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RESEARCH ARTICLE

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Unexpected terrestrial hand posture diversity in wild mountain gorillas

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Abstract

Objectives: Gorillas, along with chimpanzees and bonobos, are ubiquitously described as 'knuckle-walkers.' Consequently, knuckle-walking (KW) has been featured pre-eminently in hypotheses of the pre-bipedal locomotor behavior of hominins and in the evolution of locomotor behavior in apes. However, anecdotal and behavioral accounts suggest that mountain gorillas may utilize a more complex repertoire of hand postures, which could alter current interpretations of African ape locomotion and its role in the emergence of human bipedalism. Here we documented hand postures during terrestrial locomotion in wild mountain gorillas to investigate the frequency with which KW and other hand postures are utilized in the wild.

Materials and methods: Multiple high-speed cameras were used to record bouts of terrestrial locomotion of 77 habituated mountain gorillas at Bwindi Impenetrable National Park (Uganda) and Volcanoes National Park (Rwanda).

Results: We captured high-speed video of hand contacts in 8% of the world's population of mountain gorillas. Our results reveal that nearly 40% of these gorillas used "non-KW" hand postures, and these hand postures constituted 15% of all hand contacts. Some of these "non-KW" hand postures have never been documented in gorillas, yet match hand postures previously identified in orangutans.

Discussion: These results highlight a previously unrecognized level of hand postural diversity in gorillas, and perhaps great apes generally. Although present at lower frequencies than KW, we suggest that the possession of multiple, versatile hand postures present in wild mountain gorillas may represent a shared feature of the African ape and human clade (or even great ape clade) rather than KW *per se*.

KEYWORDS
ape, hominoid, knuckle-walking, terrestrial locomotion

1 | INTRODUCTION

African apes are unique among primates in their use of knuckle-walking (KW) hand postures during terrestrial locomotion (Owen, 1859; Straus, 1940). KW involves placing the dorsal aspect of the intermediate phalanges in contact with the ground (Owen, 1859; Garner, 1896; Straus, 1940; Schaller, 1963; Tuttle, 1967), and has been associated with a number of soft and hard tissue adaptations in the hand, wrist, and forearm (e.g., Schultz, 1936; Straus, 1940; Tuttle, 1969a, 1969b, 1970, 1967; Marzke, 1971; Yalden, 1972; Jenkins & Fleagle, 1975; Corruccini, 1978; Susman, 1979; Sarmiento, 1994; Richmond & Strait, 2000; Richmond, Begun, & Strait, 2001). KW has traditionally been described as an adaptation for efficient terrestriality in otherwise arboreal-adapted and long-fingered apes (Tuttle, 1967, 1969a, 1969b, 1970; Preuschoft, 1973; Susman, 1974, 1979; though see Almécija, Smaers, & Jungers, 2015 for an updated perspective on finger length evolution). However, KW may not be the exclusive terrestrial hand posture in adult gorillas. Doran (1997) reported that palmigrade hand postures are often used by infant mountain gorillas until around two years of age. In addition, in his pioneering behavioral research with mountain gorillas, Schaller (1963, p. 82) noted that "For brief periods, especially when holding an object, gorillas sometimes place the entire back of the hand on the ground." This hand posture has also been documented during terrestrial quadrupedalism in orangutans (Tuttle, 1967), a taxon that displays a suite of other non-KW hand postures which are generally associated with a lack of selection for terrestrial locomotor adaptations (Tuttle, 1967, 1969a, 1969b). The existence of non-KW hand postures in mountain gorillas as noted in adults by Schaller (1963) and in infants by Doran (1997) raises the possibility that non-KW hand postures may constitute a relatively common—yet unquantified—component of terrestrial locomotion in adult gorillas. If so, this may shed light on the role of KW during great ape and human evolution.

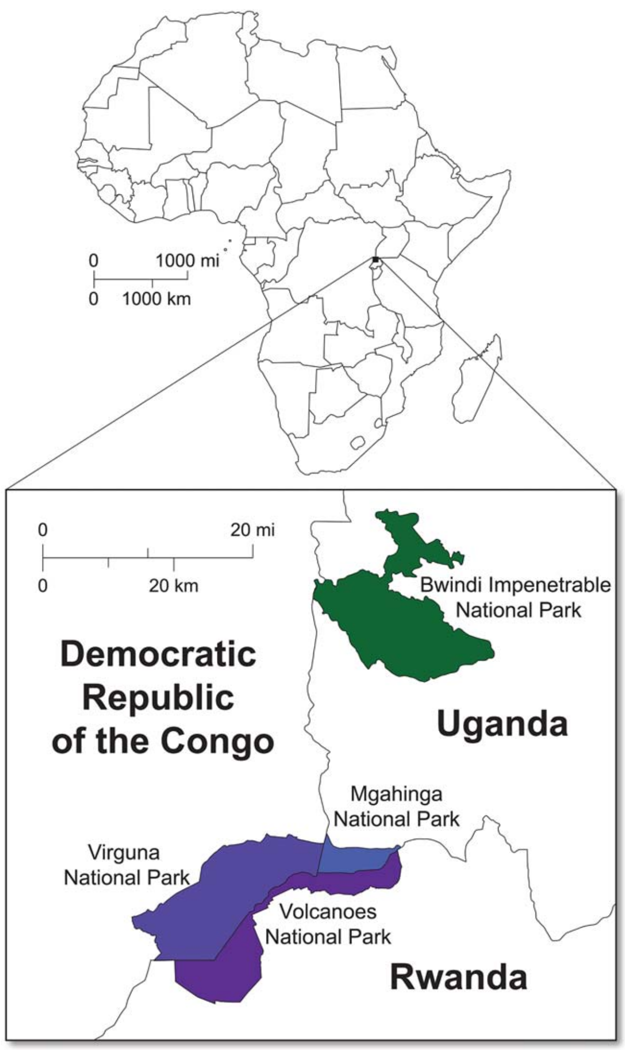

FIGURE 1 Mountain gorilla (*Gorilla beringei beringei*) habitats and study localities. Volcanoes National Park (Rwanda) is part of the Virunga Massif, which also includes Virunga National Park (Democratic Republic of the Congo) and Mgahinga National Park (Uganda), and is geographically isolated from Bwindi Impenetrable National Park (Uganda)

Knowing the extent to which non-KW hand postures occur is necessary for understanding the proximate interaction between gorillas and their environment, as well as for investigating morpho-functional signals that may shed light on the origin of KW behaviors in African apes. Whether or not KW was a shared derived trait of the African ape and human clade has been widely debated (e.g., Dainton & Macho, 1999; Richmond et al., 2001; Kivell & Schmitt, 2009; Lovejoy, Suwa, Simpson, Matternes, & White, 2009b and citations therein), and has large implications for whether KW preceded bipedalism in human evolution, and for understanding the course of locomotor evolution in great apes more generally. Yet, despite the efforts spent addressing this question, detailed data on how *extant* African apes actually utilize their hands during terrestrial locomotion in the wild is extremely scarce (Schaller, 1963; Doran, 1997). To fill this gap in our current knowledge, we recorded *ad libitum* bouts of terrestrial locomotion in approximately 8% of the world-wide population of mountain gorillas (*Gorilla beringei beringei*) at the only two remaining mountain gorilla localities (Figure 1): Bwindi Impenetrable National Park (Uganda) and the Virunga Massif in Volcanoes National Park (Rwanda). We identified frequencies of KW and non-KW hand postures (fist-walking (FW), dorsal metacarpal weight bearing (DMC), and modified palmigrady (MP), Figure 2), some of these postures having been previously undocumented in adult gorillas. The presence of alternative hand postures (i.e., besides KW) provides evidence that variety and versatility in terrestrial hand postures are a previously unrecognized component of the gorilla locomotor repertoire. These results support the hypothesis that a variety of hand postures (including KW) may have been a shared derived feature of the African ape and human clade.

2 | MATERIALS AND METHODS

2.1 | Field localities and sample composition

Video data were collected during a seven-week period in July and August, 2016. Video recordings of mountain gorillas (*Gorilla beringei beringei*) were collected both at Bwindi Impenetrable National Park (Uganda) and Volcanoes National Park (Rwanda; Figure 1). Volcanoes National Park encompasses a high-altitude montane forest where mountain gorillas regularly range from 2,630 to 3,850 m in altitude (Caillaud, Ndagijimana, Giarrusso, Vecellio, & Stoinski, 2014), while Bwindi encompasses medium-altitude to afro-montane forest (1,160–2,600 m; Robbins, Nkurunungi, & McNeilage, 2006). For this study, gorillas were generally observed in the higher altitude areas of Bwindi Impenetrable National Park (>1,800 m), and in the lower altitude areas of Volcanoes National Park (<3,400 m). At Bwindi Impenetrable National Park, data collection primarily took place in open and mixed forests, with varying amounts of understory, and to a lesser extent small swamp forests (see Nkurunungi, Ganas, Robbins, & Stanford, 2004). In particular, a large amount of data came from *Mimulopsis* spp. forests with varying degrees of vegetation covering the forest floor, from firm ground with little leaf litter to dense herbaceous plants and vines. At Volcanoes National Park, data were largely collected in the following habitat types (following Plumptre, 1993; Grueter et al.,

FIGURE 2 The four hand posture types categorized in this study. Knuckle-walking (KW, blue) involves the dorsal aspect of the intermediate phalanges contacting the ground, fist-walking (FW, orange) involves the dorsal aspect of the proximal phalanges contacting the ground, dorsal metacarpal weight bearing (DMC, red) involves the dorsum of the hand and wrist contacting the ground, and modified palmigrady (MP, purple) involves the palm contacting the ground with interphalangeal joints flexed. Photos courtesy of The Dian Fossey Gorilla Fund International, photos by Dr. Jordi Galbany

2013): mixed and *Mimulopsis* forests, *Hagenia-Hypericum* woodlands, herbaceous vegetation, and giant *Lobelia*. The forest floor varied from slight/moderate to dense herbaceous vegetation and vines. Areas of little ground cover were generally encountered less at Volcanoes National Park than at Bwindi Impenetrable National Park. Both sites involved data collection along steep terrain, although local areas of flatter ground were also present, which generally presented more ideal filming locations. At both localities, cameras were positioned along likely travel paths where it was anticipated that hand contacts would be visible. This potentially biased data collection toward more open environments. However, even in extremely dense regions, areas of local visibility were encountered (e.g., when recording an individual from behind along a newly trampled path). In addition to differences in habitat between localities, previous studies also suggest some behavioral differences between sites, including greater levels of frugivory, lower levels of food availability, larger daily travel distances and home range sizes, as well as increased climbing behaviors at Bwindi Impenetrable National Park (Sarmiento, Butynski, & Kalina, 1996; Doran & McNeilage, 2001; McNeilage, 2001; Robbins & McNeilage, 2003; Ganas & Robbins, 2004, 2005; Ganas, Robbins, Nkurunungi, Kaplin, & McNeilage, 2004; Nkurunungi et al., 2004; Wright et al., 2015).

2.2 | Video recording methodologies

All protocols and methodologies received appropriate review and approval or exemption from The Institutional Care and Use Committee (IACUC) of The George Washington University, Karisoke Research Center, the Rwanda Development Board, the Uganda Wildlife Authority, and the Ugandan National Council for Science and Technology. At each site, three or four tripod-mounted GoPro Hero 4 Backbone-modified cameras with fixed focal length lenses were used to capture video data. These cameras recorded data at 60 frames-per-second and at either 2,704 × 1,520, or 1,920 × 1,080 pixel resolution. We positioned the tripods ~0.5–1.0 m apart alongside likely travel paths of gorillas and triggered the cameras to record via a wireless remote. In addition to the tripod-mounted cameras, a handheld Sony HX-90V digital camera was also used *ad libitum* to film gorillas walking at 60 frames-per-second and at 1,920 × 1,080 resolution. All forelimb

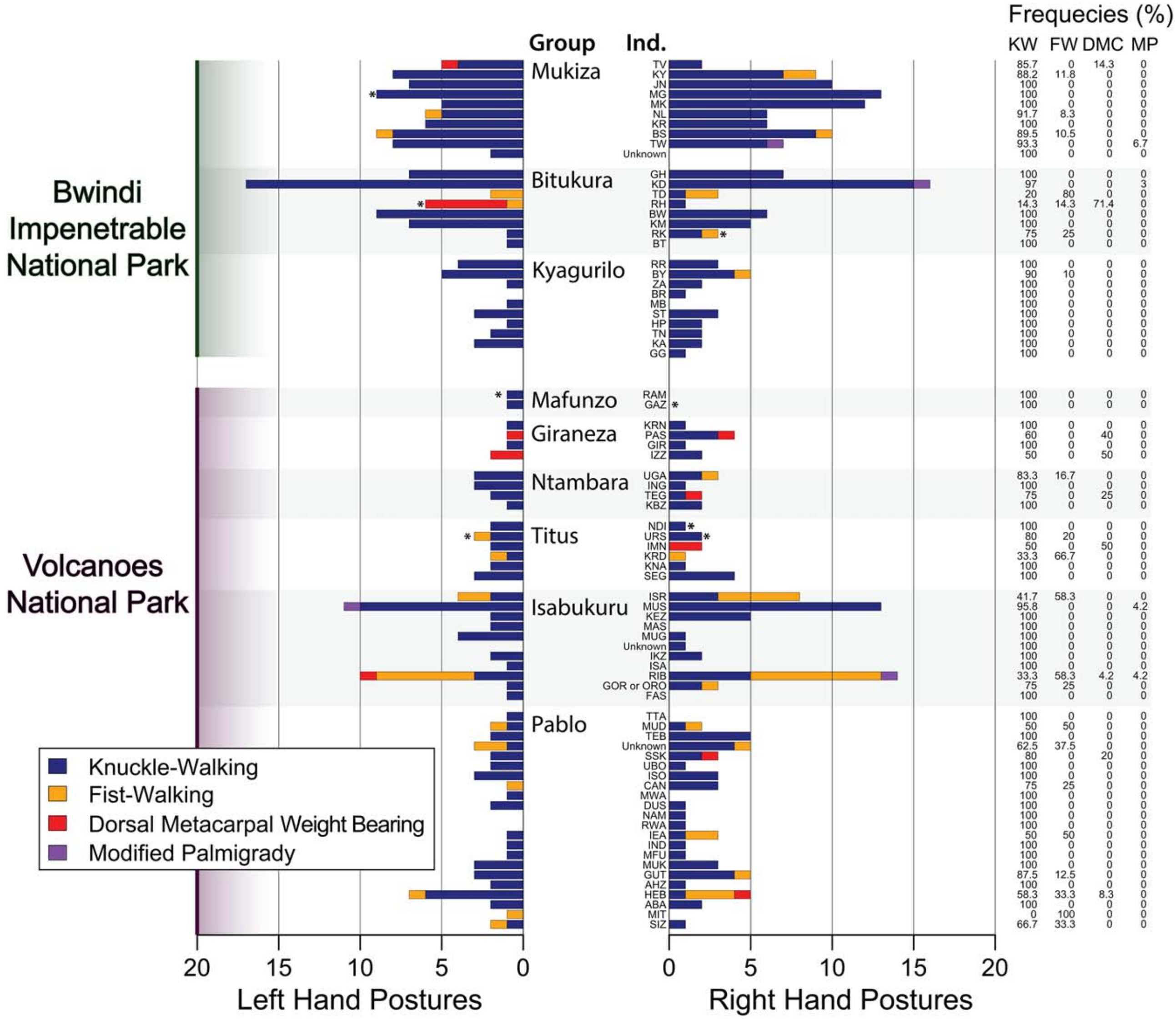

FIGURE 3 All hand contacts from Bwindi Impenetrable National Park and Volcanoes National Park, arranged by gorilla group, and by individual within each group (two or three letter abbreviation). All individuals that could not be positively identified were put into "Unknown" for each group. All left and right hand contact counts are shown to the left and right of the group identifications respectively. Frequencies of each hand posture for both hands combined are shown on the right. Color coding follows Figure 2. The asterisks (*) represent individuals (and wrist/hand side) for which an injury was either present or had been previously documented

contact events that were clearly identifiable in any of the cameras were subsequently categorized into hand posture type, resulting in a range of quantifiable hand contacts per individual between 1 and 33 contacts. This includes, for some individuals, right and left hand posture from the same stride as well as subsequent strides, whereas other individuals may have only had a single identifiable posture in a given day. We eliminated any hand contacts that were maintained during any portion of standing (i.e., any hand postures that were maintained during a period where the animal came to a complete stop), and only retained hand postures that occurred during walking strides.

2.3 | Hand posture classification

Hand postures were categorized following a modified version of the classification used by Tuttle (1967). Hand postures were classified as either (1) KW, (2) FW, (3) DMC, or (4) MP (Figure 2; Supporting information, Movies S1 and S2). Hand postures were classified as KW when the dorsal aspect of the intermediate phalanges were in contact with the ground and appeared to be the primary area of weight support for the forelimb. It is notable that in a large number of strides that were classified as KW, due to discontinuities in substrate and/or uneven ground, the palm of the hand also bore weight. FW hand postures were identified when the dorsum of the proximal phalanges, rather than the intermediate phalanges, were the primary point of contact and weight support. 'DMC' is our term for the hand posture described by Schaller (1963) and mentioned but not named by Tuttle (1967) in which the wrist undergoes extreme flexion such that the dorsum of the hand and wrist are the primary areas of weight support. This typically involved pronation of the arm such that the fingers pointed posteriorly, but could also occur with the arm between pronation and supination

TABLE 1 KW and non-KW hand posture usage

	Bwindi Impenetrable National Park		Volcanoes National Park		Total	
	Count	Frequency (%)	Count	Frequency (%)	Count	Frequency (%)
Number of individuals	28		49		77	
Number of individuals using:						
Exclusively KW hand postures	18	*64.3*	29	*59.2*	47	*61.0*
Non-KW hand postures	10	*35.7*	20	*40.8*	30	*39.0*
FW	7	*25.0*	14	*28.6*	21	*27.3*
DMC	2	*7.1*	7	*14.3*	9	*11.7*
MP	2	*7.1*	2	*4.1*	4	*5.2*
Fisher's exact *p*-value between sites		$p = .72$				
Total hand contacts	272		231		503	
KW	252	*92.6*	178	*77.1*	430	*85.5*
FW	12	*4.4*	41	*17.7*	53	*10.5*
DMC	6	*2.2*	10	*4.3*	16	*3.2*
MP	2	*0.7*	2	*0.9*	4	*0.8*
Fisher's exact *p*-value between sites		$p < .001$				

Abbreviations: KW, knuckle-walking; FW, fist-walking; DMC, dorsal metacarpal weight bearing; MP, modified palmigrady.

such that the fingers would face medially to some degree. Finally, MP refers to a hand posture where the interphalangeal joints were flexed, the wrist was extended, and the palms apparently bore a large portion of body weight. Because there were so few MP steps, we differed in definition from Tuttle (1967), and did not define this term on the basis of any particular degree of forearm pronation/supination. The few MP steps also appeared to involve a large amount of forelimb protraction, such that the degree of extension of the wrist was small. There was also some continuity between KW and MP. Because the KW category included some hand contacts where the palm bore weight, depending on the substrate these hand postures could look like MP. Here we attempted to be conservative, and any cases in which we were unclear whether a hand contact should be classified as KW or MP, we classified it as KW. However, some hand postures were clearly more similar to the MP posture illustrated by Tuttle (1967) than they were to KW.

For all hand classifications, we required that the hand either be visible while in contact with the ground or immediately before contacting the ground with no apparent change in posture immediately following touchdown. For some steps the hand assumed a KW posture prior to ground contact, and was classified as KW, even if the fingers were not 100% visible following ground contact (e.g., the fingers were in the KW position prior to touchdown, and afterwards the upright palm was still in view). However, in order to minimize false positives, FW, DMC, and MP hand contacts were typically positively identified after hand contact. For this reason, it is possible that a hand contact that was classified as KW may have changed post-contact into FW or DMC (and indeed we recorded examples of such post-contact transitions occurring). Conversely, it is unlikely that any KW hand contact was erroneously classified as FW or DMC. Therefore, any inherent error in this study likely overestimates the frequency of KW postures and underestimates the frequency of non-KW postures. Finally, a number of individuals were identified as possessing a hand or wrist injury, or having previously sustained a serious hand injury either via oral records or via written records from 2015 to 2016 (Volcanoes National Park only). While this likely under-documents all injuries, it was clear that many individuals, even with current noticeable injuries (e.g., stiff or broken fingers), still predominantly or exclusively used KW hand postures. For these individuals, the side on which an injury either exists, or was documented, is labeled in Figure 3 with an asterisk (*).

2.4 | Statistical analysis

Classifications of hand contacts were performed for each individual, and individual-specific frequencies were calculated. In a few instances, we captured data on individuals that could not be positively identified. These hand contacts were lumped together into an "Unknown" category for each gorilla group (Figure 3), which was then treated as an individual for statistical purposes in Table 1 and in Figure 3. However, it may be the case that a hand contact from an unidentified individual may belong to an already represented individual from another day or video sequence. Furthermore, all individuals within each site were pooled, and site-specific frequencies were calculated. For all individuals with known ages, frequencies of hand posture usage by age-class (infant: ≤ 3 years, juvenile: 3–6 years, subadult: 6–8 years, and adult: ≥ 8 years) and sex were calculated, and are shown in Table 2. All hand contacts from unidentified individuals were excluded from the sex and age-class breakdowns shown in Table 2. Descriptive data in Tables 1 and 2 include the full dataset, however, we also present data excluding current or previously injured individuals (*s in Figure 3) in Supporting information, Tables S1 and S2. Removing the data from the side of the injury eliminates 25 strides and two individuals from the dataset. Tests for differences between sites in frequencies of hand postures, and in number of individuals that used each hand posture, were made using a Fisher's exact test. However, the results of these tests must be interpreted with caution since there are highly unequal number of strides per individual, individuals per group, and groups per locality (one sample binomial and one sample χ^2 tests $p < .05$). In performing a Fisher's

TABLE 2 KW and non-KW hand posture usage by age class and sex

	Total		Male		Female	
Adult	**Count**	**Frequency (%)**	**Count**	**Frequency (%)**	**Count**	**Frequency (%)**
Individuals	47	–	19	–	28	–
Total hand contacts	368	–	183	–	185	–
KW	307	83.4	157	85.8	150	81.1
FW	42	11.4	21	11.5	21	11.4
DMC	15	4.1	2	1.1	13	7.0
MP	4	1.1	3	1.6	1	0.5
Subadult	**Count**	**Frequency (%)**	**Count**	**Frequency (%)**	**Count**	**Frequency (%)**
Individuals	7	–	3	–	4	–
Total hand contacts	42	–	14	–	28	–
KW	39	92.9	13	92.9	26	92.9
FW	3	7.1	1	7.1	2	7.1
DMC	0	0.0	0	0.0	0	0.0
MP	0	0.0	0	0.0	0	0.0
Juvenile	**Count**	**Frequency (%)**	**Count**	**Frequency (%)**	**Count**	**Frequency (%)**
Individuals	13		9	–	4	–
Total Hand Contacts	57	–	50	–	7	–
KW	54	94.7	47	94.0	7	100.0
FW	3	5.3	3	6.0	0	0.0
DMC	0	0.0	0	0.0	0	0.0
MP	0	0.0	0	0.0	0	0.0
Infant	**Count**	**Frequency (%)**	**Count**	**Frequency (%)**	**Count**	**Frequency (%)**
Individuals	6	–	4	–	2	–
Total hand contacts	21	–	9	–	12	–
KW	19	90.5	8	88.9	11	91.7
FW	1	4.8	1	11.1	0	0.0
DMC	1	4.8	0	0.0	1	8.3
MP	0	0.0	0	0.0	0	0.0

Abbreviations: KW, knuckle-walking; FW, fist-walking; DMC, dorsal metacarpal weight bearing; MP, modified palmigrady.

exact test we effectively binned all strides within a site, which disregards these factors.

3 | RESULTS

Data were collected on a total of nine gorilla groups (Bwindi: 3; Volcanoes: 6) totaling 503 individual hand contacts from 77 individuals (74 positively identified and 3 "unknown" individuals) including males and females from all age classes (Tables 1 and 2). Overall, 47 of 77 (61%) gorillas used exclusively KW hand postures (Bwindi: 18/28; Volcanoes: 29/49; Table 1), and 30 of 77 (39%) gorillas utilized non-KW hand postures of any type (Bwindi: 10/28; Volcanoes: 20/49). FW was the most commonly utilized non-KW hand posture and was utilized at least once by 21 of 77 individuals (27%; Bwindi: 7/28; Volcanoes: 14/49). DMC was the next most common posture and was used at least once by 9 of 77 individuals (12%; Bwindi: 2/28; Volcanoes: 7/49), and MP was the least utilized non-KW hand posture (4/77, 5% of individuals; Bwindi: 2/28; Volcanoes: 2/49). Removing data from possible or documented injured wrists and hands resulted in an overall increase in number of gorillas that used exclusively KW from 61% to 64% (Supporting information, Table S1). This is largely an effect of an increase in frequency at Bwindi Impenetrable National Park (from 64% to 71%) when removing data from injured wrists and hands, while frequencies at Volcanoes National Park remain nearly unchanged (Supporting information, Table S1).

Overall percentages of hand postures are listed in Table 1 and are shown for each individual in Figure 3. KW was used in 85% of all steps, with this percentage being higher at Bwindi Impenetrable National Park than at Volcanoes National Park (93% vs. 77%). FW, DMC, and MP hand postures were present in 11%, 3%, and 1% respectively of all hand contacts across sites, with higher percentages of non-KW hand postures occurring at Volcanoes National Park (FW: 18% vs. 4%; DMC: 4% vs. 2%; and MP: $\sim$1% at both sites). This difference in frequency of occurrence of hand postures is significant between sites (Fisher's exact test: $p < .001$). However, it should be noted that the frequency of individuals which utilized non-KW hand postures (36% at Bwindi and 41% at Volcanoes) is not significantly different between sites (Fisher's exact test: $p = .72$). Therefore, while non-KW hand postures seemed to be more common at Volcanoes National Park, it is largely because those individuals which utilized any non-KW postures did so more regularly at Volcanoes National Park than at Bwindi Impenetrable National Park. However, the sample sizes between sites are also highly biased; more individuals but fewer steps were collected at Volcanoes National Park, while larger samples of the same individual were collected from Bwindi Impenetrable National Park (Figure 3). In addition, at both sites, some specific individuals used a disproportionately high amount of non-KW hand postures (e.g., individual RH from Bwindi Impenetrable National Park, and individual RIB from Volcanoes National Park). Therefore, given these biases, the statistical tests presented here should be interpreted with caution until larger samples sizes are obtained. Removing data from possible or documented injured wrists and hands result in overall similar breakdowns in total percentages of hand posture usage (Supporting information, Table S1).

When split by age-class, frequencies of KW were generally similar between adults and non-adults, though slightly lower in adults (Table 2 and Supporting information, Table S2). Doran (1997) found that the proportion of KW increased with age until ~2 years of age. In our data set, only two individuals were under two years of age (MUG and SIZ) and each only contributed eight hand contacts to the overall dataset. Furthermore, the subadult, juvenile, and infant samples were all too small (≤56 contacts) to reliably identify non-KW events, which are expected to occur at low frequencies.

4 | DISCUSSION

Here we sought to document the type and frequency of non-KW hand postures in wild mountain gorillas. We sampled 77 gorillas (8% of the total estimated number of living mountain gorillas; Plumptre, Robbins, & Williamson, 2016) and found that nearly 40% of individuals used non-KW hand postures, and ~15% of all mountain gorilla steps involve a non-KW hand posture. One of the postures entailed bearing weight on the dorsum of the hand and wrist (DMC), as noticed by Schaller (1963). We also identified two other hand postures—FW and MP—typically associated with orangutan terrestriality (Tuttle, 1967) but previously undocumented in adult gorillas.

The proximate causes underlying an individuals' switch from KW to a non-KW hand posture appear to relate to substrate, pathology, and even individual preference. Some individuals appeared to use non-KW hand postures in response to certain environments and substrates. For instance, FW hand postures were occasionally used by individuals walking along steep slopes. The up-slope hand utilized a FW posture, and the down-slope hand utilized a KW posture. This may have served to modify effective forelimb length (from shoulder to ground) such that the up-slope limb was similar in effective length to the downslope limb, thus keeping the shoulders and trunk level. Similarly, some individuals used non-KW hand postures when walking underneath low hanging vegetation as an apparent means to lower overall body height. Secondly, occasionally non-KW hand postures were used as a response to injury or pathology. This is clearly the case for one individual (RH) who used exclusively non-KW hand postures on the left side (Figure 3, Supporting information, Movie S2). It was apparent through observation that this individual had sustained an injury to the left hand and wrist that left her unable to extend the wrist and metacarpophalangeal joints, and kept both permanently flexed. Thus DMC and FW hand postures were used to overcome this injury. However, not all injuries resulted in adoption of different hand postures; individual RK from Bwindi also had a stiff middle finger on the right hand, but was still able to use KW hand postures. Indeed, aside from RH, among all the other individuals that were identified as having, or previously having sustained, a serious hand or wrist injury, there was no clear pattern of adopting a particular non-KW hand posture (Table 1 and Supporting information, Table S1). Finally, while the above listed reasons are somewhat intuitive explanatory factors for adopting non-KW hand postures over KW hand posture (which at an overall frequency of 85% is overwhelmingly the dominant hand posture), there appears to be a degree of individual preference in hand posture. Some individuals (e.g., RIB, HEB, and ISR) utilized a number of different hand postures, and there was no immediately clear link to substrate, pathology, or age. Future studies including larger sample sizes of the individuals measured here, particularly over a greater variety of substrates, may allow for a more nuanced investigation of the relationship between age, substrate, and hand posture choice. In addition, while it is intriguing that there is a statistical difference in frequency of hand posture use between sites, we would suggest that biases and unevenness in sample size included here cannot yet be ruled out as the driver of these differences. Larger repeated measure of these individuals may allow us to link differences between sites to environmental, behavioral, or morphological differences between them.

While KW was recorded here as a single discrete hand posture, there was a large amount of variation within KW. For instance, a large number of hand contacts involved some degree of weight support by the palm. This would occur, for example, when the forest floor was discontinuous and/or covered in dense foliage and leaf litter. In these scenarios, KW would often result in the intermediate phalanges contacting the ground first and sinking into the substrate until the point where the palm would also contact the substrate and movement of the hand would cease. In many of these cases the palm appeared to be not only contacting the substrate but actively bearing weight. In fact, there was one recognizable scenario in which individuals seem to purposely adopt this KW weight-bearing palm posture. When walking along a steep slope, as happened frequently at both locations, animals would occasionally hyper-pronate the up-slope forearm (so that the palm faced laterally), while they maintained the down-slope forearm between pronation and supination (so that the palm faced medially). In this position, one or both palms could then be placed along the steep substrate, while still utilizing a KW posture. Indeed, in this and other situations, the kinematics of the hand and forearm of gorilla KW generally appear to be much more variable than previously recognized in studies of zoo and laboratory animals. In particular, the degree of forearm pronation/supination appeared to be much more variable than the generalized "palm-back" (i.e., pronated) position documented in captive western gorillas (Sarmiento, 1988; Matarazzo, 2013), and the degree of wrist flexion appears to vary from nearly fully extended to highly flexed (at touch down). Some aspects of the recorded variability in hand postures and kinematics may be attributable to the unique environment of mountain gorillas, which includes large amounts of steep, mountainous terrain. Future 2D and 3D kinematic data are needed to quantitatively evaluate the breadth and stereotypicality of hand postures in mountain and western gorillas, as well as their relationship to substrate.

The variability in hand postures documented here must also be appreciated when interpreting skeletal morphology. A healthy literature exists documenting hypothesized morphological correlates of KW, and a proportion of these studies further hypothesize relationships between presumed loading regimes and/or stress distributions to external (e.g., Richmond et al. [2001] and citations therein) and internal (Preuschoft, 1973; Oxnard, 1983; Marchi, 2005; Patel & Carlson, 2007; Lazenby, Skinner, Hublin, & Boesch, 2011; Tsegai et al., 2013; Matarazzo, 2015) bony morphology. While some of these studies are ultimately based on empirical evidence of living or cadaveric animals (e.g., Tuttle, 1967, 1969a; Tuttle & Beck, 1972; Yalden, 1972; Susman, 1974; Tuttle & Basmajian, 1974; Jenkins & Fleagle, 1975; Inouye, 1994; Wunderlich & Jungers, 2009; Matarazzo, 2013) many of these studies require significant assumptions about KW kinematics, load magnitudes, orientations, and patterns of stress distribution. The variability in hand postures discovered here suggest that more empirical data are needed to understand the "typical" kinematics or kinetics of wild African ape locomotion, before we can confidently evaluate hypothesized morphological correlates of KW. In addition, though non-KW hand postures are infrequent in mountain gorillas, studies of bone adaptation in model species have shown that loads originating from abnormal directions can be potent stimuli for bone modeling and remodeling, perhaps even more influential than loads originating from more stereotypical directions (e.g., Lanyon, 1992; Wallace, Kwaczala, Judex, Demes, & Carlson, 2013). Though less frequent than KW, these alternative hand postures may therefore have a strong and perhaps disproportionate effect on adult bone morphology. For example, African apes—especially *Pan*—are widely regarded as possessing morphologies directly related to vertical climbing and suspensory behaviors (both genetically driven and likely behaviorally induced; [e.g. Aiello & Dean, 1990; Hunt, 2016 and the numerous citations therein]). However, African apes actually spend little time practicing these locomotor behaviors. Even some of the most arboreal African apes (the Taï chimpanzees) spend only 11% of all locomotor behaviors in climbing and $<$2% in suspension (Doran, 1996). These two behaviors combined constitute an even smaller proportion of time when compared to all positional behaviors ($\sim$1.1%; Doran, 1996; Hunt, 2016). Therefore, even rare behaviors must be appreciated and acknowledged when investigating form-function hypotheses.

The presence of non-KW hand postures in mountain gorillas, as well as the similarity of these hand postures to those previously observed in orangutans during terrestrial locomotion (Tuttle, 1967; including limited KW, Tuttle & Beck, 1972; Susman, 1974), also has implications for the timing and evolution of KW in hominoids generally. At present there are two major hypotheses concerning the origin of KW[1]: (1) that KW is a synapomorphy of the African ape and human clade (Washburn, 1967; Marzke, 1971; Corruccini, 1978; Begun, 1994; Richmond & Strait, 2000; Corruccini & McHenry, 2001; Richmond et al., 2001; Begun & Kivell, 2011), and 2) that KW has arisen independently in both genera *Pan* and *Gorilla* (Dainton & Macho, 1999; Dainton, 2001; Kivell & Schmitt, 2009; Lovejoy et al., 2009b). This latter hypothesis typically relies on differing degrees of expression of bony traits often associated with KW in adults and through ontogeny (Dainton & Macho, 1999; Kivell & Schmitt, 2009), the presumed or measured kinematic/kinetic differences between hand postures in KW (Inouye, 1994; Kivell & Schmitt, 2009), and ultimately a lack of bony evidence of KW in fossil apes and early hominins (Almécija, Alba, Moyà, & Köhler, 2007, 2009; Lovejoy, Simpson, White, Asfaw, & Suwa, 2009a; Patel, Susman, Rossie, & Hill, 2009; but see McCrossin & Benefit, 1997; McCrossin, Benefit, Gitau, Palmer, & Blue, 1998; Richmond & Strait, 2000; Begun & Kivell, 2011). The data presented here illustrates that non-dominant terrestrial hand postures are used by gorillas and are in fact the same terrestrial hand postures that have been documented in captive orangutans (FW, DMC, MP, and limited bouts of KW [Tuttle, 1967; Tuttle & Beck, 1972; Susman, 1974]), despite the large differences in anatomy between gorillas and orangutans. Therefore, we suggest that the evolution of KW in African apes should be considered as an increase in frequency of an existing (although originally less frequent) hand posture rather than as the evolution of a *de novo* discrete behavior that was either present or absent at certain ancestral nodes (i.e., that KW either evolved discretely once or twice). The notion that a pre-existing but small component of a total locomotor (or postural) behavior repertoire can become predominant in some subsequent lineages is not new. A similar argument has often been invoked concerning the origin of bipedalism in hominins (e.g., Rose, 1991; Hunt, 1996). Similarly, our results, together with previous observations in orangutans, support a hypothesis that multiple hand postures are available to great apes during terrestrial locomotion (including KW), though they are utilized at different frequencies by different species.

We propose that hand postures utilized at the base of Hominidae (i.e., the great ape and human clade) likely involved a similar degree of versatility (including KW, FW, MP, and DMC). Selection for increased terrestriality in African apes may have driven the adoption of KW as the dominant hand posture as a means to increase terrestrial proficiency (Tuttle, 1967, 1969a; Susman, 1974; Tuttle & Basmajian, 1974; Susman & Stern, 1979), while non-KW hand postures were relegated to a sub-dominant usage. Under this scenario, it need not be required that any morphological features associated with KW are true synapomorphies of African apes. Indeed, some traditional morphological indicators of KW are variably expressed in adult African apes (Kivell & Schmitt, 2009) and have been found in large-bodied palmigrade or digitigrade cercopithecoids (McCrossin & Benefit, 1997; Patel et al., 2009). Similarly, if hand posture diversity were to characterize the ancestral hominid (or African ape) condition, it also does not imply that hand proportions or morphology at this node would have been orangutan- or gorilla-like. Instead, what we propose is that variability in hand postures (including KW, FW, DMC, and MP) with KW at some, likely appreciable, percentage was likely present at the ancestor of African apes and humans. Regardless of the exact frequency of KW utilization at the ancestral great ape and African ape nodes, it is also possible that independent increases in KW frequency also occurred along each of the

[1]As has been discussed by Richmond et al. (2001), KW may be thought of as a behavioral character, or as a series of bony adaptations related to the adoption of the behavior of KW. In the following citations, this distinction may or may not be explicit.

Gorilla and *Pan* lineages independently and perhaps differentially. For instance, dissimilarity in the evolution of digit proportions (Almécija et al., 2015) and/or the evolution of body mass (Tsegai et al., 2013) between *Gorilla* and *Pan* may provide anatomical bases for differential selective pressures to increase KW utilization. It may be hypothesized that larger body masses in *Gorilla* compared to *Pan* may have resulted in disproportionately large biomechanical stresses (e.g., joint moments) compared to *Pan*, even though *Gorillas* have proportionately shorter fingers. While anecdotal accounts of chimpanzee FW exist (Garner, 1896) and chimpanzee MP has been documented (Hunt, 1996), particularly in infant and juvenile chimpanzees (Doran, 1992) and in adults during arboreal locomotion (Hunt, 1991; Doran, 1993), further frequency-level terrestrial locomotor data from wild chimpanzees and bonobos, as well as data from western lowland gorillas and orangutans, are needed. Thus, future studies testing such hypotheses will require data on terrestrial hand posture from other wild apes. Nevertheless, the presence of non-KW hand postures in mountain gorillas illustrates a previously unrecognized degree of versatility and variability in hand usage during quadrupedal locomotion, and should warn against making simplistic generalizations regarding great ape locomotion. An evolutionary possibility derived from these results is that this spectrum of behavioral versatility may have been present at the base of the great ape and human clade, with KW having emerged from among these varied hand postures to become the dominant hand posture in *Pan* and *Gorilla*.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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