PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Dickinson E, Young MW, Hirschkorn GA, McKinney JC, DiMartino A, Deutsch MR, Welser KH, Granatosky MC. 2025 Ecomorphological correlates of grasping forces in strepsirrhine primates. *Proc. R. Soc. B* **292**: 20242190.
https://doi.org/10.1098/rspb.2024.2190

Received: 13 September 2024
Accepted: 18 November 2024

Subject Category:
Morphology and biomechanics

Subject Areas:
biomechanics, evolution

Keywords:
grip force, lemur, arboreal, biomechanics, muscle architecture, locomotion

Author for correspondence:
Michael C. Granatosky
e-mail: michael.granatosky@nyit.edu

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.7571814.

THE ROYAL SOCIETY
PUBLISHING

Ecomorphological correlates of grasping forces in strepsirrhine primates

Edwin Dickinson[1,2], Melody W. Young[3,4], Gabrielle A. Hirschkorn[5], Julie C. McKinney[5], Alana DiMartino[1], Michael R. Deutsch[1], Kay H. Welser[5] and Michael C. Granatosky[1,5,6]

[1]Department of Anatomy, New York Institute of Technology College of Osteopathic Medicine, Old Westbury, NY 11568, USA
[2]Department of Anthropology and Archaeology, University of Calgary, Calgary, Alberta T2N1N4, Canada
[3]Department of Biology, [4]Department of Biomedical Engineering, and [5]Duke Lemur Center, Duke University, Durham NC 27701, USA
[6]Center for Biomedical Innovation, New York Institute of Technology College of Osteopathic Medicine, Old Westbury, NY 11568, USA

ED, 0000-0002-9062-6677; MWY, 0000-0003-1760-812X; MCG, 0000-0002-6465-5386

Powerful digital grasping is essential for primates navigating arboreal environments and is often regarded as a defining characteristic of the order. However, *in vivo* data on primate grip strength are limited. In this study, we collected grasping data from the hands and feet of eleven strepsirrhine species to assess how ecomorphological variables—such as autopodial shape, laterality, body mass and locomotor mode—influence grasping performance. Additionally, we derived anatomical estimates of grip force from cadaveric material to determine whether *in vivo* and *ex vivo* grip strength measurements follow similar scaling relationships and how they correlate. Results show that both *in vivo* and anatomical grip strength scale positively with body mass, though anatomical measures may overestimate *in vivo* performance. Species with wider autopodia tend to exhibit higher grip forces, and forelimb grip forces exceed those of the hindlimbs. No lateralization in grip strength was observed. While strepsirrhine grip forces relative to their body weight are comparable to those of other primates and slightly exceed those of humans, they are not exceptional compared to other arboreal mammals or birds, suggesting that claims of extraordinary primate grasping abilities require further investigation.

1. Introduction

It is impossible to understand primate ecology, evolution and behaviour without an understanding of the constraints associated with arboreal locomotion [1–3]. Adaptations for arboreal grasping, particularly in fine branches, are considered critical drivers of early primate evolution [4–7], and classical definitions of primates [4,6] emphasize powerful grasping appendages as a hallmark feature of the order. As a result, it is widely understood that primates are highly effective graspers (with both their hands and feet) across a range of substrates [7–9]. Indeed, the ability to generate powerful grasping forces is considered essential for survival when moving on arboreal substrates [10,11], as these supports are unpredictable in nature and often three-dimensionally complex, varying in orientation, size, texture, compliance and gap distance [2–4,12]. Given the steep fitness cost of failure (e.g. falls) during arboreal locomotion, which could result in serious injury or death [13], grasping forces are considered a core functional metric upon which adaptive selection is expected to exert strong pressures [5,6,14]. Yet, despite widespread recognition of their importance in an evolutionary context, little data currently exist on the grasping abilities of primates in a comparative framework.

The basic biomechanical abilities associated with grasping (i.e. controlled manipulation of an object or substrate with the manual or pedal digits) likely originated early in tetrapod evolution [14]. Across multiple tetrapod radiations, a positive relationship between arboreality and grasping strength has been suggested, highlighting the importance of manual grip strength as an adaptation among specialized arborealists to mitigate the risks associated with falling [11,14]. However, these grasps vary drastically in both their nature and complexity, reflecting differences in gross autopodial morphology as well as the extent of neuromuscular independence between individual digits [14]. Additionally, limited work has explored the ecomorphological correlates of grasping capabilities, making direct relationships between anatomy and performance difficult to elucidate [15,16].

(a) Anatomical estimates of primate grip force

The ability to generate grasping forces is anatomically determined by the contractile properties of skeletal muscles [17–22]. Over the past decade, several studies have sought to assess the anatomical grip strength of primates, using the physiological cross-sectional area (PCSA) of digital flexor muscles as a proxy for potential grasping strength [17,18,20–22]. Digital flexor PCSA is reported to scale with positive allometry relative to body mass across a broad sample ($n = 55$) of strepsirrhines and anthropoids [20]. However, no differences in relative digital flexor strength (accounting for body mass) were reported between arboreal and terrestrial taxa, nor were any observed between locomotor modes (e.g. quadrupedal versus suspensory versus climbing specialists; [20]). A similar analysis focusing on strepsirrhines and platyrrhines [18] produced comparable findings, with a positively allometric relationship between digital flexor PCSA and body mass, but no overarching trends clearly relating to locomotor ecology.

A detailed comparison of forelimb myology in lemurids and callitrichids [19] reported a similarly positive allometric relationship between digital flexor PCSA and body mass in callitrichids, though this relationship was isometric in lemurids. Digital flexors also comprised a slightly greater proportion of total forearm PCSA in lemurids (20.3%) than in callitrichids (18.48%) and did not conform to any overarching trends relating to locomotor strategy or habitat type [19]. Finally, a recent comparison of forearm myology between macaques (*Macaca mulatta*), gibbons (e.g. *Hylobates lar*, *H. pileatus*, *Nomascus leucogenys*, *N. concolor*, *Symphalangus syndactylus*), bonobos (*Pan paniscus*) and humans (*Homo sapiens*) suggests that gibbons exhibit significantly greater digital flexor musculature (as a proportion of total forearm musculature) than other taxa, an adaptation attributed to their frequent use of ricochetal brachiation, which require strong manual grasping forces to ensure a stable pivot during locomotion [23,24].

Compared to forelimb muscles, much less is known about the digital flexor musculature of the primate foot. However, electromyographic data collected during arboreal locomotion demonstrate that pedal flexor muscles are active at higher levels and for longer durations than manual flexors during the stance phase [25]. Thus, a powerful grasping foot may be essential to arboreal quadrupedalism. Comparative myological data on the primate foot are limited to a recent study by Marchi *et al.* [21], which reported that digital flexor muscle mass and PCSA in the primate hindlimb ($n = 33$) scaled with positive allometry relative to body mass across catarrhines, platyrrhines and strepsirrhines, such that larger-bodied animals have relatively larger and stronger hindlimbs. However, no interspecific differences aligned with locomotor categories and no differences between suborders were observed. Additionally, a comparison of hindlimb myology between bonobos and gibbons revealed a similar gross morphological configuration, with strong plantar flexors and large hallucal muscles, although the triceps surae of gibbons contained a significantly longer tendon [26]. Finally, a broader comparison across hominoids [27] revealed a greater proportion of distal limb muscle mass in orangutans (*Pongo pygmaeus*) and bonobos than in gorillas (*Gorilla gorilla*) or lar gibbons, a finding attributed to the less frequent use of the foot for grasping in the latter two taxa.

(b) *In vivo* measurements of primate grip force

Direct measurements of grasping forces *in vivo* are limited to only a handful of primate species [15,22,28,29]. Broadly, two discrete categories of grasping performance have been considered: gripping forces, which reflect the contractile forces generated aroundt an object or substrate enclosed within the digits [10,11,22,30,31], and pulling forces, which reflect the magnitude of force an animal can exert in resistance to being forcibly removed from a substrate [15,32–34]. These forces are representative of differing ecological scenarios: while gripping forces approximate the compressive forces exerted by a primate's hand around a branch, pulling forces represent the force with which a primate clings to a branch to avoid being lifted away by a predator [10,14]. Of these two metrics, pulling forces represent the vast majority of *in vivo* data, both in primates and other animals [15,32–34]. These experiments have shown that many species are capable of generating bimanual grip forces that are several times their body mass to resist being pulled away from a substrate [15,32,33]. In contrast, true gripping forces (i.e. measurements of the active muscle forces generated by the animal in a static condition) have only been conducted in two platyrrhine species: common marmoset (*Callithrix jacchus*) and black-capped squirrel monkey (*Saimiri boliviensis*) [22]. Mean grasping forces for these taxa reached 74.8% and 101.0% of body weight, respectively. However, differences between left and right hands or between hands and feet were not assessed. Additionally, as only two individuals were sampled from each taxon, the degree of intraspecific variance in grasping strength remains unclear.

(c) Aims and predictions

Within this study, we propose the first comprehensive sampling of *in vivo* grip forces from the hands and feet of the strepsirrhines, an ideal model for early primate evolution [1,6]. Additionally, we aim to identify myological correlates of grip strength in the hands and feet of the same phylogenetic sample. These data will be one of the few examples directly linking biomechanical performance with associated anatomy, providing novel insights into primate evolution. Together, these data will offer essential information about primate grasping performance, a topic that is often discussed but has yet to be thoroughly investigated [1,4,6]. In doing so, we test the following explicit predictions:

Prediction 1: in vivo and anatomically predicted grip forces will scale with positive allometry relative to body mass. Anatomical predictions of primate grip force [18–21] have almost universally suggested that grasping forces scale with positive allometry relative to body mass. We predict that *in vivo* forces will follow a similar trend, with larger animals being both *absolutely* and *relatively allometrically* stronger than their smaller-bodied counterparts.

Prediction 2: Hand shape will be positively correlated with grip force. Hand shape (a ratio of hand width divided by hand length; [30]) has been positively correlated with grip strength in humans, with participants exhibiting wider hands consistently showing stronger grip forces than those with longer hands. These findings align with earlier literature suggesting that, when controlling for height, individuals with wider hands exhibit greater muscular strength [16,35–37]. We predict this relationship will also exist interspecifically among strepsirrhines.

Prediction 3: Physiological cross-sectional area will be positively correlated with grip force in both the hand and foot. The physiological cross-sectional area represents an anatomical proxy for muscle strength and has been experimentally shown to scale proportionally to a muscle's contractile force potential [38,39]. Thus, we predict that anatomical estimates of a species' grasping force potential will strongly correlate with *in vivo* forces collected from conspecifics.

Prediction 4: Locomotor mode will predict grip force, with highly arboreal taxa exhibiting stronger grasping forces than other species. The ability to generate and sustain a stable grip on substrates of variable diameter is critical to the locomotor abilities of arboreal taxa. Accordingly, across numerous tetrapod lineages, a positive relationship between arboreality and grasping strength has been reported [11,15,33]. Therefore, we predict a similar relationship among primates.

Prediction 5: Pedal grasping forces will exceed those of the hand. Quadrupedal primates are thought to successfully occupy arboreal environments by relying on their grasping feet to control balance and propulsion, freeing their hands to test unstable branches and to forage [8,25,40]. This functional decoupling of the hindlimb and forelimb should yield discernible differences in fore- versus hindlimb musculoskeletal strength, particularly in how manual and pedal digital flexor muscles are recruited for grasping during arboreal locomotion [25]. Electromyographic data from extrinsic flexor muscles in red ruffed lemurs (*Varecia rubra)* walking on a simulated arboreal substrate support this, revealing that pedal flexors are activated at higher levels and for longer durations than manual flexors during the stance phase [25]. Thus, we predict that grasping forces measured from the feet will exceed those of the hands within each taxon.

Prediction 6: Behavioural laterality (e.g. handedness) will guide bilateral differences in grip force, with stronger forces observed in the behaviourally dominant hand, but no bilateral differences will be observed in the foot. Strepsirrhines show varying degrees of laterality across species. While most species exhibit hand preferences during food grasping, object manipulation, and the tube test [41–47], this can range from a strong left-hand bias in ring-tailed lemurs (*Lemur catta*) and ruffed lemurs (*Varecia rubra and V. variegata*) to a right-hand bias in common brown lemurs (*Eulemur fulvus*) and mongoose lemurs (*E. mongoz*). Several taxa (e.g. aye-ayes (*Daubentonia madagascariensis*) and sifaka (*Propithecus* sp.)] are reported as ambipreferent, showing no clear hand dominance. In humans, behavioural lateral bias strongly corresponds with asymmetry in manual grip strength, with the dominant hand being approximately 5% stronger [30]. As such, we expect similar patterns of handedness within strepsirrhines, with the dominant hand exhibiting stronger grasping forces in each taxon. However, given that hindlimbs contribute equally during locomotion, we expect no lateralized differences in pedal grip strength.

2. Material and methods

(a) Animals and permissions

This study encompassed eleven distinct strepsirrhine primates: Mohol bushbaby (*Galago moholi*), collared brown lemur (*E. collaris*), fat-tailed dwarf lemur (*Cheirogaleus medius*), aye-aye, crowned lemur (*E. coronatus*), mongoose lemur, blue-eyed black lemur (*E. flavifrons*), ring-tailed lemur, grey mouse lemur (*M. murinus*), Coquerel's sifakas (*P. coquereli*) and ruffed lemur . Note that although some sources classify black-and-white and red ruffed lemurs as separate species (e.g. *V. variegata* and *V. rubra*, respectively) [48], we have elected to pool all ruffed lemur data under a single species, because the two species/subspecies are quite similar in all aspects of anatomy except for pelage. The subjects comprised solely adult individuals that exhibited good health without any evident pathologies. Data regarding the body mass of each specimen were provided by the husbandry staff of the Duke Lemur Center on the day of sampling. For a detailed breakdown of species-specific information such as the number of individuals, age, mass and maximal grip force, refer to electronic supplementary material, table S1 and Supplemental Data. All experimental protocols adhered to the approved guidelines of Duke University (Protocol # A183−22−10) Institutional Animal Care and Use Committee.

(b) Experimental design

We conducted grip force trials using a custom-built apparatus (figure 1). The substrate that the animals gripped consisted of two carbon fibre-embedded, three-dimensional-printed semi-lunar bisections (Markforged, Waltham, MA). To accommodate the varying body sizes of strepsirrhines in our study (e.g. the autopodia of grey mouse lemurs are considerably smaller than those of ruffed lemurs), we fabricated parts in different diameters to ensure consistent hand-wrapping posture. We selected a diameter for each individual to maintain a physiologically equivalent grasp, avoiding under- or overwrapping of the digits (figure 1).

We employed two distinct Advanced Mechanical Technology, Inc. (Watertown, MA) force plates. For the relatively low grip forces of smaller strepsirrhines (i.e. grey mouse lemurs, fat-tailed dwarf lemurs, Mohol bushbabies), we used a low-load force plate (model HE6 X 6; load capacity = 4 N), while larger animals were tested on an intermediate load force plate (model MC3A; load capacity = 100 N). The apparatus mounted the calibrated force plate, with one semi-lunar 3D-printed part attached to the plate and the other affixed to the uninstrumented handle of the grip force tester. As the animals gripped the 3D-printed semicircular pieces, the lower piece, attached to the force plate, generated a vertically oriented force directed upwards.

Most individuals spontaneously engaged with the apparatus, although some required minimal encouragement, such as gentle tapping on the hand or feet to prompt grasping. Duke Lemur Center personnel suspended and handled each individual to ensure that recorded forces only reflected single-foot forelimb or hindlimb grip strength, without bodyweight contributions. Each individual completed between five and ten grip trials from both left and right forelimbs and hindlimbs. We recorded and processed all force data using Bioware v5.4 software (Kistler; MI, USA).

We included only trials in which an isolated grip force was recorded. Using a custom MATLAB (MathWorks, Natick, MA) script, we extracted the peak grip force (N) for each trial. To minimize the influence of low-motivation trials, we isolated only the maximum grip force recorded for each limb for each individual (i.e. up to four data points per individual).

(c) Ecomorphological correlates

In addition to *in vivo* strepsirrhine grip force data, we collected myological data to compare anatomical estimates of grip strength from conspecific cadavers. Our cadaveric sample included eleven individuals from all focal taxa (electronic supplementary material, table S1), with intact, unfixed frozen specimens provided by the Duke Lemur Center Biosamples Collection. All specimens were adults without known pathologies, and none were euthanized for this study or showed tissue degradation. It was not possible to make the measurements of interest for some limbs owing to lack of tissue availability (see below).

We collected myological data using a standardized sharp dissection protocol [18–21]. After removing the skin and overlying tissues, we individually excised and weighed each digital flexor muscle (e.g. flexor digitorum profundus, flexor digitorum superficialis, opponens pollicis) in the forearm, hand, lower leg and foot. We weighed muscles to the nearest 0.01 g (or 0.001 g for grey mouse lemurs, fat-tailed dwarf lemurs and Mohol bushbabies). The muscles were then placed in 35% nitric acid to digest connective tissues between fascicles, following protocols by Herrel *et al.* [49]. After 3–12 h (depending on muscle size), muscles were removed from the acid and placed in a 50% glycerol solution to neutralize residual acid and prevent overdigestion. We then manually separated at least forty fascicles for each muscle and photographed them with a Dino-Lite Digital Microscope (AF7915MZTL; Dino-Lite USA, Torrance, CA) alongside a scale bar for digital data collection. The fascicles were measured using ImageJ [50]. Muscle mass and fascicle length were combined to compute the PCSA for each digital flexor using the formula:

$$\mathrm{PCSA} = m/lp$$

wherein m is muscle mass in grams, l represents mean fascicle length and p represents muscle density. A constant of 1.056 g cm^{-3} was applied to represent muscle density, following Murphy and Beardsley [51]. The PCSA of each digital flexor was then summed to derive a limb-specific estimate of anatomical grip force.

We also collected data on autopodial shape, body mass and behavioural laterality. The autopodial shape was calculated by dividing autopodial width by length, following [30]. Since direct measurement was not feasible during *in vivo* data collection, we derived these values from imprints of species-specific archived autopodia at the Duke Lemur Center. While not ideal, we limited the inclusion of imprints to adults matching our *in vivo* sample and, where possible, matched for sex to account for differences in hand shape that may be attributable to sexual dimorphism. Body mass was recorded prior to each trial. Finally, we gathered data on behavioural laterality (e.g. hand preference) from literature sources [41,42,47]. It should be noted that using a species-level approach to analyse laterality is suboptimal, as true handedness occurs at the individual level, even though species-level trends in laterality exist. Unfortunately, individual-level handedness data were not available for the strepsirrhines sampled in our study.

(d) Statistical analyses

All statistical analyses were conducted using *R* [52]. To assess the scaling of grip force across body size and determine the relationship between grip force and PCSA, data were first linearized (i.e. body mass was taken to the cubic root, and grip forces and PCSA to the square root, such that isometry for all slopes = 1) and subsequently log-transformed. Reduced major axis regressions were then conducted to assess changes in grip force and PCSA as a function of body mass and between PCSA

Figure 1. Schematic of the experimental setup and ideal autopodial wrapping posture (*a*). The substrate that the animals gripped consisted of two carbon fibre-embedded, 3D-printed semi-lunar bisections. The upper portion (white) of the substrate was uninstrumented and provided a solid anchor on which the autopodia could rest. The lower portion (shaded) was affixed to a force plate and recorded an upward force as the animal grasped. See Dickinson *et al*. [10] and Young *et al*. [11] for a more detailed representation of the experimental setup. Instead of using the same substrate size across species, which could lead to underwrapping or overwrapping of the digits (*b*), the substrate size was adjusted for each individual to maintain a physiologically equivalent grasping posture regardless of the individual's size (*c*). Animals were positioned so that body mass did not rest on the instrumented portion of the force plate, thus ensuring that only grasping forces were recorded.

and grip force. The slopes and 95% confidence intervals of these regressions were used to infer prevailing allometric trends following [20,53].

To assess the effects of ecomorphological correlates on grip strength performance, we conducted two linear mixed-effects models. Before performing these analyses, we scaled all maximum grip force data in two ways because grip force is expected to vary as a consequence of body mass, among other factors. First, we divided raw maximal grip forces by the body mass of each individual collected during each trial to express maximal grip force as a percentage of body weight (%BW). Since muscle force-generating potential does not scale linearly with body mass (see above), we also calculated an alternative body weight-adjusted maximal grip force metric. We first linearized the data by taking the cubic root of body mass and the square root of grip forces, then log-transformed the results. Afterwards, we regressed each adjusted measurement of grip force against body mass and calculated the residuals for further analysis. We used Shapiro–Wilk and Levene's tests to assess the normality of both body weight-adjusted metrics of maximal grip force. Since the data were not normally distributed, we rank-transformed all grip force measurements before making any statistical comparisons [54]. We constructed the linear mixed-effects models based on Winter [55] and Bates *et al*. [56], using the *R* packages 'lmerTest' [57] and 'lme4' [56]. In each model—one with body weight-adjusted maximal grip force as %BW and the other with residuals—we included body mass, autopodial shape, locomotor ecology (i.e. arboreal quadruped, vertical clinger and leapers and terrestrial; electronic supplementary material, table S1), limb (forelimb versus hindlimb) and laterality as fixed effects. Since age [28], sex [30], species [22] and individual behavioural idiosyncrasies [11] can influence grip strength performance, we treated these variables as random effects.

We conducted two additional statistical analyses to assess the role of limb laterality and interspecific differences. Since expectations for hand dominance varied by species and no species was expected to show side dominance for the hindlimbs, we ran a series of Mann–Whitney Wilcoxon tests for each species to determine whether the left and right forelimbs and hindlimbs differed within a species. As all laterality comparisons were intraspecific, maximal recorded grasping forces were analysed as %BW. To evaluate interspecific differences, we performed a series of Kruskal–Wallis tests to assess how body weight-adjusted maximal grip force (i.e. as %BW and residuals) varied between species for each limb. If we observed statistically significant differences, we conducted a Tukey *post hoc* analysis. We used the *R* packages 'kruskal.test' and 'wilcox.test' for these analyses.

It should be noted that we elected not to conduct phylogenetic analyses in the current sample. We were working with a relatively limited number of species (e.g. eleven), and with such low phylogenetic diversity, it is unclear whether additional

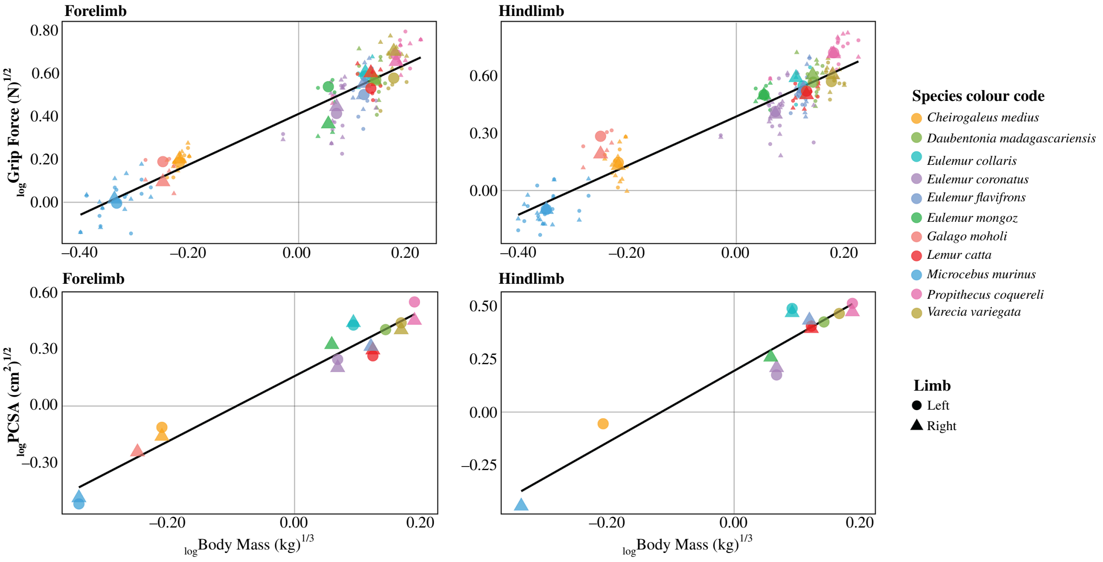

Figure 2. Bivariate regressions of *in vivo* grip force data (N) and dissection physiological cross-sectional area (PCSA; cm^2) against body mass (kg). All metrics were first linearized (i.e. the square root was taken for grip force and PCSA while the cube root was taken for body mass), then logged. *In vivo* grip force is displayed on the top row and separated by forelimb (left; $y = 1.16\,x + 0.41$, $R^2 = 0.88$) and hindlimb (right; $y = 1.28\,x + 0.39$, $R^2 = 0.87$). Physiological cross-sectional area is displayed on the bottom row and similarly separated by forelimb (left; $y = 1.73\,x + 0.16$, $R^2 = 0.95$) and hindlimb (right; $y = 1.66\,x + 0.19$, $R^2 = 0.91$). Species are depicted in different colours (see legend) and limb side is denoted so that the circles represent the left limb while the triangles represent the right side. Transparent and smaller points in *in vivo* grip force data (top) are the maximal recorded grasping forces recorded from each individual, while larger more opaque points represent species means.

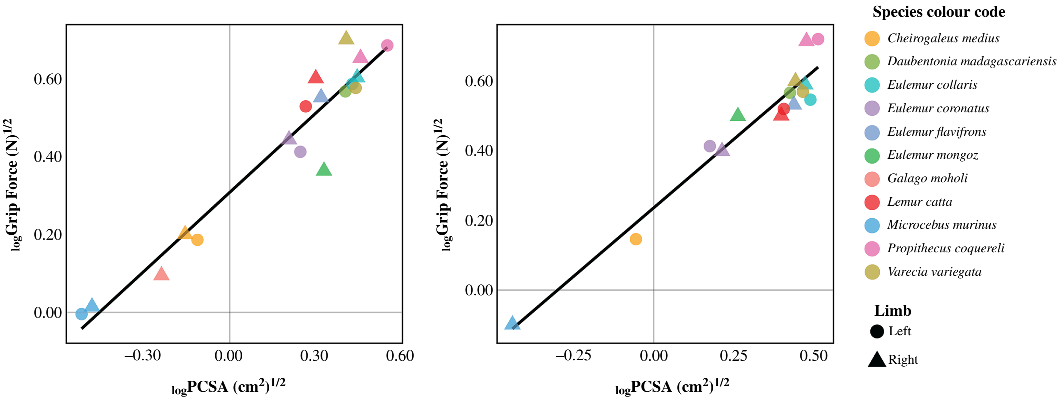

Figure 3. Bivariate regressions of forelimb and hindlimb physiological cross-sectional area (PCSA; cm^2) collected from one individual per species and species-mean *in vivo* maximal grip force data (N). Forelimb is shown on the left ($y = 0.67\,x + 0.31$, $R^2 = 0.93$) while hindlimb is shown on the right ($y = 0.79\,x + 0.24$; $R^2 = 0.94$). All metrics were first linearized (i.e. the square root was taken for grip force and PCSA) then logged. Species are depicted in different colours (see legend) and limb side is denoted so that the circles represent the left limb while the triangles represent the right side.

statistical testing is warranted. Furthermore, as only one species (Mohol's bushbaby) is not a Malagasy strepsirrhine, phylogenetic corrections would likely only serve to obscure the results presented below.

3. Results

Both *in vivo* grip forces and anatomical estimates of grip force (estimated via digital flexor PCSA) strongly correlated with body mass ($R^2 = 0.87–0.95$). Across both limbs and using both methodologies, we observed grip force scaling with positive allometry, with 95% confidence intervals consistently exceeding 1 (figure 2 and electronic supplementary material, table S2). Thus, larger strepsirrhines exhibited both *absolutely* and *relatively allometrically* stronger grip forces than smaller taxa.

Regressing anatomically derived grip forces against their *in vivo* counterparts demonstrated a strong correlation between the two methods. In the forelimb, we reported an R^2 of 0.93, with a slope of 0.68 and an intercept of 0.31. In the hindlimb, we reported a similar R^2 of 0.94, with a slope of 0.79 and an intercept of 0.24. Thus, we observed a strong and consistent relationship between a taxon's anatomical strength and *in vivo* measured strength (figure 3).

We constructed linear mixed-effect models to explore the ecomorphological correlates of grip force measured both as %BW and as a residual following the regression of grip force against body weight. Neither model showed any effect of laterality on grip force (all p-values > 0.271, table 1). However, we observed a significant effect of locomotor mode, with vertical clinging and leaping species exhibiting greater grip force compared to both arboreal quadrupeds and terrestrially inclined ring-tailed

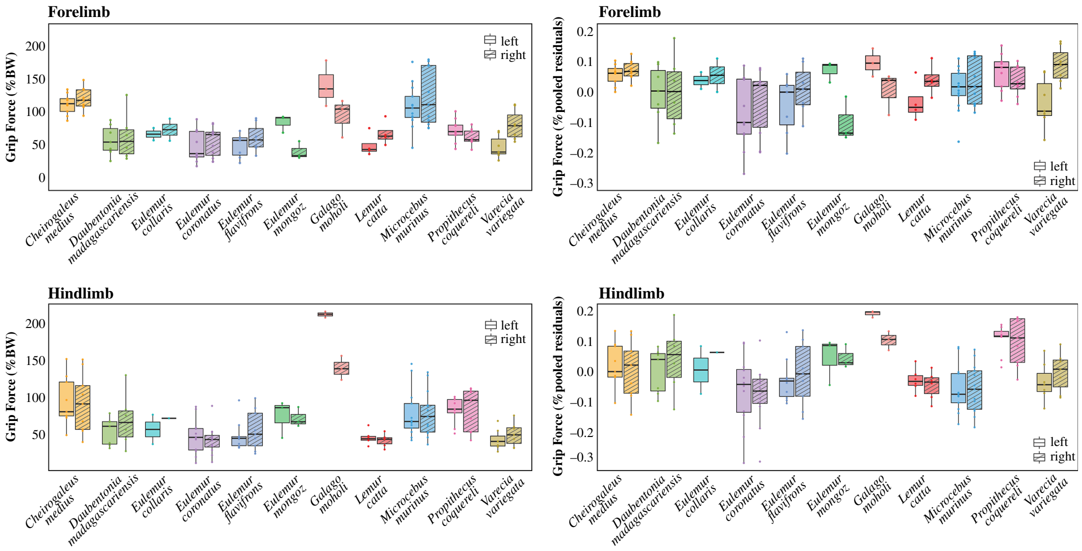

Figure 4. Box and whiskers plots of maximal recorded *in vivo* grasping forces recorded from each individual grip force presented as a percentage of body weight (%BW; left) and as a scaled allometric residual (right). Species are indicated on the *x*-axis and data are split between forelimb (top) and hindlimb (bottom). Unhashed boxes indicate left limb while hashed boxes indicate right limb.

lemurs. Specifically, vertical clingers and leapers had significantly higher grip force (%BW: vertical clingers and leapers versus arboreal quadrupeds, $p < 0.001$; vertical clingers and leapers versus terrestrial, $p < 0.001$; scaled: vertical clingers and leapers versus arboreal quadrupeds, $p < 0.001$; vertical clingers and leapers versus terrestrial, $p < 0.001$]. No significant differences in grip force were found between arboreal quadrupeds and terrestrially inclined ring-tailed lemurs (%BW: $p = 0.250$; scaled: $p = 0.560$). Both models also revealed that the forelimbs produced greater relative forces than the hindlimbs, and animals with a relatively high autopodial width relative to length had higher grip forces (electronic supplementary material, figure S1). When analysed as %BW, grip force was inversely and significantly correlated with body mass; however, this relationship was not observed when grip strength was analysed as a scaled allometric residual (table 1).

We assessed differences in laterality (i.e. left- versus right-sided limbs) for both the forelimbs and hindlimbs. Of the 21 cases, only one comparison (ruffed lemur forelimb, $p = 0.018$; figure 2–4 and electronic supplementary material, table S3) yielded statistically significant differences between contralateral limbs. Thus, we found no evidence of lateral differences in gripping force within our data.

Interspecific comparisons revealed significant differences (all p-values < 0.002) in grip force across species, both as %BW and as scaled allometric residuals, for forelimbs and hindlimbs. *Post-hoc* analyses (figure 4 and electronic supplementary material, tables S4–S7) demonstrated that these differences were largely attributable to body mass (when forces were analysed as %BW) and locomotor mode (when forces were analysed as body mass-scaled residuals).

In our %BW model, the three smallest taxa (i.e. grey mouse lemurs, fat-tailed dwarf lemurs and Mohol bushbabies) exhibited the strongest relative forelimb grip forces. In the hindlimb, grip forces as %BW followed a similar pattern, with the vertically clinging and leaping Coquerel's sifakas showing significantly higher forces than several arboreal generalists (e.g. crowned lemurs, blue-eyed black lemurs and ruffed lemurs) and the terrestrial ring-tailed lemur (electronic supplementary material, tables S4 and S5).

When we analysed grip force as a body mass-scaled residual, interspecific differences in the forelimb were minimal, with only crowned lemurs standing out as significantly weaker than both fat-tailed dwarf lemurs and Coquerel's sifakas. In the hindlimb, interspecific patterns aligned with locomotor ecology, as the vertically clinging and leaping Mohol bushbabies and Coquerel's sifakas proved significantly stronger than almost all other taxa. We observed no differences between any other taxonomic pairs (electronic supplementary material, tables S6 and S7).

4. Discussion

(a) Allometric scaling of grip forces

Both *in vivo* and anatomically predicted grip forces closely align with our predictions, scaling with positive allometry relative to body mass (figure 2 and electronic supplementary material, table S2). This supports findings from previous studies that explored the allometry of myological grip force in primate forelimbs and hindlimbs [18,20,21]. Collectively, these findings suggest that as primates increase in size, their grip forces become both *absolutely* and *relatively allometrically* stronger.

We emphasize the importance of distinguishing between grip force models that consider grip as a %BW and those that analyse grip as a residual from allometric reconstructions. Grip force, a product of muscle cross-sectional area (PCSA; cm^2), scales with a factor of 0.66 relative to body mass (a cubic variable) [58]. Presenting grip force as %BW, common in literature [11,22,32,33], inherently favours smaller-bodied taxa, which are less negatively affected by this basic scaling relationship. We therefore recommend using body-mass-scaled residuals to assess relative grip force across samples that cover a wide range

Table 1. Statistical parameters derived from linear mixed-effects models demonstrating the influence of various fixed effects on rank-transformed maximal recorded grasping forces as a percentage of body weight (%BW) and scaled allometric residuals. Since age, sex, species and individual behavioural idiosyncrasies can influence grip strength performance, we treated these variables as random effects. The categorical variables in parentheses are the reference variable. Forelimb = FL; Arboreal quadruped = AQ; Terrestrial = TERR; and Vertical clinger and leaper = VCL.

response variable	fixed effects		estimate	standard error	*df*	*t*	*p*-value
grip force (%BW)	(intercept)		425.02	32.93	82.96	12.91	**<0.001**
	locomotion (AQ)	TERR	−26.39	22.86	83.32	−1.15	0.253
		VCL	85.87	16.77	81.49	5.12	**<0.001**
	limb (FL)		−34.96	7.62	269.46	−4.59	**<0.001**
	weight		−26.22	4.82	106.53	−5.44	**<0.001**
	laterality		6.04	6.07	206.85	0.99	0.321
	autopodial shape		96.95	28.94	289.73	3.31	**0.001**
grip force (residuals)	(intercept)		202.65	38.27	85.41	5.30	**<0.001**
	locomotion (AQ)	TERR	−27.16	26.79	83.22	−1.01	0.314
		VCL	102.54	19.64	81.67	5.22	**<0.001**
	limb (FL)		−38.72	8.75	278.67	−4.43	**<0.001**
	weight		6.51	5.63	106.10	1.16	0.250
	laterality		7.62	6.90	205.18	1.10	0.271
	autopodial shape		100.04	33.34	33.34	3.00	**0.003**

Significant effects are highlighted in **bold.**

of body sizes. This approach allows for more nuanced interpretations of grip strength by accounting for the disproportionate scaling of muscle cross-sectional area and body mass (i.e. the square-cube law).

(b) Forelimb versus hindlimb grasping strength

Contrary to our predictions, forelimb grasping forces were significantly stronger than those measured in the hindlimbs. This finding is surprising for two reasons. First, the anatomical strength potential of hindlimb digital flexors in strepsirrhines exceeds that of forelimbs by *ca* 14% on average, with greater strength in 70% of taxa (figure 4 and electronic supplementary material, table S1). Additionally, previous behavioural studies suggest that pedal flexors are activated at higher magnitudes than forelimb muscles during arboreal locomotion in strepsirrhines [25]. It is possible that this discrepancy could be owing to motivational factors (see §4g below), as subjects might have been more willing to grasp with full strength using their hands than their feet, possibly because of the apparatus's positioning relative to their line of sight or a greater sense of comfort during manual grasping. Further exploration using alternative experimental setups is necessary to confirm our findings.

(c) Lateralization of grip forces

Our sample generally showed no consistent differences owing to lateralization, with only one taxon (i.e. ruffed lemurs) exhibiting differences between left- and right-sided forelimbs, and no species showing differences for the hindlimbs. The issue of laterality in nonhuman primates has long been discussed, despite the relative lack of empirical data [41,42,59]. Many species display hand preference for specific tasks; for instance, gorillas exhibit a right-hand bias during coordinated bimanual tasks (e.g. the 'tube test'), while orangutans show a preference for the left hand [47]. In strepsirrhines, a clear left-hand bias is seen in more than half of the twenty tested species, with only two families (Indriidae and Cheirogaleidae) showing ambipreferent behaviour at the population level [41–46].

However, behavioural lateralization does not appear to be linked to differences in the maximum functional capabilities of the hands. Maximal grip forces seem to be equivalent between dominant and non-dominant hands, in contrast to human data, where the dominant hand is typically reported as up to approximately 5% stronger than the non-dominant hand (5.5% in males, 4.2% in females; [30]). This difference between humans and non-human primates may reflect either the mode of lateralization (i.e. humans exhibit biases for both dexterity and strength, while nonhuman primates exhibit only the former) or the magnitude of hand bias (i.e. biases are stronger in humans than in nonhuman primates). In any case, the absence of consistent lateral biases in hand (or foot) strength between left- and right-sided limbs sets strepsirrhines apart from previously published human data.

While our analysis generally showed no consistent differences owing to lateralization, it is important to recognize a potential limitation in measuring grip force at the species level. When considering laterality, it's crucial to understand that overall species trends do not always reflect individual behaviours. For instance, although humans tend to be right-handed about 90% of the time [60], this doesn't mean that a right-handed individual uses their right hand 90% of the time and their left for only 10%; rather, they often rely entirely on their right hand for most tasks. If a similar pattern holds true for strepsirrhines, we may have missed individual-level signals of laterality in our grip force data by aggregating at the species level. Analysing grip strength data at the individual level could reveal significant differences between left and right grip strength that correspond to individual hand preferences. Therefore, the lack of observed lateralization effects in our study may reflect a methodological limitation rather than an actual absence of hand preference among strepsirrhine species. Future research should explore the relationship between laterality and grip strength to determine if these two variables are correlated.

(d) Hand shape

Previous experimental studies of the human hand have shown that autopodial shape (e.g. wide versus long hands) significantly affects grip force production, with wider autopodia (i.e. those with an aspect ratio closer to 1) capable of producing stronger grasping forces. In humans, this pattern holds for both dominant and non-dominant hands in females and for non-dominant hands in males (differences in male dominant hands approach significance, $p = 0.06$; [30]). Our findings largely align with these reports, especially in the hand, suggesting that strepsirrhines follow similar trends, with wider autopodia correlating with greater grip forces. This finding agrees with broader research on human morphology, which indicates that individuals with wider hands tend to have greater muscular strength in the forelimb, when controlling for weight [16,35–37]. Mechanically, wider hands may indicate larger intrinsic hand muscle volumes, enhancing physiological force generation, or may favourably alter the mechanical advantage of flexor muscles. These data suggest that hand shape modifications may be adaptive for improving grip force, echoing research on hand shape evolution in humans, which highlights the maximization of dexterity [61,62] and grip strength [30]. We attest that the relationship is weaker in the feet compared with the hands, and it becomes negative when grip force is assessed as a scaled residual (electronic supplementary material, figure S1). This is likely owing to the selective pressures on vertical clingers and leapers to elongate the foot, creating longer anatomical moment arms beneficial for leaping [63,64]. As such, anatomical specialization for other locomotor behaviours may obscure the relationship between grip force potential and autopodial shape.

(e) Locomotor ecology

Interspecific differences in grip strength were more pronounced in the hindlimb than in the forelimb and were significantly associated with locomotor ecology. Specifically, vertical clingers and leapers (e.g. Mohol bushbabies and Coquerel's sifakas) exhibited significantly stronger hindlimbs than other species. This suggests that vertical clinging and leaping place considerable demands on hindlimb musculature [64]. Vertical clinging and leaping have been linked to powerful extensor muscles, particularly in the knee and ankle, which drive explosive leaping movements [64]. However, vertical clinging and leaping may also induce hypertrophy across all hindlimb muscles or require powerful flexor muscles to absorb high forces during landing. Experimental data on strepsirrhine leaping suggest that hindlimb forces are similar during takeoff and landing [65], supporting the notion that powerful flexor muscles are a specific adaptation for vertical clinging and leaping, enabling these taxa to produce high grasping forces compared to more generalized arborealists or terrestrial strepsirrhines like ring-tailed lemurs.

It is important to discuss why more differences attributable to locomotor ecology were not observed. Contrary to our predictions, highly arboreal species did not exhibit greater grasping forces than their terrestrial counterparts. Several factors may explain this lack of an ecological signal. First, our sample included only one terrestrially adapted species (i.e. the ring-tailed lemur), which still spends a considerable amount of time in trees [12,48]. Strepsirrhines do not exhibit extensive variation in their locomotor repertoires [12]. To better explore whether locomotor ecology influences grasping forces, it may be more effective to examine a lineage with greater locomotor diversity (e.g. Old World monkeys [12] or marsupials [66]). Additionally, broad locomotor categories may be overly reductive, as no species adopts a single form of locomotion [12] or moves exclusively on one type of substrate [8]. A more precise approach would involve quantifying the proportion of time each species spends in trees versus on the ground or on specific substrate diameters. While some of these data are available in the literature [8,12], they were not available for all species in our sample and could not be analysed statistically without significantly reducing our sample's species diversity. We hope future studies will address these gaps and use the data provided here to examine these potential associations in greater detail.

(f) Strepsirrhine grasping strength in a comparative context

Primates are widely regarded as models of specialized arboreal species, with adaptations including strong grip forces in both the hindlimbs and forelimbs. However, prior to this study, *in vivo* grip forces had only been measured in the forelimbs of two nonhuman primate species—common marmosets and black-capped squirrel monkeys—with no data available on pedal grip strength [22]. Comparisons between these data and our findings suggest similar magnitudes of grip strength. Common marmosets and black-capped squirrel monkeys registered forces of 75% and 101% of body weight, respectively [22], which align with our data (figure 4). Our three strongest taxa in forelimb grip strength (i.e. grey mouse lemurs, fat-tailed dwarf lemurs, and Mohol bushbabies) exceeded this benchmark, falling between *ca* 100–120% of body weight, while our weakest taxa (i.e. crowned lemurs and blue-eyed black lemurs) measured slightly above 50% of body weight in manual grip strength. Hindlimb forces ranged from *ca* 45 to 200% of body weight (figure 4).

In a broader comparative context, these grip forces are somewhat comparable to those of another arboreal specialist, the brown-throated sloth (*Bradypus variegatus*), which exhibits maximal grip forces upwards of *ca* 150% of body weight [11]. While such performance is achievable for our smallest taxa (i.e. grey mouse lemurs, fat-tailed dwarf lemurs and Mohol bushbabies), the *ca* 4 kg brown-throated sloth far exceeds the force-generating potential of our larger-bodied strepsirrhines. Additionally, strepsirrhine forces are lower than those of birds, where hindlimb grip forces range from 150 to 300% of body weight [10]. Taken together, it is safe to say that strepsirrhine primates exhibit grip capabilities comparable to other arboreal primates and slightly surpass humans, whose forelimb grip strength measures around 65–70% of body weight [30]. However, proposing that primate grip force stands out as exceptional among other arboreal mammals, let alone other tetrapods, is likely false and requires considerable additional taxonomic sampling to justify.

(g) Motivation clouds the form–function relationship

It should be noted that estimating grasping force in newtons—the directly comparable measure collected during *in vivo* studies—from anatomically derived metrics is challenging [31]. This process requires information about muscle moment arms and muscle architecture dynamics that are beyond the scope of this study. Such comparisons are possible in feeding systems where joint morphology and muscle configuration allow for more accurate estimates [31,49]. Dickinson and colleagues [67], in a comparative study of avian bite force, concluded that anatomical estimates yielded bite force magnitudes that were, on average, 31.4% greater than equivalent *in vivo* measurements of the same taxa, a relationship comparable (25–36%) with that reported in raptorial birds by Sustaita and Hertel [31]. Our attempt to assess how force-generating potential in the forelimb and hindlimb correlates with PCSA demonstrated strong correlations, but slopes of only 0.68 and 0.79, respectively. While we do not claim that PCSA is a direct measure of force-generating potential during grasping, the reduced slopes indicate that attempts to estimate grasping potential from anatomy alone would likely result in overestimations compared with *in vivo* metrics. This may reflect one of two factors. First, myological models—which assume simultaneous maximal contraction of the flexor musculature—may inherently overstate grip force potential by incorporating this biologically unlikely condition. Second, as discussed by Sustaita and Hertel [31], animals may exert sub-maximal effort during *in vivo* experiments because the equipment fails to mimic the true biological conditions where maximal motivation would be required. More direct metrics linking grasping anatomy and performance are needed to firmly establish the scaling relationships between the two approaches, and caution should be exercised when discussing performance metrics without appropriate experimental validation.

5. Conclusion

Our study provides valuable insights into the allometric scaling of grip forces in primates. We found that both *in vivo* and anatomically predicted grip forces scale with positive allometry relative to body mass, supporting previous findings that primate grip strength increases with body size. This suggests that larger primates have stronger grip forces both *absolutely* and *relatively allometrically*. Our analysis also highlights the importance of distinguishing between grip force models based on body mass percentages and those using scaled residuals from allometric reconstructions. Grip force, scaling with a factor of 0.66 relative to body mass, favours smaller-bodied taxa when presented as a percentage of body weight. Using body-mass-scaled residuals provides a more nuanced assessment of relative grip strength, accounting for the disproportionate scaling of muscle cross-sectional area and body mass.

Unexpectedly, forelimb grasping forces were significantly stronger than hindlimb forces, despite the higher anatomical strength potential of hindlimb digital flexors in many strepsirrhines. This discrepancy may be owing to motivational factors or differences in experimental setup, warranting further investigation with alternative methodologies. Interspecific differences in hindlimb grip strength, strongly associated with locomotor ecology, reveal that vertical clingers and leapers like Mohol bushbabies and Coquerel's sifakas exhibit significantly stronger hindlimbs, likely owing to adaptations in muscle structure that meet the demands of explosive leaping and force absorption during landing. Our study also found no consistent lateralization effects in grip strength among the examined taxa, contrasting with the pronounced hand biases observed in humans. This absence of lateralization may reflect differences in the mode or magnitude of hand bias between humans and nonhuman primates. Finally, while our findings on hand shape suggest that wider autopodia are associated with greater grip strength—aligning with research on human morphology—the relationship between grip force and autopodial shape is weaker in the feet. This may be owing to selective pressures for elongated feet in vertical clingers and leapers, which could obscure the grip force potential associated with foot shape.

In a broader context, while strepsirrhine relative grip forces are comparable to those of other arboreal primates and slightly surpass relative human grip strength, suggesting that primate grip force is exceptional compared to other arboreal mammals or grasping tetrapods broadly is likely incorrect and would require extensive additional taxonomic sampling to support. Moreover, estimating grasping force from anatomical metrics alone is challenging and likely results in overestimations compared to *in vivo* measurements. Caution should be exercized when discussing performance metrics without appropriate experimental validation, as such speculation could obscure accurate discussions of the form and function relationship.

Ethics. All experimental protocols adhered to the approved guidelines of Duke University (Protocol # A183-22-10) Institutional Animal Care and Use Committee.

Data accessibility. All data necessary to recreate our analyses are available in the supplementary materials [68].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. E.D.: conceptualization, funding acquisition, investigation, methodology, supervision, writing—original draft; M.W.Y.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, validation, visualization, writing—original draft; G.A.H.: investigation, methodology, project administration; J.C.McK.: investigation, methodology, project administration;

A.D.: investigation, methodology; M.R.D.: investigation, methodology; K.H.W.: investigation, methodology, project administration; M.C.G.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, writing—original draft.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This project was funded by the Leakey Foundation, the Duke Lemur Center Director's Fund and the Center for Biomedical Innovation.

Acknowledgements. This project would not have been possible without the support of the Duke Lemur Center. We especially thank Erin Ehmke, Alexis Sharp and Miriam Gordon for their unwavering support and assistance. We also extend our gratitude to Jonathan Geisler and Konstantinos Mountrakis for providing access to the Anatomy Laboratory, which was essential for conducting the dissections required for this project. Finally, we thank Daniel Schmitt, Grégoire Boulinguez-Ambroise, Diego Sustaita and Tracy L. Kivell for their valuable discussions, comments and suggested revisions, which significantly improved the quality of this work.

References

1. Bloch JI, Boyer DM. 2002 Grasping primate origins. *Science* **298**, 1606–1610. (doi:10.1126/science.1078249)
2. Granatosky MC. 2020 Primate locomotion. In *Encyclopedia of animal cognition and behavior* (eds J Vonk, T Shackelford), pp. 1–7. Cham, Switzerland: Springer International Publishing. (doi:10.1007/978-3-319-47829-6_1833-1)
3. Granatosky MC, YoungJW. 2023 *Primate locomotion: a comparative and developmental perspective*, (ed. C Larsen), pp. 587–602. Hoboken, NJ: John Wiley & Sons, Ltd. (doi:10.1002/9781119828075)
4. Cartmill M. 1972 Arboreal adaptations and the origin of the order Primates. In *The Functional and Evolutionary Biology of Primates* (ed. RH Tuttle), pp. 97–122. Chicago, IL: Aldine-Atherton. (doi:10.4324/9781315132129-4)
5. Sargis EJ. 2001 The grasping behaviour, locomotion and substrate use of the tree shrews *Tupaia minor* and *T. tana* (Mammalia, Scandentia). *J. Zool.* **253**, 485–490. (doi:10.1017/S0952836901000449)
6. Sargis EJ, Boyer DM, Bloch JI, Silcox MT. 2007 Evolution of pedal grasping in primates. *J. Hum. Evol.* **53**, 103–107. (doi:10.1016/j.jhevol.2007.01.008)
7. Gebo DL. 1985 The nature of the primate grasping foot. *Am. J. Phys. Anthropol.* **67**, 269–277. (doi:10.1002/ajpa.1330670312)
8. Goodenberger KE, Boyer DM, Orr CM, Jacobs RL, Femiani JC, Patel BA. 2015 Functional morphology of the hallucal metatarsal with implications for inferring grasping ability in extinct primates. *Am. J. Phys. Anthropol.* **156**, 327–348. (doi:10.1002/ajpa.22652)
9. Szalay FS, Dagosto M. 1988 Evolution of hallucial grasping in the primates. *J. Hum. Evol.* **17**, 1–33. (doi:10.1016/0047-2484(88)90047-4)
10. Dickinson E, Young MW, Kim CJ, Hadjiargyrou M, Granatosky MC. 2022 The influence of substrate size upon pulling and gripping forces in parrots (Psittaciformes: *Agapornis roseicollis*). *J. Exp. Biol.* **225**, jeb244818. (doi:10.1242/jeb.244818)
11. Young MW, Granatosky MC, Avey-Arroyo JA, Butcher MT, Dickinson E. 2023 Grip it good: *in vivo* grip force across substrate diameters in the brown-throated three-toed sloth (*Bradypus variegatus*). *J. Zool.***319**, 254–263. (doi:10.1111/jzo.13041)
12. Granatosky MC. 2018 A review of locomotor diversity in mammals with analyses exploring the influence of substrate use, body mass and intermembral index in primates. *J. Zool.* **306**, 207–216. (doi:10.1111/jzo.12608)
13. Arlet ME, Carey JR, Molleman F. 2009 Species, age and sex differences in type and frequencies of injuries and impairments among four arboreal primate species in Kibale National Park, Uganda. *Primates* **50**, 65–73. (doi:10.1007/s10329-008-0119-9)
14. Sustaita D, Pouydebat E, Manzano A, Abdala V, Hertel F, Herrel A. 2013 Getting a grip on tetrapod grasping: form, function, and evolution. *Biol. Rev.* **88**, 380–405. (doi:10.1111/brv.12010)
15. Thomas P, Pouydebat E, Brazidec ML, Aujard F, Herrel A. 2016 Determinants of pull strength in captive grey mouse lemurs. *J. Zool.* **298**, 77–81. (doi:10.1111/jzo.12292)
16. Abe T, Loenneke JP. 2015 Handgrip strength dominance is associated with difference in forearm muscle size. *J. Phys. Ther. Sci.* **27**, 2147–2149. (doi:10.1589/jpts.27.2147)
17. Hartstone-Rose A, Leischner C, Pastor F, Marchi D. 2017 Functional adaptations of primate forearm and leg muscle fiber architecture. *Am. J. Phys. Anthropol.* **S64**, 211.
18. Boettcher ML, Leonard KC, Dickinson E, Herrel A, Hartstone-Rose A. 2019 Extraordinary grip strength and specialized myology in the hyper-derived hand of *Perodicticus potto*? *J. Anat.* **235**, 931–939. (doi:10.1111/joa.13051)
19. Dickinson E, Boettcher ML, Smith MR, Worden NA, Swindell SR, Seelye JS, Pastor F, Hartstone-Rose A. 2021 Myological variation in the forearm anatomy of Callitrichidae and Lemuridae. *J. Anat.* **239**, 669–681. (doi:10.1111/joa.13440)
20. Leischner CL, Crouch M, Allen KL, Marchi D, Pastor F, Hartstone-Rose A. 2018 Scaling of primate forearm muscle architecture as it relates to locomotion and posture. *Anat. Rec.* **301**, 484–495. (doi:10.1002/ar.23747)
21. Marchi D, Leischner CL, Pastor F, Hartstone-Rose A. 2018 Leg muscle architecture in primates and its correlation with locomotion patterns. *Anat. Rec.* **301**, 515–527. (doi:10.1002/ar.23745)
22. Young JW, Chadwell BA, O'Neill TP, Pastor F, Marchi D, Hartstone-Rose A. 2024 Quantitative assessment of grasping strength in platyrrhine monkeys. *Am. J. Biol. Anthropol.* **183**, e24900. (doi:10.1002/ajpa.24900)
23. Vanhoof MJM, van Leeuwen T, Vereecke EE. 2020 The forearm and hand musculature of semi-terrestrial rhesus macaques (*Macaca mulatta*) and arboreal gibbons (Fam. Hylobatidae). Part I. Description and comparison of the muscle configuration. *J. Anat.* **237**, 774–790. (doi:10.1111/joa.13222)
24. van Leeuwen T, Vanhoof MJM, Kerkhof FD, Stevens JMG, Vereecke EE. 2018 Insights into the musculature of the bonobo hand. *J. Anat.* **233**, 328–340. (doi:10.1111/joa.12841)
25. Patel BA, Wallace IJ, Boyer DM, Granatosky MC, Larson SG, Stern JT. 2015 Distinct functional roles of primate grasping hands and feet during arboreal quadrupedal locomotion. *J. Hum. Evol.* **88**, 79–84. (doi:10.1016/j.jhevol.2015.09.004)
26. Vereecke EE, D'Août K, Payne R, Aerts P. 2005 Functional analysis of the foot and ankle myology of gibbons and bonobos. *J. Anat.* **206**, 453–476. (doi:10.1111/j.1469-7580.2005.00412.x)
27. Payne RC, Crompton RH, Isler K, Savage R, Vereecke EE, Günther MM, Thorpe SKS, D'Août K. 2006 Morphological analysis of the hindlimb in apes and humans. II. Moment arms. *J. Anat.* **208**, 725–742. (doi:10.1111/j.1469-7580.2006.00564.x)
28. Le Brazidec M, Herrel A, Thomas P, Grégoire BA, Aujard F, Pouydebat E. 2017 How aging affects grasping behavior and pull strength in captive gray mouse lemurs (*Microcebus murinus*). *Int. J. Primatol.* **38**, 1120–1129. (doi:10.1007/s10764-017-0001-y)

29. Boulinguez-Ambroise G, Herrel A, Berillon G, Young JW, Cornette R, Meguerditchian A, Cazeau C, Bellaiche L, Pouydebat E. 2021 Increased performance in juvenile baboons is consistent with ontogenetic changes in morphology. *Am. J. Phys. Anthropol.* **175**, 546–558. (doi:10.1002/ajpa.24235)
30. Bardo A, Kivell TL, Town K, Donati G, Ballieux H, Stamate C, Edginton T, Forrester GS. 2021 Get a grip: variation in human hand grip strength and implications for human evolution. *Symmetry* **13**, 1142. (doi:10.3390/sym13071142)
31. Sustaita D, Hertel F. 2010 *In vivo* bite and grip forces, morphology and prey-killing behavior of North American accipiters (Accipitridae) and falcons (Falconidae). *J. Exp. Biol.* **213**, 2617–2628. (doi:10.1242/jeb.041731)
32. Cannata MJ, Dickinson E, Young MW, Kantounis SJ, Jacobson RN, Granatosky MC. 2024 Grip it and ribbit: mechanisms contributing to grasping in Australian green treefrogs (*Ranoidea caerulea*). *J. Herpetol.* **58**, 64–74. (doi:10.1670/23-040)
33. Herrel A, Tolley KA, Measey GJ, da Silva JM, Potgieter DF, Boller E, Boistel R, Vanhooydonck B. 2013 Slow but tenacious: an analysis of running and gripping performance in chameleons. *J. Exp. Biol.* **216**, 1025–1030. (doi:10.1242/jeb.078618)
34. Kim CJ *et al*. 2023 *Mustn1* ablation in skeletal muscle results in functional alterations. *FASEB Bioadv.* **5**, 541–557. (doi:10.1096/fba.2023-00082)
35. Aghazadeh F, Lee K, Waikar A. 1993 Impact of anthropometric and personal variables on grip strength. *J. Hum. Ergol. (Tokyo)* **22**, 75–81. (doi:10.11183/jhe1972.22.75)
36. Yakou T, Yamamoto K, Koyama M, Hyodo K. 1997 Sensory evaluation of grip using cylindrical objects. *JSME Int. J. Ser. C* **40**, 730–735. (doi:10.1299/jsmec.40.730)
37. Crawford JO, Wanibe E, Nayak L. 2002 The interaction between lid diameter, height and shape on wrist torque exertion in younger and older adults. *Ergonomics* **45**, 922–933. (doi:10.1080/00140130210162243)
38. Brand RA, Pedersen DR, Friederich JA. 1986 The sensitivity of muscle force predictions to changes in physiologic cross-sectional area. *J. Biomech.* **19**, 589–596. (doi:10.1016/0021-9290(86)90164-8)
39. Maughan RJ, Watson JS, Weir J. 1983 Strength and cross-sectional area of human skeletal muscle. *J. Physiol.* **338**, 37–49. (doi:10.1113/jphysiol.1983.sp014658)
40. Granatosky MC, Fitzsimons A, Zeininger A, Schmitt D. 2018 Mechanisms for the functional differentiation of the propulsive and braking roles of the forelimbs and hindlimbs during quadrupedal walking in primates and felines. *J. Exp. Biol.* **221**, 1–11. (doi:10.1242/jeb.162917)
41. Batist CH, Mayhew JA. 2020 Lateralization in seven lemur species when presented with a novel cognitive task. *Am. J. Phys. Anthropol.* **172**, 270–279. (doi:10.1002/ajpa.24037)
42. Ward JP, Milliken GW, Stafford DK, eds JP Ward. 1993 Patterns of lateralized behavior in prosimians. In *Primate laterality. Recent research in psychology* (eds JP Ward, WD Hopkins), pp. 43–74. New York, NY: Springer. (doi:10.1007/978-1-4612-4370-0_2)
43. Milliken GW, Forsythe C, Ward JP. 1989 Multiple measures of hand-use lateralization in the ring-tailed lemur (*Lemur catta*). *J. Comp. Psychol.* **103**, 262–268. (doi:10.1037/0735-7036.103.3.262)
44. Milliken GW, Ferra G, Kraiter KS, Ross CL. 2005 Reach and posture hand preferences during arboreal feeding in sifakas (*Propithecus* sp.): a test of the postural origins theory of behavioral lateralization. *J. Comp. Psychol.* **119**, 430–439. (doi:10.1037/0735-7036.119.4.430)
45. Leliveld LMC, Scheumann M, Zimmermann E. 2008 Manual lateralization in early primates: a comparison of two mouse lemur species. *Am. J. Phys. Anthropol.* **137**, 156–163. (doi:10.1002/ajpa.20852)
46. Schnoell AV, Huebner F, Kappeler PM, Fichtel C. 2014 Manual lateralization in wild redfronted lemurs (*Eulemur rufifrons*) during spontaneous actions and in an experimental task. *Am. J. Phys. Anthropol.* **153**, 61–67. (doi:10.1002/ajpa.22403)
47. Papademetriou E, Sheu CF, Michel GF. 2005 A meta-analysis of primate hand preferences, particularly for reaching. *J. Comp. Psychol.* **119**, 33–48. (doi:10.1037/0735-7036.119.1.33)
48. Mittermeier RA *et al*. 2010 *Lemurs of Madagascar 3* (Tropical Field Guide series). Arlington, VA: Conservation International. See https://publications.goettingen-research-online.de/handle/2/10061.
49. Herrel A, De Smet A, Aguirre LF, Aerts P. 2008 Morphological and mechanical determinants of bite force in bats: do muscles matter? *J. Exp. Biol.* **211**, 86–91. (doi:10.1242/jeb.012211)
50. Schneider CA, Rasband WS, Eliceiri KW. 2012 NIH image to imageJ: 25 years of image analysis. *Nat. Methods* **9**, 671–675. (doi:10.1038/nmeth.2089)
51. Murphy RA, Beardsley AC. 1974 Mechanical properties of the cat soleus muscle in situ. *Am. J. Physiol.* **227**, 1008–1013. (doi:10.1152/ajplegacy.1974.227.5.1008)
52. R Core Team. 2021 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.R-project.org.
53. Clemente CJ, Dick TJM. 2023 How scaling approaches can reveal fundamental principles in physiology and biomechanics. *J. Exp. Biol.* **226**, jeb245310. (doi:10.1242/jeb.245310)
54. Conover WJ, Iman RL. 1982 Analysis of covariance using the rank transformation. *Biometrics* **38**, 715–724. (doi:10.2307/2530051)
55. Winter B. 2013 Linear models and linear mixed effects models in R with linguistic applications. *arXiv* 1308.5499. (doi:10.48550/arXiv.1308.5499)
56. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
57. Kuznetsova A, Brockhoff PB, Christensen RHB. 2017 lmerTest package: tests in linear mixed effects models . *J. Stat. Softw.* **82**, 1–26. (doi:10.18637/jss.v082.i13)
58. Brown JH, West GB. 2000 *Scaling in biology*. New York, NY: Oxford University Press.
59. Fitch WT, Braccini SN. 2013 Primate laterality and the biology and evolution of human handedness: a review and synthesis. *Ann. N. Y. Acad. Sci.* **1288**, 70–85. (doi:10.1111/nyas.12071)
60. Papadatou-Pastou M, Ntolka E, Schmitz J, Martin M, Munafò MR, Ocklenburg S, Paracchini S. 2020 Human handedness: a meta-analysis. *Psychol. Bull.* **146**, 481–524. (doi:10.1037/bul0000229)
61. Feix T, Kivell TL, Pouydebat E, Dollar AM. 2015 Estimating thumb–index finger precision grip and manipulation potential in extant and fossil primates. *J. R. Soc. Interface* **12**, 20150176. (doi:10.1098/rsif.2015.0176)
62. Almécija S, Smaers JB, Jungers WL. 2015 The evolution of human and ape hand proportions. *Nat. Commun.* **6**, 7717. (doi:10.1038/ncomms8717)
63. Connour JR, Glander K, Vincent F. 2000 Postcranial adaptations for leaping in primates. *J. Zool.* **251**, 79–103. (doi:10.1111/j.1469-7998.2000.tb00595.x)
64. Demes B, Fleagle JG, Lemelin P. 1998 Myological correlates of prosimian leaping. *J. Hum. Evol.* **34**, 385–399. (doi:10.1006/jhev.1997.0203)
65. Demes B, Franz TM, Carlson KJ. 2005 External forces on the limbs of jumping lemurs at takeoff and landing. *Am. J. Phys. Anthropol.* **128**, 348–358. (doi:10.1002/ajpa.20043)
66. Amanat S, Srinivasan P, Mayer J, Bhavsar R, Ali Z, Paracha H, Granatosky MC. 2020 *Encyclopedia of animal cognition and behavior*. (eds J Vonk, T Shackelford). Cham, Switzerland: Springer International Publishing. See http://link.springer.com/10.1007/978-3-319-47829-6.
67. Dickinson E, Young MW, Granatosky MC. 2022 *In vivo* bite force in lovebirds (*Agapornis roseicollis*, Psittaciformes) and their relative biting performance among birds. *J. Zool.* **318**, 272–282. (doi:10.1111/jzo.13014)
68. Dickinson E, Young MW, Hirschkorn GA, McKinney JC, DiMartino A, Deutsch MR. 2024 Supplementary material from: Ecomorphological correlates of grasping forces in Strepsirrhine primates. Figshare. (doi:10.6084/m9.figshare.c.7571814)