 2001) strongly suggests that the hip joint was already being used habitually in extension (which implies at least an orangutan-like degree of orthograde). At about twice this age, the truncal anatomy of *Pierolapithecus* (Moya-Sola et al., 2004) was described as adapted for upright posture, as of course was that of *Oreopithecus*, where the structure of the inner ear is also consistent with upright posture (Rook et al., 2004). Thus, the weight of evidence, in our view, favors the temporal primacy of orthograde in the hominoids, rather than suggesting a compressive pronograde locomotor repertoire in the common ancestor of the hominoids.

Although positional-mode frequencies and distinctiveness are important in assessing the evolutionary origin of ape anatomy, it is rather the muscular effort required for a positional mode and the associated stresses that are likely to determine the anatomical adaptations required for

the effective performance of a given positional mode (Hunt, 1992). Some positional behaviors are, of course, inherently more stress-inducing or energetically expensive than others. But, all other things being equal, positional behaviors for which an animal is well-adapted are expected to require less muscle activity, and induce less stress in the skeleton and ligaments, than behaviors for which the animal is poorly adapted. It is argued that natural selection shapes anatomy to reduce muscular activity and structural stress in proportion to the frequency of the behavior (Basmajian, 1965; Cartmill et al., 1987; Hunt, 1991b, 1992). However, Pontzer and Wrangham (2004) demonstrated that the relationship between muscle forces and stresses and frequencies of positional modes is rather more complicated than this suggests. They noted current evidence indicating that chimpanzee terrestrial travel is energetically relatively costly (Taylor et al., 1972; Heglund and Taylor, 1988). This led them to test the hypothesis that arboreal adaptations for climbing in common chimpanzees minimize total locomotor energy expenditure (climbing and walking) by lowering the amount of energy spent climbing, a potentially costly activity. They found, however, that morphological specializations for arboreal locomotion incurred a significant energy cost, and they concluded that nonenergetic factors are more likely to be critical in shaping chimpanzee locomotor anatomy. Cartmill and Milton (1977) pointed out that a large animal is less likely to survive if it falls from any great height, because the kinetic energy which the tissues of its body must dissipate on impact increases in proportion to the cube of its linear dimensions and to the square of its terminal velocity (which is in turn increased by the low surface-to-mass ratio). Accordingly, Pontzer and Wrangham (2004) concluded that chimpanzee postcranial adaptations should be seen as adaptations to avoid falls, rather than to reduce the energy cost of climbing. Given their higher degree of arboreality, we would expect, therefore, that orangutan anatomical adaptations should be particularly directed at avoidance of falls.

Another measure of the stresses associated with positional behaviors is the dimensions of the bones and muscles of the locomotor system, which Alexander (1974) proposed should be understood largely in relation to the most strenuous activities in which they are used. Climbing and arboreal locomotion undoubtedly form the most strenuous locomotor activities of the apes, due to the effects of gravity and the discontinuous and three-dimensional nature of the substrates. Thorpe et al. (1999) showed that whereas human hindlimb muscles appear to be designed to generate large forces over a narrow range of joint positions (as required for bipedal running), chimpanzee hindlimb muscles were designed to generate smaller forces, but over a wider range of joint positions. Payne (2001) and Payne et al. (in press, a and b) found that these observations held true for all extant nonhuman apes, and concluded that nonhuman apes have a greater need than terrestrial mammals to vary muscle function throughout the joint range of motion, due to the complexities of their arboreal habitat. Orthograde postures involve the exertion of significant muscle force in more extended joint positions than either quadrupedalism or vertical climbing (Crompton et al., 2003), supporting the theory that orthograde behavior may be important in shaping the musculoskeletal morphology of all apes. Indeed, it is by some degrees that the muscular anatomy of humans is the most distinctive of all the hominoids (Thorpe et al., 1999; Payne, 2001; Payne et al., in press, a and b).

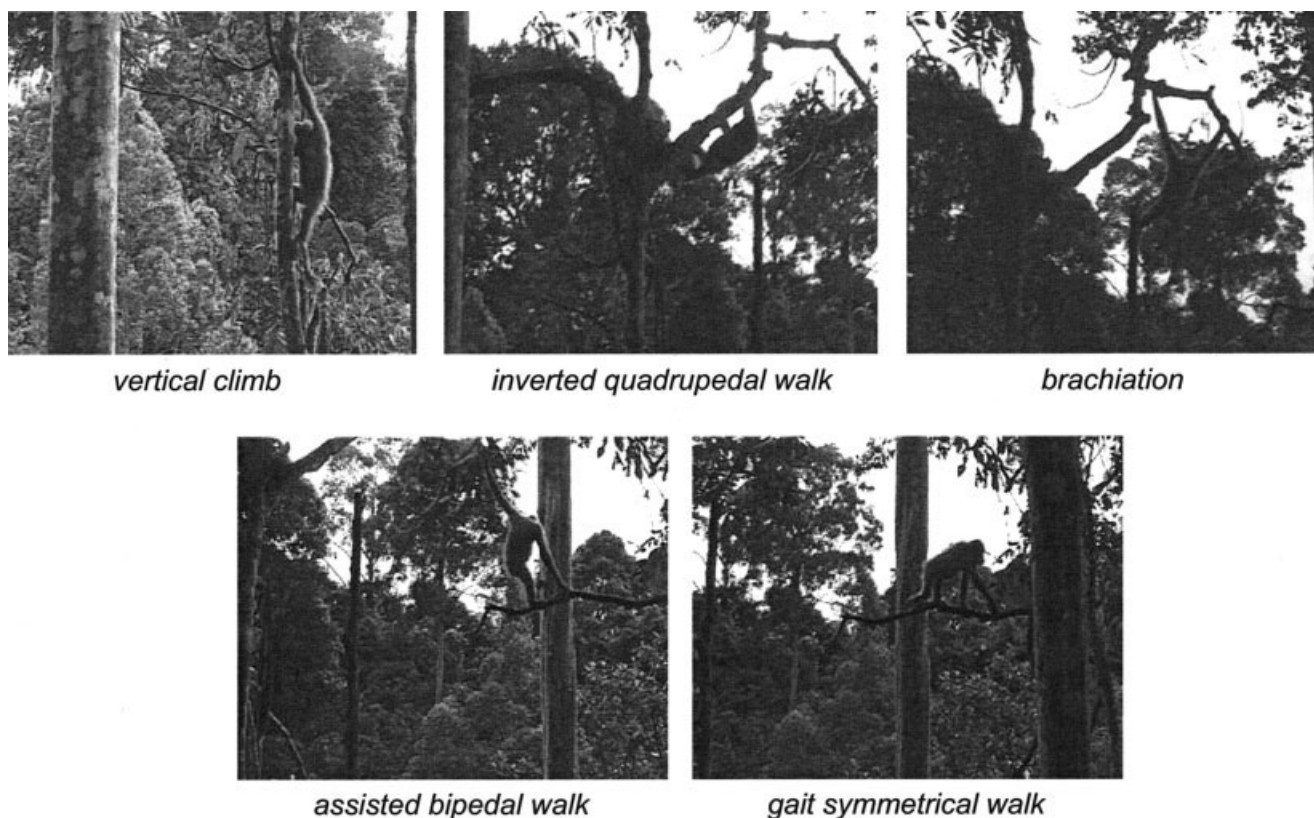
The ecological context of behavior is also an important consideration when trying to identify the potential importance of its influence on musculoskeletal design. The benefits of forelimb suspension in hominoids are already well-documented: suspension in general increases safety for animals of large body mass (Cartmill, 1974, 1985); it allows them to utilize small-diameter supports for feeding and traveling (Cant, 1987a,b; Hunt, 1992); and it extends their foraging radius (Grand, 1972), particularly in the terminal branches where high-quality fruits abound (Avis, 1962). However, the benefits provided by forelimb suspension for each of these factors are surely magnified by the use of both fore- and hindlimbs in supporting body mass.

When arboreal animals stand bipedally or quadrupedally, even on a horizontal branch, they tend to topple to one side or the other because all the support points are effectively colinear (Napier, 1967; Cartmill, 1985). Safety is therefore likely to be increased by suspension, and animals of large body mass were predicted to suspend more than smaller ones (Cant, 1987b). While this prediction is supported in hylobatids (Hunt, 1991a), it is not fully borne out by intraspecific studies of orangutans and lowland gorillas (Cant, 1987b; Remis, 1995; Thorpe and Crompton, 2005) or interspecific studies of gibbons and chimpanzees (Hunt, 1991a). Cartmill (1985) proposed that methods of resisting the toppling tendency were: 1) having relatively short limbs, thus keeping the body's center of mass close to the support; 2) having prehensile hands and feet that can grip a branch and exert a torque that resists the toppling moment; 3) suspension; or 4) reduction of body size. Clearly the benefit of hindlimb-assisted suspension, as well as forelimb-assisted compression, is that it allows a combination of options 1, 2, and 3, thus maximizing safety in a complex and uncertain habitat.

Hunt (1992) identified the small size of available weight-bearing supports in the most productive areas of fruiting trees as the most significant evolutionary pressure selecting for suspensory posture and locomotion. Assisted and unassisted orthograde forelimb suspension were seen in the context of feeding more than any other posture, leading to the conclusion that arm-hang was the key specialization that separated chimps from baboons. We argue that in an arboreal context, this assessment is based on an overly static analysis of positional behavior. Few positional modes, other than a single leap, have a clear beginning or end. Nearly all locomotor and postural modes are abstracted by the observer from a continuum of activity: such abstraction is a prerequisite of objective analysis, and the observer's judgment has to balance conflation with oversplitting. Figure 3 illustrates this point by showing five locomotor modes that might be isolated from a single 18-sec video clip of completely uninterrupted orangutan locomotion.

In the terminal branches of trees, there is almost always a multitude of additional supports available to support other limbs in tension or compression, serving the function of distributing body mass more widely and thus reducing stress on a single limb. Indeed, for feeding to take place, unimanual suspension will nearly always (even temporarily) become bimanual suspension. To select another fruit, a third or fourth limb will often make contact to bring about a shift in body position. Thus, orthograde suspension with formation of a foot contact can become orthograde suspension assisted by hindlimb compression, and this in turn can become orthograde stand assisted by forelimb suspension, simply by contact of an extremity and slight alterations in





**Fig. 3.** Five locomotor modes isolated from single 18-sec video clip of completely uninterrupted orangutan locomotion.

the position of the body's center of gravity. This, in turn, may be driven by the movement of branches in response to body weight, reaching, and environmental conditions.

A major problem with testing the hypothesis of Hunt (1992) is that as a largely irregular rather than patterned activity, the various submodes conflated under **torso-orthograde suspensory locomotion** and **bipedal walk** and similar postural modes are difficult to analyze or describe in an experimental situation. Nevertheless, it is possible that we are mistaken in looking for a single unique mode to account for the morphological similarities of the apes. It is certainly plausible that what underlies ape anatomy is the exact opposite: the ability to respond to a complex array of ecological and environmental conditions with one of a broad range (if not a continuum) of orthograde-based postures and locomotion.

## CONCLUSIONS

This paper shows that orangutan positional behavior is highly complex, representing a continuum of positional forms rather than a collection of unique and mutually exclusive positional modes, as may be seen in arboreal animals of smaller body mass. Although orangutan positional behavior is broadly similar between age-sex categories, there is some evidence to suggest that it differs at the submode level, although a larger sample size would be required to quantify this. Overall, this study showed greater levels of pronograde and orthograde compressive locomotion and reduced levels of

orthograde suspensory locomotion in comparison to other studies. Suspensory postures were also exhibited less frequently in this study than previously reported. Given the complexity of orangutan positional behavior demonstrated by this study, it is likely that differences in positional behavior between studies reflect differences in the interplay between the complex array of variables which were shown to influence positional behavior (Thorpe and Crompton, 2005).

Orangutans, alone among the apes, exhibit pronograde suspensory positional behavior. Otherwise, most postural and locomotor frequencies are similar in orangutans and African apes, and in particular, lowland gorillas. This study suggests that it is orthograde positional behavior in general, rather than forelimb suspend specifically, which characterizes the positional behavior of hominoids.

## ACKNOWLEDGMENTS

We thank the Indonesian Institute of Sciences in Jakarta, the Indonesian Nature Conservation Service in Jakarta, Medan, and Kutacane, and the Leuser Development Programme in Medan for granting permission and giving support to conduct scientific research in the Ketambe Research Station situated in the Leuser Ecosystem. We thank the European Commission and the Indonesian Government for funding the Leuser Development Programme, and our Indonesian counterpart Jito Sugardjito for his assistance. We are grateful to two anonymous reviewers for their comments on the manuscript.



## APPENDIX A. Postural mode definitions

| Postural mode<br>Postural submode (component 1/component 2/component 3)  | % bouts |
|--|---------|
| <b>Sit</b>   |         |
| <i>Sit</i> (P1a–P1f): <sup>1</sup> combines “sit,” “sit in,” “sit out,” “foot-prop sit,” “sit in/out,” “chair sit,” and “ischium sit,” as these positions were difficult to distinguish when individuals were sitting on day nests/platforms.                            | 50.50   |
| <i>Sit/forelimb-suspend</i> (P1g).   | 5.91    |
| <i>Sit/hindlimb-suspend</i> : more than half of body weight depends on one or both ischia, but one or both hindlimbs grasp overhead substrate and support more than their own weight.  | 0.22    |
| <i>Sit/forelimb-hindlimb-suspend</i> : as for “sit/hindlimb-suspend” but a forelimb and a hindlimb support more than their own weight in either contralateral or ipsilateral suspensory combination.   | 0.17    |
| <i>Sit/forelimb-compression</i> : as for “sit/forelimb-suspend,” but one or both forelimbs are below level of shoulders and support body weight in compression.  | 0.21    |
| <i>Sit/hindlimb-compression</i> : sit, with one or both hindlimbs supporting body weight in compression.   | 0.91    |
| <i>Sit/forelimb-hindlimb-compression</i> : more than half of body weight is supported by ischia, but a forelimb and a hindlimb support more than their own weight in contralateral or ipsilateral compression combination.   | 0.03    |
| <i>Sit/forelimb-suspend/hindlimb compression</i> : more than half of body weight is supported by ischia, but weight is also supported by a forelimb in suspension and a hindlimb in compression.   | 0.13    |
| <b>Squat</b>   |         |
| <i>Squat</i> (P2)  | 0.1     |
| <i>Squat/forelimb-suspend</i> : bipedal or monopedal squat in which one or both forelimbs also support weight in suspension.   | 0.25    |
| <i>Squat/forelimb-cling</i> : as for “squat/forelimb-suspend,” but one or both forelimbs cling to a vertical or near vertical substrate, supporting more than their own weight.  | 0.01    |
| <i>Stomach-squat</i> : body weight is borne primarily by feet in a squat, but protruding stomach rests on additional support and appears to support significant body mass.   | 0.06    |
| <i>Stomach-squat/forelimb-suspend</i> : as above, but with some body weight borne by one or both forelimbs in suspension.  | 0.03    |
| <b>Cling</b>   |         |
| <i>Bimanual cling</i> (P3a).   | 0.01    |
| <i>Cling/forelimb-suspend</i> (P3c).   | 0.08    |
| <i>Cling/sit/forelimb-suspend</i> : one hindlimb is in cling position and supports majority of body mass. This is aided by a forelimb in suspension and one ischium.   | 0.04    |
| <b>Pronograde stand</b>  |         |
| <i>Quadrupedal stand</i> (P4a).  | 1.48    |
| <i>Tripedal stand</i> (P4b).   | 1.26    |
| <i>Tripedal stand/forelimb-suspend</i> : tripedal posture in which free forelimb is extended in arm-hanging fashion.   | 0.10    |
| <i>Tripedal stand/hindlimb-suspend</i> : tripedal posture in which free hindlimb supports body weight in suspension.   | 0.01    |
| <i>Quadrupedal full-crouch</i> (P4c1).   | 0.10    |
| <i>Quadrupedal forelimb-crouch</i> (P4c2).   | 0.01    |
| <i>Quadrupedal hindlimb-crouch</i> (P4c3).   | 0.01    |
| <i>Tripedal hindlimb-crouch</i> : tripedal posture in which elbow is extended, but both hindlimbs are flexed.  | 0.07    |
| <i>Tripedal hindlimb-crouch/forelimb-suspend</i> : as above, but with free forelimb supporting more than its own weight in suspension.   | 0.01    |
| <i>Contralateral compression</i> : standing with torso pronograde and face downward and weight supported by a forelimb and a hindlimb on opposite sides of body.   | 0.01    |
| <i>Contralateral compression/hindlimb-suspend</i> : as for “contralateral stand,” but with remaining hindlimb in suspension.   | 0.03    |
| <i>Ipsilateral compression/forelimb-suspend</i> : torso is pronograde and on its side. Majority of body weight is supported in compression by a forelimb and hindlimb on same side of body. Significant body weight is also supported by a forelimb under suspension.    | 0.01    |
| <i>Ipsilateral compression/hindlimb-suspend</i> : as for “ipsilateral stand-forelimb suspension,” except that mass is partially supported by a hindlimb in suspension rather than a forelimb.  | 0.01    |
| <i>Pronograde stand/forelimb-suspend</i> : torso is in pronograde position, with one or both hindlimbs in quadrupedal stand position, but one or both forelimbs are abducted and support body mass through suspension above head.  | 1.16    |
| <b>Orthograde stand</b>  |         |
| <i>Extended bipedal stand</i> (P5b).   | 1.58    |
| <i>Flexed bipedal stand</i> (P5a).   | 0.18    |
| <i>Flexed bipedal stand/forelimb-suspend</i> (P5c2).   | 0.24    |
| <i>Extended bipedal stand/forelimb-suspend</i> (P5c1).   | 1.09    |
| <i>Extended bipedal stand/forelimb-compression</i> : as for “extended bipedal stand,” but one or both forelimbs are below level of shoulders and support body weight in compression.   | 0.07    |
| <i>Bipedal compression</i> : bipedal posture where legs may be angled in any position below horizontal and may be positioned on variously angled substrates, at different levels, and with different degrees of abduction/adduction and flexion/extension to each other. | 0.06    |
| <i>Bipedal compression/forelimb-suspend</i> : as above, but with significant support from one forelimb in suspension.  | 0.03    |
| <i>Monopedal stand</i> : body mass supported by standing on one leg, with insignificant contributions from other body parts.   | 0.77    |
| <i>Monopedal stand/forelimb-suspend</i> : as for “bipedal stand/forelimb-suspend,” but with only one hindlimb.   | 1.16    |
| <i>Monopedal stand/forelimb compression</i> : as for “bipedal stand/forelimb-compression,” but with only one hindlimb.   | 0.01    |

(Continued)

## APPENDIX A. (Continued)

| Postural mode  | % bouts |
|--|---------|
| Postural submode (component 1/component 2/component 3)   |         |
| <i>Monopedal stand/forelimb-hindlimb-suspend</i> : majority of body weight is supported by one hindlimb, which in most cases is rather abducted. Torso is often angled, and a fore-and hindlimb support weight in suspension, either in ipsilateral or contralateral combination.  | 0.03    |
| <i>Monopedal compression/forelimb-suspend</i> : as for “monopedal stand/forelimb-suspend,” but with the hindlimb excessively abducted or adducted. Includes flexed and extended postures.  | 0.06    |
| <i>Monopedal compression/tripedal-suspend</i> : majority of body weight is supported by one abducted or adducted hindlimb. But torso is horizontal or near horizontal, and remaining three limbs support body weight in suspension.  | 0.04    |
| <i>Monopedal compression/forelimb-hindlimb-suspend</i> : majority of body weight is supported by one hindlimb, which is abducted or adducted. Torso is often angled, and a fore- and hindlimb support weight in suspension, either in ipsilateral or contralateral combination.  | 0.20    |
| <i>Monopedal compression/hindlimb-suspend</i> : posture in which majority of body mass is supported by one hindlimb under compression, but other hindlimb supports substantial body weight under suspension. Torso can be in any position from horizontal to near vertical.  | 0.13    |
| <i>Monopedal stand/sit</i> : more than half of body weight is supported by a hindlimb in compression. However, body is learning in part-sitting posture against angled or horizontal support, and ischia contribute to supporting body mass.   | 0.03    |
| <i>Monopedal stand/hindlimb-cling</i> : orthograde posture in which majority of body weight is supported by one hindlimb, but significant body weight is supported by other hindlimb in a “cling” position.  | 0.01    |
| <b>Cantilever</b>  |         |
| <i>Extended cantilever</i> (P7a).  | 0.01    |
| <b>Orthograde forelimb-suspend</b>   |         |
| <i>Unimanual forelimb-suspend</i> (P8a).   | 1.17    |
| <i>Bimanual forelimb-suspend</i> (P8b).  | 0.15    |
| <i>Forelimb-suspend/sit</i> (P8c).   | 0.46    |
| <i>Forelimb-suspend/sit/hindlimb compression</i> : body mass is supported by one or both forelimbs, ischia, and one or both hindlimbs in compression.  | 0.01    |
| <i>Forelimb-suspend/squat</i> (P8d).   | 0.07    |
| <i>Forelimb-suspend/hindlimb compression</i> : more than half of body weight suspended from one or both forelimbs. Rest is supported by bipedal or monopedal compression. Trunk is held at least 45° above horizontal. Distinct from <i>Forelimb suspend/hindlimb cling</i> , because knees and hips may be extended or only slightly flexed, and feet may be placed on supports of any size and orientation, and do not exhibit power grip typical of cling postures. | 1.27    |
| <i>Forelimb-suspend/tripedal compression</i> : majority of body weight is suspended from one forelimb, and trunk is held at least 45° above horizontal. Rest is supported by one forelimb and both hindlimbs in compression. Knees may be flexed or extended.  | 0.01    |
| <i>Forelimb suspend/hindlimb cling</i> (P8f).  | 0.11    |
| <i>Forelimb suspend/lie</i> (P8g).   | 0.01    |
| <i>Forelimb suspend/hindlimb-compression/hindlimb cling</i> : one forelimb supports body weight in suspension, but is aided by one hindlimb in compression and other hindlimb is flexed, grasping a support in cling posture, and supporting more than its own weight.   | 0.01    |
| <b>Orthograde quadrumanous-suspend</b> : orthograde suspend where body mass may be supported by one or both hindlimbs in equal or greater proportion than one or both forelimbs.   |         |
| <i>Trunk-vertical suspend</i> (P8h): orthograde suspension using one or both hindlimbs and one or both forelimbs in tension in any combination.  | 1.95    |
| <i>Orthograde ipsilateral suspend/hindlimb compression</i> : orthograde suspension by ipsilateral fore- and hindlimb, with other hindlimb supporting more than its own weight in compression, and foot is below level of hip.  | 0.07    |
| <i>Orthograde hindlimb suspend</i> : orthograde suspension by both hindlimbs, in which hindlimbs are abducted to approximately 45° above horizontal and support all body mass. Forelimbs may be used for balance, but not weight-bearing.  | 0.03    |
| <b>Forelimb-hindlimb suspend</b>   |         |
| <i>Ipsilateral suspend</i> (P9a).  | 7.32    |
| <i>Ipsilateral suspend/hindlimb-compression</i> : suspension by ipsilateral fore- and hindlimb, and compression with remaining hindlimb. Body is relatively horizontal and on its side. All three support limbs bear approximately equal body mass.  | 0.71    |
| <i>Ipsilateral-suspend/ipsilateral-compression</i> : as above, but with ipsilateral fore- and hindlimb supporting body weight in compression. Limbs in suspension appear to support most body weight.  | 0.11    |
| <i>Ipsilateral suspend/sit</i> : majority of body weight is suspended by ipsilateral limbs, but ischia support some body mass.   | 0.08    |
| <i>Contralateral suspend</i> (P9b).  | 0.81    |
| <i>Contralateral suspend/hindlimb-compression</i> : suspension by contralateral fore- and hindlimb, with body relatively horizontal and facing downwards, and with other hindlimb supporting more than its own weight in “stand” posture.  | 0.07    |
| <b>Pronograde suspend</b>  |         |
| <i>Quadrumanous-suspend</i> (P10): inverted pronograde suspension involving both hindlimbs and one or both forelimbs. Used as feeding posture, generally with one forelimb free to harvest food.   | 3.41    |
| <i>Quadrumanous-suspend/sit</i> : as above, but with additional support from one or both ischia.   | 0.01    |

(Continued)

## APPENDIX A. (Continued)

| Postural mode<br>Postural submode (component 1/component 2/component 3)  | % bouts |
|--|---------|
| <i>Quadrumanous-suspend/lie</i> : as for “quadrumanous-suspend” but with additional support from back in horizontal position.  | 0.04    |
| <i>Forelimb-suspend/pronograde-compression</i> : as for “pronograde stand/forelimb-suspend,” but majority of body mass is borne by one or both forelimbs in tension while abducted above head. Distinct from “forelimb-suspend/hindlimb compression” because torso is pronograde. Head faces downward. | 0.27    |
| <b>Hindlimb suspend</b>  |         |
| <i>Extended bipedal hindlimb-suspend</i> : suspension from both hindlimbs, with both hips and knees extended.  | 0.36    |
| <i>Extended monopodal hindlimb-suspend</i> : suspension from one hindlimb, with extended hip and knee.   | 0.28    |
| <i>Hindlimb-suspend/forelimb-hindlimb compression</i> : suspension from one extended hindlimb, with less than half of body weight supported by a fore- and hindlimb in compression. In this study all fore- and hindlimb combinations were ipsilateral.  | 0.06    |
| <i>Hindlimb-suspend/hindlimb compression</i> : suspension from one extended hindlimb, with other hindlimb under compression. Suspended limb supports majority of body weight, and torso is normally near vertical, with head downward.   | 0.08    |
| <b>Lie</b>   |         |
| <i>Lie</i> (P13a, b, d). Includes “supine lie,” “lateral lie,” and “back lie,” as these were not possible to distinguish when orangutan was in a nest.   | 10.37   |
| <i>Lie/forelimb-suspend</i> : lie, with one forelimb supporting significant body weight.   | 0.03    |
| <i>Lie/forelimb-hindlimb-suspend</i> : lie, with one forelimb and one hindlimb supporting significant body weight.   | 0.01    |
| <i>Sit/lie</i> (P13e).   | 1.75    |
| <i>Sitlie/forelimb-suspend</i> : as for “sit/lie,” but with-additional support from one forelimb in suspension.  | 0.03    |
| <b>Postural bridge</b>   |         |
| <i>Pronograde bridge</i> (P14).  | 0.08    |
| <i>Orthograde bridge</i> : generally one forelimb and one hindlimb hold supports on each side of gap, with body spanning gap in orthograde posture, in tension. Mothers used this posture to reduce size of gap to allow, infant to cross independently at another level.                              | 0.04    |

<sup>1</sup> Where locomotor descriptions follow exact definition of Hunt et al. (1996), the code for definition in their paper is specified (e.g., P1a), and only classification details which differ in present study are provided. Where locomotor modes are specific to this study, we provide a full definition.

## APPENDIX B. Locomotor mode definitions

| Locomotor mode, submode, description  | % bouts     |
|---|-------------|
| <b>Quadrupedal walk</b>   |             |
| <i>Symmetrical gait walk</i> (L1a) <sup>1</sup>   | 8.00        |
| <i>Irregular gait walk (scramble)</i> (also called pronograde scramble) (L1c1).   | 9.36        |
| <b>Tripedal walk</b>  |             |
| <i>Tripedal walk</i> (L2): in this study, nonocomoting limb is not specified, but was most often a forelimb. Occasionally a forelimb was used in suspension to help support body weight.  | 0.22        |
| <b>Bipedal walk</b>   |             |
| <i>Extended bipedal walk</i> (L3a).   | 1.28        |
| <i>Flexed bipedal walk</i> (L3b).   | 0.36        |
| <i>Hand-assisted extended bipedal walk</i> : bipedal walk in which hindlimbs bear more than 50% of body mass in full extension, but one or both forelimbs are used to assist, either in suspension or compression and bear more than their own weight.  | 2.88        |
| <i>Hand-assisted flexed bipedal walk</i> : as for “hand-assisted extended bipedal walk,” but with hindlimbs relatively more bent.   | 0.57        |
| <i>Bipedal scramble</i> : body is orthograde and majority of body mass is borne by hindlimbs, but hindlimb kinematics are not characteristic of smooth bipedal gait. Typically, supports are small, irregularly placed, and variously angled. Hindlimbs may utilize both extension and flexion during gait cycle. | 0.14        |
| <i>Hand-assisted bipedal scramble</i> : as above, but one or both forelimbs also bear more than their own weight, either in compression or suspension. Similar to “orthograde clamber,” but majority of body mass is carried by hindlimbs.  | 2.03        |
| <b>Vertical climb</b> <sup>2</sup>  |             |
| <i>Flexed-elbow vertical climb</i> (L8a).   | 5.59 (0.60) |
| <i>Inverted flexed-elbow vertical climb</i> : ascent only on angled (20–45°) supports, whereby orangutan is effectively hanging underneath support while ascending.   | (0.50)      |
| <i>Ladder climb</i> (L8b).  | 0.18        |
| <i>Vertical scramble</i> (L8c).   | 7.08 (0.64) |
| <i>Extended-elbow vertical climbing</i> (L8d).  | 1.17 (0.46) |
| <i>Bimanual pull-up</i> (L8f).  | 1.28 (0.04) |
| <i>Vertical climb forelimbs only</i> : vertical climbing in which body mass is borne only by forelimbs in typical forelimb climbing pattern, but hindlimbs are not used for weight-bearing.   | 0.18 (0.07) |
| <b>Vertical descent</b> <sup>2</sup>  |             |
| <i>Rump-first symmetrical descent</i> (L8g1).   | 1.99 (0.28) |
| <i>Rump-first scramble descent</i> (L8g2).  | 4.45 (0.46) |
| <i>Rump-first forelimbs only descent</i> : rump-first descent in which only forelimbs are used. Hindlimbs may be used for balance, but do not bear more than their own weight.  | 0.60 (0.14) |

(Continued)

## APPENDIX B. (Continued)

| Locomotor mode, submode, description  | % bouts     |
|---|-------------|
| <i>Rump-first cascade descent</i> : equivalent to “head-first cascade descent,” but rump-first.   | 0.18        |
| <i>Rump-first extended elbow descent</i> : kinematically reverse of “vertical climb-extended elbow,” with limbs moving in sequence, normally hand over hand, foot over foot.  | 0.28 (0.07) |
| <i>Fire pole slide</i> (L81).   | 0.18 (0.04) |
| <i>Head-first descent (scramble)</i> (L8h2).  | 0.36 (0.11) |
| <i>Head-first descent (cascade)</i> (L8h3).   | 0.07        |
| <i>Pronograde slide</i> (L8k).  | 0.04 (0.04) |
| <i>Sideways vertical descent</i> (L8i).   | 1.07 (0.32) |
| <i>Cartwheel descent</i> : descent in which limbs grasp supports in motion which resembles limb sequence of human cartwheels.   | 0.14 (0.07) |
| <b>Torso-orthograde suspensory locomotion</b>   |             |
| <i>Brachiate</i> (L9a).   | 6.15        |
| <i>Forelimb swing</i> (L9d).  | 8.25        |
| <i>Flexed-elbow forelimb swing</i> (L9e).   | 0.18        |
| <i>Orthograde transfer</i> (L9f).   | 6.05        |
| <i>Orthograde clamber</i> (L9g).  | 14.37       |
| <i>Arrested drop</i> (L9h).   | 0.85        |
| <b>Torso-pronograde suspensory locomotion</b>   |             |
| <i>Inverted quadrupedal walk</i> (L10a).  | 2.28        |
| <i>Inverted tripodal walk</i> : as above, but with only three limbs.  | 0.11        |
| <i>Inverted quadrupedal run</i> (L10b).   | 0.04        |
| <i>Inverted pronograde scramble</i> (L10c).   | 1.28        |
| <b>Hindlimb swing</b> : body is held upside-down, and animal swings on one or both hindlimbs. Often used as intermediary form of locomotion to reorient body between two longer bouts of different locomotor modes.   | 0.14        |
| <b>Forelimb-hindlimb swing</b> : suspensory locomotion which may or may not follow regular limb sequence, utilizing both forelimbs and hindlimbs in both orthograde and pronograde positions.   |             |
| <i>Cartwheel swing</i> : sequence of suspensory locomotion on horizontal or negatively inclined support which resembles sequence of limb usage seen in human cartwheels.  | 0.18        |
| <i>Ipsilateral swing</i> : swinging from ipsilateral fore- and hindlimb. Exhibited as single swing to join two other modes of locomotion.   | 0.07        |
| <b>Bridge</b>   |             |
| <i>Cautious pronograde bridge</i> (L11a).   | 2.53        |
| <i>Inverted pronograde bridge</i> : as above, except with body in inverted pronograde suspension.   | 0.11        |
| <i>Lunging bridge</i> (L11b).   | 0.14        |
| <i>Supinograde bridge</i> (L11d).   | 0.04        |
| <i>Descending bridge</i> (L11e).  | 0.04        |
| <b>Leap</b> <sup>3</sup>  |             |
| <i>Pronograde leap</i> (L12a).  | 0.04        |
| <b>Drop</b> <sup>3,4</sup>  | 0.36        |
| <i>Unimanual suspensory drop</i> (L13c): as described in Hunt et al. (1996), but orangutans often tended to use one limb to maintain contact with support throughout drop, although support does not bear any weight during fall.   | 0.57        |
| <i>Bimanual suspensory drop</i> (L13d).   | 0.04        |
| <b>Sway</b> : based on tree sway (L16) of Hunt et al.’s (1996), but expanded to include any locomotion which relies on oscillation of supports to progress forward. Also includes locomotion where orangutan swings on vertical branch/liana (see text for further discussion). | 4.55        |
| <b>Ride</b> (L17): orangutans exhibit “ride” to move between different levels in canopy rather than from tree to ground (Hunt et al., 1996).  | 0.50        |

<sup>1</sup> Where locomotor descriptions follow exact definition of Hunt et al. (1996), the code for definition in their paper is specified (e.g., L1a), and only classification details which differ in present study are provided. Where locomotor modes are specific to this study, we provide full definition.

<sup>2</sup> For vertical climb and descent, values in parentheses are for angled climb.

<sup>3</sup> Landings from leaps and drops were not recorded, but were generally pronograde.

<sup>4</sup> Refers to drops in which semiposture assumed before drop was obscured from view.

## LITERATURE CITED

- Agresti A. 1990. Categorical data analysis. New York: John Wiley & Sons.
- Alexander RM. 1974. The mechanics of jumping by a dog (*Canis familiaris*). *J Zool (Lond) [A]* 173:549–573.
- Alexander RM, Jayes AS. 1983. A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *J Zool* 201:135–152.
- Avis V. 1962. Brachiation: the crucial issue for man’s ancestry. *Southwest J Anthropol* 18:119–148.
- Basmajian JV. 1965. Muscles alive: their functions revealed by electromyography. Baltimore: Wilkins and Wilkins Co.
- Begun DR. 2002. European hominoids. In: Hartwig WC, editor. The primate fossil record. Cambridge: Cambridge University Press. p 339–368.
- Boinski S. 1989. The positional behavior and support use of squirrel monkeys: ecological implications. *J Hum Evol* 18:659–677.
- Buettner-Janusch J. 1967. Origins of man. New York: John Wiley & Sons.
- Cant JGH. 1987a. Positional behavior of female Bornean orangutans (*Pongo pygmaeus*). *Am J Primatol* 12:71–90.
- Cant JGH. 1987b. Effects of sexual dimorphism in body size on feeding postural behavior of Sumatran orangutans (*Pongo pygmaeus*). *Am J Phys Anthropol* 74:143–148.



- Cant JGH. 1992. Positional behavior and body size of arboreal primates: a theoretical framework for field studies and an illustration of its application. *Am J Phys Anthropol* 88:273–283.
- Cant JGH, Youlatos D, Rose MD. 2001. Locomotor behavior of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador: general patterns and non suspensory modes. *J Hum Evol* 41:141–166.
- Cant JGH, Youlatos D, Rose MD. 2003. Suspensory locomotion of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador. *J Hum Evol* 44:685–699.
- Carlson KJ. 2005. Investigating the form-function interface in African apes: relationships between principal moments of area and positional behaviors in femoral and humeral diaphyses. *Am J Phys Anthropol* 127:312–334.
- Cartmill M. 1974. Pads and claws in arboreal locomotion. In: Jenkins FA Jr, editor. *Primate locomotion*. New York: Academic Press. p 45–83.
- Cartmill M. 1985. Climbing. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, editors. *Functional vertebrate morphology*. Cambridge, MA: Harvard Belknap Press. p 73–88.
- Cartmill M, Milton K. 1977. The lorisform wrist joint and the evolution of brachiating adaptations in the Hominoidea. *Am J Phys Anthropol* 47:249–272.
- Cartmill M, Hylander WL, Shaffland J. 1987. *Human structure*. Cambridge, MA: Harvard University Press.
- Chivers DJ. 1972. The siamang and the gibbon in the Malay peninsula. In: Rumbaugh DM, editor. *The gibbon and the siamang*, volume 1. Basel: Karger. p 103–135.
- Collis A. 2001. Siamang locomotion: implications for the arboreal clambering hypothesis. *Austral Primatol* 14:9.
- Crompton RH, Li Y, Thorpe SKS, Wang WJ, Savage R, Payne R, Carey TC, Aerts P, Van Elsacker L, Hofstetter A, Gunther MM, D'Aout K, DeClerq D. 2003. The biomechanical evolution of erect bipedality. *Cour Forsch Senckenberg* 243:115–126.
- Dagosto M. 1994. Testing positional behavior of Malagasy lemurs: a randomization approach. *Am J Phys Anthropol* 94:189–192.
- Dohlinow P, Fuentes A. 1999. *The nonhuman primates*. Mountainview, CA: Mayfield Publishing Co.
- Doran DM. 1989. Chimpanzee and pygmy chimpanzee positional behavior: the influence of environment, body size, morphology, and ontogeny on locomotion and posture. Ph.D. dissertation, State University of New York, Stony Brook.
- Doran DM. 1992a. The ontogeny of chimpanzee and bonobo locomotor behavior: a case study of paedomorphism and its behavioral correlates. *J Hum Evol* 23:139–157.
- Doran DM. 1992b. Comparison of instantaneous locomotor bout sampling methods: a case study of adult male chimpanzee locomotor behavior and substrate use. *Am J Phys Anthropol* 89:85–99.
- Doran DM. 1993. The comparative locomotor behavior of chimpanzees and bonobos: the influence of morphology on locomotion. *Am J Phys Anthropol* 91:99–115.
- Doran DM. 1996. The comparative positional behaviour of the African apes. In: McGrew W, Nishida T, editors. *Great ape societies*. Cambridge: Cambridge University Press. p 213–224.
- Doran DM, Hunt KD. 1994. Comparative locomotor behavior of chimpanzees and bonobos: species and habitat differences. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG, editors. *Chimpanzee cultures*. Cambridge, MA: Harvard University Press. p 93–106.
- Fleagle JG. 1976. Locomotion, posture and comparative anatomy of Malaysian forest primates. Ph.D. dissertation, Harvard University.
- Fleagle JG. 1980. Locomotion and posture. In: Chivers DJ, editor. *Malayan forest primates: ten years' study in tropical rain forest*. New York: Plenum Press. p 191–207.
- Fleagle JG. 1988. *Primate adaptation and evolution*. San Diego: Academic Press.
- Gilbert GN. 1981. *Modelling society: an introduction to loglinear analysis for social researchers*. London: George Allen & Unwin.
- Gittins SP. 1983. Use of the forest canopy by the agile gibbon. *Folia Primatol* (Basel) 40:134–144.
- Grand TI. 1972. A mechanical interpretation of terminal branch feeding. *J Mammal* 53:198–201.
- Hamanda Y. 1985. Primate hip and thigh muscles: comparative anatomy and dry weights. In: Hollihn U, editor. *Bimanual suspensory behavior: morphology, selective advantages and phylogeny*. Tokyo: University of Tokyo Press. p 131–152.
- Harrison T. 1987. The phylogenetic relationships of the early catarrhine primates: a review of the current evidence. *J Hum Evol* 16:41–80.
- Harrison T. 2002. Late Oligocene to Middle Miocene catarrhines from Afro-Arabia. In: Hartwig WC, editor. *The primate fossil record*. Cambridge: Cambridge University Press. p 311–338.
- Harrison T, Rook L. 1997. Enigmatic anthropoid or misunderstood ape? The phylogenetic status of *Oreopithecus bambolii* reconsidered. In: Begun DR, Ward CV, Rose MD, editors. *Function, phylogeny, and fossils: Miocene hominoid evolution and adaptations*. New York: Plenum Press. p 327–362.
- Heglund NC, Taylor CR. 1988. Speed, stride frequency, and energy cost per stride: how do they change with body size and gait? *J Exp Biol* 138:301–318.
- Hofstetter AM, Niemitz C. 1997. Comparative gait analyses in apes. In: Niemitz C, editor. *Proceedings of the 5th International Congress of the German Primatological Society*. Berlin: Freie Universitaet Berlin. p 73.
- Hunt KD. 1989. Positional behavior in *Pan troglodytes* at the Mahale Mountains and the Gombe Stream National Parks, Tanzania. Ph.D. dissertation, University of Michigan, Ann Arbor.
- Hunt KD. 1991a. Positional behavior in the Hominoidea. *Int J Primatol* 12:95–118.
- Hunt KD. 1991b. Mechanical implications of chimpanzee positional behavior. *Am J Phys Anthropol* 86:521–536.
- Hunt KD. 1992. Positional behavior of *Pan troglodytes* in the Mahale Mountains and Gombe Stream National Parks, Tanzania. *Am J Phys Anthropol* 87:83–105.
- Hunt KD. 2004. The special demands of great ape locomotion and posture. In: Russon AE, Begun DR, editors. *The evolution of thought: evolutionary origins of great ape intelligence*. Cambridge: Cambridge University Press. p 172–189.
- Hunt KD, Cant JGH, Gebo DL, Rose MD, Walker SE, Youlatos D. 1996. Standardised descriptions of primate locomotor and postural modes. *Primates* 37:363–387.
- Kano T, Mulawwa M. 1984. Feeding ecology of the pygmy chimpanzees *Pan paniscus* of Wamba. In: Susman RL, editor. *The pygmy chimpanzee*. New York: Plenum Press. p 233–274.
- Larson SG. 1998. Parallel evolution in the hominoid trunk and forelimb. *Evol Anthropol* 87:87–99.
- MacKinnon J. 1971. The orang-utan in Sabah today. A study of a wild population in the Ulu Segama reserve. *Oryx* 11:141–191.
- MacKinnon J. 1974. The behavior and ecology of wild orangutans (*Pongo pygmaeus*). *Anim Behav* 22:3–74.
- MacLachly L. 2004. The oldest ape. *Evol Anthropol* 13:90–103.
- MacLachly L, Gebo D, Kityo R, Pilbeam D. 2000. Postcranial functional morphology of *Morotopithecus bishopi*, with implications for the evolution of modern ape locomotion. *J Hum Evol* 39:159–183.
- Moya-Sola S, Kohler M. 1996. The first *Dryopithecus* skeleton: origins of great-ape locomotion. *Nature* 379:156–159.
- Moya-Sola S, Kohler M, Alba DM, Casanovas-Vilar I, Galindo J. 2004. *Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. *Science* 306:1339–1344.
- Napier JR. 1967. Evolutionary aspects of primate locomotion. *Am J Phys Anthropol* 27:333–342.
- Payne RC. 2001. Musculoskeletal adaptations for climbing in hominoids and their role as exaptations for the acquisition of bipedalism. Ph.D. dissertation, University of Liverpool.
- Payne RC, Crompton RH, Isler K, Savage R, Vereecke EE, Günther MM, Thorpe SKS, D'Aout K. In press. Morphological analysis of the hindlimb in apes and humans. Part I: comparative anatomy. *J Anat*.
- Payne RC, Crompton RH, Isler K, Savage R, Vereecke EE, Günther MM, Thorpe SKS, D'Aout K. In press. Morphological analysis of the hindlimb in apes and humans. Part II: Moment arms. *J Anat*.

- Pilbeam DR. 2002. Perspectives on the Miocene Hominoidea. In: Hartwig WC, editor. The primate fossil record. Cambridge: Cambridge University Press. p 301–310.
- Pontzer H, Wrangham RW. 2004. Climbing and the daily energy cost of locomotion in wild chimpanzees: implications for hominoid locomotor evolution. *J Hum Evol* 46:317–335.
- Remis M. 1994. Feeding ecology and positional behavior of western lowland gorillas (*Gorilla gorilla gorilla*) in the Central African Republic. Ph.D. dissertation, Yale University, New Haven, CT.
- Remis M. 1995. Effects of body size and social context on thear-boreal activities of lowland gorillas in the Central African Republic. *Am J Phys Anthropol* 97:413–433.
- Remis M. 1998. The effects of body size and habitat on the positional behavior of lowland and mountain gorillas. In: Strasser E, Fleagle J, Rosenberger A, McHenry HM, editors. Primate locomotion—recent advances. New York: Plenum Press. p 95–106.
- Rijksen HD. 1978. A field study on Sumatran orangutans (*Pongopygmaeus abelli*, Lesson 1827): ecology, behavior and conservation. Wageningen: Veenman.
- Rook L, Bondioli L, Casali F, Rossi M, Kohler M, Moya-Sola S, Macchiarelli R. 2004. The bony labyrinth of *Oreopithecus bambolii*. *J Hum Evol* 46:349–356.
- Ruff CB. 1989. New approaches to structural evolution of limb bones in primates. *Folia Primatol (Basel)* 53:142–159.
- Ruff CB, Runestad JA. 1992. Primate limb bone structural adaptations. *Annu Rev Anthropol* 21:407–433.
- Runestad JA. 1994. Humeral and femoral diaphyseal cross-sectional geometry and articular dimensions in Prosimii and Platyrrhini (primates) with application for reconstruction of body mass and locomotor behavior in Adapidae (primates, Eocene) Ph.D. dissertation, Johns Hopkins University School of Medicine.
- Senut B. 2003. Palaeontological approach to the evolution of hominid bipedalism: the evidence revisited. *Cour Forsch Senckenberg* 243:25–134.
- Senut B, Pickford M, Gommery D, Mein P, Cheboi K, Coppens Y. 2001. First hominid from the Miocene (Lukeino formation, Kenya). *C R Acad Sci [IIA]* 332:137–144.
- Srikosamatara S. 1984. Notes on the ecology and behavior of the hoolock gibbon. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N, editors. The lesser apes. Edinburgh: Edinburgh University Press. p 242–257.
- Sugardjito J. 1982. Locomotor behavior of the Sumatran orang utan (*Pongo pygmaeus abelii*) at Ketambe, Gunung Leuser National Park. *Malay Nat J* 35:57–64.
- Sugardjito J, van Hooff JARAM. 1986. Age-sex class differences in the positional behavior of the Sumatran orang utan (*Pongo pygmaeus abelii*) in the Gunung Leuser National Park, Indonesia. *Folia Primatol (Basel)* 47:14–25.
- Taylor CR, Caldwell SL, Rowntree VJ. 1972. Running up and down hills: some consequences of size. *Science* 178:1096–1097.
- Thorpe SKS, Crompton RH. 2005. Locomotor ecology of wild orangutans (*Pongo pygmaeus abelii*) in the Gunung Leuser Ecosystem, Sumatra, Indonesia: a multivariate analysis using log-linear modeling. *Am J Phys Anthropol* 127:58–78.
- Thorpe SKS, Crompton RHC, Günther MM, Ker RF, Alexander RM. 1999. Dimensions and moment arms of the hind- and forelimb muscles of common chimpanzees (*Pan troglodytes*). *Am J Phys Anthropol* 110:179–199.
- Tuttle RH, Cortwright D. 1988. Positional behavior, adaptive complexes, and evolution. In: Schwartz J, editor. Orang-utan biology. New York: Oxford University Press. p 311–330.
- van Schaik CP, Mirmanto E. 1985. Spatial variation in the structure and litterfall of a Sumatran rainforest. *Biotropica* 17: 196–205.
- Warren RD, Crompton RH. 1997. Locomotor ecology of *Lepilemur edwardsi* and *Avahi occidentalis*. *Am J Phys Anthropol* 104: 471–486.
- Wrangham RW, Conklin-Brittain NL, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in food abundance. I. Antifeedants. *Int J Primatol* 19: 949–970.
- Young NM. 2003. A reassessment of living hominoid postcranial variability: implications for ape evolution. *J Hum Evol* 45:441–464.
- Young NM, MacLatchy L. 2004. The phylogenetic position of *Morotopithecus*. *J Hum Evol* 46:163–184.