



# Pelvic shape variation among gorilla subspecies: Phylogenetic and ecological signals

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## ARTICLE INFO

### Article history:

Received 15 January 2019

Accepted 24 September 2019

Available online 24 October 2019

### Keywords:

Gorilla

Pelvis

Os coxae

Ecomorphology

Neutral evolution

## ABSTRACT

Gorillas occupy habitats that range in elevation from 0 to 3850 m. Populations at higher elevations tend to be less arboreal than lowland populations. Variation in habitat-specific behaviors among closely related populations makes gorillas a unique model to study the relationship between locomotion and morphology. The pelvis reflects differences in locomotion in other primates, and thus may also reflect locomotor differences among gorillas. We tested the hypothesis that pelvic morphology exhibits clinal variation across elevation within *Gorilla*. Using 3D geometric morphometrics and principal components analysis (PCA), we characterized pelvic shape in three gorilla subspecies representing 14 localities across gorillas' full elevation range: western lowland gorillas (*Gorilla gorilla gorilla*), mountain gorillas (*Gorilla beringei beringei*), and Grauer's gorillas (*Gorilla beringei graueri*). We found that the first principal component (PC1) usually reflects differences between western and eastern gorillas in the lateral margin of the ilium and, in males, the obturator foramen. When sexes are considered together, the second principal component (PC2) indicates some separation between *G. b. beringei* and *G. b. graueri*, albeit with considerable overlap, corresponding to the shape of the iliac crest. When sexes were analyzed separately, there was no distinction. Phylogenetic generalized least squares regression was used to evaluate the relationship between elevation and pelvic shape under varying phylogenetic assumptions. Models were compared to assess how phylogenetic adjustment affects model fit. Neither of the first two PCs nor overall shape yielded a significant relationship with elevation in any of the pooled-sex and individual-sex samples. This suggests that covariation between pelvic morphology and elevation is sex-specific and dependent on phylogenetic assumptions. Our results find complex interactions between sex, phylogeny, elevation, and pelvic morphology, suggesting that there is not one ecomorphological pattern that characterizes all gorillas.

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## 1. Introduction

The pelvis has been the focus of much attention in primate evolutionary anatomy because its gross morphology reflects the influence of multiple potentially competing selective pressures. The pelvis contributes to the size and shape of the trunk, which has

been implicated in both the evolution of orthograde postures in apes (e.g., Ward, 1991; Hammond et al., 2013; Middleton et al., 2017) and thermoregulatory adaptation (Ruff, 1993, 1994; Simpson et al., 2008; Betti et al., 2013, 2014; Betti, 2017; Betti and Manica, 2018). The pelvis must also accommodate the demands of birth, and its morphology is central to debates over the evolution of human birth (e.g., Rosenberg and Trevathan, 2002; Wells et al., 2012; Fischer and Mitteroecker, 2015; Wells, 2015; Moffett, 2017; Ruff, 2017). Locomotor behavior is another major selective force acting on pelvic morphology, both as it pertains to the evolution of

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bipedalism (e.g., Stern and Susman, 1983; McHenry, 1986; Rak, 1991; Ruff, 1995; Marchal, 2000; Lovejoy, 2005; Lovejoy et al., 2009a, b; Kibii et al., 2011; Claxton et al., 2016; Lewton and Scott, 2017) and the evolution of locomotion in other fossil primates (Straus, 1929; Godfrey et al., 1997; Köhler and Moyà-Solà, 1997; Rook et al., 1999; Hammond et al., 2013; Morgan et al., 2015).

Given that the pelvis is under such diverse selective demands, considerable research effort has been invested in identifying the adaptive significance of pelvic variation in living apes and fossil hominins. In the case of locomotor adaptation, fossil discoveries (e.g., *Ardipithecus ramidus*; Lovejoy et al., 2009a) and advances in evolutionary modeling (Grabowski et al., 2011; Lewton, 2012; Hammond and Almécija, 2017) are revealing an increasingly complex evolutionary history of hominoid pelvic morphology and its locomotor implications.

For example, an existing paradigm posits that the *Pan/Homo* last common ancestor (LCA) resembled a modern member of the genus *Pan* (e.g., Wrangham and Pilbeam, 2001; Pilbeam and Lieberman, 2017). Although chimpanzees probably represent good ancestral models for key aspects of body form, such as overall body size (e.g., Grabowski and Jungers, 2017), brain size (e.g., Almécija and Sherwood, 2017), and vertebral length (e.g., Pilbeam, 2004; Williams and Russo, 2015; Williams et al., 2016; Thompson and Almécija, 2017), other anatomical regions (Lovejoy et al., 2009a, b; Almécija et al., 2013, 2015) challenge this paradigm, highlighting the mosaic nature of hominoid body shape evolution (e.g., Almécija, 2016). For the case of the pelvis, a recent analysis of the lower ilium length suggested that the *Pan/Homo* LCA most likely resembled that of *Gorilla* rather than *Pan* or *Homo* (Hammond and Almécija, 2017). These results emphasize the need for more

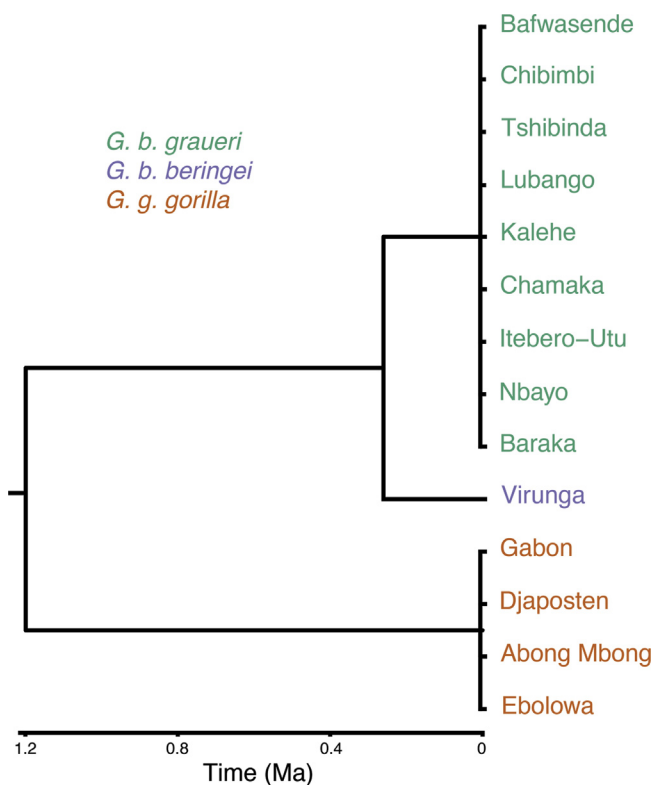
thorough investigation of the morphological variation represented in living great apes and how, if at all, locomotor behavior is reflected in pelvic morphology. This requires a fine-grained approach that accounts for small-scale diversification over relatively short spans of evolutionary time, like those represented in the hominin fossil record (e.g., Haile-Selassie et al., 2012; DeSilva et al., 2013).

Recently, morphologists have turned to gorillas as an extant model due to the range of ecological and behavioral variation observed within this small clade (e.g., Inouye, 1994; Sarmiento, 1994; Taylor, 1997a, b; Inouye, 2003; Tocheri et al., 2011; Ruff et al., 2013, 2018; Dunn et al., 2014; Knigge et al., 2015; Jabbour and Pearman, 2016). As our appreciation for gorilla diversity has grown over time, several taxonomies have been proposed. Here, we use the taxonomy put forth by Groves (1967), which has found wide acceptance (e.g., Stanford, 2001; Robbins, 2011). This schema recognizes two species: western gorillas (*Gorilla gorilla*) and eastern gorillas (*Gorilla beringei*). Both species are comprised of two subspecies. *Gorilla gorilla* is comprised of western lowland (*Gorilla gorilla gorilla*) and Cross River (*Gorilla gorilla diehli*) gorillas. *Gorilla beringei* is comprised of Grauer's gorillas (*Gorilla beringei graueri*) and mountain gorillas (*Gorilla beringei beringei*). Since pelvises of *G. g. diehli* are not available in museum collections, this subspecies was excluded from the present study.

### 1.1. Gorilla evolution, ecology, and behavior

Independent molecular phylogenetic studies have yielded the same tree topology for the genus *Gorilla*. However, estimates of node dates and branch lengths vary considerably depending on model assumptions and included loci (Arbogast et al., 2002). Here, we use a composite phylogeny derived from studies of nuclear DNA (Fig. 1; Thalmann et al., 2007; McManus et al., 2014; Roy et al., 2014), because they incorporate more loci than mitochondrial studies. Reconstructions of past population dynamics differ, but nearly all agree on a series of population bottlenecks in all subspecies from the Last Glacial Maximum to the present (Jensen-Seaman and Kidd, 2001; Thalmann et al., 2007, 2011; Bergl et al., 2008; McManus et al., 2014; Tocheri et al., 2016). The loss of genetic diversity during these bottlenecks likely affected phenotypic diversity as well (Lande, 1975; Adkison, 1995; Fraser et al., 2011; Xue et al., 2015). Large-scale losses of genetic diversity reduce the pool of variation on which natural selection can act, potentially inhibiting adaptation to the demands of specific habitats. In this scenario, habitat vegetation structure would be a poor predictor of phenotype and populations in similar habitats would not necessarily be expected to resemble each other. Differences among populations, therefore, are more likely to reflect population history. Given the complex demographic history of gorilla populations, there is a reasonable likelihood that morphological variation across the genus may be, to some degree, a product of nonadaptive processes like genetic drift, as has been observed in the human pelvis (Betti et al., 2013, 2014; Betti, 2017; Betti and Manica, 2018). To date, studies of morphological variation in gorillas have not attempted to account for the effects of population history using quantitative measures of phylogenetic distance.

Gorilla habitats are distributed along an elevation and ecological gradient across equatorial Africa, where they range in elevation from zero to approximately 3850 m above sea level (Fig. 2; Groves, 1967; Goodall, 1977; Doran and McNeilage, 1998; Yamagiwa et al., 2005; Caillaud et al., 2014; Robbins and Robbins, 2018). *Gorilla gorilla gorilla* has the lowest elevation range, from zero to 600 m above sea level. At the other extreme, *G. b. beringei* ranges from 2500 m to as high as ~3850 m above sea level (Caillaud et al., 2014). As documented elsewhere (Goodall, 1977; Yamagiwa and Mwanza,



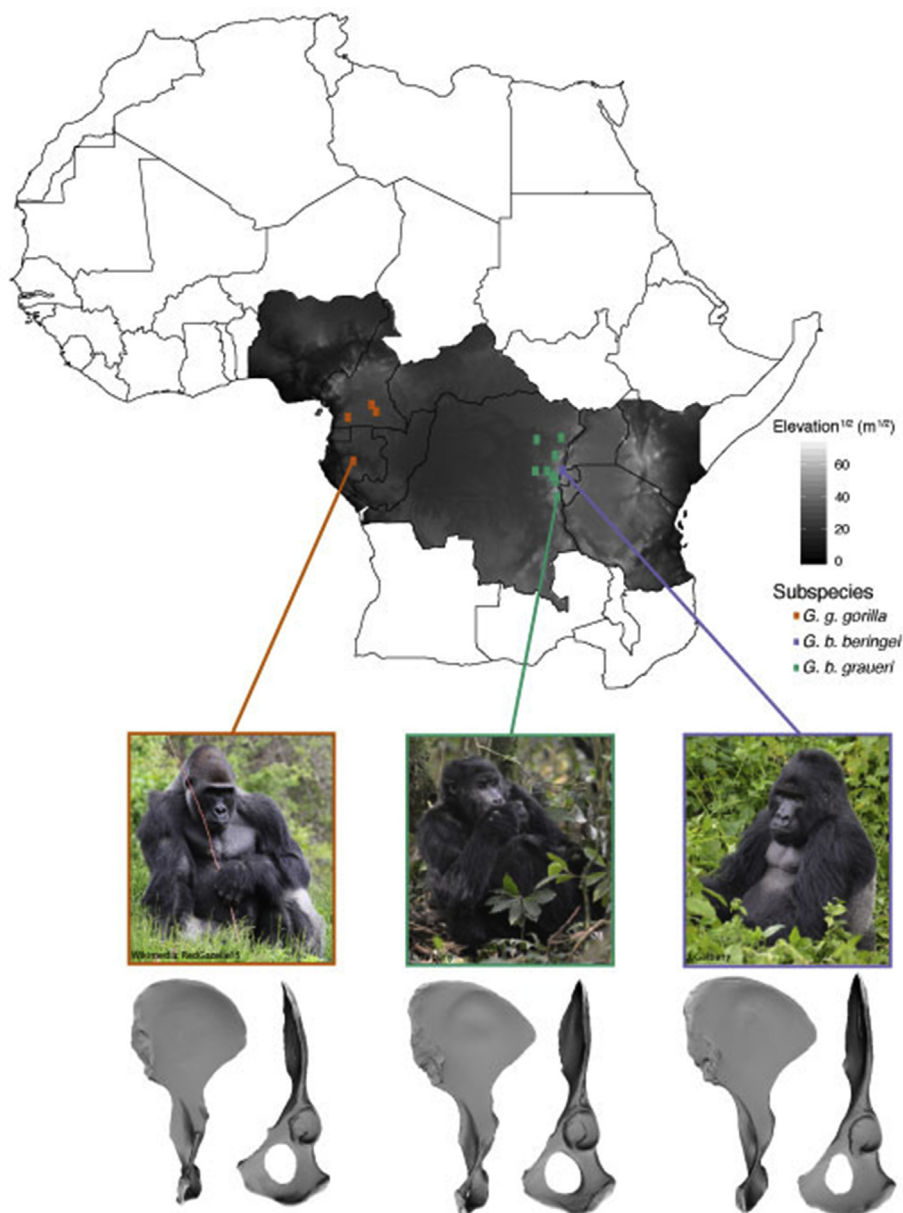
**Figure 1.** Composite phylogeny derived from studies of nuclear DNA. Divergence dates are from Thalmann et al. (2007), McManus et al. (2014) and Roy et al. (2014). Phylogenetic relationships among populations within subspecies are unresolved and are thus treated as polytomies.

1994; Doran and McNeillage, 1998; Yamagiwa et al., 2004, 2005) and confirmed by museum collection archives explored in this study, the widest elevation range is observed in *G. b. graueri*, with some populations overlapping with *G. g. gorilla* and others overlapping with *G. b. beringei*.

The vegetation structure of gorilla habitats changes with elevation, and these differences in habitat ecology are associated with corresponding differences in behavior (Goodall, 1977; Yamagiwa and Mwanza, 1994; Doran and McNeillage, 1998; Hall et al., 1998; Yamagiwa et al., 2005). In general, gorilla habitats at lower elevations have a greater availability of fruit than those from higher elevations. As such, *G. g. gorilla* incorporates the greatest proportion of fruit into its diet (Rogers et al., 1990, 2004; Remis, 1993, 1995; Tutin et al., 1995; Doran and McNeillage, 1998; Goldsmith, 1999; Brugiére and Sakom, 2001; Remis et al., 2001; Doran et al., 2002; Doran-Sheehy et al., 2009). In contrast, *G. b.*

*beringei* from the Virunga Massif consumes very little fruit and instead relies on terrestrial herbaceous vegetation (e.g., Fossey and Harcourt, 1977; Vedder, 1984; Watts, 1984; McNeillage, 2001), while the lower elevation population from Bwindi Impenetrable National Park (maximum elevation = 2500 m) consumes a greater proportion of fruit than its Virunga counterpart (Stanford, 2001; Robbins and McNeillage, 2003; Stanford and Nkurunungi, 2003; Ganas et al., 2004). As predicted from its elevation distribution, the diet of *G. b. graueri* is intermediate between *G. g. gorilla* and *G. b. beringei*. Diets of Grauer's gorilla populations living at higher elevations resemble Bwindi *G. b. beringei*, while populations from lower elevations more closely resemble *G. g. gorilla* in their increased reliance on fruit (Casimir, 1975; Goodall, 1977; Yamagiwa and Mwanza, 1994; Hall et al., 1998; Yamagiwa et al., 2004, 2005).

The frequency of climbing and above-ground nesting in *G. g. gorilla* varies seasonally with the availability of fruit. During the wet



**Figure 2.** Geographic range and elevation of studied populations with representative pelvises of each gorilla subspecies. Elevation has been log-transformed for visualization purposes, but untransformed elevation measures were used in all analyses. Photos of *Gorilla beringei* subspecies courtesy of The Dian Fossey Gorilla Fund International (taken by Jordi Galbany) and Wikimedia contributor RedGazelle15.

fruiting season, *G. g. gorilla* spends more time feeding in trees (Remis, 1998, 1999), has longer day ranges (Goldsmith, 1999), and nests in trees (Remis, 1993; Tutin et al., 1995; Brugiere and Sakom, 2001; Mehlman and Doran, 2002) more so than during the dry season. Climbing in *G. g. gorilla* is also associated with a greater availability of large trees capable of supporting their large bodies (Remis, 1999).

In contrast, Virunga *G. b. beringei* is the least frugivorous and is the most terrestrial gorilla subspecies (Doran, 1997; Remis, 1998) due to the relative lack of available fruits in their habitat. Virunga *G. b. beringei* is often characterized as being almost exclusively terrestrial. However, individuals of all body sizes and age classes have been observed climbing (Doran, 1997; J. Galbany, pers. comm.). According to Sarmiento et al. (1996), *G. b. beringei* from Bwindi Impenetrable National Park, Uganda, climbs more than Virunga *G. b. beringei*, consistent with predictions based on its more frugivorous diet. The dietary variation in *G. b. graueri* is also reflected in its locomotor behavior. Highland *G. b. graueri* from Tshibinda, Kahuzi-Biega National Park in Democratic Republic of Congo climbs to access seasonally available fruits. However, fruit makes up a lesser proportion of its diet than in *G. g. gorilla* (Goodall, 1977).

Unfortunately, the few studies of gorilla locomotor behavior that exist do not characterize locomotor behavior in a standardized way. This precludes testing hypotheses directly relating pelvic morphology to observed locomotor behavior. Taken together, these studies support Goodall's (1977) suggestion that variation in diet composition is linked to variation in vegetation at the habitat level. As a corollary, the association between climbing behavior and fruit acquisition suggests that vegetation, as with elevation, can be used as a proxy for the relative prevalence of arboreal and terrestrial behaviors at the local level. This relationship can thus be used to make inferences about gorilla locomotor repertoires in the absence of comparable behavioral data.

## 1.2. Gorilla postcranial morphology

The ecological and behavioral diversity in *Gorilla* has made this genus a popular model for determining the degree to which skeletal morphology is fine-tuned to the demands of their specific habitats (e.g., Inouye, 1994; Sarmiento, 1994; Taylor, 1997a, b; Inouye, 2003; Tocheri et al., 2011; Ruff et al., 2013, 2018; Dunn et al., 2014; Knigge et al., 2015; Jabbour and Pearman, 2016). Several studies have described postcranial variation across gorilla subspecies and populations and its correspondence to differences in locomotor behavior. The morphology of the bones of the hands and feet bear some of the strongest signals of locomotor adaptation. More terrestrial populations have relatively shorter hands (Schultz, 1934; Sarmiento, 1994; Inouye, 1994, 2003; Almécija et al., 2015; Jabbour and Pearman, 2016), which have been attributed to differences in patterns of weight bearing and the biomechanical demands of terrestrial locomotion (Etter, 1973; Patel and Wunderlich, 2010). The joint surfaces of the tarsus also appear to reflect differences in arboreality and terrestriality in gorillas. The hallux facet of the medial cuneiform indicates a greater degree of hallux adduction in *G. g. gorilla* compared to *G. b. beringei* (Schultz, 1934; Tocheri et al., 2011). In the latter study, the sample of primarily highland *G. b. graueri* was indistinct from *G. b. beringei*, consistent with their similar locomotor regimes. In the talus, the surface area of the lateral malleolus (Dunn et al., 2014) and the topography of the trochlear surface (Dunn et al., 2014; Knigge et al., 2015) match predictions based on the foot positions used during arboreal and terrestrial locomotion.

In the long bones of the limbs, there does not appear to be a relationship between inter- and intra-limb length proportions and

locomotor behavior (Inouye, 2003; Ruff et al., 2013, 2018; Jabbour and Pearman, 2016), but proportions in long bone structural properties do appear to bear a locomotor signal (Ruff et al., 2013, 2018). These findings are consistent with other work demonstrating a plastic response to habitual loading in diaphyseal strength (Bass et al., 2002). Linear dimensions of the scapula do not differentiate between *G. g. gorilla* and *G. b. beringei* in the ways predicted by the shoulder biomechanics of climbing and terrestrial behaviors (Taylor, 1997a, b).

Taken together, these studies suggest that locomotor adaptations are reflected in some postcranial elements, but not all, or only in some specific morphological aspects (e.g., shaft mechanical properties, specific joints). Since there is not a generalizable pattern across the postcranium, it is necessary to examine behavior/morphology relationships in individual bones. Here, we contribute to this effort by characterizing variation in gorilla pelvis shape (Fig. 3) and its relationship to habitat variation and inferred locomotor behavior using elevation as an ecological proxy.

## 1.3. Pelvic morphology and function

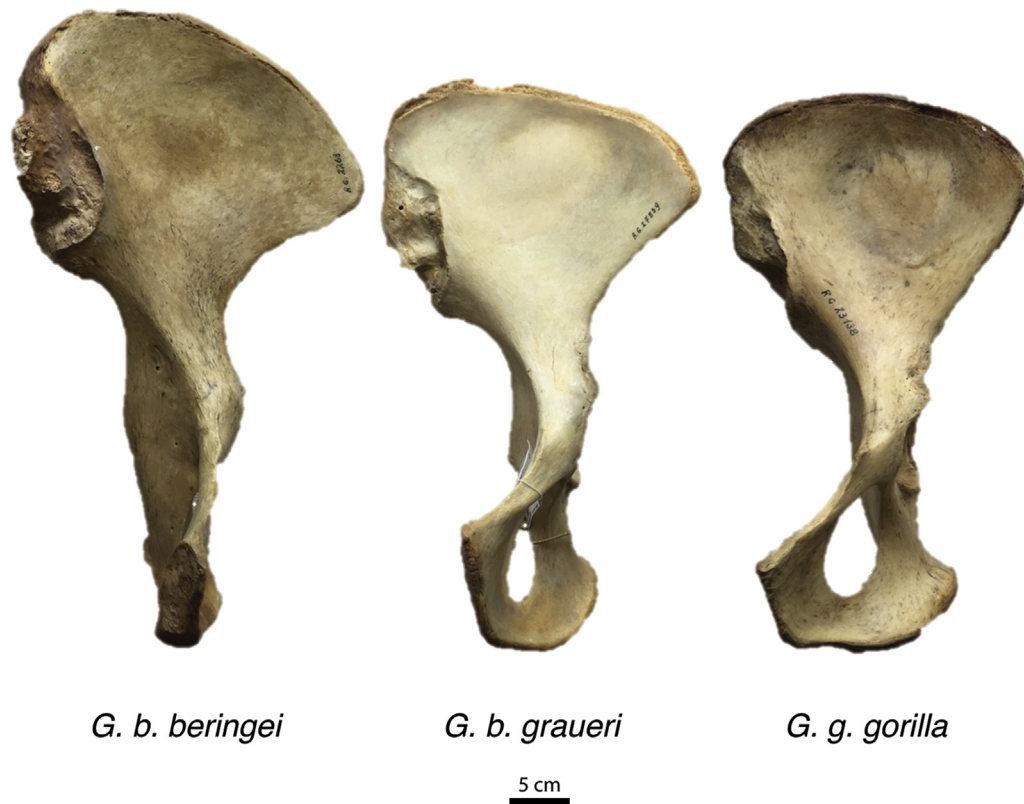
Despite the central role of the pelvis as an attachment site for several muscle groups involved in locomotion, there have been relatively few studies relating pelvic morphology to locomotor behavior in non-human primates. The pelvis is highly evolvable (Grabowski et al., 2011; Lewton, 2012; Betti, 2017; Huseynov et al., 2017), allowing for variation in individual modules to arise over relatively short spans of evolutionary time. This lends plausibility to the suggestion that adaptive differences related to locomotor behavior may have evolved since the divergence of extant gorilla taxa from their last common ancestor.

Lewton (2015) described differences in iliac breadth, lower ilium height, and lower ilium cross-sectional area among locomotor categories in strepsirrhines, which may relate to specialization of the gluteal muscles for generating propulsive force in leaping (Lewton, 2015). Differences in iliac length and breadth in anthropoids using different locomotor behaviors have also been related to differences in size and orientation of hip flexors and extensors (Hammond and Almécija, 2017), which are known to have differing functional capabilities tracking different locomotor categories (Hammond, 2014). The erector spinae, quadratus lumborum, and latissimus dorsi muscles attach to the iliac crest (Gregory and Raven, 1950; Diogo et al., 2010), and differences in ilium size and shape might thus reflect differing functional demands in spinal and forelimb musculature. The quadratus lumborum muscles provide mediolateral stability to the trunk, while the latissimus dorsi muscles extend and adduct the arm. These two muscles and their functions play important roles in forelimb-dominated climbing behavior (Ward, 1991; Middleton et al., 2017; Ward et al., 2018) and variation in their attachments may reflect differences in function related to climbing. Collectively, these studies point to the ilium in particular as a likely site for detecting signals of locomotor adaptation in the pelvis.

Less attention has been paid to the ischium and pubis. The length and dorsal projection of the ischium and the associated length of the moment arm of the gluteal muscles have been suggested to affect the range of hip extension (Fleagle and Anapol, 1992; Lewton and Scott, 2017; Kozma et al., 2018). Differences in the length of the pubis have been associated with locomotor differences in some primates, but this trait does not appear to vary among apes (Lewton and Dingwall, 2016; Ward et al., 2018).

In modern humans, Betti and colleagues (Betti et al., 2013, 2014; Betti, 2017; Betti and Manica, 2018) described a significant effect of climate on overall pelvic morphology and an even larger effect of population history while maintaining the functional demands of





**Figure 3.** Representative female pelvises from each subspecies (*G. g. gorilla*: RMCA 23138; *G. b. graueri*: RMCA 27839; *G. b. beringei*: RMCA 2263). Differences in iliac shape are visually apparent. Left pelvises are shown to same scale in ventral view.

bipedal locomotion. Signatures of neutral evolution were more prevalent in the false pelvis than the true pelvis, which [Betti et al. \(2013\)](#) hypothesized may be due to the obstetric constraints imposed on the true pelvis. So, while the ilium appears to be the region with the most potential for identifying locomotor adaptation, it may also be the most prone to neutral evolutionary processes like genetic drift.

#### 1.4. Aims

The present study examines the structure and adaptive significance of morphological variation in the gorilla pelvis by addressing three research questions:

- (1) Are there differences in pelvic shape among gorilla subspecies?
- (2) If there are differences in pelvic shape among gorilla subspecies, is there a relationship between shape and habitat elevation? If so, this would suggest that gorilla pelvic morphology is finely tuned to locomotor differences even across short evolutionary timescales.
- (3) Does the inclusion of phylogenetic information into models of ecology/morphology relationships improve model fit? This would suggest that the inclusion of phylogenetic information improves a model's ability to appropriately identify ecology/morphology relationships compared to models that do not.

Differences in pelvic shape among subspecies are visually apparent in their representative photographs ([Fig. 3](#)). The shape of the iliac blade at its ventral margin and the anterior superior iliac

spine (ASIS) has a distinct appearance, particularly in *G. b. beringei*. Our first aim is to quantify this shape variation using geometric morphometrics to describe patterns of morphological difference in the gorilla pelvis. Based on our visual observations, we expect that gorilla subspecies are distinct in their pelvic shape and that iliac shape contributes heavily to the major axes of shape variation. Our second aim is to use regression analyses to evaluate how closely dimensions of pelvic shape track habitat elevation and inferred locomotor behavior. Since numerous putative adaptations have been identified throughout the gorilla postcranium, we expect to find evidence of adaptation in the gorilla pelvis as well. Our third aim is to build on previous approaches to gorilla ecomorphology by examining how different assumptions about the role of phylogeny affect the outcomes and fits of our regression models. Since it is unlikely that any axis of phenotypic variation is completely phylogenetically independent, we expect that including phylogenetic information will improve the fit of our models. Comparing alternative models will allow us to make a more realistic assessment of the relationship between elevation and pelvic shape beyond that which would be expected under neutral genetic drift.

Genetic drift has the potential to drastically affect phenotypic evolution ([Lande, 1975](#)), especially in small populations (e.g., [Lande, 1975](#); [Adkison, 1995](#); [Fraser et al., 2011](#); [Savolainen et al., 2013](#)). The complex demographic history ([Jensen-Seaman and Kidd, 2001](#); [Thalmann et al., 2007, 2011](#); [Bergl et al., 2008](#); [McManus et al., 2014](#); [Tocheri et al., 2016](#)) and either endangered (*G. b. beringei*: [Hickey et al., 2018](#)) or critically endangered (*G. g. gorilla*: [Maisels et al., 2016](#); *G. b. graueri*: [Plumptre et al., 2016](#)) status of all of the gorilla subspecies indicate multiple past instances of population decline, suggesting that strong drift effects likely influenced the genetic and phenotypic evolution of gorillas in both the recent and

deep past. We therefore predict strong signals of drift, as reflected in high degrees of phylogenetic signal consistent with a Brownian motion model of phenotypic evolution.

Previous studies of gorilla ecomorphology have divided samples into subspecies and habitat elevation categories. However, habitat elevation varies on a continuous scale. Here, we use continuous elevation data for each sample locality to provide a finer grained characterization of the relationship between continuous elevation data and pelvic shape both among and within groups. This study uses three-dimensional geometric morphometrics (3DGM) to quantify pelvic shape variation in a sample of 54 wild adult gorillas covering the entire elevation spectrum of their distribution. 3DGM is capable of characterizing variation in complex shapes, and data derived from 3DGM can be subjected to a wide variety of statistical tests (Rohlf and Marcus, 1993; Adams et al., 2004; McNulty and Vinyard, 2013). The present study seeks to identify signatures of adaptive variation and posit their functional significance based on their broader musculoskeletal context. These findings can be used to develop and explicitly test hypotheses regarding the biomechanical role of morphological variants in different environments and their association to specific locomotor behaviors.

## 2. Materials and methods

### 2.1. Sample

Morphometric data were collected from 3D surface scans of pelves from 54 wild gorillas available in museum collections or as part of naturally-accumulated skeletal assemblages (14 *G. g. gorilla*, 22 *G. b. graueri*, and 18 *G. b. beringei*) representing adult males and females. Adult status was determined by complete eruption of the third molar and fusion of the ilium, ischium, pubis, and iliac crest. Sample composition and sources are detailed in Table 1.

### 2.2. 3D surface scanning

Scans were collected using a NextEngine Desktop 3D Scanner (NextEngine, Malibu), Geomagic Capture (3D Systems, Rock Hill), or 3D photogrammetry. Laser scanning, light scanning, and photogrammetric modeling have previously been demonstrated to produce 3D models of comparable quality (Guidi et al., 2007; Aguilar et al., 2009; Slizewski et al., 2010; Fourie et al., 2011; Tocheri et al., 2011; Katz and Friess, 2014; Magnani et al., 2016; Porter et al., 2016; Shearer et al., 2017). The left innominate bone was digitized. In instances where the left innominate was damaged or unavailable, a model of the right bone was created and mirrored in Geomagic Studio (3D Systems, Rock Hill). In one instance, a fully

articulated pelvis was scanned; articulation did not affect landmark placement.

The protocol for scanning with the NextEngine Desktop scanner followed that described in Hammond et al. (2016). When using the NextEngine scanner, pelves were secured onto the NextEngine turntable using the NextEngine gripper and putty. Due to the large size of gorilla pelves, NextEngine scans were collected in Extended Mode. All NextEngine scans were collected using high-definition settings. Point cloud data were aligned in NextEngine Scan-Studio HD and exported as a polygonal model (wavefront or OBJ files). Right bones were mirrored in PolyWorks v. 11.0–12.0 software (InnovMetric, Quebec). As Scan Studio has limited options for model cleaning, scans were cleaned of topographic irregularities using the IMEdit module PolyWorks, comparable to what has been done in other studies (e.g., Tocheri et al., 2011; Garvin and Ruff, 2012).

Our scanning protocol for the Geomagic Capture structured light scanner was first implemented in Hammond et al. (2018) and generally follows the extensive laser scanning protocol outlined in Hammond et al. (2016). Briefly, the Capture scanner is operated through Geomagic Studio software. When using the Geomagic Capture scanner, pelves were secured to the turntable using putty and the turntable gripper. The field of view was adjusted to capture as much of the bone as possible and the exposure was adjusted to ensure optimal lighting conditions for scanning. Multiple 360-degree scanning rotations (consisting of 10 'Medium' resolution scans each) were required to capture all views of the bone. Each scan rotation was aligned using the 'Global Registration' tool, and points were combined into a single object. The specimen was then repositioned on the turntable and the process was repeated to capture the remaining surfaces of the bone. After multiple sets of scans were aligned, they were first manually aligned to each other and then subsequently the alignment was refined via the Global Registration best-fit feature. A polygonal model was created from the aligned objects using the 'Wrap' tool. Minor postprocessing of surface models was conducted in Geomagic Studio, as is common practice in studies using scan data (e.g., Tocheri et al., 2011; Garvin and Ruff, 2012; Hammond et al., 2016, 2018).

For photogrammetric modeling, the specimen was placed on its dorsal surface, directly on a table with a black photography drape and scale card. Photographs were taken using a Nikon D700 digital single-lens reflex camera equipped with a macro lens (Nikon AF Micro Nikkor 105 mm f/2.8) and stabilized on a tripod. 25–30 photographs with a scale bar were taken from all angles to ensure maximum coverage of the specimen. The specimen was then flipped onto its ventral surface, and a second set of 25–30 photographs was taken of the dorsal side. Exposure time and aperture stop were adjusted to account for inconsistent lighting conditions and to

**Table 1**  
Gorilla sample by subspecies, sex, and collection.<sup>a</sup>

|       | <i>G. g. gorilla</i> | <i>G. b. graueri</i> (lowland) | <i>G. b. graueri</i> (highland) | <i>G. b. beringei</i> |
|-------|----------------------|--------------------------------|---------------------------------|-----------------------|
| NMNH  | 0 F, 1 M             | —                              | —                               | 1 F, 3 M              |
| RMCA  | —                    | 6 F, 5 M                       | 1 F, 2 M                        | 2 F, 0 M              |
| RBINS | —                    | 2 F, 5 M                       | —                               | —                     |
| NRM   | —                    | —                              | —                               | 3 F, 3 M              |
| AMNH  | —                    | —                              | 0 F, 1 M                        | —                     |
| CMNH  | 6 F, 7M              | —                              | —                               | —                     |
| MGSP  | —                    | —                              | —                               | 2 F, 4 M              |
| Total | 6 F, 8 M             | 8 F, 10 M                      | 1 F, 3 M                        | 8 F, 10 M             |

Abbreviations: AMNH = American Museum of Natural History, New York, NY, USA; CMNH = Cleveland Museum of Natural History, Cleveland, Ohio, USA; MGSP = Mountain Gorilla Skeletal Project, Musanze, Rwanda; NMNH = US National Museum of Natural History, Washington, DC, USA; NRM = Swedish Museum of Natural History, Stockholm, Sweden; RBINS = Royal Belgian Institute of Natural Sciences, Brussels, Belgium; RMCA = Royal Museum for Central Africa, Tervuren, Belgium.

<sup>a</sup> Total number of gorilla males (M,  $n = 31$ ) and females (F,  $n = 23$ ) is shown by subspecies, sex, and collection. Highland and lowland samples are separated into those >1000 m and those <1000 m, though the analyses performed here treat elevation as a continuous variable.

maximize visibility of the bone's surface. Photographs were imported into Agisoft Photoscan Professional (Agisoft LLC, St. Petersburg) in two chunks, one for each set of photographs. The background of each photograph was masked to improve alignment and reduce processing time. Both chunks were aligned separately at high accuracy to produce a sparse cloud. After confirming the correct alignment of the photographs, a dense cloud was generated at medium quality. This setting reduces processing time while still producing a high-resolution model. The dense cloud was then cleaned of any remaining background points using the lasso tool. Meshes for each chunk were aligned using three homologous landmarks on each scan. The dense clouds from the aligned models were then merged. The resulting model was scaled by placing landmarks on the scale bar in the original photographs. Completed models were exported as PLY files. Photogrammetric scans were cleaned of any stray vertices using the 'Remove Unreferenced Vertex' function and reduced using the 'Quadratic Edge Decimation' tool in MeshLab (Cignoni et al., 2008). The 3D models produced by these methods have previously been found to yield equivalent morphometric results (Weinberg et al., 2004; Majid et al., 2005; Fourie et al., 2011; Tocheri et al., 2011; Porter et al., 2016).

### 2.3. Geometric morphometrics

3D coordinate data were collected by L.M.F. using Landmark Editor software (Wiley et al., 2005). 23 fixed landmarks (Table 2; Fig. 4) were collected on each specimen. One female *G. b. graueri* was chosen to serve as the 'atlas' specimen for subsequent semi-automated landmark placement (see below). An additional 71 landmarks (Fig. 4) were placed on the atlas to be treated as curve-sliding semilandmarks during analysis. These characterize the contours of the iliac crest, lateral margin of the ilium, greater sciatic notch, and obturator foramen. Landmark coordinates were exported to R (R Core Team, 2017) for analysis.

A semiautomatic protocol in the 'morpho' R package (Schlager, 2017) was implemented to place semilandmarks. This process

aligns specimen meshes to the atlas mesh using the previously assigned fixed landmarks and uses the thin-plate spline algorithm to project the semilandmarks from the atlas specimen onto the target specimen. Generalized Procrustes analysis (Dryden and Mardia, 1998) was performed on the resulting coordinate data using the 'morpho' package. Curve-sliding semilandmarks were slid according to the minimal bending energy criterion to ensure compatibility with future datasets with greater shape disparity (Gunz and Mitteroecker, 2012). Principal components (PC) analysis was performed to reduce the dimensionality of the Procrustes-aligned coordinates and identify the principal axes of morphological variation in the sample. Variation along PC axes were visualized using the thin-plate spline algorithm (Bookstein, 1989) to warp the specimen closest to the average shape to the extreme values of each PC using the R package 'geomorph' (Adams et al., 2017).

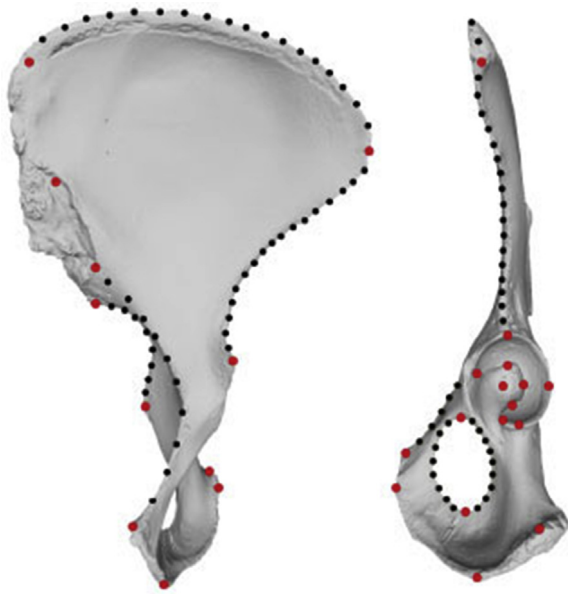
### 2.4. Locality elevation

Quantitative elevation data for specimen collection localities were collected. Names of collection localities were sourced from museum catalogs and their latitude/longitude coordinates were recorded from Google Earth (see Supplementary Online Material [SOM] Table S1). In instances where searches did not yield results, alternative spellings, alternative site descriptions (Cooper and Hull, 2017), and one collector's biography (R.L. Garner; Rich, 2012) were used to locate the collection site. Elevation data for each set of latitude/longitude coordinates were extracted from a SRTM 90 m resolution digital elevation model in the 'raster' R package (Hijmans, 2017) or maximum published values when available. When the maximum elevation was not available, we elected to use the median value from a 10 km buffer, following Gordon et al. (2013). While this measure does not necessarily reflect the amount of time populations spend at different elevations, it attempts to address uncertainty in historical collection sites, heterogeneity in the gorillas' actual habitats, and the potential influence of human settlement. Specimens for which no locality

**Table 2**  
Fixed landmarks collected from each pelvis scan.<sup>a</sup>

| #  | Fixed landmarks  |
|----|--|
| 1  | Most cranial point on sacroiliac joint   |
| 2  | Most caudal point on ventral margin of the symphysis, on symphyseal surface                                |
| 3  | Most caudal point on outer rim of acetabulum   |
| 4  | Most dorsal point on outer rim of acetabulum   |
| 5  | Cranial termination of lunate surface  |
| 6  | Most cranial point on inner rim of lunate surface  |
| 7  | Most dorsal point on inner rim of lunate surface   |
| 8  | Most caudal point on inner rim of lunate surface   |
| 9  | Caudal termination of lunate surface   |
| 10 | Center of acetabular fossa   |
| 11 | Most medially projecting point on ischium, on ischial tuberosity   |
| 12 | Most dorsally projecting point on ischium, on ischial tuberosity   |
| 13 | Most laterally projecting point on ischium, on ischial tuberosity  |
| 14 | Ventral termination of ischial tuberosity  |
| 15 | Ischial spine  |
| 16 | Pubic tubercle; most medial point on pubis, cranial to pubic symphysis                                     |
| 17 | Most cranial point on rim of the obturator foramen   |
| 18 | Intersection of arcuate line and sacroiliac joint  |
| 19 | Point on iliac tuberosity corresponding to the medial extent of iliac crest, on inner surface of the ilium |
| 20 | Most laterally projecting point of anterior superior iliac spine, on inner surface of ilium                |
| 21 | Most cranial point on outer rim of the acetabulum  |
| 22 | Cranial termination of greater sciatic notch   |
| 23 | Most posterior point on rim of obturator foramen   |

<sup>a</sup> Semilandmark placement, characterizing the contours of the iliac crest, lateral margin of the ilium, greater sciatic notch, and obturator foramen, is described in the text and shown in Figure 4.



**Figure 4.** Landmarks collected from each specimen. Fixed landmarks are indicated in red. Curve-sliding semilandmarks defining the iliac crest, lateral margin of the ilium, greater sciatic notch, and obturator foramen are indicated in black. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

information could be found were excluded from this study. Localities and their associated elevations are presented in Table 3.

## 2.5. Statistical analyses

The R code for the statistical analyses described below has been provided in the [SOM S1 File](#).

**Between-sex MANOVA** Multivariate analysis of variance (MANOVA) was performed across all shape PCs in the combined-sex sample to test for systematic differences in mean PC scores for females and males. Note that this procedure only tests for differences in mean shape along a particular axis of variation and does not describe or test for differences in patterns of covariation between shape and other explanatory variables.

**Multivariate allometric regression** Gorillas exhibit a high degree of sexual dimorphism, and size-related differences in shape between females and males may confound the relationship between elevation and shape (e.g., [Jungers et al., 1995](#)). To evaluate this

influence, a multivariate regression of scores for each PC axis against the log-transformed centroid sizes of each individual was performed in 'geomorph' for the combined-sex, female, and male samples. Statistical significance of this relationship was assessed using a randomization procedure with 5000 iterations in which the model fit is compared against the fit of models using randomized shape variables. If the model of the observed data yields a better fit than 95% of the randomized models, the relationship between the independent and dependent variables is considered statistically significant.

**Phylogenetic signal: Blomberg's K** In general, closely related gorilla populations live at similar elevations ([Groves, 1967](#); [Goodall, 1977](#); [Doran and McNeillage, 1998](#); [Yamagiwa et al., 2005](#); [Caillaud et al., 2014](#)), introducing nonindependence among data points due to their shared evolutionary history ([Pagel, 1992, 1999](#); [Freckleton et al., 2002](#); [Barr, 2014](#); [Barr and Scott, 2014](#)). The degree to which phylogenetic relationships structure the observed morphological data (phylogenetic signal) was evaluated using Blomberg's K. In essence, Blomberg's K assesses how well the observed tip data fit the expectations of Brownian motion along a given phylogeny. This is quantified as the ratio between the mean squared errors around the phylogenetic mean before ( $MSE_0$ ) and after (MSE) correcting for the expected covariance under Brownian motion ([Blomberg et al., 2003](#); [Revell et al., 2008](#)). If the observed data are consistent with Brownian motion (i.e., high phylogenetic signal),  $MSE_0$  and MSE will be equal, and  $K = 1$ . If the tip taxa are less similar to each other than would be expected under Brownian motion (i.e., high phylogenetic signal), MSE will be larger than  $MSE_0$ , and  $K < 1$ . Deviations from  $K = 1$  suggest the potential influence of other evolutionary mechanisms including, but not limited to, adaptation. Blomberg's K is also advantageous in that it performs relatively well on small phylogenies ([Blomberg et al., 2003](#)) and has been generalized for multivariate datasets ([Adams, 2014](#)).

The multivariate generalization of Blomberg's K ([Adams, 2014](#)) was calculated across all Procrustes coordinates using the 'geomorph' package ([Adams et al., 2017](#)) to assess the phylogenetic structure of variation in overall shape at the locality level. Individual univariate estimates of Blomberg's K were also performed for the first two PCs. A composite phylogeny among subspecies was constructed using node dates from phylogenetic studies using nuclear genomes ([Fig. 1](#); [Thalmann et al., 2007](#); [McManus et al., 2014](#); [Roy et al., 2014](#)). As the phylogenetic relationships among the populations that make up subspecies have not been resolved, localities representing the same subspecies were treated as polytomies with negligible (i.e., zero) branch lengths.

**Table 3**  
Sample localities and elevation.<sup>a</sup>

| Subspecies            | Locality                    | Maximum elevation (m) | Females | Males |
|-----------------------|-----------------------------|-----------------------|---------|-------|
| <i>G. g. gorilla</i>  | Gabon                       | 0                     | 0       | 1     |
|                       | Ebolowa, Cameroon           | 602                   | 2       | 3     |
|                       | Abong Mbong, Cameroon       | 692                   | 4       | 2     |
|                       | Djaposten, Cameroon         | 710                   | 0       | 2     |
| <i>G. b. graueri</i>  | Bafwasende Territory        | 568                   | 2       | 5     |
|                       | Chamaka                     | 622                   | 1       | 0     |
|                       | Road to Itebero-Utu         | 773                   | 2       | 0     |
|                       | Tshibinda, West Kivu        | 1159                  | 0       | 1     |
|                       | Kalehe, South Kivu          | 1388                  | 0       | 1     |
|                       | Nbayo, Mt. Kahuzi           | 2350                  | 1       | 0     |
|                       | Chibimbi, North of Mt. Kivu | 1669                  | 0       | 1     |
|                       | Baraka, Forest Sibakwa      | 1850                  | 3       | 4     |
|                       | Lubango                     | 2000                  | 0       | 1     |
|                       | Virunga Massif              | 3850                  | 8       | 10    |
| <i>G. b. beringei</i> |                             |                       | 23      | 31    |
| Total                 |                             |                       |         |       |

<sup>a</sup> Locality latitude and longitude are available in [SOM Table S1](#).



**Elevation regression** To evaluate the relationship between habitat elevation and overall pelvic shape, multivariate regressions of the Procrustes coordinates against locality elevation were performed in the 'geomorph' package. Two regressions were performed: one assuming complete phylogenetic independence and one using a covariance matrix that reflects the expected covariance among the tip data under Brownian motion, resulting in a covariances proportional to phylogenetic distance. For each locality, the mean shape as represented by Procrustes coordinates was calculated. This was repeated using the combined-sex, female, and male samples.

To examine the relationships between elevation and individual axes of shape variation, two regression analyses were performed on the first two PCs individually for the combined sex, female, and male samples. The first was a generalized least squares regression that assumes phylogenetic independence among all of the data points. The second was a modified version of phylogenetic generalized least squares (PGLS) regression in which the expected covariance between observations of two taxa is proportionate to the phylogenetic distance between them (Grafen, 1989; Symonds and Blomberg, 2014). This differs from other PGLS approaches in that it does not include a measure of phylogenetic signal to transform branch lengths. As such, the PGLS regressions reported here reflect an assumption of complete phylogenetic signal under a Brownian motion model of evolution. Both sets of regression analyses were performed using the 'caper' package (Orme et al., 2018).

For each sample, the fits of the regression models were compared using the Akaike information criterion corrected for small sample sizes (AICc) to evaluate the fit of a model while penalizing for model complexity (Akaike, 1974; Hurvich and Tsai, 1989). Models with the lowest AICc values and highest AIC weights were selected as the best fit of the two models. Model fitting and comparisons were performed using the 'mvMORPH' package (Clavel et al., 2015).

### 3. Results

#### 3.1. Principal components analysis

The distribution of subspecies along the first two PCs is illustrated in Figure 5. PC1 explains 28.7% of the total variance in the combined-sex sample, 44.6% of the total variance in the female sample, and 24.4% of the total variance in the male sample. In the combined-sex and female samples, PC1 differentiates *G. gorilla* (negative values) and *G. beringei* (positive values) with two *G. g. gorilla* specimens overlapping with the range of *G. b. beringei*. In the male sample, *G. gorilla* overlaps almost completely with the lower end of the range for *G. beringei*. In all samples, more positive PC1 scores are associated with a mediolaterally wider iliac blade, caudal sloping of the lateral half of the iliac crest, and a greater projection of the ASIS, giving the lateral ilium a 'beaked' appearance (see also Fig. 6). In the male sample, more positive scores are also associated with a more mediolaterally narrow obturator foramen. There is no apparent separation between females and males in the combined sex sample along either of the first two PCs.

PC2 explains 15.9% of the total variance in the combined-sex sample, 12.6% of the total variance in the female sample, and 20.9% of the total variance in the male sample. There is some differentiation between *G. b. graueri* and *G. b. beringei* along PC2 in the combined-sex and male samples, and the *G. b. beringei* range is entirely within that of *G. b. graueri* along PC2 in females. In the combined-sex sample, *Gorilla beringei graueri* has generally more positive scores that correspond to a greater lateral projection of the ASIS, though there is considerable overlap in the ranges of PC2 scores for *G. b. graueri* and *G. b. beringei*.

In the combined-sex and female samples, more positive scores along PC2 correspond to a greater caudal sloping of the lateral half of the iliac crest, while more negative values are associated with a more transversely oriented iliac crest. These shape changes are very subtle in the female sample, and this may be the reason for PC2 explaining a relatively small part of the overall shape variance. Males exhibit the opposite pattern: more negative values are associated with greater lateral projection and caudal sloping of the lateral half of the iliac crest and ASIS.

PC3 explains 11.4% of the total variance in the combined-sex sample, 8.4% of the total variance in the female sample, and 13.7% of the total variance in the male sample. There is no apparent differentiation among subspecies on this axis, and the morphological significance of variation along this axis is unclear. As such, regression analyses of elevation against PC3 and subsequent PCs were not performed.

#### 3.2. Between-sex MANOVA

Mean PC scores for the combined-sex dataset are significantly different between females and males on only PC3 ( $p < 0.01$ ,  $F[1,52] = 17.66$ ) and PC4 ( $p < 0.01$ ,  $F[1,52] = 41.75$ ). These axes accounted for 11.4% and 7% of the total variance, respectively, and did not appear to differentiate subspecies or populations.

#### 3.3. Multivariate allometric regression

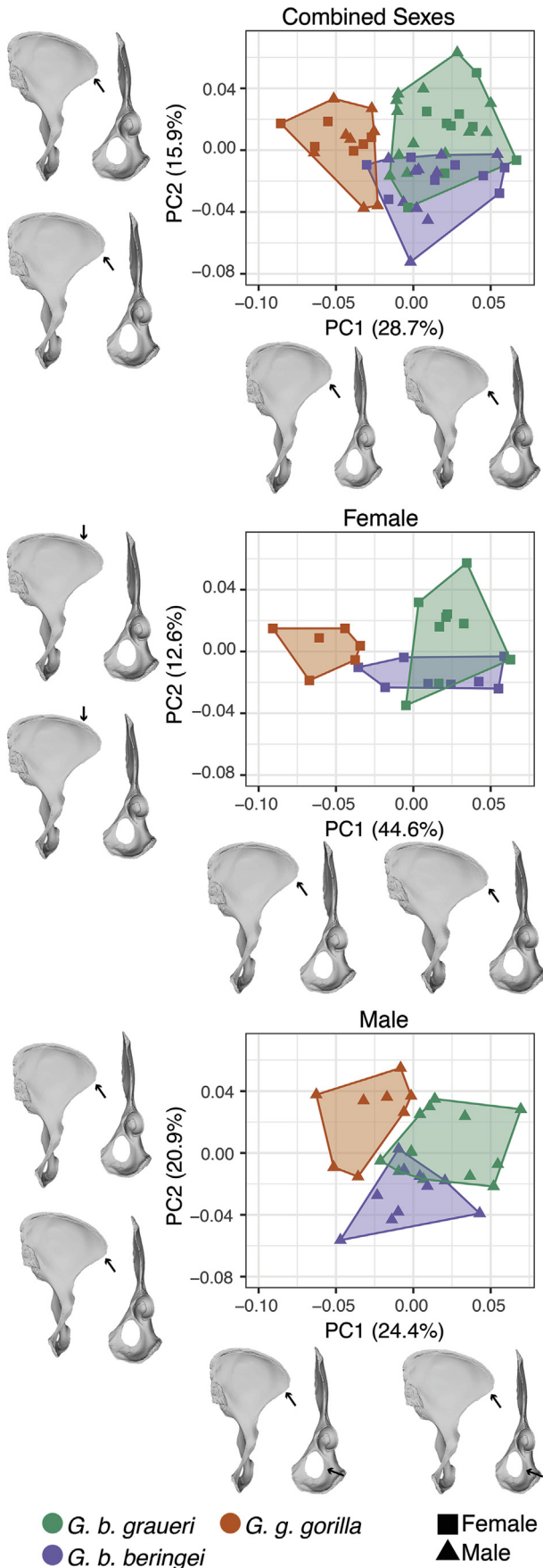
Results of the multivariate least-squares allometric regressions of all Procrustes coordinates against log-transformed centroid size are summarized in Table 4. The combined-sex sample yielded a significant relationship ( $p = 0.01$ ,  $r^2 = 0.08$ ). The female sample also had a significant allometric relationship ( $p = 0.01$ ,  $r^2 = 0.26$ ). The male sample did not have a significant allometric relationship ( $p = 0.07$ ). In both the female and combined-sex samples, the ASIS projects further laterally and the lateral half of the iliac crest slopes further caudally as overall size increases.

#### 3.4. Phylogenetic signal: Blomberg's K

Estimates of the multivariate Blomberg's K for overall shape as reflected by the Procrustes coordinates yielded K-values less than one for the combined-sex ( $K = 0.002$ ), female ( $K = 0.003$ ), and male ( $K = 0.002$ ) samples. K-values less than one indicate that the populations studied here are less similar in shape than would be expected under Brownian motion (i.e., low phylogenetic signal). K-values indicated nearly no phylogenetic signal in all samples for both PC1 (combined-sex:  $K = 0.01$ , female:  $K = 0.01$ , male:  $K = 0$ ) and PC2 (combined-sex:  $K = 0$ , female:  $K = 0$ , male:  $K = 0$ ), indicating a greater degree of similarity among populations than expected under Brownian motion.

#### 3.5. Multivariate elevation regression

Results of the multivariate regressions of all Procrustes coordinates against elevation are summarized in Table 4. Regression models that did not assume phylogenetic covariation did not indicate a significant relationship in either the combined-sex ( $p = 0.09$ ) or the female ( $p = 0.30$ ) samples. The male sample, however, did have a significant relationship ( $p = 0.05$ ,  $r^2 = 0.17$ ). When the covariance matrix is adjusted to reflect phylogenetic distance, there was not a significant relationship in either the combined-sex ( $p = 0.10$ ) or male ( $p = 0.56$ ) samples. The female sample, however, did have a significant relationship ( $p < 0.01$ ,  $r^2 = 0.43$ ).



### 3.6. Individual PC elevation regression and model selection

Summary statistics and AICc values are presented in Table 5. There were no significant relationships for the first PC irrespective of data partitioning and phylogenetic assumptions (Fig. 7a–c).

For PC2, there were no significant relationships in the combined-sex sample (Fig. 7d). The female sample exhibited a significant relationship under Brownian motion ( $p < 0.01$ ,  $r^2 = 0.85$ ), while the phylogenetically independent model did not ( $p = 0.07$ ,  $r^2 = 0.44$ ; Fig. 7). In the male sample, the model assuming Brownian motion was not significant ( $p = 0.53$ ,  $r^2 = 0.04$ ), while the PGLS model was significant ( $p = 0.050$ ,  $r^2 = 0.37$ ; Fig. 7f). In all cases, the GLS yielded a better fit than the PGLS model.

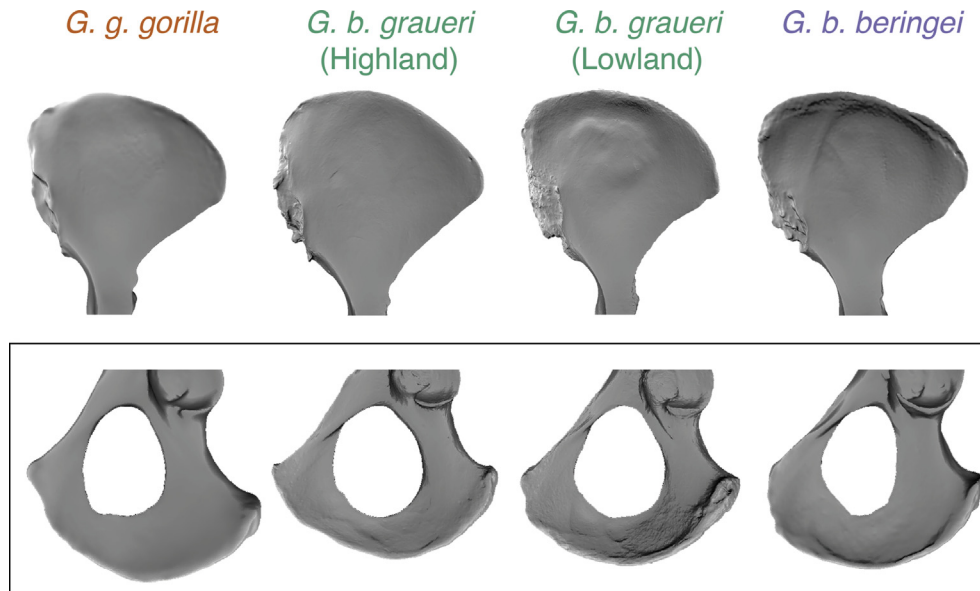
## 4. Discussion

### 4.1. Summary of results

The present study sought to quantitatively characterize variation in the pelvis of gorilla subspecies that live at different elevations and that engage in arboreal behaviors with different frequencies. Previous research on elevation/morphology relationships in gorillas has identified several postcranial morphologies that match expectations derived from observations of locomotor behavior. The present study built on this body of work by evaluating whether there is a relationship between habitat-specific behavior and pelvic morphology in a framework that also accounts for phylogenetic relationships. To this end, we addressed three research questions: (1) Do gorilla subspecies differ in their pelvic morphology? (2) Is there a relationship between habitat elevation and pelvic morphology across gorillas? and (3) How does the inclusion of phylogenetic information affect the fit of elevation/morphology regression models and our interpretation of ecomorphological relationships?

In the combined-sex and female samples, there are species-level differences in the morphology of the ASIS. *Gorilla beringei* tends to have a more laterally projecting ASIS and the lateral half of the iliac crest slopes caudally. In *G. gorilla*, the iliac crest forms a more symmetrical arc. This was not the case in the male sample; there is substantial overlap among all three subspecies on PC1. However, male *G. b. graueri* tend to have a more projecting ASIS as well as a more mediolaterally narrow obturator foramen. In the female sample, PC1 accounts for more than three times the variation represented by PC2 (12.6%), suggesting that species-level differences in the shape of the lateral ilium are the predominant sources of morphological variation among females. This strong interspecific signal is likely attenuated when both sexes are analyzed together by the overlapping ranges of subspecies along PC1 in males. As a result, the combined-sex sample appears to reflect species-level differences, but these differences account for a lesser portion of the overall variance than they do in females.

**Figure 5.** Plots of second vs. first principal components (PC2 vs. PC1) for the combined-sex, female, and male samples. In each case, *G. beringei* tends to have higher PC1 scores than *G. gorilla* with some overlap, especially in males. In all of the samples, more positive PC1 scores indicate a greater lateral projection of the anterior superior iliac spine (indicated by black arrows in the figure) and caudal sloping of the lateral iliac crest. More positive PC1 scores are also associated with a dorsoventrally narrow obturator foramen in males (indicated by red arrow in figure). In each sample, *G. b. graueri* tends to have higher PC2 scores than *G. b. beringei*, albeit with considerable overlap between the two. In females, the *G. b. beringei* PC2 range is completely within that of *G. b. graueri*. In the combined-sex and female samples, more positive PC2 scores reflect a greater degree of caudal sloping of the lateral iliac crest. In males, however, more negative scores reflect greater caudal sloping of the lateral iliac crest. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)



**Figure 6.** Representative ilia (above, in ventral view) and obturator foramina (below, in ventrolateral view) of *G. g. gorilla*, *G. b. graueri*, and *G. b. beringei*. The lateral projection of the anterior superior iliac spine in *G. beringei*, and particularly *G. b. graueri*, is evident. Images of ilia are called to the same vertical height, and images of obturator foramina are scaled to the same vertical height. Specimens shown include CMNH-B 1704 (*G. g. gorilla*), RMCA 27756 (lowland *G. b. graueri*), RMCA 1001 (highland *G. b. graueri*), and RMCA 2558 (*G. b. beringei*).

**Table 4**  
Summary statistics from multivariate regression models.<sup>a</sup>

| Model              | Type | <i>p</i>        | <i>r</i> <sup>2</sup> |
|--------------------|------|-----------------|-----------------------|
| Combined allometry | GLS  | <b>0.01</b>     | <b>0.08</b>           |
| Female allometry   | GLS  | <b>0.01</b>     | <b>0.26</b>           |
| Male allometry     | GLS  | 0.07            | 0.06                  |
| Combined elevation | GLS  | 0.09            | 0.13                  |
| Combined elevation | PGLS | 0.10            | 0.12                  |
| Female elevation   | GLS  | 0.30            | 0.17                  |
| Female elevation   | PGLS | <b>&lt;0.01</b> | <b>0.43</b>           |
| Male elevation     | GLS  | <b>0.05</b>     | <b>0.17</b>           |
| Male elevation     | PGLS | 0.56            | 0.09                  |

Abbreviations: GLS = generalized least squares; PGLS = phylogenetic generalized least squares.

<sup>a</sup> Significant results are indicated in bold.

**Table 5**  
Summary statistics from regression models for individual PCs.<sup>a</sup>

| Model        | Type | <i>p</i>        | <i>r</i> <sup>2</sup> | AICc          | AIC weight |
|--------------|------|-----------------|-----------------------|---------------|------------|
| Combined PC1 | GLS* | 0.11            | 0.20                  | −61.31        | 0.95       |
|              | PGLS | 0.45            | 0.05                  | −55.29        | 0.05       |
| Female PC1   | GLS* | 0.45            | 0.10                  | −28.55        | 0.96       |
|              | PGLS | 0.48            | 0.09                  | −22.35        | 0.04       |
| Male PC1     | GLS* | 0.21            | 0.17                  | −49.39        | 1.00       |
|              | PGLS | 0.50            | 0.05                  | −33.24        | 0          |
| Combined PC2 | GLS* | 0.09            | 0.22                  | −68.36        | 1.00       |
|              | PGLS | 0.13            | 0.18                  | −44.44        | 0          |
| Female PC2   | GLS* | 0.07            | 0.44                  | −38.19        | 1.00       |
|              | PGLS | <b>&lt;0.01</b> | <b>0.85</b>           | <b>−27.49</b> | <b>0</b>   |
| Male PC2     | GLS* | <b>0.01</b>     | <b>0.57</b>           | <b>−60.36</b> | <b>1</b>   |
| Combined PC1 | PGLS | 0.53            | 0.04                  | −39.46        | 0          |

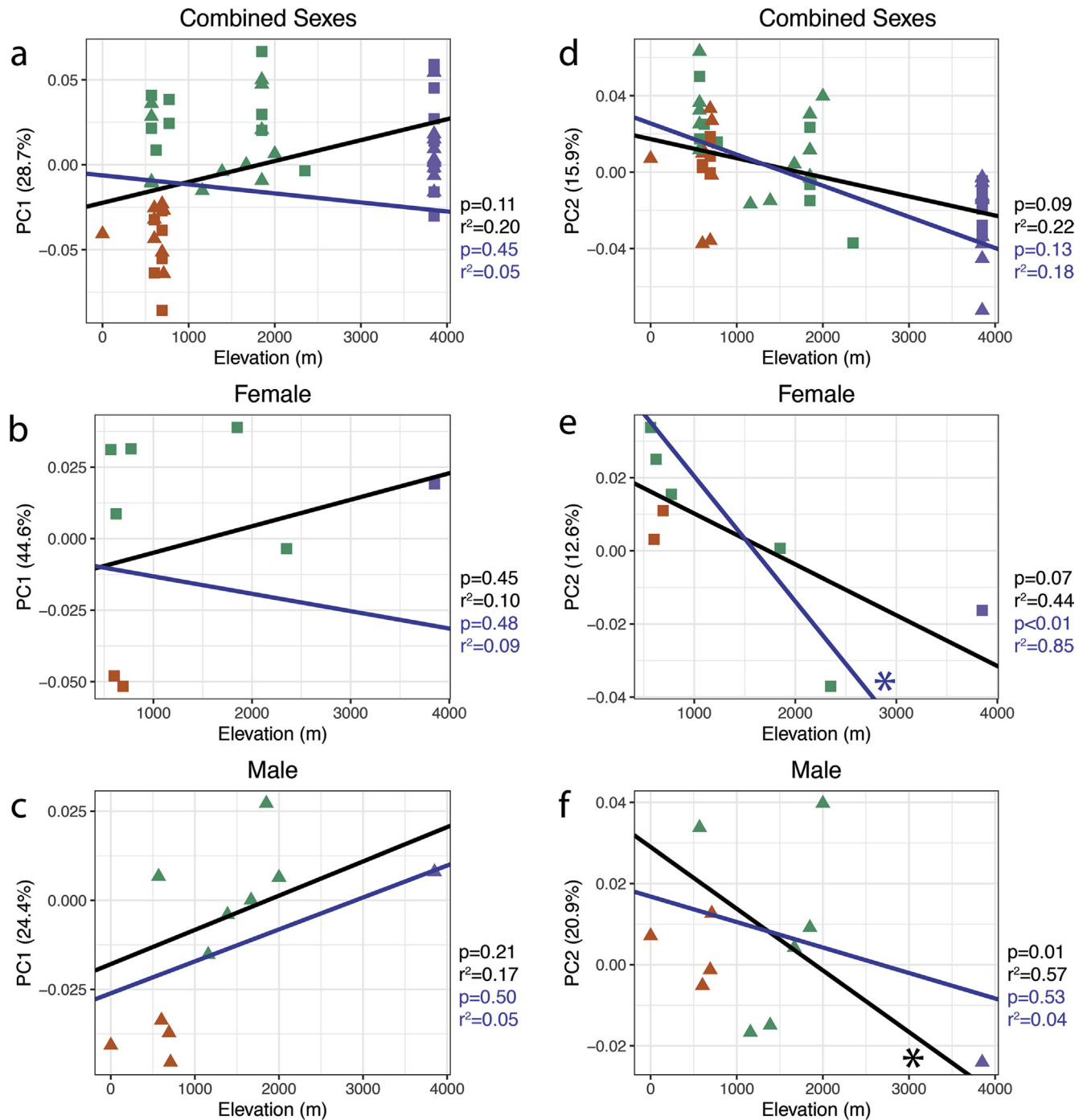
Abbreviations: AICc = Akaike information criterion corrected for small sample size; AIC weight = Akaike information criterion weight; GLS = generalized least squares; PGLS = phylogenetic generalized least squares.

<sup>a</sup> Significant results are in bold. Best-fit models are indicated by asterisk.

Patterns of morphological variation and variance explained are more variable among samples on PC2. PC2 accounts for 15.9% of the overall variance in the combined-sex sample and corresponds to differences in the caudal sloping of the lateral iliac crest. There is

some distinction between *G. b. graueri* and *G. b. beringei*, albeit with considerable overlap. The more positive scores characteristic of *G. b. graueri* reflect a greater degree of caudal sloping than that observed in *G. b. beringei*. In females, PC2 explains much less of the shape variation (12.6%) than PC1 (44.6%), and the *G. b. beringei* range is entirely within that of *G. b. graueri* on this axis. Unlike the combined-sex sample, there is no distinction between *G. b. graueri* and *G. b. beringei*. In terms of morphology, variation along this axis corresponds to very subtle differences in the shape of the iliac crest. The lack of meaningful differentiation among groups, low percentage of variance explained, and barely discernible morphological variation along PC2 appear to suggest that this axis may reflect random variation. In the male sample, PC2 explains 20.9% of the total variance. Unlike the combined-sex sample, more positive scores indicate a lesser degree of caudal sloping. There may be some distinction between *G. b. beringei* and the other two subspecies, with *G. b. beringei* having a greater degree of caudal sloping, though there is considerable overlap in the scores for all three subspecies. The differences in variance explained, group discrimination, and morphological significance of PC2 among samples suggests that after interspecific variation, the secondary sources of pelvic variation differ according to the composition of the sample and are not common between sexes.

It is possible that differences in pelvic shape among gorilla subspecies have functional consequences. Several hip muscles relevant to locomotion have attachments on the iliac blade, and differences in iliac shape may reflect functional differences in muscular configuration (see also Hammond and Almécija, 2017). For instance, the large gluteus maximus and iliopsoas muscles attach to the iliac blade and are the primary extensors and flexors of the hip, respectively (Gregory and Raven, 1950; Stern, 1971; Diogo et al., 2010). The lesser gluteal muscles also attach to the ilium and are involved in internal rotation of the hip, among other actions (Gregory and Raven, 1950; Stern and Susman, 1983; Diogo et al., 2010). Differences were also observed in the relative size of the obturator foramen (Figs. 5 and 6). The obturator foramen, the overlying obturator membrane, and the adjacent bony pubis and ischium are attachment sites for the obturator externus and obturator internus muscles. These muscles laterally rotate the thigh, an



**Figure 7.** Plots of phylogenetic generalized least squares regressions. Points represent mean PC values for each locality. The first principal component against elevation is shown for the combined-sex (a), female (b), and male (c) samples. The second principal component against elevation is shown for the combined-sex (d), female (e), and male (f) samples. Models in which that do not include phylogenetic adjustment are in black, and models using the phylogenetic covariance matrix are in blue. Significant relationships are indicated with an asterisk. The only significant relationships were in females on PC2 with phylogenetic adjustment and in males on PC2 without phylogenetic adjustment. None of the combined-sex models were significant. Regression statistics are presented in Table 5. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

important concomitant movement of hip abduction during vertical climbing in apes (Stern and Larson, 1993; Hammond, 2014), and so an expanded area of origin for these muscles could reflect more powerful lateral rotation abilities related to increased climbing behaviors. Likewise, a beaked or more laterally projecting ilium might also reflect differences in mechanical advantage of the gluteus minimus and scanorius muscles, which originate along the lateral border of the ilium and are involved in hip abduction,

rotation, and flexion. However, the differences observed in pelvic shape and the functional implications for the associated muscles remain speculative until detailed dissection work and biomechanical modeling are available for these gorilla subspecies.

Prior to addressing the relationship between elevation and pelvic shape, the potential influence of sexual dimorphism was evaluated. Mean PC scores for females and males along the leading two PCs were not significantly different, indicating that the most



prevalent axes of shape variation cannot be attributed to sex differences. There were significant differences in mean scores between sexes along PC3 and PC4; however, these axes were excluded from subsequent regression analyses because they explain relatively little of the overall shape variation. Differences in size accounted for a small portion (8%) of the variance in overall shape when females and males were examined together, and a greater portion of the variance in females (26%). Males, however, did not have a significant relationship. This suggests that the allometric signal present in the full sample is driven primarily by the stronger signal in the female sample. This combined with shape differences restricted to lesser PCs points to complex interactions between sex, size, and pelvic shape and suggested that it would be appropriate to perform separate analyses for females and males.

Similar to allometric scaling relationships, there are also sex differences in the relationships between phylogeny, elevation, and overall pelvic shape. The relationship between overall size and elevation when sexes were combined was not significant either before or after adjusting the covariance matrix to reflect phylogenetic distance. When females were analyzed alone, the shape/elevation relationship was only significant after phylogenetic adjustment, and elevation explained a substantial amount of the variation in overall shape (43%). The opposite pattern was found in males; the shape/elevation relationship was only significant prior to phylogenetic adjustment and explained less of the variation in overall shape (17%). Given that there is not a significant ecomorphological signal for the combined-sex sample and that females and males yield significant relationships only under different treatments of phylogenetic information, there does not appear to be a singular pattern of covariation between overall shape and elevation that can be applied across gorillas as a whole. These findings do not indicate, however, that individual axes of variation do not bear a relationship with elevation.

Estimates of phylogenetic signal for Procrustes coordinates and the first two PCs all yielded low K-values that often approached zero, indicating a lesser degree of similarity among populations than would be expected based on their phylogenetic distance. This was surprising given the separation of subspecies along the first two PCs (Fig. 5). However, phylogenetic signal was not calculated at the level of the subspecies, but rather at the level of the individual populations that constitute the subspecies. It is possible that the assumed lack of phylogenetic structure within subspecies due to unresolved population-level polytomies overwhelms the signal that would be expected among subspecies based on their distributions in PC space.

There are several potential explanations for this. It may be that pelvic morphology truly bears no indication of its phylogenetic history at all. As such, the clustering of subspecies in PC space would be a matter of coincidence. Since at least some aspects of pelvic morphogenesis is regulated by genes and are thus heritable, this scenario is unlikely. Alternatively, it is possible that gorilla populations have not been isolated long enough for genetic drift to establish systematic, selectively neutral differences among populations that would yield a pattern of variation consistent with Brownian motion. Given the long lifespans of gorillas and the relatively short period of time over which they have diverged, this is the more likely explanation. This may be an unavoidable problem when applying phylogenetic comparative methods to recently diverged populations of long-lived species. However, insufficient divergence time should not be assumed a priori, and it is still prudent to compare multiple evolutionary models with different phylogenetic assumptions.

The regressions for PC1 against elevation were not significant in any of the samples (Fig. 7a–c), indicating that elevation is not the primary source of shape variation in the gorilla pelvis. As with the multivariate regressions for overall shape, the combined-sexes

sample did not bear a significant relationship between PC2 and elevation (Fig. 7d), regardless of phylogenetic assumptions. Females, however, had a significant relationship between PC2 and elevation under Brownian motion, and this model yielded a better fit than the phylogenetically independent model. Under this model, elevation explained a substantial portion (85%) of the variance along PC2. Males, on the other hand, did not have a significant relationship under Brownian motion, but did when assuming phylogenetic independence. This model had the best fit but explained less of the variance along PC2 than it did in females (57%). The strong relationships found in the female sample should be treated with caution, however, as PC2 explains relatively little of the overall shape variation, and its morphological significance is minor.

While there was evidence of significant relationships between elevation and various aspects of pelvic morphology, these patterns only emerged when females and males were analyzed separately and under different phylogenetic assumptions. Given that ecomorphological relationships were significant only under very specific circumstances that differed between sexes, there is not a single pattern of covariation between shape and elevation that characterizes gorillas as a whole.

In the case of the gorilla pelvis, the morphology of the ASIS more closely tracks elevation in females than it does in males. This resembles the ‘ecological sex’ phenomenon described by Gordon et al. (2013), in which body size was more strongly correlated with ecological variables in females than males in *Propithecus*. The present study found sex differences in both mean shape (i.e., PC3 and PC4) and the patterns of shape change associated with differences in habitat elevation. It is therefore plausible that female and male gorillas adapt to their habitats in different ways, perhaps as a consequence of other sex-specific selection pressures.

These findings also have more general implications for comparative morphology. First, when seeking to describe relationships between ecology and morphology, it is critical that other potential influences, like sex, are taken into account. Second, though the phylogenetically independent models had the best fit in the current study, the sensitivity of the results to different treatments of phylogenetic information emphasize the need for critical assessment of the role of phylogenetic structure in the tip data. Third, great apes may indeed offer complementary models of ecophenotypic diversity that better characterize morphological evolution in the fossil record. While modern human models have been invaluable in efforts to examine how ecology might have shaped morphological evolution in the past, unique aspects of human biology like reduced sexual dimorphism may not be generalizable to other hominoids, both living and extinct.

#### 4.2. Broader implications

The pelvis plays a central role in reconstructing locomotor behavior in fossil hominoids and, as such, a detailed understanding of the patterns of pelvic variation in living apes is critical to the interpretation of fossil diversity. Unfortunately, the fragmentary nature of the fossil record and uncertainty surrounding the phylogenetic positions of postcranial fossils makes interpretation of pelvic variation difficult. Extant models of ecological variation, however, offer a promising route forward.

Modern humans occupy an extraordinary breadth of environments and exhibit considerable phenotypic variation, making them an intuitive model for ecogeographic variation in fossil hominins. Indeed, much insight into phenotypic evolution has been gained using human models, including in pelvic shape (Betti et al., 2013, 2014; Betti, 2017; Betti and Manica, 2018). However, some unique aspects of human biology may not apply to extinct taxa. One such point of departure is the greatly diminished level of sexual

dimorphism in modern humans compared to their fossil predecessors like *Australopithecus* (e.g., Richmond and Jungers, 1995; Lockwood et al., 1996; Gordon et al., 2008). As von Cramon-Taubadel and Smith (2012) noted, studies of adaptive and neutral evolutionary processes at fine-grained taxonomic levels in other hominoids may be helpful for disentangling these processes in the fossil record. Modern gorilla populations are phylogenetically close, ecologically diverse, and have documented behavioral differences related to their specific habitats. This combination of factors makes them a promising alternative model of large-bodied, highly sexually dimorphic, and ecologically diverse hominoids. While no extant model perfectly reflects the processes underlying fossil diversity, multiple models and multiple evolutionary hypotheses (i.e., adaptive vs. nonadaptive processes) can improve the confidence with which we draw conclusions about the role of ecology in shaping phenotypic evolution in great apes and humans.

There is an increasingly prevalent view that the pelvic evolution of the extant apes was characterized by homoplasy due to similar biomechanical demands (Lovejoy et al., 2009a, b; Hammond et al., 2013; Hammond and Almécija, 2017). Evaluation of this hypothesis rests on our ability to reconstruct the ancestral condition, polarize observed differences from this condition, and characterize the evolutionary processes that generated these character states. Evolutionary modeling of lower ilium length in hominoids found similar proportions between *Gorilla* and Miocene hominoids (Hammond and Almécija, 2017), suggesting that living gorillas may be particularly important in further studies of hominoid pelvic evolution. There is considerable variation both among and within hominin pelvises (Marchal, 2000; Häusler and Berger, 2001; Kibii et al., 2011; Claxton et al., 2016; Ward et al., 2015; Hammond et al., 2018), and new discoveries reveal an increasingly complex picture of hominin pelvic evolution. This variation is particularly pronounced in the iliac crest, iliac pillar, and ASIS. This appears to be the case in gorillas as well. Here, variation in the iliac crest and ASIS accounted for the largest proportions of overall shape variance (i.e., PC1 and PC2), and was effective at differentiating between species and subspecies to some degree.

Moving beyond the fossil record, a more comprehensive understanding of how populations can or cannot adapt to their specific habitats can improve the development of conservation strategies targeted to specific populations. The lack of a clear signal of pelvic adaptation to ecologically-mediated behavior suggests that pelvic adaptation may be somehow constrained or that there simply has not been enough time since their divergence for gorilla populations to accrue pelvic adaptations to locomotor behavior. While the period of time over which modern gorilla diversity arose is short in the evolutionary sense, it is long compared to the rate of anthropogenic habitat modification and destruction. Ultimately, a population's survival depends on a vast constellation of interacting phenotypes. The present findings, while restricted to a single phenotype, illustrate the need to consider not only how organisms vary, but also the broader evolutionary context in which this variation arose.

#### 4.3. Limitations and future directions

There are several limitations to the present study. Relatively few gorilla populations are represented in osteological collections, and the sample sizes for most of these populations are small. These sampling issues are particularly problematic when estimating phylogenetic signal. Nonetheless, we tried to sample as broad a range as possible. Collection localities were often recorded in museum catalogs using colonial or outdated names and often reflected the names of nearest towns or roads. As such, the locations of the points and buffers used to extract elevation may data may not reflect the elevation of the habitat itself or the parts of the habitat

gorillas use regularly. While there are some unavoidable weaknesses in the current dataset, effort was taken to mitigate their effects on the study results. Future work aiming to integrate morphological, ecological, and phylogenetic data should take these factors into consideration during study design and interpretation of findings. In particular, larger clades with larger sample sizes for each tip taxon may offer further insight into anatomical correlates of ecology-specific behaviors in primates beyond those presented here.

#### 5. Conclusions

The present study evaluated the adaptive significance of variation in gorilla pelvic shape. First, 3D geometric morphometric analysis revealed differentiation among gorilla species in the morphology of the ilium, and partial differentiation between subspecies in the morphology of the ilium and obturator foramen. Second, phylogenetic comparative analyses indicated that tests of the relationship between habitat elevation and pelvic shape can yield different results in females and males with different assumptions about the degree of phylogenetic signal. Further research is needed to determine the functional implications of these shape differences and their impact on climbing ability.

Lastly, comparisons of model fits with different phylogenetic assumptions found that phylogenetically independent models had the best fits in each comparison. PC2 was the only axis that bore a significant relationship with elevation, however this was only the case when sexes were analyzed separately with different treatments of phylogenetic information. The strongest relationship with elevation was for PC2 in females after phylogenetic adjustment. This finding suggests that female gorilla pelvises may be more finely tuned to their habitat-specific locomotor demands than those of males, though the subtlety of shape change along this axis makes the functional significance of this pattern difficult to interpret. The differences in model fit and significance between sex groupings emphasize the importance of critically considering how phylogenetic effects and other factors like sex will be handled when designing comparative morphological studies.

This research contributes to a broader research effort to elucidate how ecology-specific behaviors and phylogenetic history are—or are not—reflected in the skeletal morphology of great apes. Gorillas have proven to be a particularly valuable model for studying morphological evolution across short spans of evolutionary time due to their ecological and behavioral diversity despite having a relatively recent last common ancestor. The results from this study indicate that, at least in the pelvis, the relationship between habitat ecology and morphology is complex and is potentially confounded by other influences like sex and phylogeny. While differences in iliac morphology were observed and bore a significant relationship to elevation in some cases, there is no single unified pattern that characterizes pelvic morphological variation across all of *Gorilla* in terms of adaptation to specific habitats.

Future studies of morphological variation in very closely related taxa should also attempt to account for other environmental factors like annual rainfall that may shape primate habitats and thus their behavior and morphology. These environmental factors are tightly interrelated, and research on their relationship to morphology will require more sophisticated modeling to parse out their relative effects. We conclude that due diligence in exploring multiple evolutionary explanations is critical to drawing meaningful conclusions about the significance of phenotypic diversity.

#### Acknowledgments

The authors thank the curators and staff at the US National Museum of Natural History, Royal Museum for Central Africa, Royal

Belgian Institute of Natural Sciences, Swedish Museum of Natural History, American Museum of Natural History, and Cleveland Museum of Natural History. We also acknowledge the Rwandan government for permission to study skeletal remains curated by the Mountain Gorilla Skeletal Project in Rwanda, which has been made possible by the continuous efforts of researchers, staff and students from the Rwanda Development Board's Department of Tourism and Conservation, Gorilla Doctors, Dian Fossey Gorilla Fund International's (DFGI) Karisoke Research Center, The George Washington University, New York University College of Dentistry, Institute of National Museums of Rwanda, and other universities in Rwanda and the USA, by infrastructural support from DFGFI, and by funding from the National Science Foundation (BCS-0852866, BCS-0964944, BCS-1520221), National Geographic Society's Committee for Research and Exploration (8486-08), and The Leakey Foundation. Additional funding for this work was generously provided by the National Science Foundation (BCS 1232393, BCS 0852866, BCS 0964944, BCS 1520221), Wenner-Gren Foundation, Leakey Foundation, National Geographic, the Agencia Estatal de Investigación and European Regional Development Fund (CGL2017-82654-PO), Generalitat de Catalunya (CERCA Programme), the GWU Lewis N. Cotlow Fund, and the GWU William Warren Endowment. Support for L.M.F. was generously provided by the GWU Presidential Merit Fellowship. We thank Nicolas Gauthier and Alexander Prucha for programming assistance, Jordi Galbany for sharing photographs, Jeroen Smaers for advice on regression model comparisons, and Jane Meiter for assistance with photogrammetric modeling. We thank three anonymous reviewers for their feedback, which greatly improved the manuscript.

## Supplementary Online Material

Supplementary online material to this article can be found online at <https://doi.org/10.1016/j.jhevol.2019.102684>.

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