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Sex differences in positional behavior of chimpanzees (*Pan troglodytes schweinfurthii*) living in the dry and open habitat of Issa Valley, Tanzania

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Abstract

Objectives: Many early fossil hominins are associated with savanna-mosaic paleohabitats, and high sexual dimorphism that may reflect differences in positional behavior between sexes. However, reconstructions of hominin behavior and the selective pressures they faced in an open habitat are limited by a lack of studies of extant apes living in contemporary, analogous habitats. Here, we describe adult chimpanzee positional behavior in the savanna-mosaic habitat of the Issa Valley, Tanzania, to test whether Issa chimpanzees show larger sex-differences in positional behavior than their forest-dwelling counterparts.

Materials and Methods: We quantified and compared adult locomotor and postural behavior across sexes (6 females, 7 males) in the riparian forest (closed) and miombo woodland (open) vegetation types at Issa Valley (13,743 focal observations). We then compared our results to published data of chimpanzee communities living in more forested habitats.

Results: Issa females and males both spent less time arboreally in open vegetation and showed similar locomotor and postural behavior on the same substrates, notably using a high level of suspensory locomotion when arboreal. Females were, however, more arboreal than males during locomotor behavior, as well as compared with females from other communities. Issa males behaved similarly to males from other communities.

Conclusion: Results suggest that open habitats do not elicit less arboreal behaviors in either sex, and may even select for suspensory locomotion to effectively navigate an open canopy. An open habitat may, however, increase sex differences in positional behavior by driving female arboreality. We suggest this is because of higher energetic demands and predator pressures associated with open vegetation, which are likely

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exaggerated for reproducing females. These results have implications for the interpretation of how sexual dimorphism may influence reconstructions of hominin positional behavior.

KEYWORDS
African apes, ecomorphology, hominin origins, locomotor behavior, savanna-mosaic

1 | INTRODUCTION

A shift from forest to savanna habitat holds a central role in hypotheses about hominin speciation and key behavioral transitions. In particular, sparse and heterogenous vegetation associated with savanna-mosaics has been hypothesized to select for increased terrestrial travel and arboreal climbing (as opposed to other arboreal behaviors such as suspension; Rodman & McHenry, 1980; Shipman, 1986; MacLatchy et al., 2023; Senut et al., 2018). However, a high degree of sexual dimorphism interpreted for some australopith taxa (e.g., *Australopithecus afarensis*; Alemseged, 2023; Gordon, 2013; Gordon et al., 2008; Grabowski et al., 2015; Haile-Selassie et al., 2010; Plavcan et al., 2005; Richmond & Jungers, 1995; but see Reno et al., 2003) that lived in savanna-mosaic habitat (Blumenthal et al., 2017; Bonnefille, 2010; Cerling et al., 2011; Su & Haile-Selassie, 2022) has led some to suggest exaggerated sex differences in positional behavior (Hunt et al., 2021; Stern & Susman, 1983; Susman et al., 1984). Specifically, smaller females are suggested to be more arboreal and larger males more terrestrial given that (1) living primates show a negative association between body mass and arboreality (e.g., Cant, 1992; Doran, 1993a, 1996; Fan et al., 2013; Fleagle & Mittermeier, 1980), and (2) smaller (assumed female) specimens more regularly display morphology considered advantageous for arboreal locomotion (i.e., wider pelves and relatively shorter hindlimbs; Cartmill, 1985; Hunt et al., 2021) compared with presumably male specimens (Haile-Selassie et al., 2010). Understanding variation in positional behavior of apes living in different habitats may help to refine our functional interpretations of morphological variation in extant and fossil hominids and inform hypotheses about hominid evolution in different paleoenvironments (Carlson, 2005; Carlson et al., 2006; Hunt, 1991a; Hunt et al., 2021; Thorpe & Crompton, 2006). However, how vegetation affects substrate use and positional behavior of males and females differently has never been tested in extant hominids.

Chimpanzees (*Pan troglodytes*) are unique among nonhuman great apes (hereafter "great apes") in living across a range of habitat types, from tropical forest to seasonal savanna-mosaics (Humle et al., 2016; van Leeuwen et al., 2020). Chimpanzees thus provide a valuable natural experiment to examine how great ape positional behavior varies across habitat types and explore evolutionary hypotheses about adaptation to dry, open habitats as a driver for hominin (e.g., Domínguez-Rodrigo, 2014; Hunt, 1994; Rodman & McHenry, 1980; Senut et al., 2018) and hominid (MacLatchy et al., 2023) evolution. Studies of chimpanzee positional behavior have, however, to date focused on forest sites (Mahale and Gombe, Tanzania; Hunt, 1991b, 1992; Taï National Park, Ivory Coast; Doran, 1993a, 1993b; Kibale National Park, Uganda; Sarringhaus et al., 2014) (Figure 1), limiting our understanding of the causes and extent of variation and plasticity in *Pan* behavior.

To address the lack of data on great ape positional behavior in open habitats, we quantitatively characterized adult chimpanzee (*Pan troglodytes schweinfurthii*) positional behavior in the Issa Valley, Tanzania, a savanna-mosaic that is analogous to paleohabitat reconstructions of early hominin sites (Levin et al., 2008; Schoeninger et al., 2003; Senut et al., 2001; Su & Haile-Selassie, 2022; White et al., 2009). We (Drummond-Clarke et al., 2022) previously showed that although Issa chimpanzees spent more time in locomotor behaviors than their forest-dwelling counterparts, they were not more terrestrial and more frequently used suspensory locomotion. These results are in contradiction to hominin evolutionary hypotheses that a more open habitat drove increased terrestriality (Napier, 1967; Rodman & McHenry, 1980; Sockol et al., 2007) and increased climbing of more sparsely distributed trees (Senut et al., 2018). Here, we follow-up those results and investigate potential sex differences in positional behavior across the chimpanzee habitat gradient by characterizing variation between females and males across (1) vegetation types within the Issa Valley savanna-mosaic habitat, and (2) within the context of previously studied forest chimpanzee communities. Specifically, we test the hypotheses that:

1. Habitat variables (such as openness and vegetation structure) are more important than body mass as determinants of adult chimpanzee positional behavior. If so, we predicted that adult females and males would (i) show the same change in positional behavior frequency between vegetation types (i.e., more terrestrial locomotion in open vegetation due to more sparsely distributed feeding trees) and, (ii) exhibit similar positional behavior on substrates of the same characteristics, and more specifically on flexible substrates in the canopy.
2. Sex differences in arboreality are exaggerated in open habitat. Specifically, we hypothesized that living in a savanna-mosaic habitat will be a stronger driver of arboreality for females than males. If supported, we expected differences in arboreality between sexes to be larger at Issa than in communities in forest habitats and, in particular, Issa females to be more arboreal than females of forest-dwelling communities.

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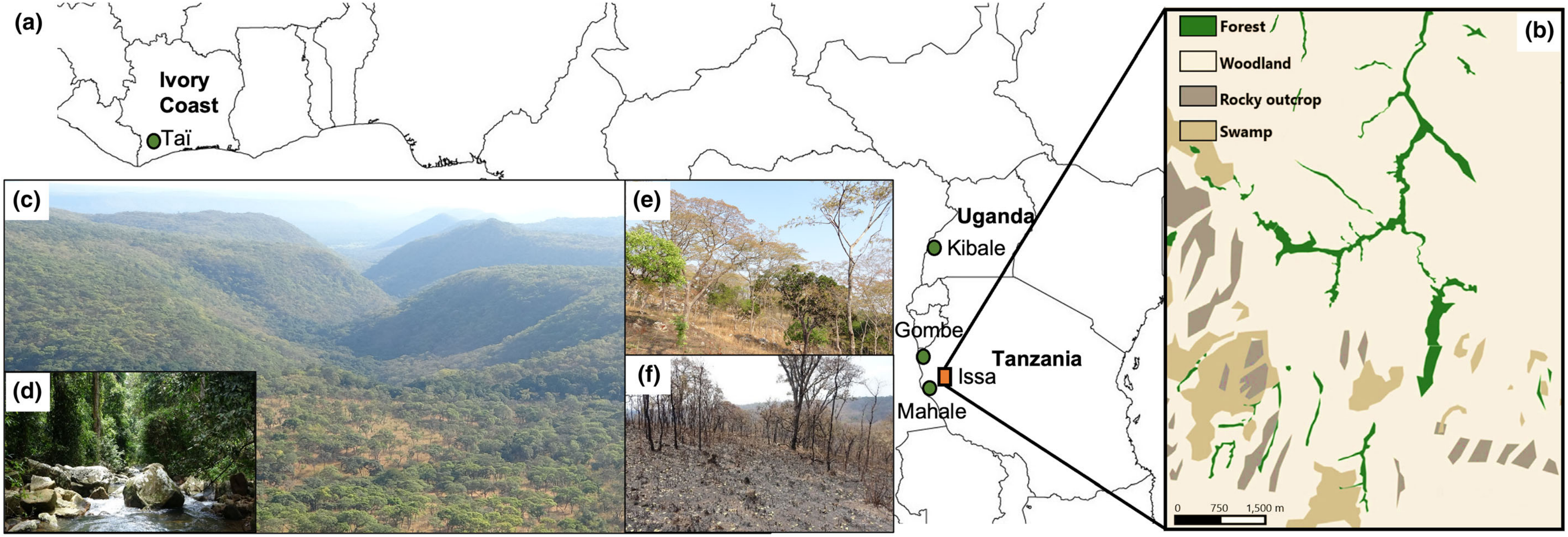

FIGURE 1 The Issa Valley study site. (a) Location of Issa valley in western Tanzania, and of more forested chimpanzee sites previously studied for positional behavior. Forested sites are represented by green circles, savanna by orange rectangle. Notably, Taï hosts the western subspecies (*Pan troglodytes verus*), all other sites host eastern chimpanzees (*Pan troglodytes schweinfurthii*). (b) The Issa Valley mosaic vegetation map. (c) View of the landscape looking north up Issa Valley. The chimpanzees use principally two vegetation types: (d) the riparian forest, closed vegetation that covers less than 7% of the landscape and (e) the miombo woodland, open vegetation which covers >80% of the landscape and is burnt annually by grass fires (f).

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1.1 | General patterns of forest-dwelling chimpanzee positional behavior

Field studies of forest chimpanzee positional behavior have demonstrated that chimpanzees (eastern; *P. t. schweinfurthii*, and western; *Pan troglodytes verus*) are best characterized as terrestrial travelers (average 90% of total travel time) and arboreal feeders (average 85% of total feeding time; Doran & Hunt, 1994; Hunt, 2016). The vast majority of their time is spent in stationary positions (hereafter referred to as "posture" or "postural behaviors"), spending less than 20% of their time in locomotor behaviors (or "locomotion", defined as any movement involving body mass displacement) (Doran & Hunt, 1994; Hunt, 2016; Williams et al., 2023).

Averaged across forest sites of Mahale (M-group), Gombe (Kasekela), Taï (North-group; taken from Hunt, (2020)), and Kibale (Ngogo; Sarringhaus et al., 2014), adult chimpanzees spend the majority of their waking hours sitting (63%), as this is the main posture used during feeding, resting, and grooming (Doran, 1993b; Hunt, 1992). The next most exhibited behavior is quadrupedal walking (14%), which is the main mode of terrestrial locomotion, closely followed by lying (13%). Much of the remainder of their time is spent in suspensory (3.3%), climbing (1%), and bipedal (0.3%) behaviors, which, although relatively rare, are critical for chimpanzees to forage in the canopy and are hypothesized to be important influencers of ape anatomy (Hunt, 1991b; Keith, 1923; Lovejoy et al., 2009; MacLatchy et al., 2023; Prang et al., 2021; Thompson et al., 2018; Tuttle, 1967).

Chimpanzees use vertical climbing (ascent and descent; Table S1) to negotiate vertical supports angled greater than 45° (mainly tree trunks and lianas; Hunt et al., 1996) between the ground and the canopy to access arboreal foods, for nesting, or for avoiding predators. This mode of locomotion includes biomechanically distinct submodes depending on the direction of travel and width of the substrate being climbed: flexed-elbow climbing is generally used on smaller substrates less than 20 cm wide, where flexed forelimbs help to elevate the body and extended hindlimbs provide propulsion (Hunt et al., 1996; Thorpe & Crompton, 2006). Supports >20 cm wide are more likely to evoke extended-elbow climbing, where propulsion is generated by the extended forelimbs (Hunt, 1991a, 1992; Hunt et al., 1996; Neufuss et al., 2017). While substrate width can have the same effect on forelimb position during downclimbing, moving with gravity means the limbs are used for braking rather than propulsion, which may induce larger forelimb joint angles (Fannin et al., 2023), and can involve "sliding" or "cascade" modes of descent (Hunt et al., 1996; Thorpe & Crompton, 2006) (Table S1). Chimpanzees use suspensory postures (e.g., forelimb suspend) and locomotion (e.g., forelimb swing; Table S1) to safely navigate thin, flexible substrates (i.e., terminal branches, where food is most often located) by displacing their body mass below the support to reduce the risk of falling (Cartmill, 1985; Saunders et al., 2018). Similarly, bipedalism is also used most commonly in the terminal branches (Drummond-Clarke et al., 2022; Hunt, 1994; Stanford, 2006) and may also be an important locomotor strategy for large-bodied, orthograde apes to navigate flexible supports (Drummond-Clarke et al., 2022; Thorpe et al., 2007).

1.2 | Current understanding of variation in chimpanzee positional behavior

Despite the general cross-community similarities in adult chimpanzee positional behavior described above, there is also clear variation within and between communities (e.g., Doran & Hunt, 1994; Sarringhaus et al., 2014). Primarily, females are consistently more arboreal than males (Doran & Hunt, 1994), which has been linked to their smaller body mass (20%–30% less than males; Carter et al., 2008; Doran, 1993a, 1996; Grabowski et al., 2015; Pusey et al., 2005). Body mass is suggested to affect the frequency of arboreality and thus primate positional behavior by dictating how many arboreal pathways are available to an animal and how they navigate thin supports (Cant, 1992; Doran, 1993a; Fleagle & Mittermeier, 1980). However, tests of this hypothesis in chimpanzees have produced mixed results. Taï chimpanzees are the only community to show significant sex differences in how individuals move once in the trees (hereafter arboreal locomotor behavior), whereas Gombe and Mahale individuals only show sex differences in positional behavior related to the amount of time spent in the trees (hereafter level of arboreality; Doran, 1993a; Doran & Hunt, 1994). Although there is documented variation in body mass between (*P. t. verus* is larger than *P. t. schweinfurthii*) and within chimpanzee subspecies, there is no evidence of subspecific variation in sexual dimorphism (e.g., Carter et al., 2008; Pontzer, 2017; Pusey et al., 2005). It is therefore unlikely that variation in sex differences in (arboreal) positional behavior between communities is due to body size (Doran, 1993a).

Intracommunity variation in positional behavior is indicative of morphology (i.e., because of sexual dimorphism), but also differences in selective pressures depending on ecological context (related to sex, predator risk, and social interactions, among others; Cant, 1992; Karr & James, 1975; Saunders et al., 2018). For example, higher nutritional demands associated with gestation and lactation (Dufour & Sauther, 2002; Murray et al., 2009; Thompson et al., 2012; Thompson & Wrangham, 2008) and predator risk to dependent young (Bezanson, 2009; Monteza-Moreno et al., 2020) may drive high female arboreality. In contrast, resource defense is an important aspect of male chimpanzee ecology, selecting for terrestrial travel in the form of patrols (Boesch & Boesch-Achermann, 2000; Drummond-Clarke et al., 2023; Goodall, 1979; Watts et al., 2006; Watts & Mitani, 2001; Wilson & Wrangham, 2003). Notably, open, heterogenous vegetation characteristic of savanna-mosaic habitats is associated with increased terrestriality (Domínguez-Rodrigo, 2014; Lindshield et al., 2021; Rodman & McHenry, 1980), but also increased energetic demands (Wessling et al., 2018) and perceived predator risk that may increase arboreality (Fornof et al., 2023; Lindshield et al., 2017; Monteza-Moreno et al., 2020). Although variation in positional behavior in relation to habitat structure is widespread across the primates (e.g., *Colobus badius*; Gebo & Chapman, 1995, *Pongo*; Manduell et al., 2011, 2012) including *P. troglodytes* (Drummond-Clarke et al., 2022), how sex and habitat interact to influence chimpanzee substrate use and positional behavior remains poorly understood. Additional studies that expand our understanding

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of intracommunity variation in chimpanzee positional behavior across an ecological gradient (in particular in dry and open environments), are necessary to better understand the role of habitat on sex differences in positional behavior. Chimpanzees of the Issa Valley not only live in one of the driest sites that chimpanzees inhabit (van Leeuwen et al., 2020), but also use open (woodland) and closed (forest) vegetation types within their habitat (Drummond-Clarke et al., 2022; Giuliano et al., 2022). Observations of the Issa chimpanzee community thus offer a rich comparative dataset to test how vegetation type influences positional behavior in females and males, within and between sites.

2 | METHODS

2.1 | Study site and subjects

The Issa Valley is a savanna-mosaic habitat located in western Tanzania, with rugged topography ranging from ~1050 to 1750 m in elevation (Figure 1). The site is dominated by miombo woodland (86% of landscape) interspersed with riparian forest strips (<7%) as well as swamps and grassland (Figure 1b), although chimpanzees were only observed in woodland and forest vegetation. Woodland vegetation is characterized by deciduous trees (predominantly *Brachystegia*, *Julbernardia* and *Isoberlinia* spp.) with discontinuous canopies and a grassy understory (Figure 1e,f). Riparian forest vegetation is characterized by evergreen and semi-deciduous vegetation, continuous canopies and open or liana dense understories (Piel et al., 2017; Russak, 2014) (Figure 1d). These vegetation types differ significantly in aspects of vegetation structure that affect arboreal substrate availability and openness; the miombo woodland has half the tree density of the forest (Piel & Stewart, unpublished data), and significantly lower tree height, crown height, and canopy connectivity (van Leeuwen, 2019). Thus, the riparian forest is considered as "closed" vegetation, whereas the miombo woodland is "open" (Figure 1).

At the time of the current study, the community consisted of 29 individuals, which were individually identifiable. We only include adults in this study (a total of 13 individuals; seven males and six females, five of which had dependent young), as there was an insufficient number of individuals per subadult age category for meaningful comparisons.

2.2 | Data collection

Data collection methods followed those outlined in Drummond-Clarke et al. (2022) and are further described in Supplementary Material 1 in Data S2. Data collection methods were in concordance to previous studies of chimpanzee positional behavior to allow for intercommunity comparisons (Doran & Hunt, 1994; Hunt, 1992; Sarringhaus et al., 2014). We recorded focal individual positional behavior every 2 min during 1 h follows, standardizing positional behavior into modes and submodes following the hierarchical scheme set out in Hunt et al. (1996) and reflecting modifications by Thorpe and Crompton (2006) (see Table S1). At the 2 min mark we also recorded vegetation type (forest vs. woodland), substrate type (e.g., arboreal [terminal branch, central tree] and terrestrial supports), and arboreal substrate diameter.

During a total of 459 observation hours, we obtained a total of 13,743 instantaneous observations of positional behavior, of which 2849 were locomotor and 10,412 were postural bouts (482 were nonvisible; Table 1). Observations were distributed across sexes, vegetation types, and seasons.

2.2.1 | Classification of supports/substrates

Weight bearing substrates were principally split into terrestrial and arboreal. Arboreal substrates included three categories: (1) central tree (tree trunk including base of branches that join onto it); (2) branches (secondary and terminal supports that form the tree crown); (3) lianas. Terrestrial substrates included the ground, fallen tree trunks, boulders, and vertical rock face. If there were multiple supports used (i.e., hands and feet on different branches), the support that bore the most weight was used (judged by position and amount of bending of branch; Thorpe et al., 2007). For arboreal bouts, the diameter of the substrate was recorded. Arboreal substrate diameter was grouped into four categories based on kinematic qualities used in previous studies (Doran, 1993a,b; Hunt, 1992); very thin and flexible supports (<3 cm), larger flexible supports (3–10 cm), more stable supports that can still be gripped by an adult chimpanzee hand (10–20 cm), and nonflexible supports greater than 20 cm.

2.3 | Statistical analysis

We ran all statistical tests in R studio v4.3.2 (R Core Team, 2023), with levels of significance set at $p < 0.05$. Raw data were used to calculate means for all analyses. Normality of data was assessed using Shapiro–Wilcox test and variance was assessed using Levenes test. When data were normally distributed, parametric tests were used for pairwise comparisons (e.g., between the sexes) because of their higher statistical power, but significance checked against the nonparametric test equivalent to avoid Type I and Type II errors that can arise using parametric tests on discrete (frequency) data. Follows for each individuals were aggregated to single data points within analytical categories to avoid repeated sampling and to reduce the degree of dependence within analytical categories (Sarringhaus et al., 2014). The percentage of time spent moving was calculated as the proportion of 2 min samples that individuals engaged in locomotion. Level of arboreality was calculated as the percent of observations when individuals were on arboreal supports relative to total observations (i.e., arboreal + terrestrial supports). Level of arboreality and the percentage of time each individual spent in each mode and submode were calculated as a proportion of the overall positional behavior profile, and for postural and locomotor behavior separately (see below). We averaged all results

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TABLE 1 Number of 2 min scans per adult sex category and vegetation type recorded throughout the study period (2020 and 2021 combined).

	Vegetation type season									
	Riparian forest				Miombo woodland					
Focal sex/ID	Early dry	Late dry	Wet	Forest total	Early dry	Late dry	Wet	Woodland total	Total scans	N locomotion
Female	1241	1558	1141	3940	1077	1075	637	2789	6729	1336
Ba.	67	310	149	526	55	89	94	238	764	133
Ju.	293	307	265	865	194	146	137	477	1342	244
Ki.	192	251	107	550	235	121	79	435	985	196
Ko.	205	234	210	649	281	286	64	631	1280	301
Ma.	173	197	193	563	74	267	124	465	1028	189
Za.	311	259	217	787	238	166	139	543	1330	273
Male	962	1169	822	2953	1859	1459	743	4061	7014	1511
Bo.	142	156	26	324	316	225	125	666	990	197
El.	197	214	136	547	247	209	41	497	1044	209
Im.	146	227	244	617	386	232	108	726	1343	296
Kit.	82	14	76	172	124	62	40	226	398	99
Mb.	123	181	84	388	364	214	84	662	1050	214
Sa.	77	213	115	405	140	257	67	464	869	164
Wa.	195	164	141	500	282	260	278	820	1320	332
Grand Total	2203	2727	1963	6893	2936	2534	1380	6850	13,743	2847

Note: Both sexes spent roughly equal amounts of time in both habitats, although females slightly more time in the forest (58.5% of overall time) and males in the miombo (57.9%).

across months, since temporal or seasonal variation was not the focus of the current study.

2.3.1 | Postural behavior

Interdependence of sequential observations separated by small-time intervals (in this case 2 min) is problematic in analyses of postural behavior data since postural bouts (starting when a posture, such as sitting, is first recorded until a change of positional mode) often have a duration longer than 2 min. To ensure independence of postural scans, we thus collapsed consecutive duplicates during a single focal observation for subsequent analyses (following Hunt, 1992; Sarringhaus et al., 2014) (Table S2a). The frequencies of main postural modes were normally distributed across sexes, and therefore we used *t*-tests to examine differences in postural behavior between sexes in the Issa community. We then checked for differences in postural behavior between vegetation types for each sex category independently (e.g., female sitting in forest vs. female sitting in woodland) using Wilcoxon Signed Rank test, as sex-specific vegetation data were not normally distributed, and paired.

2.3.2 | Locomotor behavior

In contrast to chimpanzee postural behavior, locomotor bouts—defined as the beginning of locomotor activity to stopping locomotion— are regularly interrupted by bouts of rest or change of locomotor mode, avoiding problems of interdependence between locomotor observations. Therefore, all observations of locomotion were subsequently analyzed (following Hunt, 1992; Sarringhaus et al., 2014). All main locomotor modes were normally distributed and of equal variance between sex and vegetation type categories. Differences between sexes were thus analyzed using *t*-tests and differences between sexes by vegetation type were analyzed using two-way ANOVA with repeats (to account for data point interdependence as the same individuals are represented in each vegetation type) and Tukey's post-hoc comparisons. Arboreal substrate diameter used during locomotor behavior was also compared by sex and vegetation type using two-way ANOVA with repeats.

2.3.3 | Intercommunity comparison

Statistical comparisons between other chimpanzee communities were limited to the mean data presented in the published literature. All intercommunity comparisons were thus qualitative. Postural frequencies with collapsed consecutive data points were compared to Kibale (Ngogo; Sarringhaus et al., 2014), Mahale (M-group) and Gombe (Kasakela; Hunt, 1992), and postural frequencies with noncollapsed consecutive data points were used in comparison to Taï (North-group; Doran, 1993b) (Table 2). For comparisons on locomotor behavior, different studies used different groupings of locomotor modes into

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TABLE 2 Summary of intercommunity comparison of chimpanzee positional behavior (adults only).

Site community	Issa NA			Kibale Ngogo	Taï N group	Mahale M group	Gombe Kasekela
Subspecies	(*P.t.s*)			(*P.t.s*)	(*P.t.v*)	(*P.t.s*)	(*P.t.s*)
Citation	Drummond-Clarke et al., 2022; Current study			Sarringhaus et al., 2014	Doran 1989; Doran, 1993a	Hunt 1989; Hunt, 1992	
Habitat/ vegetation type	Savanna-mosaic	Riparian forest	Miombo woodland	Dense forest	Dense forest	Mosaic forest	Mosaic forest
% Overall arboreality							
Male	43.8	47.9	39.3	-	48.9	32.9	37.4
Female	67.9	75.5	60.7	-	64.8	47.8	68.4
% Time as locomotion	22.0	19.2	24.3	17.0	15.0	18.0	18.0
% Locomotor arboreality[a]							
Male	15.6	26.7	11.0	-	14.7	8.2	
Female	40.2	57.6	28.2		18.2	12	
Postural behavior[b]							
Sit/Lie	91.0/73.0	-	-	92.0/77.0	92.0/-	-/90.0	-/90.0
Suspend	3.0/8.2			2.2/7.5	1.5/-	-/4.2	-/4.2
stand	1.9/5.5			2.4/8.0	5.9/-	-/1.7	-/4.3
Locomotor behavior[c]							
Quad. walk	81.0	75.4	87.2	77.0	86.0	92.0	92.0
Male	88.8	83.8	82.9	86.0	86.6	93.6	96.5
Female	74.9	66.9	91.4	69.0	85.6	91.3	89.5
Climb	10.5/11.5	13.0/-	9.3/-	11.8/-	-/11.0	-/5.9	-/6.0
Male	7.7/7.8	11.1/-	5.9/-	-	-/11.1	-/5.1	-/3.5
Female	13.7/15.2	14.8/-	12.7/-	-	-/10.9	-/7.7	-/8.9
Suspensory	5/5.2	7.9/-	2.4/-	5.6/-	-/1.3	-/0.9	0.5
Male	2.3/2.4	3.8/-	1.4/-	2.4/-	-/1.1	-/0.8	-/0.0
Female	7.7/8.0	12.0	3.3/-	8.9/-	-/1.4	-/0.9	-/0.5
Bipedal	1.0	1.7	0.7	1.8	1.2	0.3	-
Male	0.5	0.6	0.5	-	1.2	0.3	-
Female	1.6	2.5	0.6	-	1.2	0.2	-

Note: Issa forest and woodland columns represent values for these distinctive vegetation types within the Issa habitat, whereas "savanna-mosaic" is the mean across the entire site. All values show mean percentages.

Abbreviations: *P.t.s*, *Pan troglodytes schweinfurthii*; *P.t.v*, *Pan troglodytes verus*.

[a] Values for Mahale and Taï taken from Carlson (2005). For Gombe, estimated from Hunt (1992) and Doran and Hunt (1994). Ngogo value provided by Sarringhaus (unpublished data).

[b] First value presents frequencies with noncollapsed consecutive scans of the same behavior, second value presents frequencies with consecutives collapsed.

[c] Two values are given for locomotor behavioral frequencies to allow comparison to past studies: First value represents locomotor categories based off modern classification schemes following Sarringhaus et al. (2014), "climb" includes modes vertical climb and vertical descent, "suspensory" includes modes arrested drop, bimanual pull-up, clamber, forelimb swing, transfer, and unimanual forelimb twist; "other" includes bridge, drop, ride/sway, and forelimb–hindlimb swing. The second value represents grouping of modes following Doran and Hunt (1994), suspensory includes as above + dropping and riding, "climbing" includes as above + bridging and swaying. Where only one value is given, locomotor categories included the same modes. Analyses of Issa locomotor ecology were run using first values based on modern classification schemes.

locomotor broader categories. As such we present two values per locomotor category for Issa (following the different categorical groupings) to facilitate comparison of general locomotor behavior across communities (see Table 2).

3 | RESULTS

We present first an overview of the general positional behavioral profile of Issa adult chimpanzees (posture and locomotion pooled). We

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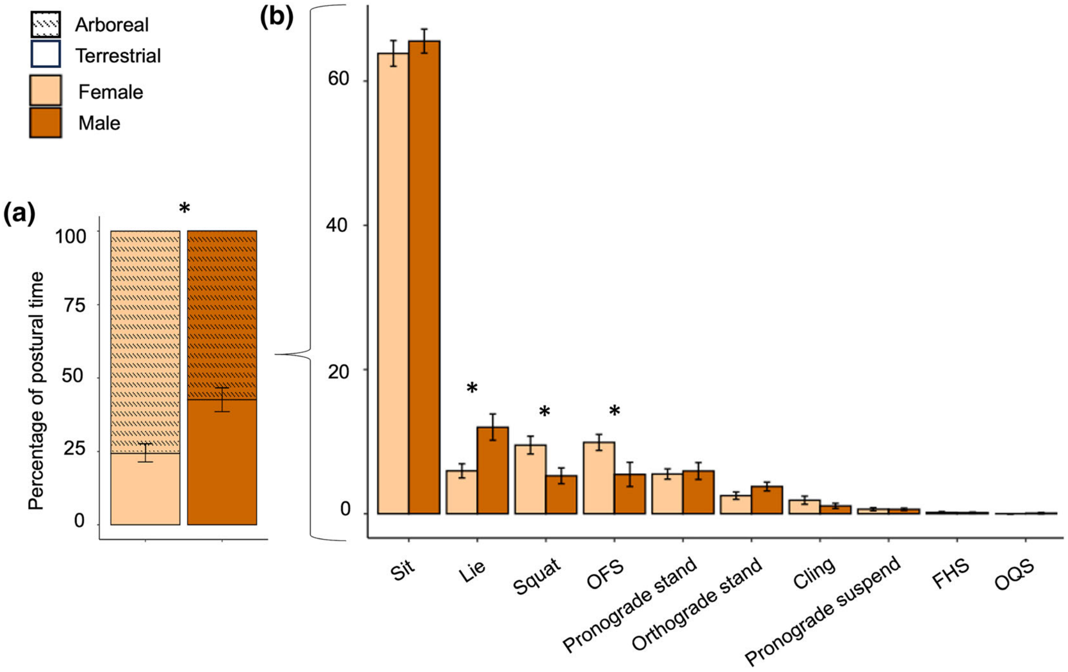

FIGURE 2 Postural behavioral profiles of Issa Valley females (light orange) and males (dark orange), averaged across vegetation types. (a) Level of arboreality versus terrestriality during postural time. Issa chimpanzees (sexes pooled) spent on average 65% of their observed postural time in the trees, but females were significantly more arboreal during postural behaviors than males. (b) Frequencies of main postural modes shown by Issa adults. Stars indicate significant differences between sexes. Error bars show standard error from the mean. FHS, forelimb–hindlimb suspend; OFS, orthograde-forelimb suspend; OQS, orthograde-quadrupedal suspend.

then consider posture and locomotion separately to investigate how positional behavior and substrate use compares between sexes and vegetation types. Finally, we present arboreal locomotion specifically to test whether females and males move differently in the canopy.

3.1 | General positional behavior profile

Overall, Issa chimpanzees (sexes pooled) spent 78% of their time in postural behaviors, with less than a quarter of their time spent in locomotion (Table 2). About 57% of their total observation time was spent arboreally. Considered by vegetation type they spent more time in locomotor behaviors in the woodland compared to the forest ($F = 6.62$, $p = 0.026$), but significantly less time arboreally ($F = 7.75$, $p = 0.018$; Table 2). There were no significant sex differences in time spent in locomotion ($F = 0.55$, $p = 0.474$), but females were overall significantly more arboreal than males (68% vs. 44%; $F = 16.91$, $p = 0.002$). The highest level of arboreality was thus shown by females in the forest (76%), and the lowest level of arboreality by males in the woodland (39%; Table 2).

3.2 | Postural behavior

Issa chimpanzee postural mode frequencies are presented in Figure 2. Issa chimpanzees (sexes pooled) spent on average 65% of their observed postural time in the trees, regardless of vegetation type ($F = 4.82$, $p = 0.051$). Issa chimpanzees spent by far the most postural time sitting (65%), with the next most common postural mode, lie, only accounting for 9% of postural behavior. Females were, however, significantly more arboreal ($F = 8.88$, $p = 0.012$); Figure 2a, and spent more time in forelimb suspensory ($t = 2.16$, $p = 0.042$) and squatting ($t = 2.81$, $p = 0.01$) postures, but less time lying ($t = -3.60$, $p = 0.002$) than males (Figure 2b).

Considered together, Issa chimpanzees spent less time sitting (62% vs. 68%; $t = -3.20$, $p = 0.008$) but more time in forelimb suspensory postures (10% vs. 6%; $t = 4.17$, $p = 0.001$) in the forest than in woodland vegetation. However, considered by sex, only males showed a difference in postural mode frequency between vegetation types, using orthograde-forelimb suspension less when in the woodland compared to the forest (3% vs. 8%, $V = 21.00$, $p = 0.036$).

3.3 | Locomotor behavior

Averaged across sexes, Issa chimpanzees spent 28% of their total locomotor time arboreally, and spent over 80% of all locomotor time quadrupedal walking, 10% climbing, and 5% in suspensory locomotion, with bipedal and other forms of locomotion each accounting for less than 2% of locomotor time (Figure 3a). Issa chimpanzees were significantly more arboreal in the forest than in the woodland (39% vs. 18%; $t = 5.99$, $p < 0.001$), and thus spent more time in solely arboreal locomotor behaviors (vertical climbing [$F = 10.01$, $p = 0.009$] and suspensory locomotion [$F = 19.36$, $p = 0.001$]), and less time quadrupedal

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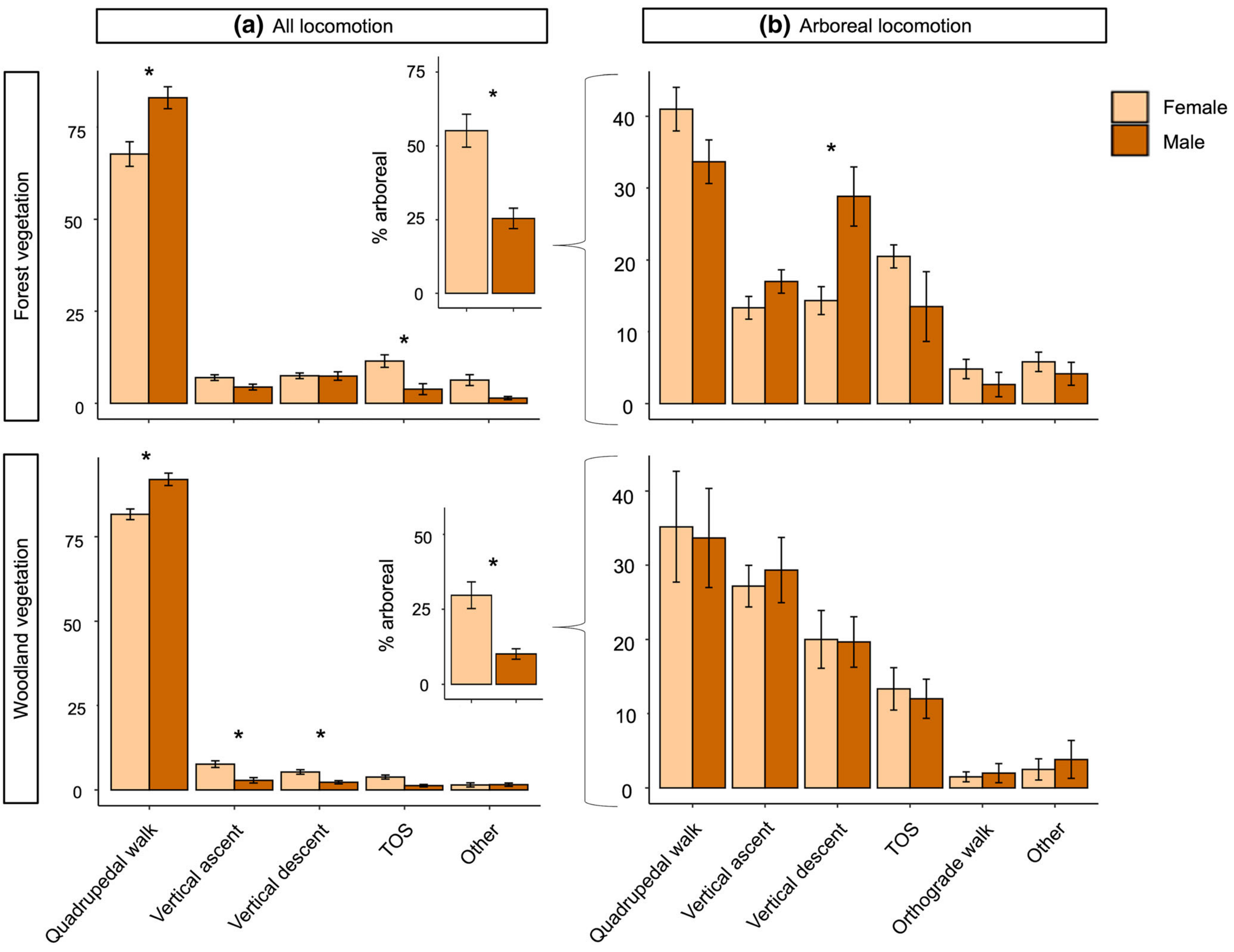

FIGURE 3 Locomotor behavior of females (light orange) and males (dark orange) between forest (top row) and woodland (bottom row) vegetation types at Issa. (a) Main locomotor mode frequencies during locomotor observation time at Issa (arboreal and terrestrial). Note negative correlation between level of arboreality (graph inserts) and percentage of overall locomotor time spent quadrupedal walking as although used in the trees too, quadrupedal walking is the main terrestrial locomotor mode. Both sexes used less arboreal locomotion in the woodland compared with forest, but females were consistently more arboreal than males in both vegetation types. (b) Arboreal locomotor behavior (i.e., not including terrestrial behavior). The only significant difference between sexes was when in the forest females spent less time in vertical descent than males when in the forest. Females spent significantly less time vertical ascent climbing when in the forest compared to when in the woodland. Stars indicate significant differences between sexes. Error bars show standard error from the mean. "Other" includes bridge, drop, ride/sway, and forelimb–hindlimb swing. TOS, torso-orthograde suspend.

walking ($F = 20.82$, $p < 0.001$), in the forest compared to woodland (Table 2).

Considered by sex, females were significantly more arboreal ($F = 29.65$, $p < 0.001$) and spent significantly less time quadrupedal walking ($F = 24.3$, $p < 0.001$), and more time in suspensory ($F = 17.23$, $p = 0.002$), and climbing ($F = 18.15$, $p = 0.001$) behaviors than males (Table 2). When climbing was divided into vertical ascent and descent, females engaged in ascent significantly more than males (7% vs. 4%; $F = 16.03$, $p = 0.002$), but not descent (6% vs. 5%).

Tukey's post-hoc comparisons showed that changes in frequencies of locomotor behavior between vegetation types varied by sex (Table S2b). When in the forest females spent significantly less time quadrupedal walking ($p = 0.012$) and more time in suspensory locomotion ($p = 0.003$) compared to in the woodland (Figure 3a). To the contrary, males did not change their frequency of quadrupedal walking or suspensory locomotion significantly with vegetation type, but exhibited less vertical descent in the woodland compared to forest ($p = 0.003$; Figure 3a). Further, the extent of differences between males and females depended on vegetation type (Figure 3a). Males notably showed a low frequency of vertical ascent climbing compared with females in the woodland ($p = 0.003$), but not in the forest. Females only used suspensory locomotion significantly more than males in the forest, but not in the woodland ($p < 0.001$; Figure 3a).

We found further variation in the frequency of locomotor submodes (Table S2c). Males and females varied in the frequency of different types of suspensory locomotion; whereas males spent more

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than half of suspensory locomotion as forelimb swinging, females were more diverse, distributing their suspensory locomotion across three submodes: transfer (30%), forelimb swing (20%) and clamber (20%). When considered by vegetation type, both sexes used arrested drop more and forelimb swing less during suspensory locomotion in the woodlands compared to the forest. Both sexes also tended toward a higher frequency of extended-elbow (as opposed to flexed-elbow) vertical ascent in the woodland compared to forest (Table S2c).

3.4 | Arboreal locomotor behavior

When terrestrial, quadrupedal walking was the dominant behavior (90%) for both sexes, regardless of vegetation type (Table S2). Once in the trees, however, locomotor behavior was much more varied, with 42% spent vertical climbing, 36% quadrupedal walking, and 14% engaged in suspensory behaviors (sexes pooled). Averaged across sexes, the only arboreal locomotor mode to show a significant difference with vegetation type was vertical ascent climbing, which was engaged in more frequently in the woodland compared to the forest (28% vs. 14%, $F = 12.90$, $p = 0.004$; Table S2b).

Considered by sex, we found no difference in arboreal locomotor mode frequencies between females and males when arboreal locomotor behavior was pooled across vegetation types (Table S2b). However, Tukey's post-hoc comparisons showed that, in the forest, females spent less time vertical descent climbing than males ($p = 0.024$; Figure 3b). Further, females where the only sex to change their arboreal locomotor behavior significantly between vegetation types, spending more time vertical ascent climbing in the woodland than forest ($p = 0.011$; Figure 3b).

Across all arboreal locomotion (sexes and vegetation types pooled), 59% was exhibited on substrates <10 cm in diameter (of which only 7% was on <3 cm diameter), and 41% on substrates >10 cm in diameter (22% 10–20 cm, 19% > 20 cm; Table S2d). Use of substrates 10–20 cm in diameter was the only category to differ significantly between sexes, being used more by males than females (31% vs. 18%; $F = 5.9$, $p = 0.033$). When female and male frequencies were pooled, the use of substrates 3–10 cm in diameter was significantly higher in the forest compared with woodland (59% vs. 39%; $F = 9.0$, $p = 0.012$), whereas use of substrates >20 cm in diameter showed a trend toward being lower in the forest ($F = 4.1$, $p = 0.067$; Table S2d). Use of substrates <3 cm and between 10 and 20 cm in diameter did not differ significantly between vegetation types (Table S2d). When substrate use was considered by locomotor mode, Issa chimpanzees (sexes pooled) predominantly used substrates <10 cm in diameter for all locomotor modes except vertical ascent and descent (Figure 4). Substrate diameter use did not differ significantly with vegetation type during specific locomotor modes, although during vertical climbing (ascent and descent) the use of substrates >20 cm in diameter approached significance between vegetation types (woodland > forest, $F = 3.9$, $p = 0.075$) (Table S2d).

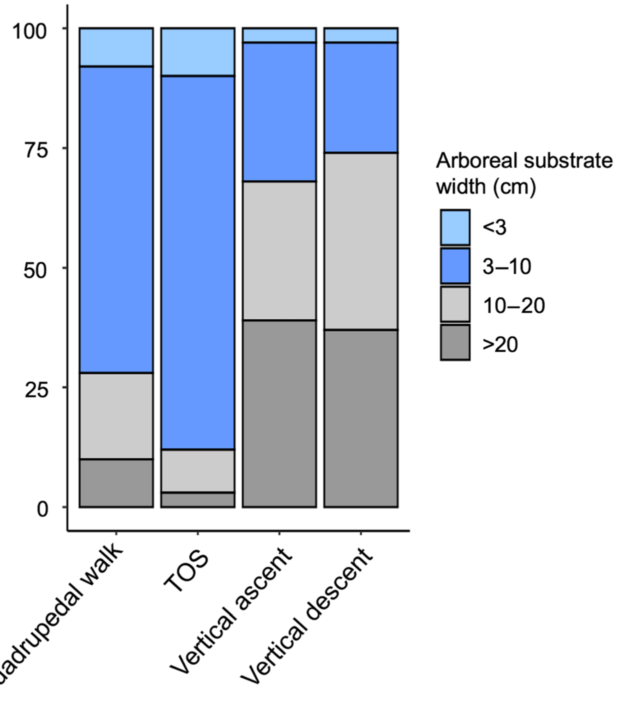

FIGURE 4 Arboreal substrate width used by Issa chimpanzees (sexes pooled) during principle arboreal locomotor categories, averaged across vegetation types. Substrates considered flexible (smaller than 10 cm in diameter) are in shades of blue, substrates considered nonflexible (larger than 10 cm) are depicted in gray. Note vertical climbing (including ascent and descent) is the only locomotor category to be practiced mostly on substrates wider than 10 cm.

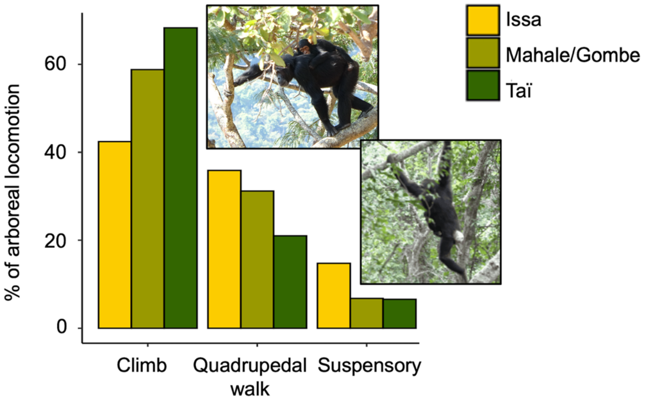

FIGURE 5 Intercommunity comparison of arboreal locomotor behavior frequencies (sexes pooled). Note Issa has a high level of suspensory and quadrupedal locomotion (both behaviors associated with low angled, thinner substrates, i.e., terminal branches), but low level of climbing (vertical ascent and descent combined; a behavior associated with highly angled, wider substrates, i.e., trunks) compared with the more forested sites. Photo credits RCDC/GMERC.

3.5 | Intercommunity comparison

Intercommunity comparisons are summarized in Table 2 and Figure 5. Comparisons of the general positional behavior profiles (sexes pooled)

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show Issa chimpanzees spent more time in locomotor behaviors than forest-dwelling chimpanzees. Where possible, collapsing consecutive data points of postural modes decreased the frequency of the most common "sitting" posture and increased the relative frequency of less common postures across sites. Although such "collapsed" and "non-collapsed" postural frequencies were only available for Issa (Table S2a) and Kibale (Sarringhaus et al., 2014), a similar pattern is assumed in sites where only one value is available (i.e., the frequency of sitting would decrease for Mahale/Gombe if consecutive data points were not collapsed). Comparisons of postural time showed that chimpanzees (sexes pooled) at Gombe and Mahale spent more time sitting/lying than at Issa, Kibale, and Taï (Table 2). Issa and Kibale chimpanzees also spent a similar proportion of postural time in suspensory behaviors (~8%), with Mahale and Taï chimpanzees spending half the amount of time in suspensory postures (4%). Notably, Issa chimpanzees exhibited higher inter-sex variation in postural behavior (with significant differences in orthograde-forelimb suspension, squat, and lie) than adults at Kibale, which only showed sex differences in time engaged in pronograde stand (females = 11% males = 5%; Sarringhaus et al., 2014). Whereas Taï chimpanzees showed sex differences in their postural behavior (Doran, 1993a), no results were presented of specific postural behaviors so no further comparisons are possible.

Although Issa chimpanzees spent more time locomoting than individuals from other communities, they spent less locomotor time using quadrupedal walking (83%) and more time in suspensory and climbing behaviors (15% combined) than all communities except Ngogo (quadrupedal walking 77%; climbing and suspensory 19%; Table 2). However, considering arboreal locomotion only, Issa chimpanzees showed a low frequency of climbing but high frequency of suspensory locomotion compared with other sites (although arboreal locomotor frequencies were not available for Ngogo; Figure 5). Issa locomotor mode frequencies were most similar to Kibale and Taï chimpanzees, the most forested sites included in this comparison. Further, Issa and Kibale showed similarities in locomotor submode frequencies (Table S2c). Unfortunately, there is no such fine-scale data available for the other chimpanzee sites for further comparisons. Issa chimpanzees showed a larger difference between sexes in overall locomotor behavior than chimpanzees at Taï, Mahale, (Doran, 1993a; Doran & Hunt, 1994) and Kibale (Sarringhaus et al., 2014), all of which exhibited no significant differences between adult males and females. The only other sex differences in locomotor behavior were reported from Gombe, where, in a pattern similar to Issa, females engaged in significantly more climbing and less quadrupedal walking than males (Doran & Hunt, 1994). Taï chimpanzees showed sex differences in arboreal locomotion, but again no results were presented of specific locomotor behaviors for a more detailed comparison (Doran, 1993a).

4 | DISCUSSION

Here, we provide the first characterization of sex differences in chimpanzee positional behavior and substrate use in a savanna-mosaic habitat, with the aim of testing the hypothesis that sex differences in adult positional behavior are more pronounced in open habitat compared to more forested habitats, specifically because of high female arboreality. Results highlight significant sex differences in positional behavior among Issa chimpanzees, largely due to differences in the level of arboreality, that support our hypotheses. Below we interpret our results in the context of published findings from forest-dwelling chimpanzees, to better characterize variation in chimpanzee positional behavior across their environmental range and the implications for reconstructing fossil hominid positional behavior.

4.1 | Habitat openness and chimpanzee positional behavior

We hypothesized that habitat variables such as vegetation type, and specifically openness, would have a similar effect on variation in adult chimpanzee positional behavior despite differences in body mass. To test this hypothesis, we compared adult female and male postural and locomotor behavior, as well as substrate use, across open and closed vegetation types within their savanna-mosaic habitat. We found that female and male positional behavior differed in similar ways between vegetation types and on varying substrates, supporting our hypothesis.

Our characterization of positional behavior highlights how both female and male chimpanzee locomotor behavior differs with changes in vegetation structure at Issa, with implications for potential differences in skeletal morphology (e.g., Hunt et al., 2021). As would be predicted in open vegetation with more sparsely distributed arboreal substrates (and food sources), both males and females spent more time in locomotion but less time in the trees in the woodland compared to forest. Less time spent in the trees resulted in a reduction of arboreal locomotor behaviors but had little effect on postural behavior. In other words, differences in level of arboreality during locomotor (but not postural) behaviors were the main determinant of variation in positional behavior with vegetation type. Although this is indicative of more terrestrial travel between arboreal food sources in open vegetation, differences in how Issa chimpanzees move once in the trees of the forest versus woodland suggests differences in tree structure may also have an important influence on chimpanzee positional behavior. In particular, Issa chimpanzees increased the frequency of vertical ascent climbing in woodland compared with forest trees. Access to the canopy in the woodland compared to the forest at Issa is characterized by predominantly vertical arboreal supports >10 cm in diameter (accentuated by a lack of lianas) (Figure 1; van Leeuwen, 2019). We thus suggest that the observed increase in extended (rather than flexed) elbow climbing (Table S2c), as well as vertical ascent climbing of large substrates in woodland vegetation are interlinked (Hunt, 1992; Hunt et al., 1996; Neufuss et al., 2017), and would likely become significant with a larger sample of climbing observations. Combined with previous observations suggesting chimpanzees primarily use climbing substrates smaller than 20 cm in diameter (Hunt, 1992), and the lack of (small-diameter) lianas in the woodland,

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FIGURE 6 Example of a low, wide canopy woodland tree (*Brachystegia microphylla*) in the rugged Issa landscape, hypothesized to facilitate suspensory locomotion out of trees rather than vertical descent climbing. Predominant tree genera in the woodland (*Brachystegia* spp., *Julbernardia* spp.) have wide, short crowns consisting of mostly horizontal, (rather than vertical) branches, perhaps limiting vertical climbing and rather facilitating more energy efficient suspensory locomotor modes such as forelimb swing, transfer, drop, and assisted-bipedalism. Images (a–c) show stills from Video S1 of an adult male using suspensory locomotion on a flexible branch to lower themselves out of the canopy to the ground, without using vertical descent climbing. Photo and video credits RCDC/GMERC.

this supports a hypothesis that changes in substrate use (and therefore locomotor behavior) between vegetation types are likely because of availability, rather than preference (Manduell et al., 2012).

That Issa chimpanzees increased vertical ascent, but not descent, in woodland trees is, however, surprising if chimpanzees are limited primarily to vertical supports to enter and exit the canopy. Our observations suggest this pattern may be due to Issa chimpanzees using suspensory behaviors (i.e., arrested drop or transfer; which make up a higher proportion of suspensory behavior in the woodland (50%) than in the forest [36%; Table S2c]) to descend from woodland trees; both locomotor submodes are practiced on flexible and/or horizontal branches rather than vertical trunks and are also considered more energetically efficient than vertical descent climbing (Thorpe et al., 2007). The use of nonvertical climbing behaviors to exit trees could be facilitated by two features of the Issa woodland landscape: (1) the lower tree height and wider tree crowns compared with the forest that allow the chimpanzees to effectively “drop off” from the terminal branches that flex toward the ground with their body weight (Supplementary Videos 1-3; Figure 6), and (2) the rugged, hilly nature of the woodland landscape, which means that often after climbing into the canopy, chimpanzees were at equal height to adjacent rocky outcrops. Chimpanzees could thus access the ground horizontally from the terminal branches, rather than needing to move vertically to exit the tree crown (Supplementary Videos 1-3; Figure 6).

Apes are typically distinguished from other primates by their highly mobile shoulder and elbow joints (Almécija et al., 2021; Keith, 1891; Larson, 1993; Lee et al., 2023; Rose, 1974). Although it is generally accepted that mobile forelimbs are functionally adaptive to reduce the risk of falling and energetic costs of climbing in the face of increasing body size (Pontzer & Wrangham, 2004), the role of specific positional behaviors is disputed. Vertical ascent climbing and (mostly postural) suspensory behaviors have been at

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the forefront of discussions (e.g., Almécija et al., 2021; Hunt, 1991a, 2016; Williams et al., 2023), and more recently vertical descent, or “downclimbing” (Fannin et al., 2023). It should however be noted that in the latter, highly-positioned (highly-flexed shoulder joint and highly-extended elbow joint) forelimbs were observed during controlled braking during downclimbing, but the seperation between these phases of the downclimbing gait (i.e., pausing locomotion to “hang” from the substrate) and suspensory posture is unclear (e.g., Druelle et al., 2024). Our results demonstrate how suspensory locomotion can also be used to move out of the canopy; that is, used as a vertical, rather than just horizontal, movement as standardly defined (Hunt et al., 1996), making use of flexible, low branches especially in more open, rugged landscapes (Figure 6). We therefore suggest the distinction between vertical descent and suspension in behavioral and anatomical studies may not be so clear cut, and suspensory locomotion may be an important behavior to move between the canopy and ground in open habitat. This has implications for reconstructions of the locomotor repertoires of early hominins and hominids that lived in open, wooded habitats as early as 21 million years ago (Peppe et al., 2023), which have previously been associated with more vertical climbing rather than suspension (e.g., MacLatchy et al., 2023; Senut et al., 2018).

Overall, both Issa female and male chimpanzees spent more time in locomotor behaviors than forest-dwelling chimpanzees but retained a high level of arboreality with a notably high proportion of time using suspensory locomotor behaviors. This finding suggests (1) more locomotor time in open vegetation is not limited to terrestrial substrates, but is also arboreal, (2) open vegetation encourages a diverse arboreal locomotor repertoire to effectively navigate the tree crowns, despite a broken canopy with limited arboreal pathways, and (3) that this may be facilitated by a rugged landscape. More data on feeding-tree crown structural characteristics across vegetation types within Issa is necessary to test what structural aspects of trees (i.e., crown shape, number, diameter, and orientation of branches) in open vegetation encourage terminal branch locomotor behaviors. Data from Kibale on arboreal locomotor behavior and substrate use, as well as detailed vegetation structure comparisons, would also be insightful, since Kibale chimpanzees exhibit similar locomotor behavioral frequencies to Issa, despite Kibale being more forested than Issa (Drummond-Clarke et al., 2022) (Table 2). Information on the rates of vertical climbing and suspensory behaviors from Fongoli, a savanna site but with flat topography (Pruetz & Bertolani, 2009), would be particularly insightful for investigating the role of topography on locomotor behavior.

4.2 | Positional behavior sex differences and vegetation openness

We also tested the hypothesis that a savanna-mosaic habitat drives sex differences in positional behavior, specifically via increased female arboreality. In keeping with previous studies of forest-dwelling chimpanzees, Issa females were significantly more arboreal than males during overall positional behavior (Doran & Hunt, 1994). However, in support of our hypothesis that open vegetation drives female arboreality, Issa females showed higher arboreality than females in forested communities (40% vs. <20% at other sites; Table 2). This also means that Issa chimpanzees showed significant differences in locomotor behavior between sexes, with females having a more diverse locomotor repertoire than males (consisting of more suspensory and climbing behaviors) that varied more between vegetation types (Figure 3). Notably, once in the trees, females spent significantly more time vertical ascent climbing when in woodland compared to forest, whereas males showed no significant change in arboreal locomotor behavior between vegetation types (Table 2). These locomotor differences are perhaps due to females retaining high arboreality in the woodland despite fewer arboreal pathways, requiring them to more regularly (1) climb into trees and (2) use a more diverse locomotor repertoire to move on arboreal substrates of different characteristics. That females spent more time vertical ascent (but not descent) climbing than males when in the woodland suggests that rather than females climbing into the trees more often than males, female vertical ascent climbing bouts may have been longer (increasing the likelihood of recording the behavior during 2-min observational scans). Preliminary results suggest this could be due to exaggerated differences in tree height use between sexes (with females climbing higher) in the woodland compared with the forest; both females and males spent the majority of arboreal time above 10 m in the forest (78% and 65%, respectively), whereas females spent 52% of arboreal time above 10 m in the woodland, compared with 31% for males (unpublished data). Differences could also be due to variation in climbing speed, but further study of locomotor velocity is required to test this. Since arboreality was previously found to be associated with foraging in both sexes (Drummond-Clarke et al., 2022), and there was no large difference in level of terrestriality between sexes during foraging at Issa (e.g., females 12% vs. males 14% in woodland; unpublished data), this difference in climbing does not seem to be linked to males foraging more terrestrially than females.

A key anti-predator behavior in primates is increased arboreality (*Cebus capucinus imitator*; Monteza-Moreno et al., 2020, chimpanzees; Lindshield et al., 2017). Whilst savanna-mosaics are associated with higher perceived predation risk (Coleman & Hill, 2014; Fornof et al., 2023; Gaynor et al., 2019), other factors such as smaller body mass and group size can also increase perceived predator risk and drive arboreality. Although adult female *P. t. schweinfurthii* are not considerably smaller than males (and likely too large to be key prey for many predators [Zuberbühler & Jenny, 2002]), females often have (small) dependent infants who are vulnerable (during the study period, five of the six females had dependent offspring). Although further comparisons of females with and without dependent offspring are necessary to test this hypothesis, the only female without a dependent in the study also practiced the lowest levels of arboreality (47%, compared with 61% female mean). Observations from Gombe also suggest a similar pattern (K. D. Hunt, personal communication). We therefore propose that higher perceived predation risk for females,

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and in particular those with infants, could be driving increased arboreality compared to males at Issa.

Another explanation for high arboreality at Issa, especially in females, may be the higher energetic stresses associated with a savanna-mosaic habitat compared to more forested habitats (Wessling et al., 2018), increasing the need to forage, which is primarily an arboreal behavior. Importantly, there are additional energy costs incurred to females associated with gestation, lactation, and infant care (Dufour & Sauther, 2002; Thompson et al., 2012; Thompson & Wrangham, 2008). More research is needed on male and female feeding rates and nutrition, but we suggest female chimpanzees living in savanna habitat may incur a "double" selection for high arboreality related to a need for higher nutritional intake.

4.3 | Implications for hominid evolution

As our closest living relatives, and the only extant ape to live in a savanna-mosaic habitat, chimpanzees provide valuable models to test hypotheses about hominid evolution in open, seasonal habitats (e.g., Drummond-Clarke, 2023; Drummond-Clarke et al., 2022; Hunt, 1994; Lindshield et al., 2021; Moore, 1996; but see Lovejoy et al., 2009). Here, we demonstrate through a study of chimpanzee positional behavior that a savanna-mosaic habitat, which is the reconstructed palaeohabitat of many early hominins (Levin et al., 2008; Schoeninger et al., 2003; Senut et al., 2001; Su & Haile-Selassie, 2022; White et al., 2009) and hominids (Peppe et al., 2023), could select for arboreality in a large-bodied, semi-arboreal ape despite low tree density. In contrast to hypotheses that highlight the importance of vertical climbing (in particular on large substrates) on shaping early hominin (e.g., Gebo, 1996; Prost, 1980; Senut et al., 2018), and perhaps Miocene ape (MacLatchy et al., 2023) anatomy, our results suggest that a savanna-mosaic habitat could select for a diverse locomotor repertoire, including suspensory behaviors. Behavioral patterns in the mosaic landscape of Issa chimpanzees thus support the interpretation that "arboreal" morphological features of early hominin upper limbs are functionally significant, including those for suspensory behavior, rather than phylogenetic retentions (e.g., *Ardipithecus ramidus*; Prang et al., 2021). Moreover, observations from Issa indicate that wide, open-crown woodland trees (with abundant terminal branch fruits) in an otherwise sparse and rugged landscape, could select for frequent terminal branch locomotion, including suspension and assisted-bipedalism; locomotor behaviors used by orangutans (Thorpe et al., 2007) and chimpanzees (Hunt, 1992, 1994) to navigate flexible terminal branches, even in a savanna-mosaic habitat (Drummond-Clarke et al., 2022). Thus, such evidence offers support to hypotheses that emergence of hominin locomotor bipedalism occurred in an arboreal context (Drummond-Clarke et al., 2022; Thorpe et al., 2007).

Although more data from other savanna chimpanzee communities are needed (e.g., Fongoli and Assirik, Senegal; McGrew et al., 1981; Pruetz, 2014, Semliki, Uganda; Hunt & McGrew, 2002, Moyen Bafing, Guinea; Debetencourt et al., 2024), our findings of greater adult sex differences in locomotor behavior at Issa compared with more forested sites supports open habitat as a driver of inter-sex behavioral heterogeneity. Early hominins are characterized as having high sexual dimorphism, including larger differences in body mass between males and females than chimpanzees; *P. t. schweinfurthii* females weigh on average 79% male body mass, whereas *A. afarensis* females are estimated to be 63% and *A. africanus* females 66% of their male counterparts (Grabowski et al., 2015, 2018). Given a high degree of sexual dimorphism in early hominins, these body mass differences might further accentuate positional behavioral differences between the sexes. Behavioral observations of Issa chimpanzees support interpretations of larger, presumed-male australopiths being more terrestrial, in which a larger body size would reduce predation risk associated with terrestriality and open habitats, and smaller, presumed-female australopiths using a higher frequency of arboreal behaviors in response to higher predation risk and energetic demands associated with gestation and dependent offspring (e.g., Hunt, 2020).

4.4 | Conclusions and future directions

Here, we presented the first detailed characterization of positional behavior of adult chimpanzees living in a savanna-mosaic habitat. By quantifying female and male chimpanzee behavior across vegetation types, our results show that females and males both adjust their behavior in a similar way to more open vegetation (increasing time spent in locomotion, and reducing level of arboreality). However, the effect of vegetation type on positional behavior varies by sex, with females changing their behavior more to maintain high levels of arboreality despite a less connected canopy. In light of low sexual dimorphism in chimpanzees, we suggest that sex differences in positional behavior are likely influenced by high energetic demands and predation pressures linked to living in a savanna-mosaic habitat. Such pressures are exaggerated further for reproducing females. Our results also highlight the need to consider suspensory locomotion as an important positional behavior for early hominids and hominins in open habitats and its potential role in shaping ape forelimb and shoulder anatomy.

Future studies should combine fine-scale vegetation structure and positional behavior quantification to better investigate what particular aspects of vegetation structure (e.g., tree height, connectivity, branch diameter, and angle) have a significant influence on chimpanzee positional behavior. There is also a need for data on predation pressure (e.g., encounter rates, density, and diversity) within and between sites to understand its role on positional behavior in different vegetation types, and on each sex. Finally, more data are needed on the positional behavior of *P. t. verus* populations (which are currently limited to Taï), especially from dry habitats (i.e., Assirik, Fongoli), to explore potential variation between eastern and western chimpanzee populations. Positional behavior data from Fongoli would also enable investigations into the effect of landscape topography (i.e., flat vs. rugged) on chimpanzee positional behavior.

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AUTHOR CONTRIBUTIONS

Rhianna C. Drummond-Clarke: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); resources (supporting); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Tracy L. Kivell:** Conceptualization (equal); funding acquisition (equal); methodology (supporting); resources (equal); supervision (lead); writing – review and editing (equal). **Lauren Sarringhaus:** Conceptualization (equal); methodology (supporting); writing – review and editing (supporting). **Fiona A. Stewart:** Conceptualization (equal); funding acquisition (equal); project administration (lead); resources (equal); writing – review and editing (equal). **Alex K. Piel:** Conceptualization (equal); funding acquisition (equal); investigation (supporting); project administration (lead); resources (equal); supervision (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available upon reasonable request from the first author, and will be made freely available upon completion of their PhD.

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