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Chapter 10

The Special Demands of Great Ape Locomotion and Posture

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Introduction

Amidst the welter of competencies that could be labeled “intelligence”, the great apes repeatedly demonstrate numerous high-level abilities that distinguish them from other mammals and ally them with humans (Griffin 1982; Parker & Gibson 1990; Russon, Parker & Bard 1996; Suddendorf & Whiten 2001). **Self-concept** is argued to be among this set of distinctive

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abilities. It is often viewed as an integral aspect of advanced intelligence, one that some have argued allows great apes to have a theory of mind (Heyes 1998 and references therein). Among the abilities that co-occur with it in humans are symbolic play, simple altruism, reciprocal relationships, a concept of planning, and pleasure in completion of complex tasks (Povinelli & Cant 1995).

Until recently, the demands of locomotion and posture, together referred to as **positional behavior** (Prost 1965), were not explicitly considered to correlate with any aspect of primate intelligence or its evolution, self-concept included. Primate intelligence is most often hypothesized to have evolved either for negotiating complex social problems, or for mapping and resolving complicated foraging challenges (for an overview, see Russon this volume a). Chevalier-Skolnikoff, Galdikas and Skolnikoff (1982: 650) suggested instead that, at least for orangutans, locomotor demands were "the single major function for which the advanced cognitive abilities . . . evolved." Povinelli and Cant (1995) subsequently refined and expanded this hypothesis, asserting that self-concept in orangutans evolved to enable these large-bodied apes to negotiate thin, compliant (i.e., flexible) branches during suspensory locomotor bouts, particularly when crossing gaps in the canopy. They

c10rfa041 c10rfa074 c10rfa075 c10rfa016 c10rfa074 hypothesized that the unpredictable response of compliant weight-bearing structures when weight is transferred onto them, the need for several such structures to support the weight of a single individual, and the erratic orientation of supports together require that large primates such as great apes have an “ability to engage in a type of mental experimentation or simulation in which one is able to plan actions and predict their likely consequence before acting” (Povinelli & Cant 1995: 409). In order to move safely in the forest canopy, orangutans and perhaps other great apes must be able to step outside themselves and imagine how their body and its movements will affect fragile, easily deformable branches and twigs. I will refer to these argument as the “Povinelli and Cant hypothesis,” cognizant of Chevalier-Skolnikoff *et al.*’s contribution.

This hypothesis is consistent with evidence that only massive primates, the great apes, have a concept of self. Evidence rests heavily on one measure, mirror self-recognition (MSR), which is often taken as particularly informative about self-concept. Gallup (1970, 1982, 1991) forcefully argued that MSR is found only in species that possess a self-concept, and Parker (1996) contended it is displayed only in species that also display high-level imitation. Chimpanzees and orangutans consistently recognize themselves in mirrors, as do a few gorillas, whereas other nonhuman primates do not (Gallup 1970; Lethmate & Ducker 1973; Miles 1994; Nicholson & Gould 1995; Patterson 1984; Patterson & Cohn 1994; Suarez & Gallup 1981; Swartz *et al*. 1999; see reviews by Gallup 1991; Inoue-Nakamura 1997)[1]. Although other capacities that co-occur with self concept such as symbolic play, simple altruism, reciprocal relationships, a concept of planning, and pleasure in completion of complex tasks are not a cleanly identifiable in any species, narratives of the daily lives of great apes in captivity and in the wild convince me they have these capacities.

From the positional side, this hypothesis has not been systematically evaluated. This chapter attempts to craft informed estimates of locomotor and postural frequencies for each of the apes in order to place positional behavior in the context of Povinelli and Cant hypothesis, as well as other prominent hypotheses on the evolution of great ape intelligence, namely foraging-related ecological pressures and social pressures.

A-Head

Background

The connection between primate positional behavior and self-concept or other higher cognitive capabilities receives *prima facie* support from research on great apes – they are unusually suspensory. However, quantitative studies of apes' positional behavior are relatively recent and the meaning of these data is still in contention. Perhaps one source of the contention is that positional behavior theory has a long history, and thus a deep timescale to add heft to opposing hypotheses. Currently, two distinct positional modes (or categories – I will use modes here) are most often argued to be responsible for ape anatomy: vertical climbing and arm-hanging. The two modes have quite different demands relative to the Povinelli and Cant hypothesis.

Early research on ape functional anatomy was grounded in anatomical research, a field already well developed by the nineteenth century (Owen 1835; Savage & Wyman 1847; Tyson 1699), rather than in ape positional behavior study, which began in earnest only in the 1960s. Keith's (1891) contention that brachiation was the behavior for which ape specializations were evolved permeated early research on ape positional behavior. Keith and other anatomists argued that adaptation to hand-over-hand under-branch suspensory locomotion ("brachiation") selected for shared ape traits such as long forelimbs, long, curved digits, mobile shoulders, elongated scapulae, broad (i.e., human-like) torsos, short, stiff backs, no tail, and a predominance of muscles that flex the elbow, extend the humerus, and raise the arm. Comparison of ape and monkey muscle

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weights largely supported Keith's hypothesis (Ashton & Oxnard 1964).

Data on wild ape behavior failed to corroborate the brachiation hypothesis. Mountain gorillas (Tuttle & Watts 1985 and references therein), chimpanzees (Goodall 1968; Reynolds 1965) and even orangutans (Harrison 1962) brachiated less than theory demanded. Although brachiation made up >50% of locomotion among hylobatids (Fleagle 1980), 20% among bonobos (Susman 1984), and >10% in orangutans (Cant 1987a), another mode, "quadrumanous climbing" (i.e., "four-handed" movement in which feet and hands grip a support), was even more common, 31% in orangutans, and 31% in bonobos. Quadrumanous climbing quickly replaced brachiation as the positional mode for which ape "brachiating" characters were considered to have evolved (Cartmill & Milton 1977; Fleagle 1976; Kortlandt 1974; Mendel 1976; Tuttle 1975; Tuttle *et al*. 1979). The mode lacked a widely agreed upon, rigorous definition, but it has encompassed, among other behaviors, brachiation, quadrupedal walking on slightly inclined boughs, irregular-gait walking on thin supports, vertical climbing, gap crossing suspensory behaviors, clambering (a hindlimb assisted brachiation), and forelimb-assisted bipedalism. The more suspensory of these behaviors are those that Povinelli and Cant hypothesize to be related to self-concept in orangutans, but other behaviors are more similar to quadrupedal walking or bipedalism. Because quadrumanous climbing conflates kinematically different behaviors that require different anatomical adaptations, it seems to have outlived its usefulness. Hunt *et al*. (1996) strongly recommended discarding the term entirely and instead reporting its constituent modes separately.

Of the component positional modes in quadrumanous climbing, vertical climbing was often singled out as the most important shared ape locomotor mode. Long arms were hypothesized to facilitate ascending large diameter trunks (Cartmill 1974; Kortlandt 1974), and vertical climbing on smaller diameter supports was argued to require shoulder mobility to allow alternate reaching for new handholds. Large muscles that retract the humerus and flex the elbow were seen as vertical climbing propulsors (Fleagle *et al*. 1981; Jungers *et al*. 1982).

Notably, vertical climbing does not pose the sorts of intellectual demands that Povinelli and Cant link to suspension. Vertical supports are not compliant, either because they are large (hence the need for a robust, divergent great toe in apes) and do not deform under weight, or because smaller supports are stabilized by the weight of the suspended climber, in particular by weight depending on the trailing hindfoot, which makes deformation minor and predictable.

Quantitative positional behavior data on chimpanzees (Hunt, 1989, 1991a, b) provided only partial support for a vertical climbing hypothesis. Hunt's data showed that vertical climbing was only slightly more common in apes than monkeys (0.9% of behavior versus 0.5%), and large diameter vertical climbing was rare. Unimanual forelimb suspension (arm-hanging) was more common than anticipated, and much more common among chimpanzee than monkeys (4.4% versus 0.0%). Hunt suggested that ape shoulder mobility allows much greater joint excursion than is necessary for vertical climbing. He suggested that shoulder mobility, scapula shape, torso shape, wrist mobility and some muscular adaptations are adaptations to arm-hanging, but most ape muscular specializations and their gripping great toe fit a vertical climbing hypothesis. Finger curvature and length were suggested to be adaptations to arm-hanging and vertical climbing. Hunt's (1991a) review of ape positional behavior studies then available concluded that arm-hanging and vertical climbing were the behaviors most clearly identifiable as shared among all apes.

Doran (1989, 1996) disagreed. She argued for a return to a vertical-climbing-only hypothesis, since her data showed that "climbing" was more common than suspensory behaviors among Taï, Ivory Coast chimpanzees. Her evidence in support of the vertical climbing hypothesis is weak, most importantly because vertical climbing was not one of her locomotor categories. As currently conceived (most eloquently by Fleagle *et al*. 1981), the climbing hypothesis is a *vertical* climbing hypothesis. The mode Doran sometimes refers to as "climbing" (e.g., Doran 1996) is not vertical climbing, but short-hand for the catch-all mode "quadrumanous climbing and scrambling" (Doran 1989: 328). Whereas most anatomists read "vertical climbing" when Doran writes "climbing", her climbing mode pooled suspensory modes (such as clambering, bridging, tree swaying), quadrupedalism (scrambling), and an unknowable proportion of true vertical climbing. In contrast to this liberality, her suspensory mode was narrowly defined to include only "alternating hand to hand progression beneath substrate" (Doran 1989: 328).

In this chapter I attempt to adjust for this and other biases to craft informed estimates of locomotor and postural frequencies for each ape species, after which I place positional behavior in the context of the Povinelli and Cant and other hypotheses on great ape intelligence and its evolution. I standardized and recalculated available data to allow comparability. Rather than providing ranges of possible frequencies or qualitative estimates, I provide exact values, but offer reliability judgments

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to offset this false accuracy. I formulate predictions drawn from Povinelli and Cant's hypothesis, and then test them against positional behavior estimates. My aims are to work towards resolving debates over how great ape positional behavior should be characterized, and to apply these findings to the question of whether some distinctively great ape forms of arboreal positional behavior demand high-level intelligence that may take the form of a self-concept.

Like others, I assume that cognitive capacities, which rely on expensive brain tissue, are unlikely to have evolved or to be maintained unless they serve important functions (see Russon, this volume a), and therefore that living species that have a self-concept use it.

A-Head

Povinelli and Cant Predictions

It is the non-stereotyped, figure-it-out-as-you-go nature of some locomotor or postural modes that is central to Povinelli and Cant's argument. They argue that primates that locomote on stable supports, stable either because the animal is light or the support is large, locomote using stereotyped, preprogrammed movements (cognitively simple action schemata). These movements are less cognitively challenging than those on unstable supports. Movement on compliant or fragile supports must be planned, and plans must be adjusted moment-to-moment as supports are found to be more or less compliant than estimated. Highly intelligent primates may be those that must locomote in a more moment-to-moment, calculating, context-contingent manner. I will call these cognitively challenging positional repertoires *self-concept eliciting positional regimes* (**SCEPRs**), and I will refer to individual modes as **SCEP modes**.

Chevalier-Skolnikoff *et al*. (1982) and Povinelli and Cant (1995) c10rfa016 c10rfa074 conceived of the SCEPR as a locomotor repertoire. I argue that postures can require a work-it-out-as-you-go approach as well. An orangutan may walk on a large support to the periphery of a tree, but reaching out, grasping a small support among the terminal branches, and assuming an arm-hanging posture requires the consideration of the compliance and fragility of supports and an accommodation to unexpected compliance. Arm-hanging chimpanzees may make a number of small adjustments to posture (e.g., gripping a different support with one foot, but leaving the other grips unchanged) that can leave them, over a period of minutes, meters from their starting point and suspended from completely different supports, without ever locomoting. These postural behaviors require individuals to be aware of and respond to various degrees of compliance.

The following testable predictions grow out of the Povinelli and Cant hypothesis:

(1) Great apes that have demonstrated the ability to form self-concepts will have SCEPRs, and vice versa.

(2) If the 11 kg siamang has a SCEPR compared to the anatomically near-identical 6 kg gibbon, the siamang should have a more cognitively sophisticated self-concept than gibbons.

(3) Species with great body weight dimorphism and similar SCEPRs, or with great differences in SCEPR between the sexes should exhibit sex differences in self-concept.

(4) In comparisons among species, the more common SCEP modes are in a species' positional repertoire, the more compliant supports are, and/or the more critical SCEP modes are to survival, the more robust and sophisticated should be self-conception.

Positional Mode Definitions

I followed Hunt *et al.*'s (1996) positional mode definitions, and greater detail is presented there. Here, categories such as "sit" and "lie" need no elaboration. Other modes that have been defined differently in different studies require some explanation.

"Stand" is quadrupedal or tripedal posture (P4 in Hunt *et al.*). In the "biped" mode weight is borne by hindlimbs, usually without significant assistance from the forelimbs (Hunt *et al*. mode P5). In the "squat" (P2) mode the heels only contact the support. "Cling" is a torso orthograde (i.e., erect) posture where hands and feet grip a relatively vertical support; the elbows and knees are quite flexed (P3). "Arm-hang" (= forelimb-suspend, P8) is a one- or very rarely two-handed forelimb suspension, typically engaged in on small-diameter and therefore compliant supports, sometimes assisted by a hindlimb (P8a). "Arm-foot hang" (P9a, b) is suspension from a foot and a hand; the torso is parallel to the ground, usually engaged in on relatively small supports. Both postures are argued to exert the same sorts of selective pressures as suspensory locomotion. Both apply to the forest's horizontal structure, where Povinelli and Cant argue the greatest locomotory difficulties occur.

Among locomotor modes "walk" (L1), "leap" (L 12), and "run" (L5) are straightforward. "Climbing" throughout means "vertical climbing" (L8). It refers to a behavior wherein the individual ascends or descends a vertical or near-vertical support much as a person would ascend or descend on a ladder. "Bipedal" includes both walking and running, using hindlimbs alone and forelimbs only for incidental support. Chimpanzees use it on relatively large supports (Hunt 1989). “Scramble” (L1c(1)) is quadrupedal walking on small, often flexible, approximately horizontal supports. Orientation of supports is irregular, and the gait itself looks irregular in consequence. Scrambling requires some appreciation of compliance. “Brachiate” refers to hand-over-hand suspensory movement underneath branches, and includes the rapid, stereotyped ricochetal brachiation of gibbons. “Clamber” is a torso-upright suspensory locomotion different from brachiation in that the hindlimbs also provide support, with their grip above the center of gravity of the individual, in orangutans, often near the ear (Cant 1987a). “Suspensory” is a miscellaneous category that encompasses below branch behaviors that cannot be considered brachiation or clamber, such as tree sway. “Transfer” (L9f) often begins with bimanual forelimb-suspension, and may contain a brachiation-like gap-closing motion (a “lunge”), wherein a hand grasps a small support in an adjacent tree, after which a branch is pulled toward the animal with a hand over hand or hand over foot motion. Weight is gradually transferred to the adjacent tree. The torso remains more or less orthograde throughout; more weight is born by the forelimbs than the hindlimbs.

These last 5 modes, scramble, brachiate, clamber, suspensory movement, and transfer are all used on small, flexible supports and require

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awareness of support compliance and fragility. These modes, along with the two postural modes (arm-hanging and arm-foot hanging), form the core of a SCEPR.

Biases

Studies reviewed here utilized four sampling modes, instantaneous (focal), instantaneous (scan), continuous (bout) (Altmann 1974) and continuous (meters/kilometer) (Tuttle & Watts 1985). Recent work suggests these sampling methods are rather comparable (Doran 1992). Instantaneous scan sampling theoretically yields positional mode frequencies that are quite similar to those produced by instantaneous focal sampling (Altmann 1974). Continuous bout sampling under-represents long-duration bouts and over-represents short-duration bouts. . In theory, comparability between instantaneous sampling and bout sampling is not expected. In practice, the two sampling regimes yield quite similar positional mode frequencies, because bout lengths vary little (Doran 1992). Meters/kilometers and bout sampling regimes would yield identical figures if velocity were constant, and it is rather constant in chimpanzees, (Hunt 1989) and probably other species. I will assume figures based on meters/kilometer and bout sampling are roughly equivalent, based in part on the comparability of instantaneous and bout sampling.

As positional data have accumulated, it has become apparent that positional mode frequency estimations for regimes with only 5 or 10 modes are relatively robust with respect to sampling differences. Table 10.1 includes two studies of different hylobatids that yielded quite similar mode frequencies, despite having been conducted by different researchers on different species, at different times, and at different sites. Three studies of bonobo locomotion had sample sizes that varied by an order of magnitude, yet they yielded quite similar mode frequencies (Table 10.4). It seems that when N's reach 100 or so, mode frequencies are rather reliable even in the face of large sample size differences.

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A second bias is introduced by differences in the level of habituation to human observation. Poorly habituated individuals tend to run, leap and brachiate at unnaturally high frequencies. Unhabituated individuals are less likely to flee when arboreal, leading to oversampling of arboreal behaviors, while terrestrial behaviors are often undersampled because targets are obscured by foliage. Habituated individuals have higher frequencies of walking versus running, transferring versus leaping, posture versus locomotion, and terrestriality versus arboreality.

A common compromise when reporting data on poorly habituated subjects is reporting arboreal and terrestrial observations separately, under the assumption that even though terrestrial behaviors may be undersampled, the relative proportions of terrestrial modes to one another will be accurate. With a similar rationale, locomotion and posture are often reported separately, assuming that even if unhabituated animals locomote more often, the relative proportions of individual locomotor modes is representative. Unfortunately, these divisions are sometimes perpetuated in later studies after subjects are habituated in order to allow comparability.

There is little question that the best comparisons between species will be made on habituated subjects using methods that record relative frequencies of every positional mode in the study population's entire positional repertoire, whether locomotor or postural, and in both arboreal and terrestrial contexts. It is no surprise that studies with large sample sizes were conducted on populations habituated for a decade or more. Four pioneers, Goodall, Nishida, Boesch, and Fossey, habituated populations on which more than 2/3 of the observations below are based. Of course, short studies on unhabituated populations are vastly better than nothing. Here I consider these potential biases before including data in tables. Sometimes I report data from short-term studies for the sake of completeness, but exclude them from calculations and discussion. To allow comparability, I calculated locomotor and postural mode frequencies separately.

The most serious bias in positional study is using non-comparable positional mode definitions. I attempt to compensate for this bias with adjustments explained below.

Calculations of Postural Mode Frequencies

Hylobatids

Four studies have reported hylobatid postural mode frequencies (Table 10.1). I divided hylobatids into two groups, the siamang (*Hylobates syndactylus*) and other gibbon species. While anatomically similar, siamangs weigh approximately 11 kg, whereas gibbons average only 6 kg (Plavcan & van Schaik 1997; Smith & Jungers 1997). Larger primates leap less and climb quadrumanously more (Fleagle 1976).

Insert Table 10.1 about here

Gibbons

Two gibbon studies observed subjects in all behavioral contexts, rather than, e.g., only during feeding or travel, and sample sizes, while small, are well above 100 (322 and 655). However, these data included only two postural modes, sit and arm-hang; I assume postural modes other than sit and arm-hang were rare. The average of the two studies is reported in Table 10.1.

Siamang

One siamang study observed individuals only when feeding; a second recorded all behavioral contexts. Feeding observations undersample sitting and oversample arm-hanging (i.e., suspension), since frugivores arm-hang most often when gathering fruits. Only two postural modes (sit, arm-hang) were recorded, and sample sizes were small. I assume the broader study offers the better estimate, despite its small sample size.

Great apes

Orangutan

Three positional studies on orangutans yielded over 6,000 observations. However, observations were limited to arboreal feeding in two studies, and to arboreal travel and resting in a third. The arboreal limitation likely introduces little bias because Bornean orangutans are highly arboreal (females nearly 100%, males 80%; Rodman 1979) and Sumatran orangutans are completely arboreal (Povinelli & Cant 1995). Context, however, may introduce bias. Standing and arm-hanging were much more common during travel and resting, whereas arm-foot hang was much more common during feeding. To adjust for this bias, frequencies were weighted by context (Table 10.2). Five studies have reported activity budgets (Galdikas 1978; MacKinnon 1977; Rijksen 1978; Rodman 1979; Wheatley 1982), from which I calculated an average activity budget of 42.7% feed, 39.6% rest, and 17.4% travel. I multiplied postural mode frequencies during feeding by 0.427, and resting + travel by 0.396 + 0.174. Given the similarity of values between studies before weighting, the weighted average in Table 10.2 is a good estimate.

Insert Table 10.2 about here

Bonobo

Bonobos are poorly habituated and therefore their posture is poorly characterized. The only study to date (Table 10.2) yielded 132 observations made on subjects feeding arboreally on fruit. Bonobos have terrestrial knuckle-walking adaptations virtually identical to those of chimpanzees, and their diets include significant amounts of terrestrial herbaceous vegetation (Malenky *et al.* 1994), suggesting they spend a significant amount time on the ground. Since arboreal and terrestrial postures differ dramatically in apes, the absence of terrestrial observations likely introduces significant bias. These biases and the low sample size make this estimate poor.

Chimpanzee

Three studies of chimpanzee posture have yielded over 20,000 observations (Table 10.2). Although one study was limited to 3 postural modes, the unsampled modes represent only 5% of posture in the other studies. Frequencies for all three studies, even with this bias, are quite similar. Studies by Doran (1989) and Hunt (1989) yielded much larger sample sizes; these were used to generate a best estimate. The biggest difference between the two studies is less frequent suspensory behavior in West than East African chimpanzees.

Gorillas

Because mountain gorillas live in montane habitats nearly devoid of climbable trees, whereas lowland gorillas live in rainforest, postural profiles might be expected to differ considerably. Data support that expectation. A study of the Karisoke mountain gorillas yielded a prodigious

2,300 hours of observation; another study generated 10,674 observations. I averaged values from both studies to produce the estimates in Table 10.2.

Lowland Gorillas remain poorly habituated. The terrestrial positional behavior of this presumably quite terrestrial subspecies is largely unknown. Remis (1995) reported that for 382 first sightings (the most objective measure of terrestriality for poorly habituated subjects), 59% were terrestrial and 41% were arboreal. Data were limited to wet-season observations. Remis tabulated arboreal postural data for females, group males, and lone males. I pooled male data, then averaged male and female frequencies to get mid-sex averages (Table 10.2). I estimated lowland gorilla terrestrial behavior assuming that wet and dry season behavior differ little. This assumption seems reasonably sound because the proportion of time spent on the ground is similar in wet and dry seasons (Remis 1999). I estimated lowland gorilla terrestrial plus arboreal postural frequencies using mountain gorilla terrestrial behavior to estimate the missing lowland gorilla terrestrial data, then weighting terrestrial (i.e. mountain gorilla) frequencies by 0.59 (the proportion of time spent in terrestrial behavior in the lowland gorilla) and arboreal frequencies by 0.41 (proportion of arboreality).

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Calculations of Locomotor Mode Frequencies

Hylobatids

Gibbon

Locomotor mode frequencies are available for three gibbon species (N = 684; Table 10.3). *H. lar* were observed during feeding and travel modes, contexts that presumably sample most gibbon locomotor activity. I pooled travel and feeding observations to make this study comparable to others. The three species differed. *H. agilis* displayed more leaping than other species, *H. lar* much more climbing activity, and *H. pileatus* more brachiation. I averaged the three studies to produce the gibbon positional profile in Table 10.3.

Insert Table 10.3 about here

Siamang

Two studies totaling 1,414 observations document siamang locomotor behavior (Table 10.3). In one study, siamangs were observed during feeding and travel contexts. I pooled these observations to afford comparability. Gittins (1983) reported more brachiation, Fleagle (1980) found more climbing. These differences could reflect mode definition biases, in which case averaging ameliorates the bias.

Great apes

Orangutan

In two studies male and female orangutans were observed during travel only (Sugardjito 1982; Sugardjito & van Hooff 1986). A third study observed females during feeding and travel (Cant 1987a), but only in arboreal contexts. Travel-only data overestimate walking, and female-only data underestimate quadrupedalism. In other words, these two studies' biases offset one another. Assuming no locomotion occurs during resting, travel plus resting contexts account for over 97% of orangutan locomotion. The remainder is building sleeping nests (0.8%) and social display (1.5%). Nest building is mostly postural (all my chimpanzee nest building observations were). No data exist for social display. I averaged the two travel studies then averaged these values with travel+feeding values to yield a best estimate (Table 10.4).

Insert Table 10.4 about here

Bonobo

Three bonobo studies provided similar numbers of observations, but only

Doran (1989) observed partly habituated individuals; her values are reported in Table 10.4. Unhabituated bonobos leaped and brachiated as they fled observers. Doran found bonobos too poorly habituated to make terrestrial observations. No estimate of the relative frequency of arboreal versus terrestrial behavior is available, so it is unclear how representative of the bonobos' entire locomotor repertoire these data are. They seem unlikely to offer more than a crude estimate.

Chimpanzee

Two studies offer chimpanzee arboreal locomotor data (Table 10.4). Comparability between the two studies is problematic. Hunt (1992) defined vertical climbing as hand-over-hand ascents on supports angled greater than 45°, whereas Doran (1996) pooled vertical climbing with other modes in a quadrumanous climbing category. This is critical to the current discussion because her data do not distinguish SCEP modes, i.e., those typically used on compliant supports such as transfer, tree sway or clamber, from modes used on stable supports. To estimate compliant-support modes in *P.t. verus*, I estimated the proportion of each of the constituent modes in Doran's climbing category (Table 10.4) by assuming that her quadrumanous climbing and scrambling mode contained proportions of transferring, vertical climbing and other modes in the same proportions found in *P. t. schweinfurthii*. Vertical climbing was indeed the largest component of "climbing" (nearly 90%), but other modes were significant at both East African sites. I multiplied these proportions by 11% (Doran's value for "climbing," see Table 10.4) to yield the *P.t.verus* estimate in Table 10.5. I calculated the chimpanzee locomotor profile by averaging values for Gombe, Mahale and the *P. t. verus* estimate (Table 10.5).

Insert Table 10.5 about here

Mountain Gorilla

Tuttle and Watts (1985) provided frequencies from a 2,300 hour study. Doran (1996) recorded 1,848 instantaneous samples. Although Doran again pooled scramble with vertical climbing, these modes are uncommon in the mountain gorilla and therefore probably bias these observations little. I averaged these two locomotor profiles to provide an estimate (Table 10.5).

Lowland Gorilla

I recalculated Remis' (1995) data to produce a midsex average. One difficulty is that Remis' "scramble" involved "suspension by forelimbs with substantial support from hindlimbs (in compression)" wherein "weight was distributed relatively evenly across four limbs" (1995: 417). The "scramble" mode is more commonly defined as torso-pronograde quadrupedal walking, distinguished by its unpatterned gait (Hunt *et al.* 1996). Scramble *sensu* Remis is a mode that ranges between forelimb-assisted bipedalism and hindlimb assisted brachiation. I divided her "scrambling" value, placing half in brachiation and half in bipedalism, to yield the approximation in Table 10.5. As above, I then used terrestrial mountain gorilla data to produce a weighted lowland gorilla estimate, assuming 59% terrestrial and 41% arboreal behavior.

Discussion

Postural profiles (Table 10.6) for the seven ape taxa reviewed here provide one profile that is probably biased (the arboreal bonobo study), two profiles that are merely estimates but have no identified biases, and four profiles derived from long-term studies for which known biases have been corrected or that suffer no known biases. Locomotor profiles (Table 10.7) are derived from limited, biased studies in two cases, estimated in 3 species, and derived from long-term studies on well-habituated populations in two cases. We expect primates with a self-concept, great apes, to have SCEPRs compared to primates without self-concept, e.g., monkeys.

Baboon positional frequencies provide this contrast. Data were collected using identical methods to those for Mahale and Gombe chimpanzees (Hunt 1991b).

Posture

Compared to baboons, SCEP postures (arm-hang, arm-foot hang) occurred more often in all apes except the mountain gorilla. Gibbons and siamangs frequently use SCEP modes during posture. Cannon and Leighton (1994) found that gibbon supports during locomotion are quite stable even compared to macaques, just as Povinelli and Cant note, but suspensory postures are engaged in on small, compliant supports (Grand 1972; Gittins 1982 illustrates this spectacularly). The Povinelli and Cant hypothesis predicts that gibbons and siamangs will have self-conception, though perhaps less so than arboreal great apes. The larger siamang engaged in arm-hanging more often than gibbons, suggesting siamangs must accommodate more to compliant supports, and therefore have a more SCEPR than gibbons.

Among great apes, orangutans demonstrated the highest frequency of the SCEP modes arm-hang and arm-foot hang. They also stood the most. Suspensory postures among chimpanzees were only a tenth as common, despite similar body weights. Chimpanzees emerged overall as generalists. Mountain gorillas were distinctive only for their high frequency of squatting and lying. Lowland gorillas had a distinctively high frequency of bipedalism. Bonobo profiles are not compared because they reflect arboreal feeding only.

SCEPR postures constituted ≥35% of all posture among gibbons, siamangs and orangutans. Among chimpanzees, mountain gorillas, lowland gorillas, baboons and perhaps bonobos, SCEP modes made up less than 5% of all postures. Posture typically makes up the vast majority of positional behavior (e.g., 85% in chimpanzees, Hunt 1989). Some experts suggest that relatively immobile postures produce too little stress on the musculoskeletal system to demand morphological adaptations. My view is that while locomotion is more stressful and dangerous because falls are more likely, posture is five times more common. If posture exerts significant selective pressures, all Asian apes have profoundly greater SCEPRs than African apes or baboons.

Insert Tables 10.6 and 10.7 about here

Locomotion

Brachiation, clamber, transfer and miscellaneous suspensory modes constituted 59% or more of all Asian ape locomotor behavior. As Povinelli and Cant maintained, orangutans have high frequencies of locomotor SCEP modes, such as clamber and transfer. African apes, compared to Asian apes, are quadrupedal walkers. Walking, a distinctly un-SCEP mode, made up >60% of all locomotion in African apes, but constituted <15% in all Asian apes. Even scrambling, a walking-like compliant support mode, was uncommon among African apes. While African apes do not have a SCEPR compared to orangutans, they may still be SCEPR-selected compared to monkeys. Walking constituted 97% of baboon locomotor behavior. In the same forested habitat, walking constituted 91.8% of chimpanzee behavior. Walking made up only 64.4% of lowland gorilla behavior. Mountain gorillas are distinctive for their high frequencies of squatting and running, neither part of a SCEPR. *In toto*, SCEP modes made up less than 4% of all locomotor modes among the African apes. These locomotor data suggest that among the great apes, orangutans alone exhibit a distinct SCEPR.

Although the bonobo data are not directly comparable to the complete ape data set, arboreal-only behavior can be compared (Table 10.8). Bonobos and chimpanzees, in this limited comparison, are nearly indistinguishable; suspension represents <15% in both. Walking, likewise, is seen in similar frequencies in the two species. It is considerably less

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common among orangutans and gorillas. Although the catch-all category "quadrumanous climbing" makes comparisons tentative, gorillas appear much more Asian in this comparison than either *Pan* species. Suspensory mode frequencies in the lowland gorilla are exceeded among the great apes only by the orangutan, a quite unexpected result. They also exhibited distinctively high frequencies of bipedal posture, bipedal locomotion, and squatting. The lowland gorilla data are reliable in this comparison, since the missing terrestrial data are not a factor. These data leave that status of lowland gorillas as likely exhibitors of a SCEPR, but the case is equivocal.

Insert Table 10.8 about here

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In summary, Tables 10.6, 10.7 and 10.8 suggest that suspensory positional modes such as arm-foot hang, arm-hang, orthograde clamber, transfer and brachiate are more common in orangutans than other great apes, and more common in all apes than in monkeys. Sitting and quadrupedal walking, distinctively un-SCEP modes, were considerably more common among African apes than orangutans.

Among chimpanzees, unimanual forelimb-suspension (arm-hanging) and vertical climbing were distinctively common, compared to baboons, but their positional regime was unremarkable compared to other great apes.

Bonobos, at least from evidence in Table 10.8, are indistinguishable from chimpanzees. Their high proportion of leaping in Table 10.7 is likely a reflection of poor habituation, and the seemingly distinctive level of climbing is an artifact of arboreal-only observations.

Gibbons have the highest frequency of leaping among the apes. Gibbons and siamangs, not surprisingly, are brachiation and arm-hanging specialists, but only postural modes show evidence of a need to accommodate compliant supports, and even this evidence is circumstantial.

Predictions

None of the predictions growing out of Povinelli and Cant's hypothesis were corroborated unequivocally, though some evidence is supportive.

(1) Apes demonstrating self-concepts were predicted to have SCEPRs. Only orangutans clearly exhibit a SCEPR, but other apes have varying expressions of a SCEPR compared to monkeys. Estimates presented here suggest that great apes' SCEPRs rank: orangutan $\gg$ lowland gorilla $>$ chimpanzee ($=$ bonobo) $>$ hylobatids $\gg$ mountain gorilla. Povinelli and Cant might predict lowland gorillas to have a self-concept, but mountain gorillas, for which we have little

laboratory cognitive evidence, should not. Chimpanzees have a less demanding SCEPR than lowland gorillas, yet they appear to express self-concept equal to that of orangutans, and have been among the most successful on MSR tests (Gallup 1970; Povinelli *et al.* 1997). Equivocal evidence suggests that bonobos have a chimpanzee-like low-level SCEPR, yet they, too, pass the MSR mark test (Walraven *et al.* 1995) and exhibit symbolic behavior perhaps beyond that of common chimpanzees (Savage-Rumbaugh *et al.* 1993). Hylobatids have a postural but not a locomotor SCEPR, but offer little evidence of self-concept (Hyatt 1998; Inoue-Nakamura 1997). Some gibbons exhibit evidence of passing the mark test (Ujhelyi *et al.* 2000), and others examine body parts in mirrors (Hyatt 1998). Other indications of symbolic behavior or self-concept are lacking. While positional behavior suggests that self-concept should roughly follow the pattern of orangutan $\gg$ lowland gorilla $>$ chimpanzee $=$ bonobo $>$ hylobatids $\gg$ mountain gorilla, MSR results and other self-concept indicators suggest orangutan $=$ chimpanzee $=$ bonobo $\geq$ mountain gorilla $\gg$ hylobatids, with lowland gorillas unknown. This evidence does not support the Povinelli and Cant hypothesis.

(2) Siamangs have a SCEPR in their high frequency of arm-hanging, and are therefore predicted to have more sophisticated self-conception than closely related gibbons. No siamang has yet passed the MSR mark test (Hyatt 1998), but the contrast in SCEPR among the hylobatids suggests that as a program to test the compliant support hypothesis, further research is warranted.

(3) If SCEPRs are comparable, the heavier gorilla and orangutan males should display more sophisticated self-concepts than females. Gorillas did not meet the prerequisite comparability of male and female SCEPRs. Although Remis (1995) found very little difference in male and female positional mode frequencies, her observations were arboreal only, and females are much more arboreal than males (58% vs. 24%). Orangutan results are negative. Female orangutans engage in more clambering (47.8% vs. 38%) but males engage in more tree swaying (24% vs. 9.7%) (Table 10.9). Both behaviors should require a self-concept, so overall male and female SCEPRs appear comparable. No sex differences in self-concept have yet been noted in orangutans (Inoue-Nakamura 1997 and references therein). This result is consistent with the compliant support hypothesis, but is not support for it.

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Insert Table 10.9 about here

In chimpanzees, females have a more pronounced SCEPR than males. Females arm-hang more often and from smaller supports, and females brachiate more than males (Hunt, 1992). Males have high frequencies of un-SCEP postures such as sit (Hunt 1992). The Povinelli and Cant hypothesis predicts that female chimpanzees should exhibit a more sophisticated self-concept; no such difference has been observed. This observation is at odds with the compliant support hypothesis.

(4) The more profound the SCEPR, the more robust and sophisticated self-concepts should be. No indices of self-concept sophistication exist, but robustness can be indexed by the proportion of individuals within a species that exhibit it and how early in development it appears. The consistency of success on self-concept measures is orangutan = chimpanzee = bonobo ≥ lowland gorilla ≫ hylobatids, with mountain gorillas unknown and hylobatid data contested. Their SCEPRs, rank orangutan ≫ lowland gorilla > chimpanzee (= bonobo) > hylobatids ≫ mountain gorilla. No age differences in self-concept acquisition are yet apparent (Inoue-Nakamura 1997). c10rfa050

The compliant support hypothesis is not supported by these data.

Conclusions

A comparison of ape positional behavior repertoires confirms Povinelli and Cant's contention that orangutans position themselves among compliant and unpredictable supports, but the positional behavior of other apes does not clearly support their hypothesis. Positional mode frequencies presented here support only one of four predictions developed from the compliant support hypothesis. Apes with a self concept were predicted to have self concept eliciting positional regimes, but only orangutans clearly demonstrated a SCEPR. The compliant support hypothesis predicts that siamangs will evince greater evidence of self concept than gibbons or mountain gorillas. No such difference has been observed, but further investigation seems warranted. Orangutans possess far more elements of a SCEPR than other great apes, which predicts more advanced self conception in orangutans, but this has not been observed. Mountain gorillas do not have a SCEPR, yet there seems to be no sentiment among ape researchers that their cognitive sophistication or concept of self is different from that of lowland gorillas. Female chimpanzees should show greater expression of self-concept than males, but there is no objective evidence for such a sex difference, and my objective opinion is that there is not one.

Orangutans offer a challenge to the social brain hypothesis in that their society is simple, yet they are cognitively complex. African apes offer a challenge to the compliant support hypothesis, as perhaps do hylobatids. Gorillas, with their simple foraging regime compared to other apes, offer a challenge to the foraging complexity hypothesis. Casting the net more widely, spider monkeys (*Ateles* spp.) offer a challenge to both the social complexity and foraging demands hypotheses. Spider monkeys have social relationships, group sizes and composition, and diet similar to those of chimpanzees. Social complexity and foraging hypotheses would predict their concept of self and other cognitive abilities should rival those of chimpanzees, yet *Ateles* have shown no evidence of a self-concept or any other form of high-level intelligence comparable to great apes, or even to *Cebus* (Chevalier-Skolnikoff 1991). c10rfa015

It might be argued that self-concept evolved in one of the common ancestors of apes due to SCEPRs, as the compliant support hypothesis suggests, and has been retained for use in other contexts. This seems unlikely, since self-concept is presumably dependent on large, metabolically expensive brains, and it would disappear without selective pressure to maintain it. If it were to be retained, a non-SCEPR selective pressure for self-concept must have appeared just as African apes were losing their ancestral SCEPR. This coincidence seems unlikely.

Resolution of the evolutionary origins of great ape self concept and other evidence of higher intelligence, therefore, awaits further study of positional behavior as well as of the complexity of social relationships, diet, food resource distribution, food chemistry, and their intelligence itself. The best conclusion concerning the compliant support hypothesis is at present a tentative one: if foraging demands explain intelligence little compared to the demands of sociality, and if our understanding of orangutans as rather anti-social apes holds, and if phylogenetic inertia is insufficient to explain the retention of orangutan intelligence, then a locomotor origin for self-conception in orangutans is possible, but its origin in other apes is unexplained.

A broader conclusion concerning the evolution of self-concept and other higher cognitive abilities among other apes is similarly tentative. Among the apes, species with massive bodies have a concept of self, and smaller primates do not, even when they have SCEPRs, complex foraging regimes, and/or demanding social lives. Great apes may have larger brains not because the have unique selective pressures impinging on them, but because they can. Perhaps we must fall back on the hypothesis that organisms with larger bodies have lower costs for maintaining relatively large brains (Jerison, 1973), and therefore "intelligence" (including cognition involved in self conception) is found among the great apes simply because it is less expensive for massive primates than it is for other primates. From this perspective, increased locomotion among compliant supports derives from the same cause as presence of self-concept – great body weight – but the two are not causally connected.

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Endnote

1. Povinelli and Cant suggest that most gorillas have lost their capacity for self-recognition secondarily, as part of an adaptation to terrestriality, maintaining that the ability of the lowland gorilla Koko to recognize herself in a mirror (Patterson 1984) is an unrepresentative exception. c10rfa070 Recent work, however, suggests that gorillas do exhibit MSR (Swartz *et al.* 1999). c10rfa097 This seems in keeping with other evidence of self-concept implicit in Koko's signing ability.

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c10tab001 Table 10.1. *Hylobatid Postural Modes (percentages)*

	Sit	Lie	Stand	Squat	Cling	Biped	Arm-hang	Hand-foot hang
Hylobates agilis[1]	65.5	0.0	0.0	0.0	0.0	0.0	34.5	0.0
Hylobates pileatus[2]	61.7	0.0	0.0	0.0	0.0	0.0	38.3	0.0
Gibbon average	**63.6**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**36.4**	**0.0**
Hylobates syndactylus[3]	47.0	0.0	0.0	0.0	0.0	0.0	53.0	0.0
Hylobates syndactylus[4]	38.3	0.0	0.0	0.0	0.0	0.0	61.7	0.0
Siamang best est.	**47.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**53.0**	**0.0**

1 [1] Gittins (1983). Percentage of 322 bouts sampled by 10-minute scan surveys. c10rfa035

2 [2] Srikosamatara (1984). Percentage of 655 5-minute scan surveys. c10rfa090

3 [3] Chivers (1972). Percentage of 234 5-second instantaneous focal surveys. c10rfa017

4 [4] Fleagle (1976). Percentage of 1,376 postural bouts during feeding. c10rfa026

c10tab002 Table 10.2. *Great ape Postural Modes (percentages)*

	Sit	Lie	Stand	Squat	Cling	Biped	Arm-hang	Hand-foot hang
Pongo[1]	46.0	0.0	24.4	0.0	0.0	0.0	29.7	0.0
Pongo[2]	42.1	0.0	6.7	0.0	0.0	3.8	17.8	30.0
Pongo[3]	49.0	0.0	1.0	0.0	0.0	2.0	12.0	36.0
Pongo weighted avg.	**45.6**	**0.0**	**15.5**	**0.0**	**0.0**	**1.1**	**23.3**	**14.1**
Bonobo[4]	**90.0**	**3.0**	**2.0**	**0.0**	**0.0**	**0.0**	**5.0**	**0.0**
P.t. verus[5]	80.0	5.0	15.0	0.0	0.0	0.0	0.0	0.0
P.t. verus[6]	75.8	16.8	5.8	0.0	0.0	0.0	1.6	0.0
P.t. schweinfurthii[7]	75.2	15.1	3.0	0.8	0.4	0.4	5.3	0.0
Chimpanzee best est.	**75.5**	**16.0**	**4.4**	**0.4**	**0.2**	**0.2**	**3.5**	**0.0**
Mountain Gorilla[8]	60.0	1.3	2.7	35.4	0.0	0.2	0.0	0.0
Mountain Gorilla[9]	73.4	20.1	6.5	0.0	0.0	0.0	0.1	0.1

Mtn. Gorilla average	**66.9**	**10.7**	**4.6**	**17.7**	**0.0**	**0.1**	**0.1**	**0.0**
Lowland Gorilla[10]	48.3	8.3	4.6	31.5	0.0	5.1	1.9	0.0
Lowland Gorilla est.[11]	**59.3**	**9.7**	**4.6**	**23.3**	**0.0**	**2.2**	**0.8**	**0.0**

[1] Sugardjito & van Hooff (1986). Percentage of 5,836 bouts during arboreal travel and resting, Sumatran orangutans

[2] Cant (1987a). Percentage of 350 bouts while feeding on figs, Bornean females.

[3] Cant 1987b. Percentage of time spent in each bout during 1,682 minutes of focal arboreal feeding observations, Sumatran females.

[4] Kano & Mulavwa (1984). Percentage of 132 instantaneous time-point surveys during arboreal feeding on fruit.

[5] Sabater Pi (1979). Percentage of bouts during186 hours of continuous sampling.

[6] Doran (1989). Percentage of 8,660 1-minute time-point samples.

[7] Hunt (1989). Percentage of 11,848 2-minute time-point samples.

[8] Tuttle & Watts (1985). Percentages each bout makes up of total bouts observed in 2300 hr of continuous bout sampling.

[9] Doran (1996). Percentage of 10,674 one-minute instantaneous focal samples on Karisoke gorillas.

[10] Calculated from Remis (1995), Table 10.9.

[11] Calculated assuming terrestrial postures of Lowland and Mountain Gorillas are similar; weighted following Remis' (1995) estimate that Lowland Gorillas are 41% arboreal and 59% terrestrial (see text).

c10tab003 Table 10.3. *Gibbon Locomotor Modes (percentages)*

	Walk	Climb	Leap	Run	Biped	Scramble	Brachiate	Clamber	Suspensory	Transfer
H. agilis[1]	3.5	6.3	23.9	0.0	0.0	0.0	66.3	0.0	0.0	0.0
H. lar[2]	0.0	34.2	9.3	0.0	5.2	0.0	51.2	0.0	0.0	0.0
H. pileatus[3]	0.0	6.0	8.7	0.0	0.9	0.0	84.4	0.0	0.0	0.0
Gibbon avg	**1.2**	**15.5**	**14.0**	**0.0**	**2.0**	**0.0**	**67.3**	**0.0**	**0.0**	**0.0**
H. syndatylus[4]	0.0	10.0	0.0	0.0	11.0	0.0	80.0	0.0	0.0	0.0
H. syndatylus[5]	0.0	54.3	3.2	0.0	4.1	0.0	37.9	0.0	0.0	0.0
Siamang avg	**0.0**	**32.2**	**1.6**	**0.0**	**7.6**	**0.0**	**59.0**	**0.0**	**0.0**	**0.0**

[1] Gittins (1983). Percentage of 255 10-minute scan surveys. c10rfa035

[2] Fleagle (1980). Percentage of 211 pooled feeding and travel bouts; continuous focal sampling. c10rfa027

[3] Srikosamatara (1984). Percentage of 218 5-minute scan surveys. c10rfa090

[4] Gittins (1983). Percentage of 208 10-minute scan surveys. c10rfa035

[5] Fleagle (1980). Percentage of 1206 pooled feeding and travel bouts; continuous focal sampling. c10rfa027

c10tab004

Table 10.4. *Great ape Locomotor Modes (percentages)*

	Walk	Climb	Leap	Run	Biped	Scramble	Brachiate	Clamber	Suspensory	Transfer
Orangutan[1]	13.0	10.0	0.0	0.0	0.0	0.0	21.0	41.0	0.0	15.0
Oranutang[2]	10.8	9.8	0.0	0.0	0.0	0.0	19.8	43.0	0.0	16.8
Orangutan[3]	12.0	31.3	0.0	0.0	0.0	0.0	10.6	39.4	1.2	5.6
Orangutan est	**12.0**	**20.6**	**0.0**	**0.0**	**>0.0**	**0.0**	**15.5**	**40.7**	**0.6**	**10.8**
Bonobo[4]	34.0	20.0	18.0	0.0	8.0	0.0	20.0	0.0	0.0	0.0
Bonobo[5]	31.0	31.0	10.0	0.0	6.0	0.0	21.0	0.0	0.0	0.0
Bonobo[6]	35.3	50.4	3.1	0.0	1.5	0.0	8.9	0.0	0.0	0.0
Bonobo est.	**35.3**	**50.4**	**3.1**	**0.0**	**1.5**	**0.0**	**8.9**	**0.0**	**0.0**	**0.0**
P.t. verus[7]	86.1	11.0	0.3	0.0	1.2	0.0	1.3	0.0	0.0	0.0
P.t. verus (est.)[8]	86.1	9.6	0.3	0.0	1.2	0.5	1.3	0.0	0.1	0.8
P.t. schweinfurthii[9]	91.8	5.1	0.2	0.8	0.4	0.1	0.8	0.0	0.1	0.6
P.t. schweinfurthii[10]	91.8	4.8	0.0	1.4	0.4	0.4	0.2	0.0	0.0	0.2
P.t.s. average[11]	91.8	5.0	0.1	1.1	0.4	0.3	0.5	0.0	0.1	0.4
Chimp. est.[12]	**89.9**	**6.5**	**0.2**	**0.7**	**0.7**	**0.3**	**0.8**	**0.0**	**0.1**	**0.5**
Mountain Gorilla[13]	95.6	0.2	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0

Mountain Gorilla[14]	96.5	<1.7	0.0	0.0	1.6	>0.0	0.1	0.0	0.0	0.0
Mtn Gorilla est.	**96.0**	**≤ 1.0**	**0.0**	**1.0**	**0.8**	**≥ 0.0**	**0.1**	**0.0**	**0.0**	**0.0**
Lowland Gorilla[15]	18.8	46.6	0.0	0.0	13.7	0.0	8.7	0.0	3.2	8.0
L. Gorilla est.	**64.4**	**19.7**	**0.0**	**0.6**	**6.1**	**0.0**	**3.6**	**0.0**	**1.3**	**3.3**

[1] Sugardjito (1982). Percentage each mode makes up of all bouts observed during 219 hr of continuous bout sampling; Sumatran orangutans; during travel only.a

[2] Sugardjito & van Hooff (1986). Percentage each mode makes up of 10,601 bouts observed; Sumatran orangutans; continuous bout sampling for travel only

[3] Cant (1987a). Percentage each mode makes up of all bouts observed during 4,360 minutes of continuous bout sampling. Bornean females only were observed during feeding and travel

[4] Susman *et al*. (1980). Percentage each mode makes up of 131 arboreal feeding bouts.

[5] Susman (1984). Percentage each mode makes up of 1,722 arboreal bouts, mostly during feeding.

[6] Doran (1996). Percentage each mode makes up of 1,461 1-minute time-point samples. Arboreal locomotion only; mid-sex average.

[7] Doran (1996), Table 16.3. Mid-sex averages of percentages of 1,417 one-minute instantaneous time-point samples

[8] Doran values recalculated, assuming the proportion that scramble, tree sway and transfer making up "climbing" is the same as at Mahale and Gombe. Percentages of each mode constituting climbing taken from Table 10.5.

[9] Percentages of 1,751 2-minute instantaneous time-point samples at Mahale Mountains; midsex averages. Reanalyzed data originally presented in Hunt (1992).

[10] Percentages of 484 2-minute instantaneous time-point samples at Mahale Mountains; midsex averages. Reanalyzed data from Hunt (1992).

[11] Average of Gombe and Mahale data. Note that values are virtually identical to Hunt (1991a).

[12] Average of *P.t. verus* estimate, Gombe frequencies, and Mahale frequencies.

[13] Tuttle & Watts (1985). Percent of each kilometer constituted by each mode in 2300 hr of continuous bout sampling; midsex average for 4 adults.

[14] Doran (1996). Percentage each mode makes up of 1,848 1-minute time-point samples; midsex average.

[15] Remis (1995). Percentage of 122 one-minute instantaneous time-point sample; arboreal, wet season observations only; midsex average. Calculated from Remis (1995), Table 11.

c10rfa076

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c10tab005 Table 10.5. *Percentage of each constituent locomotor mode in Doran's "climbing" category, for chimpanzees*

Mode	Mahale[1]	Gombe[1]	Mean
Vertical Climbing	86.4	88.9	87.7
Scramble	1.7	7.4	4.6
Suspensory (Tree Sway)	1.7	0.0	0.8
Transfer (= Bridge)	10.2	3.7	6.9

1 [1] data from Hunt (1992)

c10tab006 Table 10.6. *Summary Postural Mode Frequencies Percentages*

	Mode								
	Sit	Lie	Stand	Squat	Cling	Biped Stand	Arm-hang	Hand-foot Hang	Quality of Profile[1]
Gibbon	63.6	0.0	0.0	0.0	0.0	0.0	36.4	0.0	Reliable
Siamang	47.0	0.0	0.0	0.0	0.0	0.0	53.0	0.0	Estimate
Orangutan	44.8	0.0	14.6	0.0	0.0	1.3	22.3	15.0	Reliable
Bonobo[2]	90.0	3.0	2.0	0.0	0.0	0.0	5.0	0.0	Arboreal
Chimpanzee	75.5	16.0	4.4	0.4	0.2	0.2	3.5	0.0	Reliable
Mtn. Gorilla	66.9	10.7	4.6	17.7	0.0	0.1	0.1	0.0	Reliable
L. Gorilla	59.3	9.7	4.6	23.3	0.0	2.2	0.8	0.0	Estimate
Papio anubis[3]	75.3	4.0	19.7	0.2	0.3	0.1	0.2	0.0	Reliable

1 [1] Values categorized as "estimate" are considered approximate frequencies.

2 [2] Bonobo estimates are shown for completeness; they are not discussed because they reflect arboreal feeding only.

3 [3] Percentage of 1,555 2-minute instantaneous focal observations; midsex average. From Hunt (1991).

c10tab007 Table 10.7. *Summary Locomotor Mode Percentages*

	Mode										
	Walk	Climb	Leap/ Hop	Run	Biped. Walk	Scramble	Brachiate	Clamber	Other Susp.	Transfer	Quality of Profile
Gibbon	1.2	15.5	14.0	0.0	2.0	0.0	67.3	0.0	0.0	0.0	Small Ns
Siamang	0.0	32.2	1.6	0.0	7.6	0.0	59.0	0.0	0.0	0.0	Estimate
Orangutan	12.0	20.6	0.0	0.0	0.0	0.0	15.5	40.7	0.6	10.8	Estimate
Bonobo	35.3	50.4	3.1	0.0	1.5	0.0	8.9	0.0	0.0	0.0	Arboreal
Chimpanzee	89.9	6.5	0.2	0.7	0.7	0.3	0.8	0.0	0.1	0.5	Reliable
Mtn. Gorilla	96.0	<1.0	0.0	1.0	0.8	>0.0	0.1	0.0	0.0	0.0	Reliable
L. Gorilla	64.4	19.7	0.0	0.6	6.1	0.0	3.6	0.0	1.3	3.3	Estimate
Papio anubis[1]	97.0	0.7	0.5	1.6	0.0	0.0	0.0	0.0	0.0	0.0	Reliable

[1] Percentage of 497 2-minute instantaneous focal observations; midsex average. From Hunt (1991).

c10tab008 Table 10.8. *Percentages of Arboreal Locomotor Modes In Bonobos and Other Great Apes*

	Bonobo[1]	Mahale Chimpanzee[2]	Gombe Chimpanzee[3]	Orangutan[4]	Lowland Gorilla[5]
Quadrupedal walk	35.3	31.1	38.0	12.0	18.8
"Quadrumanous climb"	50.4	51.7	55.8	31.4	46.6
Suspension	8.9	14.4	3.1	56.8	19.9
Bipedalism	1.5	1.7	3.1	0.0	13.7
Leap	3.1	1.1	0.0	0.0	0.0
N	1461	178	45	4,360 min.	122

[1] After Doran (1996), Table 16.5. One-minute instantaneous focal observations; midsex average. c10rfa023

[2] Two-minute instantaneous focal observations; midsex average

[3] Two-minute instantaneous focal observations; midsex average

[4] Values for "quadrumanous climbing" were calculated by pooling values for climb, scramble and transfer. Values for suspension were obtained by adding brachiation, clamber and miscellaneous suspensory modes.

[5] Calculated from Remis (1995), Table 11. One-minute instantaneous focal observations; midsex average. See discussion above for discussion of regularization of Remis' locomotor modes. c10rfa076

c10tab009 Table 10.9. *Sex Differences in Orangutan Locomotor Behavior (percentages)*[1]

	Walk	Climb	Brachiate	Clamber	Tree Sway[2]
Male	8.0	9.0	21.0	38.0	24.0
Female	13.3	10.3	18.5	47.8	9.7

[1] From Sugardjito & van Hooff (1986), Table II. Percentage each mode makes up of 10,601 bouts observed; continuous bout sampling for travel only c10rfa094

[2] Pooled with "transfer" in other tables.