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Sex differences in bonobo (*Pan paniscus*) terrestriality: implications for human evolution

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Summary - *Recent finds in hominin fossil environments place the transition to terrestriality in a wooded or forested habitat. Therefore, forest-dwelling apes can aid in understanding this important evolutionary transition. Sex differences in ape locomotion have been previously attributed to sexual dimorphism or ecological niche differences between males and females. This study examined the hypothesis that differential advantages of terrestrial travel may impact mating success in male bonobos. We examined whether males are more terrestrial when there are mating benefits for fast travel. We analyzed behavioral data on wild bonobos over a ten-month period in the Lomako Forest, DRC and examined the proportion of time spent at lower heights compared to higher heights between adult females and males relative to their location to feeding contexts with high mating frequencies. We found a significant interaction between sex and height class away from food patches ($F=4.65$, $df = 1$, $p < 0.05$) such that females were primarily arboreal whereas there was no difference between males across height classes. However, there was also a significant interaction between sex and height class ($F = 29.35$, $df = 1$, $p < 0.0001$) for adults traveling near or entering a food patch. Males often arrived at food patches terrestrially and females arrived almost exclusively arboreally. We found a significant difference between the expected and observed distribution of matings by food patch context ($G = 114.36$, $df = 4$, $p < 0.0001$) such that most mating occurred near or in a food patch. These results suggest that males may travel terrestrially to arrive at food patches before cohesive parties of females arrive arboreally, in order to compete with other males for mating access to these females. Such intrasexual selection for sex differences in locomotion may be important in considerations of the evolution of locomotion strategies in hominins in a forested environment.*

Keywords - *Hominin, Locomotion, Sexual dimorphism, Sexual selection.*

Introduction

Studies of sex differences of locomotion in wild primates are important to our understanding of the evolutionary connection between behavior and morphology in both living and extinct human and non-human primates (Strasser *et al.*, 1998; D'Août & Vereecke, 2011). Unlike studies of non-human primates, hypotheses on the origin of human terrestrial travel have rarely incorporated differing male and female travel strategies (Boinski & Garber, 2000). This perspective can have a direct impact on our thinking about the evolution of human locomotion. In addition, the growing body of paleoenvironmental data linking early hominin shifts to terrestrial bipedalism in woodland or forested environments underscores the relevance of studies of forest ape locomotion to our understanding of both bipedality and terrestriality (Andrews & Humphrey, 1999; Ward *et al.*, 1999; WoldeGabriel *et al.*, 2001; Senut, 2006; Lovejoy, 2009). Studies ranging from observations of chimpanzee bipedal feeding posture (Hunt, 1994b, 1996), primate vertical climbing (Fleagle *et al.*, 1981), orangutan use of upright locomotion to increase stability on unstable slender branches (Thorpe *et al.*, 2007), and bipedality during water-wading (Wrangham *et al.*, 2009) have expanded considerations of possible ecological contexts for the evolutionary advantages of human bipedality in woodland or forested environments in both arboreal and terrestrial contexts. While the use of terrestriality or bipedality in some behavioral contexts such as bipedal threat displays (Jablonski & Chaplin, 1993) or the energetics of infant carrying (Watson *et al.,* 2009) can be examined in ape studies, other hypotheses, such as the importance of provisioning by males, have no direct ape model for comparison (Lovejoy, 2009).

Many studies have found that body size has a significant impact on primate locomotion behavior with larger individuals, sexes, or species showing consistent differences including being more terrestrial, using larger arboreal supports, as well as other locomotion differences (Fleagle, 1978,1985; Doran, 1993b; Gebo & Chapman, 1995; McGraw, 1998). Sexual dimorphism is also related to dietary niche separation in primates (Pokempner & Kamilar, 2008). Although differences in methodology, however, can make comparisons of locomotion strategies among studies and species difficult (Dagosto & Gebo, 1998), sex differences in locomotion among ape species have been related to sexual dimorphism in body weight or skeletal morphology, with smaller females being more arboreal than the larger and more terrestrial males (Doran, 1993a,b, 1996, 2009; Hunt, 1994a). This includes orangutan females which are more arboreal than larger males (Cant, 1987; Galdikas, 1988) with adult males typically coming to the ground to travel longer distances (Rodman & Mitani, 1987), although Thorpe & Crompton (2005, 2006) found only small sex differences in the type of locomotion used during arboreal travel in Sumatran orangutans when all behavioral and ecological variables are taken into account. Chimpanzee females are also more arboreal than chimpanzee males although there was considerable inter-site variability in the degree of arboreality that varied with habitat (Doran, 1996). Doran (1993b) found that sex differences in substrate height use in chimpanzees at Taï were related to females resting more arboreally and not to height differences during feeding despite sex differences in diet. She also found that males use less quadrupedalism, climbing, and bipedalism than females, particularly while feeding. Doran (1993b) proposed that females and their infants suffer more frequently from predation than males, and that this selects for greater female arboreality. Among lowland gorillas, females are more arboreal than males (Remis, 1999; Doran, 2009) and use more suspensory postures and bipedal modes than males (Remis, 1995). These studies point to sex differences in locomotor strategies that may be present in all great apes.

Although locomotion strategies are often interpreted as adaptations to habitat structure or foraging strategies, sex differences in ape locomotion are by nature multifunctional and often context dependent (Doran, 1996). Studies have recognized the importance of differences in energetic and nutritional requirements of the sexes associated with reproductive state or the risks of falls (Altmann & Samuels, 1992; Pontzer & Wrangham, 2004, 2006), as well as the effects of male rank (Hunt, 1994a) or environment (Videan & McGrew, 2001, 2002) on locomotion or ranging behavior. However, it is important to also consider the possible impact of sexually selected behavioral strategies on locomotion patterns.

Sexual selection can result in sex differences in many aspects of behavior and morphology (Darwin, 1871; Andersson, 1994). The degree of sexual dimorphism is strongly related to intrasexual selection in the form of male-male competition in polygynous primates (Mitani *et al.,* 1996). Intrasexual selection for locomotion speed and effectiveness may also be an important factor especially when males and females range separately such as in fission-fusion species like chimpanzees and bonobos. Differences in male locomotor patterns in these species, therefore, may reflect different male strategies to gain access to females that are dispersed within the group's territory while avoiding rival or dominant males, neighboring males, and predators.

This study investigates sex differences in bonobo locomotion and tests both the sexual dimorphism and sexual selection hypotheses for male terrestriality. Bonobos exhibit equivalent sexual dimorphism to chimpanzees, with males being about 30% heavier than females (Jungers & Susman, 1984). Under the sexual dimorphism hypothesis, we predicted that males would exhibit terrestriality in most contexts, except during feeding in food patches. Alternatively, modes of travel to food patches that allow males to arrive before females, therefore, may be an important component of male-male competition in bonobos. At Lomako, White & Wood (2007) previously noted that most matings happen in food patches at the start of a feeding bout with mating priority determined by won decided aggressive interactions among the males before the females enter the food tree. Although terrestrial travel by chimpanzees is energetically more expensive (Pontzer *et al.,* 2011; Pontzer & Wrangham, 2004) and more vulnerable to terrestrial predators (Doran, 1993b), predominantly leopard at Lomako (Badrian & Malenky, 1984), it is less risky, in terms of injury from falls, and probably faster than arboreal travel over long distances at higher speeds of locomotion. If sexual selection explains male terrestriality, we predicted a sex difference in height during travel near and entering food patches with males exhibiting more terrestriality than females. Females, in contrast, should travel more arboreally at all times to find and access more food patches and to potentially avoid terrestrial predators. We also predicted that most mating would occur near, entering, or in food patches.

Methods

Data were collected on non-provisioned bonobos at the N'dele field site (0° 51' N, 21° 5' E) in the Lomako Forest Reserve, Democratic Republic of Congo. The study site consists of approximately 40 km² of mapped trails and features a mosaic of forest types but is principally evergreen polyspecific rain forest with some areas of secondary and swamp forest (White, 1992a,b). We analyzed 248 hrs of focal animal observation collected between October 1984 and July 1985 of known individuals from two communities and a splinter group. During the study period (and excluding infants), the Bakumba community consisted of eight adult males, one subadult male, four juvenile males, 14 adult females, five adolescent females, four juvenile females; the Eyengo community consisted of five adult males, three subadult males, one juvenile male, nine adult females, two adolescent females, one juvenile female; and the splinter group consisted of five adult males, one adult female, and four adolescent females.

Behavioral data were collected using two-minute focal animal sampling (Altmann, 1974). The activity, height class, and party size were recorded for the focal animal as well as context of the time point. See Table 1 for height classes. Individuals were classified as in a food patch if they were in a food tree or vine canopy that contained food that was eaten by at least one party member. We considered individuals to be near a food patch if they were in the immediate vicinity of a food patch, either in the adjacent tree or vine or in the understory or on the ground below the food patch canopy (< 50 m). Individuals on the main access branch or other entrance branches were recorded as entering a food patch but were not considered "in" the patch until they were on a branch or the trunk of the feeding tree. Finally, individuals travelling out of a food patch were classified as leaving a food patch. Changes in party composition from individuals leaving or joining a party and all social behavior was recorded *ab libitum* (Altmann, 1974).

Given the non-independence of data on focal animal height, we used one-zero scoring to count if an individual had been observed at least once for each height class per sighting. For example, if an individual was observed in height classes 2, 4, and 6 these were scored as '1' whereas height classes 0, 1, 3, 5, 7, 8, and 9 were scored as '0'. We grouped height classes 0, 1, and 2 (< 10 m) and labeled this category as 'low' whereas height classes > 2 (> 10 m) were considered to be 'high' (Tab. 1). We summed height class scores for adult females and males during travel per month by height class and converted counts to proportions of total counts per month within sexes to account for differences in the number of focal follows between females

Tab. 1 - Height classes.

	HEIGHT CLASS	HEIGHT (M)
LOW	0	Ground
	1	1 to 5
	2	6 to 10
HIGH	3	11 to 15
	4	16 to 20
	5	21 to 25
	6	26 to 30
	7	31 to 35
	8	36 to 40
	9	above 40

and males. Finally, we separated these counts based on location to a feeding patch. We generated two data subsets: 1) travel outside of a food patch and 2) travel near (< 50 m) and entering a food patch. Thus, we exclude data on travel while in or leaving a food patch for this analysis. A small number of months did not include any sightings in a specific food patch context for either females or males. We analyzed height class proportions from 9 months for females and 8 months for males when near or entering a food patch and 9 months for both females and males outside a food patch. These data are provided in the Supplementary Material. We ran a two-way ANOVA for each data subset with height class and sex as fixed effects and an interaction between height class and sex using the built-in ‘stats’ package in R, version 3.5.2 (R Core Team, 2017) and visualized data using ggplot2 (Wickham, 2016).

We also examined the distribution of mating by food patch context by comparing the observed data to an expected frequency calculated from two-minute time points in each context during all focal sampling. These data are available in the Supplementary Material. We compared these vectors using a G-test of goodness-of-fit (Sokal & Rohlf, 2011) using the R package ‘DescTools’ (Signorell *et al.,* 2019).

Results

There was a significant interaction between height class and sex ($F=4.65$, $df = 1$, $p < 0.05$) for out of patch travel with males spending more time at lower levels than females although both males and females were predominantly at higher levels (Fig. 1). We also found a significant interaction between height class and sex ($F = 29.35$, $df = 1$, $p < 0.0001$) when individuals were near or entering a food patch but, unlike females, males spent a preponderance of time at lower levels when near or entering a food patch.

The observed distribution of matings ($N = 41$) by food patch context was significantly different to the expected distribution ($G = 114.36$, $df = 4$, $p < 0.0001$). Mating was most frequent when entering or in a food patch (Fig. 2).

Discussion

These results add a further possible advantage of terrestriality, beyond sexual dimorphism or ecological niche, associated with the sexual selection of differential male reproductive strategies in bonobos. We found that males engaged in terrestriality near and entering food patches whereas females were predominately arboreal in the same contexts. We did find a significant interaction between sex and height class on travel outside of food patches, however, males were less terrestrial outside of food patches. Nonetheless, we cannot completely discount sexual dimorphism as a functional hypothesis for male terrestriality in this species. Given that few differences in bonobo feeding ecology exist between females and males, there does not appear to be support for the ecological niche hypothesis for sex differences in locomotion (White, 1992a). Further, females typically feed first in food patches so that fast travel to these sites by males does not reflect competition for access to the available food (White & Wood, 2007). While Kano (1992) made some observations of males collecting food at artificial feeding sites prior to the arrival of other individuals, this situation is

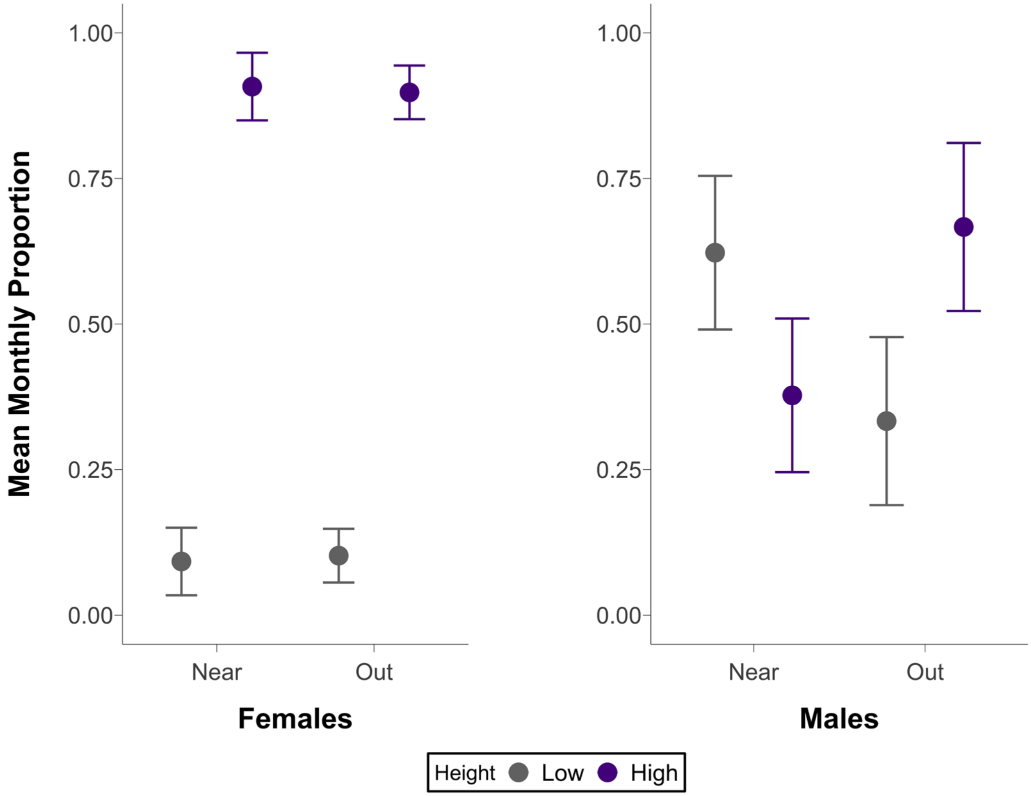

Fig. 1 - Proportion of time near/entering a food patch and outside a food patch at each height class for females and males. The colour version of this figure is available at the JASs website.

different to arboreal food patches whose access points are more limited than terrestrial feeding sites. The reproductive advantage of terrestriality is presumably dependent on the unique bonobo social and ranging patterns and, as such, may not apply to other ape species. Therefore, this study provides further support that terrestriality may infer different advantages depending on either ecological or social conditions or both.

The start of feeding bouts in discrete food patches, typically fruit trees, represents an important time of male-male competition for mating opportunities (White & Wood, 2007). The pattern of male-male competition for mating in bonobos, therefore, involves males travelling fast and often alone on the ground to food trees, while the females travel more slowly with others through the trees. These early arriving males then dispute control of the main arboreal access route into the food patch through male-male aggressive interactions, with the winner evicting other males from the food tree (White & Wood, 2007). This high-ranking male then mates with many, if not all, of the females as they arrive at the food patch before the feeding bout starts (White & Wood, 2007). It is, therefore, important to males to arrive at food patches before the females have entered. As not all community males travel to all food patches and there are often multiple parties in multiple food patches throughout the community range, mating is not restricted to the highest-ranking male in the community but is biased towards the highest-ranking male at any one location.

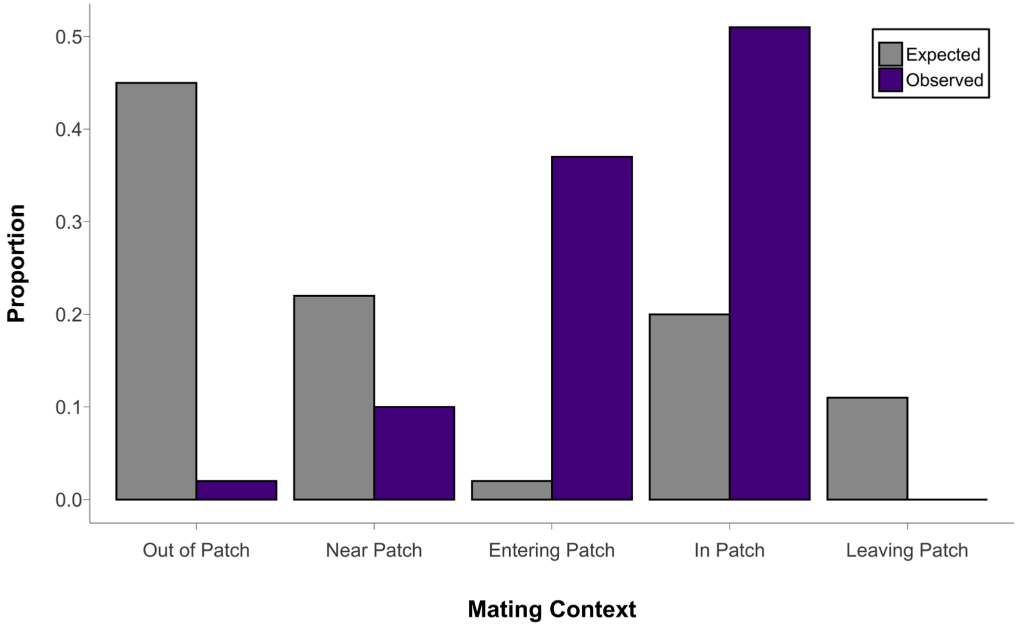

Fig. 2 - Expected vs. observed distribution of mating by food patch context. The colour version of this figure is available at the JASs website.

Males may also gain additional mating opportunities by travelling to more than one food patch.

The results of this study should, however, be interpreted with caution because of the small sample sizes involved. Observation of terrestrial travel by Lomako bonobos can be difficult. The bonobos at this site have two major contexts for terrestrial travel: ground foraging and direct travel to a distant food patch. When the bonobos were travelling on the ground to forage on terrestrial herbaceous vegetation (THV) such as *Haumania* sp., or aquatic plants, insects, or fish, they typically moved slowly and in varying directions and were relatively easy to follow. Observations of this ground foraging could last up to 6 hours. In contrast, it is very difficult to follow bonobos engaged in fast terrestrial travel to food trees so that these sample sizes were small.

An additional complication in this study is that most bonobo mating is presumably non-reproductive. Bonobos mate throughout the sexual and reproductive cycles (Thompson-Handler *et al.,* 1984; Thompson-Handler, 1990). Male strategies to obtain more mating with females may reflect factors other than male-male competition for reproductive success such as competition for social support from females (e.g., Surbeck *et al.,* 2010). Males, however, mate most frequently with those females with large swellings and with either no or independent offspring (White *et al.,* 1998). These females are presumably closest to ovulating (but see Reichert *et al.,* 2006), but only future, more detailed studies could determine if the male strategy of controlling access into food trees actually translates into male reproductive success. Curiously, male reproductive skew is greater, on average, in bonobos than chimpanzees (Surbeck *et al.,* 2017; Ishizuka *et al.,* 2018, but see McCarthy *et al.,* 2020). However, despite all these limitations, this study suggests the possible advantage of terrestriality associated with the sexual selection for differential male and female reproductive strategies.

This study prompts the consideration of how sexual selection may contribute to the evolution of locomotor strategies in hominins. While we note that the patterns observed here may be limited to forested environments with continuous canopy, paleoenvironmental data suggest that this habitat type was present in the geographic ranges of hominin taxa in which major shifts in locomotor strategies may have occurred (WoldeGabriel *et al.*, 2001, 2009). Further study on locomotion in other bonobo populations and other extant great apes could help discern whether or not our results are population or species-specific. Indeed, unique aspects of bonobo behavioral ecology underscores that sexual selection for male terrestriality could be less important than other factors, such as body mass, in hominin evolution as a whole. Additional research is needed to further test functional hypotheses for sex differences in terrestriality in the great apes as these results can contribute to our understanding of the evolution of locomotion in humans.

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Author contributions

FJW conceived of the project, secured funding, and collected the data. All authors participated in data analysis and writing/editing of the manuscript.

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