

## BRIEF REPORT

### Are Bonobos (*Pan paniscus*) Really More Bipedal Than Chimpanzees (*Pan troglodytes*)?

ELAINE N. VIDEAN<sup>1\*</sup> AND W.C. MCGREW<sup>1,2</sup>

<sup>1</sup>Department of Zoology, Miami University, Oxford, Ohio

<sup>2</sup>Department of Sociology, Gerontology, and Anthropology, Miami University, Oxford, Ohio

Of the living apes, the chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*) are often presented as possible models for the evolution of hominid bipedalism. Bipedality in matched pairs of captive bonobos and chimpanzees was analyzed to test hypotheses for the evolution of bipedalism, derived from a direct referential model. There was no overall species difference in rates of bipedal positional behavior, either postural or locomotory. The hominoid species differed in the function or use of bipedality, with bonobos showing more bipedality for carrying and vigilance, and chimpanzees showing more bipedality for display. *Am. J. Primatol.* 54:233–239, 2001. © 2001 Wiley-Liss, Inc.

**Key words:** bipedal; chimpanzee; bonobo; positional behavior; posture; locomotion

#### INTRODUCTION

The evolution of hominid bipedality (i.e., habitual upright posture and locomotion) has long been recognized as a crucial element in the transition from “ape to man” [Darwin, 1886; DuBrul, 1962; Rose, 1991]. Examination of the environmental and behavioral conditions under which bipedality exists in non-human species may illustrate conditions under which hominid bipedality evolved. Several extant primate species have been examined as possible primate models for the evolution of bipedalism: hamadryas (*Papio hamadryas*) and gelada (*Theropithecus gelada*) baboons, chimpanzee (*Pan troglodytes*), and bonobo (*Pan paniscus*) [DeVore & Washburn, 1966; Goodall & Hamburg, 1974; Zihlman et al., 1978; Wrangham, 1980; Hunt, 1994; Savage-Rumbaugh, 1994; Zihlman, 1996]. The use of extant primate species as referential models to study the evolution of bipedalism has met with criticism, but such study may lead to a better understanding of the influence of various hypothesized selection pressures and anatomical correlates on the evolution of bipedalism in hominids. Most current models for the evolution of hominid bipedalism focus on the chimpanzee or bonobo.

Contract grant sponsor: Miami University.

\*Correspondence to: Elaine N. Videan, Department of Zoology, Miami University, Oxford, OH 45056. E-mail: videanen@muohio.edu

Received 5 December 2000; revision accepted 1 May 2001

The chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*) are the closest living relatives of *Homo sapiens* [Sibley et al., 1990; Horai et al., 1992; Takahata & Satta, 1997]. Both chimpanzee [Goodall & Hamburg, 1974; Stanford, 1996] and bonobo [Zihlman et al., 1978; Susman, 1987; Savage-Rumbaugh, 1994; Zihlman, 1996] have been promoted as the ideal model for the last common ancestor. Chimpanzee-based models for the evolution of bipedalism have focused on behavioral ecology and have identified carrying, vigilance, and tool use as possible selection pressures for bipedalism [Kortlandt, 1962; Goodall & Hamburg, 1974]. Zihlman et al. [1978] based the bonobo model for the evolution of bipedalism on comparisons of skeletal and morphological characteristics with both hominids and common chimpanzees. Despite the equivocality of competing models, the bonobo is typically presented as being more bipedal in popular works and textbooks. Bonobos have been referred to as excellent bipeds with a predisposition for bipedal behavior [Zihlman, 1996; deWaal, 1997; Relethford, 2000]. The striking cover photograph for a new popular book on human origins features two bipedal bonobos [deWaal, 2001]. Only further behavioral and morphological study of the ecology and anatomy of the two *Pan* species can help clarify which is the more appropriate referential model for the evolution of human bipedalism.

Previous research on the positional behavior of bonobos is limited, due to poor observation conditions in the wild and the scarcity of subjects in captivity. Positional behavior of wild bonobos has been studied only at Lomako Forest in the Democratic Republic of Congo and is limited to arboreal locomotion [Susman et al., 1980; Susman, 1984; Doran, 1993]. Early studies revealed high levels of suspensory locomotion, particularly leaping and diving, and bipedality [Susman et al., 1980; Susman, 1984], but later research revealed less bipedality and suspensory locomotion [Doran, 1993]. Terrestrial locomotor data are crucially needed, since later research showed that bonobos are as terrestrial as chimpanzees [Hohmann & Fruth, 1993]. Tightly designed behavioral studies of the two *Pan* species are needed to clarify which species offers the more appropriate referential model for the evolution of human bipedalism [Doran, 1993].

A variety of behavioral differences have been cited in relation to chimpanzees and bonobos, with possible implications for modeling selection pressures in the evolution of bipedalism. Savage-Rumbaugh [1994] and others [Cameron, 1993; Thompson, 1994] have hypothesized that many behavioral patterns are unique to one or the other *Pan* species. These patterns include tool use during bipedal display for chimpanzee, and increased bipedal food and infant transport for bonobo, and are related to hypotheses for the evolution of human bipedalism, such as carrying and agonistic display. Overall, behavioral differences between bonobo and chimpanzee that are important to the hypothesized selection pressures for the evolution of human bipedalism seem to have been exaggerated [Stanford, 1998].

The goal of this study is to test hypothesized behavioral differences in bipedality between chimpanzees and bonobos in order to devise a direct referential model for the evolution of bipedalism. To develop a referential model for the evolution of bipedalism based on both species of *Pan*, the hypothesis that there are compelling differences between the two species in areas related to bipedality must be tested. From this, we make two predictions: First, rates of terrestrial bipedal posture and locomotion in bonobos exceed rates in chimpanzees. Second, the relative frequency of the types of functional performance of terrestrial bipedality (both posture and locomotion) differs between bonobos and chimpanzees.

TABLE I. Demography of Paired Subjects (Bonobo/Chimpanzee), Ranked by Age

Subject	Sex	Age (yr)	Origin	Rearing
Vernon/CJ	Male/male	30/31	Wild/wild	Mother/mother
Jimmy/Moose	Male/male	21/29	Wild/wild	Mother/mother
Toby/Big Daddy	Male/male	21/30	Wild/wild	Mother/mother
Louise/Alpha	Female/female	27/15	Captive/captive	Nursery/nursery
Lisa/Muffin	Female/female	18/18	Captive/captive	Mother/mother
Lady/Junie	Female/female	18/33	Wild/wild	Mother/mother
Susie/Pepper	Female/female	18/32	Wild/wild	Mother/mother
Lucy/Jana	Female/female	10/11	Captive/captive	Mother/mother
Mambo/Radar	Male/male	8/9	Captive/captive	Unknown/mother
Donny/Martin	Male/male	6/7	Captive/captive	Mother/mother
Virgil/Bo	Male/male	5/6	Captive/captive	Mother/mother
Ricky/Billy	Male/male	4/6	Captive/captive	Nursery/mother
Vir/Chester	Male/male	3/3	Captive/captive	Mother/mother
Tamia/Beta	Female/mother	3/5	Captive/captive	Mother/mother

## METHODS

### Study Subjects and Sites

The bonobos lived at the Cincinnati Zoo and Botanical Gardens ( $n = 5$ ) and at the Columbus Zoo and Aquarium ( $n = 9$ ), both in Ohio (Table I). Ages were based on known and estimated birthdates in the Bonobo Species Survival Plan (SSP) [Reinartz & Leus, 1998]. Goodall's [1986] system of four age-classes was used: infant (0–4 yr), juvenile (5–7 yr), adolescent (8–14 yr), and adult (14+ yr). Bonobo SSP and zoo records showed which subjects were wild-born (i.e., origin in the Democratic Republic of Congo, Africa) or captive-born. Subjects were classed as nursery-reared if the infant was taken from its mother shortly after birth and reared by humans for at least 6 months.

The chimpanzee sample was matched as precisely as possible to the 14 bonobos, on the basis of sex, age, origin, and rearing. They were chosen from a population of chimpanzees at the University of Texas M.D. Anderson Cancer Center Science Park (UTMDACC), near Bastrop, Texas (Table I). No previously published study comparing the two species has paired subjects in any way.

The bonobos at the Cincinnati Zoo were observed in an outdoor enclosure approximately  $50 \times 15$  m. The substrate was predominately moderate to steep grassy slopes. There was an additional area of flat grass near a small pool of water. The enclosure contained several arboreal structures, including an overturned tree with a diagonally sloped trunk, boughs, and branches, as well as portable environment-enrichment objects, such as tubs, balls, and browse. The bonobos at the Columbus Zoo were also observed in a roughly circular outdoor area with a diameter of 43 m. The substrate was predominantly flat and grassy, with several areas of moderately grassy slopes. Arboreal structures included living trees and bushes of various species and suspended ropes, and portable objects included browse and burlap sacks. A small artificial stream ran through the enclosure. The chimpanzees at UTMDACC were observed in circular outdoor enclosures 22 m in diameter. The substrate was of flat sand and grass with two to three elevated flat wooden platforms ( $2 \times 4$  m each). "Arboreal" structures included horizontal and sloped wooden beams, horizontal metal pipes, and suspended ropes, and additional portable objects included barrels, balls, and browse.

### Data Collected

Terrestrial positional behavior of the bonobos and chimpanzees was recorded over a 4-mo period by instantaneous focal-subject observations every 30 sec for a 45-min observation period [Altmann, 1974]. E.N.V. recorded terrestrial positional behavior by type, function, and substrate. Data were recorded on a hand-held computer (Psion WorkAbout) operating the Noldus Observer software package. Terrestrial bipedality, its function, and its substrate were recorded on an all-occurrence basis for both the focal subject and nonfocal subjects present during the observation. This resulted in a mean of 8.9 hr ( $\pm 1.33$ ) of observation per individual for the bonobos, and 8.8 hr ( $\pm 1.02$ ) of observation per individual for the chimpanzees. Positional behavioral categories followed Hunt et al. [1996]. Bipedal behavior was either postural or locomotor, and each of these was either assisted or unassisted. Assisted bipedality was defined as orthograde posture or locomotion in which the legs support more than half the body weight with minimal support from another body part. Categories for functions of bipedality were adapted from Hunt [1994].

### Data Analysis

Observational data were summarized within species as hourly rates and relative frequencies of positional behavior and relative frequencies of the functions of positional behavior for each subject. Counts of bipedal events were also translated into percentages, across subjects, and within species. Statistical analyses used SPSS Software 6.1. The test statistic for all paired Wilcoxon *T*-tests was calculated by generating mean ranks ( $\pm$  standard deviation) and converting those into *z*-scores.

## RESULTS

The two species did not differ in overall proportions of locomotion or posture, when compared using matched pairs of individuals (Table II). Mature captive bonobos overall averaged  $81.6 \pm 11.0\%$  of their positional behavior as posture. These values overlap greatly with those of the captive chimpanzees ( $88.1 \pm 6.2\%$ ), as well as those reported for wild chimpanzees (83%, Mahale; 82%, Gombe [Hunt, 1992]).

Mean rates of bipedality varied widely across individuals, ranging from 0.00 to 4.12 bipedal bouts per hr, across the two species and bipedal categories. Immature chimpanzees and bonobos were typically more bipedal than their mature counterparts. Immature chimpanzees averaged 1.70 postural bipedal bouts and 0.87 locomotor bipedal bouts per hr, whereas mature chimpanzees averaged 0.53 postural bouts and 0.43 locomotor bouts per hr. Immature bonobos averaged 1.95 postural bipedal bouts and 2.29 locomotor bipedal bouts per hr. Mature bonobos, however, averaged only 0.64 postural bipedal bouts and 0.29 locomotor bipedal bouts per hr. Tight comparison of the two species, based on matched pairs, shows chimpanzees exhibited higher rates of postural unassisted bipedality than did

**TABLE II. Comparison of Relative Frequency of Locomotion and Posture in Bonobo (B) and Chimpanzee (C)**

Type of positional behavior	Number of subjects	Sample size <sup>a</sup>	B>C pairs	C>B pairs	Z score	<i>P</i> -value
Total posture	14	14	8	6	-0.69	0.48
Total locomotion	14	14	6	8	-0.66	0.51

<sup>a</sup>Sample size = (total number of subjects)–(tied pairs).

**TABLE III. Comparison of Hourly Rates of Bipedality of Bonobo (B) and Chimpanzee (C)**

Type of bipedality	Number of subjects	Sample size <sup>a</sup>	B>C pairs	C>B pairs	Z score	P-value
Total posture	14	14	6	8	-0.72	0.24
Assisted	14	14	8	6	-0.66	0.26
Unassisted	14	14	3	11	-2.29	0.01 <sup>b</sup>
Total locomotion	14	14	7	7	-0.66	0.26
Assisted	14	11	6	5	-1.15	0.12
Unassisted	14	13	6	7	-0.52	0.30

<sup>a</sup>Sample size = (total number of subjects)-(tied pairs).

<sup>b</sup>Significant one-tailed (Paired Wilcoxon T-test, see text for details).

bonobos ( $P = 0.01$ , Table III). In addition, there was no difference between the species for overall postural or locomotor bipedality.

Patterns of the functional performance of bipedality were similar for mature and immature individuals, within each species. However, mature chimpanzees and bonobos appeared to use more bipedality for vigilance than did immature individuals. Mature bonobos used 62.6% of postural and 20.0% of locomotor bipedality for vigilance, whereas immature bonobos used only 27.8% of postural and 4.5% of locomotor bipedality for vigilance. Similar trends were seen in chimpanzees, with matures using 43.3% of postural and 7.5% of locomotor bipedality for vigilance, and immatures using only 20.9% and 0.0% of postural and locomotor bipedality, respectively. In paired species comparisons, bonobos used more locomotor bipedality for the function of vigilance ( $P = 0.04$ ) and came close to doing so for carrying ( $P = 0.09$ ), in comparison with chimpanzees (Table IV). Chimpanzees used more postural bipedality ( $P = 0.04$ ) for the function of display and came close to doing so for locomotion ( $P = 0.08$ , Table IV).

**TABLE IV. Relative Frequencies of the Functions of Bipedality in Bonobo (B) and Chimpanzee (C)**

Functions	Number of subjects	Sample size <sup>a</sup>	B>C pairs	C>B pairs	Z score	P-value
Carry						
Postural	14	8	4	4	-0.35	0.73
Locomotor	14	12	10	2	-1.85	0.07
Vigilance						
Postural	14	13	6	7	-0.21	0.83
Locomotor	14	5	5	0	-2.02	0.04 <sup>b</sup>
Feed/Forage						
Postural	14	7	5	2	-0.59	0.55
Locomotor	14	6	3	3	-0.42	0.68
Display						
Postural	14	13	3	10	-2.38	0.02 <sup>b</sup>
Locomotor	14	12	5	7	-1.173	0.08
Play						
Postural	14	8	4	4	-0.28	0.78
Locomotor	14	6	2	4	-0.11	0.92

<sup>a</sup>Refers to statistical sample size: (sample size)-(tied pairs).

<sup>b</sup>Significant two-tailed (Paired Wilcoxon T-test, see text for details).

## DISCUSSION

Using captive populations to test species-typical adaptations is always risky. However, the fact that the percentage of positional behavior devoted to posture or locomotion in these captive populations approximates that of their wild counterparts, at least for chimpanzees, is reassuring (Table II).

Tight quantitative comparison of the rates of bipedality revealed no real difference between the two *Pan* species. The one difference found, in unassisted posture, shows chimpanzees to exhibit higher levels than bonobos (Table III). This was manifest in higher rates of upright agonistic display, especially by adult male chimpanzees. However, this difference was consistent across age classes. Therefore, neither species appears to be a better overall model for the evolution of hominid bipedalism, as based on a propensity for hominoid bipedal behavior.

Species differences did appear in the function or use of bipedality. Bonobos showed more bipedality in carrying and vigilance; chimpanzees showed more bipedality in display (Table IV). The difference in bipedality used for vigilance appears to be driven by high rates of vigilance in mature individuals, rather than immatures. The social hierarchy of the captive bonobos seemed to be dominated by females, and adult male display was never observed (Videan, unpublished data). These differences suggest that it is not frequency but usage of bipedality that distinguishes these congeneric species. The implication of these differences may relate to differences in environment (i.e., “furnishings”) or may translate into a real species difference.

Popular views to the contrary, the results of this study suggest that there is no difference between chimpanzees and bonobos in rates of terrestrial bipedality. Further observational studies of wild and captive populations are needed. Experimental study of the contexts in which bipedal carrying, vigilance, feeding, and display occur, both in captivity and in nature, may help identify the selective pressures that shaped bipedalism [Videan, 2000]. Differences in social behaviors might account for some differences seen in the use of bipedality, and can only add to our understanding of all the possible behavioral repertoires of our hominid ancestors. A composite model, rather than a single-species referential model, based on both species of *Pan* might yield a more useful explanation for the evolution of bipedalism in hominids.

## ACKNOWLEDGMENTS

We thank Linda Marchant for arranging contacts at the Cincinnati and Columbus zoos; Jill Pruett for arranging contacts at the University of Texas M.D. Anderson Cancer Center Science Park; the staff and volunteers at the Cincinnati Zoo and Botanical Gardens, Columbus Zoo and Aquarium, and University of Texas M.D. Anderson Cancer Center Science Park; and Terri Roth, Linda Kelly, Beth Pohl, Dusty Lombardi, Susan Lambeth, Steve Shapiro, and Jessica Powell.

## REFERENCES

- Altmann J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227–267.
- Cameron DW. 1993. The pliocene hominid and protochimpanzee behavioral morphotypes. *J Anthropol Arch* 12:386–414.
- Darwin C. 1886. *Descent of man, and selection in relation to sex*. New York: D. Appleton.
- De Vore I, Washburn SL. 1996. Baboon ecology and human evolution. In: Howell FC, Bouriere F, editors. *African ecology and human evolution*. Chicago: Aldine Publishing Co. p 335–367.
- deWaal F. 1997. *Bonobo: the forgotten ape*. Berkeley: University of California Press. p 53.
- deWaal F. 2001. *Tree of origin: what primate behavior can tell us about human social*



## Bipedality in Bonobo and Chimpanzee / 239

- evolution. Cambridge: Harvard University Press.
- Doran DM. 1993. Comparative locomotor behavior of chimpanzees and bonobos: the influence of morphology on locomotion. *Am J Phys Anthropol* 91:83–98.
- DuBrul EL. 1962. The general phenomenon of bipedalism. *Am Zool* 2:205–208.
- Goodall J, Hamburg DA. 1974. Chimpanzee behavior as a model for the behavior of early man: new evidence on possible origins of human behavior. In: Hamburg DA, Brodie HKH, editors. *American handbook of psychiatry*. Vol. 6. New York: Basic Books. p 14–43.
- Goodall J. 1986. *The chimpanzees of Gombe: patterns of behavior*. Cambridge: Belknap Press of Harvard University.
- Hohmann G, Fruth B. 1993. Field observations on meat sharing among bonobos (*Pan paniscus*). *Folia Primatol* 60:225–229.
- Horai S, Satta Y, Hayasaka K, Kondo R, Inque T, Ishida T, Hayashi S, Takahata N. 1992. Man's place in Hominoidea revealed by mitochondrial-DNA genealogy. *J Mol Evol* 35:32–43.
- 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. 1994. The evolution of human bipedalism: ecology and functional morphology. *J Hum Evol* 26:183–202.
- Hunt KD, Cant JGH, Gebo DL, Rose MD, Walker SE, Youlatos D. 1996. Standardized descriptions of primate locomotor and postural modes. *Primates* 37:363–387.
- Kortlandt A. 1962. Chimpanzees in the wild. *Sci Am* 206:128–138.
- Reinartz G, Leus K. 1998. World holdings in EEP and SSP: listed by institution. Milwaukee County Zoological Gardens.
- Relethford JH. 2000. *The human species: an introduction to biological anthropology*. Mountain View: Mayfield Publishing Company. p 229.
- Rose MD. 1991. The process of bipedalization in hominids. In: Coppens Y, Senut B, editors. *Origine(s) de la bipédie chez les hominides*. Paris: Éditions de Centre National de la Recherche Scientifique. p 37–48.
- Savage-Rumbaugh ES. 1994. Hominid evolution: looking to modern apes for clues. In: Quiatt D, Itani I, editors. *Hominid culture in primate perspective*. Niwot: University of Colorado Press. p 7–49.
- Sibley CG, Comstock JA, Alquist JE. 1990. DNA hybridization evidence on hominoid phylogeny: a reanalysis of the data. *J Mol Evol* 30:202–236.
- Stanford CB. 1996. The hunting ecology of wild chimpanzees: implications for the evolutionary ecology of pliocene hominids. *Am Anthropol* 98:96–113.
- Stanford CB. 1998. The social behavior of chimpanzees and bonobos: empirical evidence and shifting assumptions. *Curr Anthropol* 39:399–420.
- Stern Jr JT, Susman RL. 1983. The locomotor anatomy of *Australopithecus afarensis*. *Am J Phys Anthropol* 60:279–317.
- Susman RL, Badrian NL, Badrian AJ. 1980. Locomotor behavior of *Pan paniscus* in Zaire. *Am J Phys Anthropol* 53:69–80.
- Susman RL. 1984. The locomotor behavior of *Pan paniscus* in the Lomako forest. In: Susman RL, editor. *The Pygmy chimpanzee: evolutionary biology and behavior*. New York: Plenum Press. p 369–393.
- Susman RL. 1987. Pygmy chimpanzees and common chimpanzees: models for the behavioral ecology of the earliest hominids. In: Kinzey WG, editor. *The evolution of human behavior: primate models*. Albany: State University of New York Press. p 72–86.
- Takahata N, Satta Y. 1997. Evolution of the primate lineage leading to modern humans: phylogenetic and demographic inferences from DNA sequences. *Proc Natl Acad Sci U S A* 94:4811–4815.
- Thompson J. 1994. Cultural diversity in the behavior of *Pan*. In: Quiatt D, Itani J, editors. *Hominid Culture in Primate Perspective*. Niwot: University of Colorado Press. p 95–115.
- Videan EN. 2000. *Bipedality in bonobo (Pan paniscus) and chimpanzee (Pan troglodytes): implications for the evolution of bipedalism in hominids*. Master's thesis. Oxford, OH: Miami University.
- Wrangham RW. 1980. Bipedal locomotion as a feeding adaptation in gelada baboons, and its implications for hominid evolution. *J Hum Evol* 9:329–331.
- Zihlman AL, Cronin JE, Cramer DL, Sarich VM. 1978. Pygmy chimpanzee as a possible prototype for the common ancestor of humans, chimpanzees, and gorillas. *Nature* 275:744–746.
- Zihlman AL. 1996. Reconstructions reconsidered: chimpanzee models and human evolution. In: McGrew WC, Marchant LF, Nishida T, editors. *Great ape societies*. Cambridge: Cambridge University Press. p 293–304.