

CORRECTION

Correction: The influence of substrate size upon pulling and gripping forces in parrots (*Psittaciformes*: *Agapornis roseicollis*)

Edwin Dickinson, Melody W. Young, Charles J. Kim, Michael Hadjiargyrou and Michael C. Granatosky

There were errors in *J. Exp. Biol.* (2022) **225**, jeb244818 (doi:10.1242/jeb.244818).

An incorrect earlier version of Fig. 3 was mistakenly uploaded twice and used as the final version of both Figs 2 and 3 of this paper. The original and corrected versions are shown below.

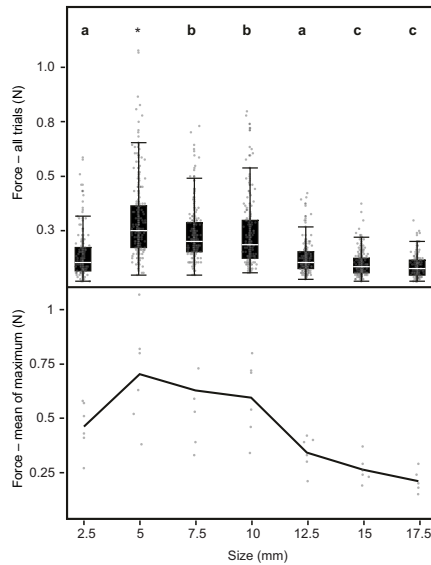


Fig. 2 (original). Box-and-whisker plots of pulling forces in *Agapornis roseicollis*, measured across a range of perch diameters.

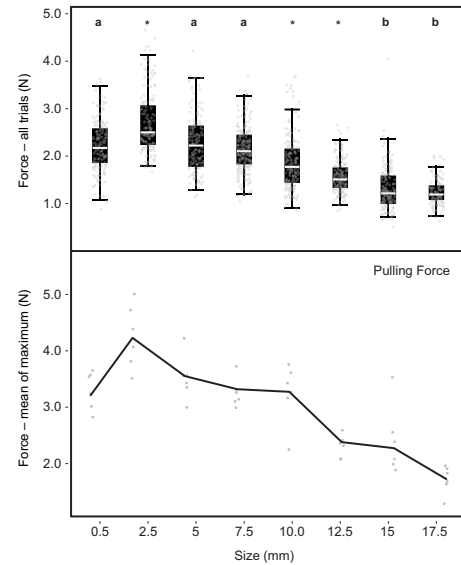


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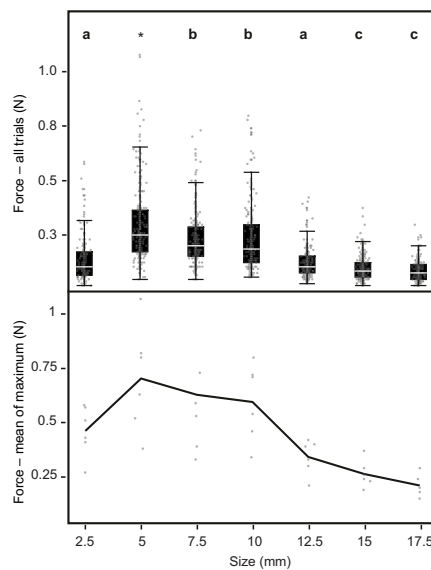


Fig. 3 (original). Box-and-whisker plots of gripping forces in *Agapornis roseicollis*, measured across a range of perch diameters.

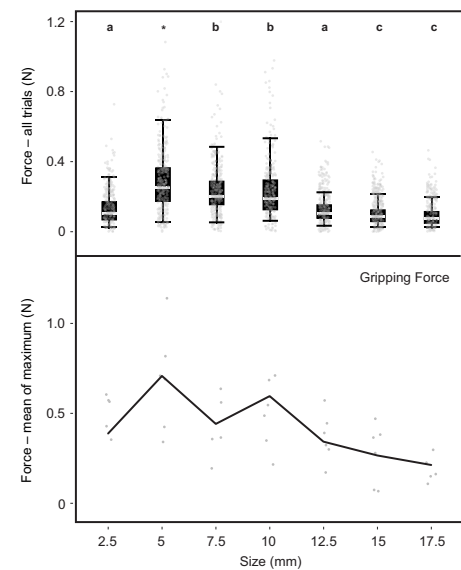


Fig. 3 (corrected). Box-and-whisker plots of gripping forces in *Agapornis roseicollis*, measured across a range of perch diameters.

The online full text and PDF versions of the paper have been corrected. Both the journal and the authors apologise to readers for not spotting this error, which does not impact the results or conclusions of the paper.

RESEARCH ARTICLE

The influence of substrate size upon pulling and gripping forces in parrots (*Psittaciformes: Agapornis roseicollis*)

Edwin Dickinson^{1,*}, Melody W. Young^{1,2}, Charles J. Kim², Michael Hadjiargyrou³ and Michael C. Granatosky^{1,4}

ABSTRACT

The ability to securely grasp substrates of variable diameter is critical to arboreal animals. Arboreal specialists have emerged across several vertebrate lineages – including mammals, lizards and amphibians – and several attempts have been made to quantify their grasping performance, by measuring either gripping (i.e. forces generated about an object or substrate enclosed within the digits) or pulling (i.e. the ability to resist being removed from a substrate) forces. In this study, we present data on both pulling and gripping performance across a range of substrate diameters (0.5–17.5 mm) within a model parrot species (*Agapornis roseicollis*). Parrots represent an ancient arboreal lineage, allowing us to compare their abilities with those of arboreal specialists within other tetrapod groups. Data were collected using 3D-printed perches of variable diameter, and forces were registered using either an AMTI low-load force plate (grip force) or a Harvard Apparatus portable strength tester (pull force). Gripping forces peaked at a 5 mm diameter perch, while pulling forces were greatest at a 2.5 mm diameter. All forces strongly diminished above 10 mm size, suggesting grip force is optimized when utilizing small perches, a finding which corresponds to observational studies of preferential perching habits among free-ranging parrots. Relative grasping performance (adjusted for body size) in parrots is roughly equivalent to that of other arboreal specialists from other tetrapod lineages, but low when compared with that of raptorial birds that utilize their feet during aerial prey capture. Further taxonomic sampling is encouraged to contextualize how grasping performance varies in an adaptive evolutionary context.

KEY WORDS: Grasping, Arboreality, Functional morphology, Length–tension relationship, Biomechanics

INTRODUCTION

The ability to generate and sustain a stable grip around substrates of variable diameter is critical to arboreal taxa, which are required to constantly navigate an often-unpredictable locomotor habitat. Given the steep fitness cost of failure in this endeavor – which could result in serious injury or even death – grasping forces can be considered a core functional metric upon which adaptive selection is anticipated to exert strong pressures. Within this context, grasping

forces have been collected *in vivo* from several vertebrate lineages, including amphibians (Manzano et al., 2008; Fabre et al., 2019), lizards (Herrel et al., 2013; da Silva et al., 2014), birds (Ward et al., 2002; Sustaita and Hertel, 2010) and mammals (Nevins et al., 1993; Iwanami et al., 2005; Thomas et al., 2016; Le Brazidec et al., 2017). In this study, we present two metrics of quantifying grasping performance – pull force and grip force – within an ancient arboreal avian lineage (*Psittaciformes*), to compare the relative grip performance of highly arboreal birds with that of similar specialists within other tetrapod clades.

Gripping, pulling and the origins of grasping

The ability to generate a grasping force using the manual or pedal digits is widespread across terrestrial tetrapods. Despite the anatomical and physiological specializations that differentiate birds, mammals, lizards and frogs, each of these lineages has evolved arboreal specialists for which grasping is key to locomotion (Sustaita et al., 2013). Indeed, it has been previously suggested that the basic biomechanical abilities associated with grasping (i.e. controlled manipulation of an object or substrate with the manual or pedal digits) likely originated in basal tetrapods (Iwaniuk and Whishaw, 2000). This notion is reinforced by broad comparative studies of limb musculature across tetrapods, which is highly conservative and near-universally retains the ability to flex and extend the digits sufficiently to facilitate at least a rudimentary grasp (Abdala and Diogo, 2010). However, the nature and complexity of these grasps vary drastically, reflecting both grades of manual/pedal morphological complexity and the presence or absence of accessory flexor muscles to support more varied digital postures. Indeed, between 16 and 33 variants of grasping (grouped broadly into power versus precision grasps) are defined within the human hand alone (Elliott and Connolly, 1984; Cutkosky, 1989; Feix et al., 2009). As such, a tight definition of specific grasping behaviors is necessary to design and implement experimental studies of performance.

Broadly, two discrete categories of experimental grasping data have been collected *in vivo*; namely, grip forces (which reflect specifically the contractile forces generated about an object or substrate enclosed within the digits) and pulling forces (which reflect the magnitude of force an animal can exert in resistance to being forcibly removed from a substrate). These forces are representative of differing ecological scenarios: while gripping forces can approximate, for example, the compressive forces exerted by the talons of a raptor around its prey, pulling forces are more representative of, to continue the above example, the force with which a small mammal might cling to a branch to avoid being lifted away by said raptor. As these forces reflect different anatomical/physiological sources (the former reflecting only the contraction of the digital flexors, and the latter further incorporating both the passive clinging force generated by penetration of the claws into the substrate and the potential resistance of tendon locking mechanisms), it is important to differentiate these streams of data

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as distinct activities to avoid conflating dissimilar measurements of functional performance.

Previous measurements of grasping performance

Of these two metrics, pulling forces represent the vast majority of *in vivo* data. These experiments have demonstrated that highly arboreal lizards (e.g. dwarf chameleons) and primates (e.g. mouse lemurs) are both capable of generating bimanual grip forces in excess of 10 times their own body mass in resistance to being pulled away from a substrate. As both species habitually locomote using narrow arboreal substrates, their pulling capacity has been connected to this aspect of their ecology (Thomas et al., 2016), especially as arboreal chameleons outperform their terrestrial counterparts in pulling force (Herrel et al., 2013). However, both dwarf chameleons and mouse lemurs are also small-bodied prey animals vulnerable to aerial predators and, as such, their extraordinary pulling performance might also reflect a defensive adaptation in resistance to raptors and sympatric predators, rather than representing adaptations to arboreality per se.

Broadly similar pulling forces have also been measured in a handful of birds (Ward et al., 2002), though these experimental trials were not measured to failure (i.e. the birds were pushed to break their balance, but were not pulled away until their grasp was broken) and are thus not wholly comparable to other experimental studies. Analyzing these data within an ecological context, owls – a lineage that utilizes forceful talons to grasp and crush prey – exhibit particularly high forces for their body size, suggesting that hunting behaviors may have some influence in driving performance (Ward et al., 2002).

By contrast, isolated gripping forces have been collected in only a single species of parrot (Roderick et al., 2019) and a handful of raptorial avian taxa (Sustaita and Hertel, 2010). Within Pacific parrotlets, grip forces register at slightly above body weight (~150% BW; Roderick et al., 2019) regardless of the material used for the perch. Within raptors, meanwhile, a strong influence of hunting ecology upon grip forces can be observed. A comparison of grip force between hawks (a family that typically kill by using their talons to suffocate or penetrate their prey) and falcons (which typically kill prey using their beak) revealed, as predicted, a significant increase in relative grip force within the talon-killing hawks (Sustaita and Hertel, 2010). Thus, among avians, predation strategies would appear a strong determinant of pulling and gripping performance. However, it is not clear how other ecological variables, such as perching and/or climbing frequency and the degree of arboreality, might impact grasping performance in birds.

Arboreal adaptations within Psittaciformes

Parrots (Order Psittaciformes) are an ancient arboreal lineage that collectively exhibit numerous anatomical adaptations towards their locomotor environment (Waterhouse, 2006; Ksepka et al., 2011; Ksepka and Clarke, 2012; Zelenkov, 2016). The parrot tarsometatarsus is short and broad relative to that of other avians, reducing the tendency to pitch when climbing vertically or roll when navigating narrow branches (Norberg, 1986; Provini and Höfling, 2020; Young et al., 2022b). Meanwhile, their zygodactylous digits are long, with an elongated penultimate phalanx that may facilitate firm grasps around a broad array of substrate sizes (Kavanagh et al., 2013), as well as dexterous manipulation in which the foot is used to pass items into the beak (Collar, 1997). Parrots have also been demonstrated to co-opt their beak as a functional limb when climbing vertical substrates, an exaptation unique to the order (Young et al., 2022a). A recent analysis of positional behaviors

within free-ranging parrots demonstrates a strong preference for arboreal substrates, with a particular bias towards small and terminal branches from which new fruit growth and leaf-buds may be foraged (Granatosky et al., 2022). Thus, it may be anticipated that the grasping capabilities of parrots may be optimized towards small substrates to maximize performance upon these narrow terminal branches, which are inherently unstable and may readily oscillate under the animal's mass – necessitating a firm grasp to maintain stability.

Aims and hypothesis

Within this study, we present *in vivo* pulling and gripping forces across a range of substrate sizes (0.5–17.5 mm) from six rosy-faced lovebirds (*Agapornis roseicollis*). In so doing, we test the overarching hypothesis that grip force within parrots will be optimized towards maximizing stability on their preferred substrate sizes; namely, narrow and terminal branches sufficiently small in diameter (>5 mm) that the toes of the bird are completely wrapped around the substrate during perching (Granatosky et al., 2022). We therefore predict that forces will be highest on these narrow substrates and decrease sequentially thereafter as substrates become larger. We further predict that peak pulling forces in arboreally specialized parrots will be relatively similar in magnitude (after adjusting for body size) to those of arboreal specialists within other tetrapod lineages (i.e. mouse lemurs and dwarf chameleons, both of which exhibit pull forces of 10–15 times their respective body masses), illustrating a shared influence of arboreality in driving grip forces across highly arboreal taxa.

MATERIALS AND METHODS

Subjects and permissions

Our sample comprised six adult (all between 1 and 2 years of age) rosy-faced lovebirds, *Agapornis roseicollis* (Vieillot 1818), all of which presented free of any observable pathology and were of approximately equivalent mass (48.8±2.8 g). Animals were communally housed at the Animal Care Facility in the College of Osteopathic Medicine at New York Institute of Technology. Animals were provisioned with seeds and fresh water, and were inspected daily to ensure good health. All experimental protocols were approved by the Institutional Animal Care and Use Committee at the New York Institute of Technology (protocol number: 2021-MG-03).

Measurement of pulling forces

Pulling forces were collected using a calibrated portable strength tester (Model 761066; Harvard Apparatus, Holliston, MA, USA), to which only two basic modifications were made. Firstly, the machine's default testing bar was replaced with a series of custom-built composite perches. These perches were designed using CAD software and 3D printed to specification, then given an epoxy coat and covered in fine sand to give a naturalistic texture that would encourage the birds to grip as normally as possible. Secondly, the machine was rotated 90 deg such that, rather than an animal grasping the bar and being pulled horizontally away, the bird could perch atop the bar and be pulled vertically away. Data collection using this machine otherwise followed a well-established protocol (e.g. Ruiz et al., 2014; Chen et al., 2018; Huang et al., 2018; Xu et al., 2019), and birds were rested for at least 2 h between trial periods to mitigate the potential impact of fatigue.

Pulling forces were measured from a single hindlimb per trial. A notation of which limb was measured during each trial was made to subsequently assess interlimb differences in pull force. Data were

collected over eight increments of perch diameter: 0.5, 2.5, 5, 7.5, 10, 12.5, 15 and 17.5 mm.

Measurement of gripping forces

Gripping forces were collected using a calibrated AMTI small-load force plate (model HE6×6; Watertown, MA, USA) in combination with a second series of custom-built composite perches. Unlike the solid perches utilized for pulling forces, these perches comprised two pieces (Fig. 1), which remained separated at all times. While the upper half of the perch was not altered in any way, the lower half of the perch was instrumented via connection to the small-load force plate. As the bird approached the perch, it naturally wrapped its foot around the substrate, generating a compressive force. The Z-magnitude of this force – which measured the vertical displacement of the lower half of the perch upwards under gripping – was used as our measurement of intrinsic grip force. As with pulling forces, forces were collected from only one limb at a time, and a notation of which limb was measured during each trial was made to assess interlimb differences in gripping force.

Because of the requirement of keeping the upper and lower halves of the perch separate during experiments (to prevent interference with our force data), the smallest perch size (0.5 mm) could not be replicated in this experiment. Thus, gripping forces were collected over seven perch diameters (2.5–17.5 mm).

Data analysis

Pulling forces were visually displayed on the machine after each trial, and were manually recorded before the machine was zeroed in anticipation of the next bird. Gripping forces were collected and exported for analysis using the software package AMTI NetForce (v3.6.04). All statistical analysis was conducted using R v4.1.1 (<http://www.R-project.org/>). Normality of datasets was determined using Shapiro–Wilk and Levene’s tests, and all gripping and pulling data underwent rank transformations prior to any statistical comparisons (Sokal and Rohlf, 1995).

Two linear mixed effect models were created, each assessing the effect of substrate size and foot (left or right) on gripping and pulling force, respectively, while accounting for individual

idiosyncrasies as a random effect following Winter (2013 preprint) and Bates et al. (2015). The R packages ‘lmerTest’ (Kuznetsova et al., 2017) and ‘lme4’ (Bates et al., 2015) were used for these analyses. *Post hoc* Tukey–Kramer HSD tests were then run between each perch size. Finally, to remove the potential influence of low-motivation trials and to provide a sample-level signal of grasping performance which could be compared with previously collected data within other taxa, we calculated an average for each experimental condition using each individual bird’s highest force trial.

RESULTS

A total of 1254 trials for pulling force and 1942 trials for gripping force were measured across substrates (Tables 1 and 2, Figs 2 and 3). Raw data from all trials are presented in Table S1. Differences between the left and right foot were significant during pulling but not grasping (Tables 3 and 4). During both pulling and gripping, the highest magnitudes of forces were measured at small diameters. Pull forces peaked significantly at 2.5 mm (2.76 ± 0.73 N), and were generally high at 7.5 mm diameter and below (Fig. 2). Indeed, forces at 0.5, 5.0 and 7.5 mm were all statistically indistinguishable from one another, but were significantly reduced from forces at 2.5 mm and universally greater than forces at any perch diameter above this range (Fig. 2). In terms of grip forces, peak values were obtained at a 5 mm diameter perch (0.29 ± 0.17 N) and the significantly strongest forces were found within the range 5–10 mm (Fig. 3).

To control for the potential confounding influence of low-motivation trials, we also calculated a mean-of-maximum metric, i.e. the average of each bird’s highest trial at each perch diameter. This yielded the same pattern in terms of perch sizes (Table 2), but force magnitudes were increased to be more reflective of maximal performance. Thus, prediction 1 – that grasping forces in parrots would be greatest on narrow substrates that closely reflect their preferential perch sizes – was largely supported.

Pull force data were subsequently compared against those of arboreal specialists within other lineages for which *in vivo* experimental data have been previously published (Fig. 4). In addition, we also included, as a reference, a generalized model taxon with a generic and varied habitat and locomotor repertoire (*Mus musculus*) and data from a handful of raptorial avians. From these, a ratio of pull force relative to body mass was calculated. The strongest relative pull forces were observed within the Chamaeleonidae (~15:1). Mouse lemurs exhibited a pull-to-body mass ratio of ~1100% BW, while our parrots had a value of 900% BW. The generalized mouse model, meanwhile, exhibited a pull-to-body mass ratio of just 500% BW. However, it should be noted that data for chameleons, mouse lemurs and mice all registered simultaneous bimanual gripping, whereas data from our parrots were both: (a) measured from a single limb, and (b) measured from the

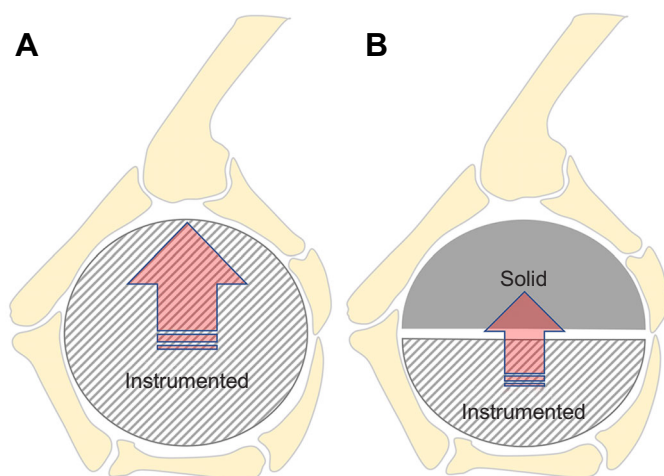


Fig. 1. Schematic illustration of the experimental design. (A) A fully instrumented perch, atop which the bird was placed before being removed with a vertical pull, during which event the magnitude of forces exerted in resistance to being moved was registered. (B) The composite perch design, from which intrinsic gripping forces were measured as the vertical displacement of the lower (instrumented) hemi-perch towards the upper, solid hemi-perch.

Table 1. Average pulling and gripping forces in *Agapornis roseicollis*, measured across a range of perch diameters

Perch diameter (mm)	Pulling force (N)	Gripping force (N)
0.5	2.23±0.51 (n=160)	N/A
2.5	2.76±0.73 (n=156)	0.13±0.10 (n=242)
5.0	2.28±0.60 (n=146)	0.29±0.17 (n=295)
7.5	2.16±0.46 (n=208)	0.23±0.13 (n=280)
10.0	1.84±0.56 (n=175)	0.23±0.16 (n=246)
12.5	1.57±0.34 (n=152)	0.12±0.07 (n=292)
15.0	1.31±0.39 (n=155)	0.10±0.05 (n=335)
17.5	1.23±0.27 (n=102)	0.09±0.05 (n=252)

The number of trials per condition is indicated in parentheses.

Table 2. Mean-of-maximum pulling and gripping forces in *A. roseicollis*, measured across a range of perch diameters

Perch diameter (mm)	Pulling force (N)	Gripping force (N)
0.5	3.22	N/A
2.5	4.28	0.47
5.0	3.55	0.71
7.5	3.31	0.63
10.0	3.27	0.60
12.5	2.38	0.34
15.0	2.20	0.23
17.5	1.73	0.21

Data were calculated by taking the average of each bird's highest trial within each experimental condition, to control for the influence of low motivation cycles.

hindlimb, as opposed to the forelimb. Thus, prediction 2 – that parrots would show a generally similar level of grasping performance to other arboreal specialists – was tentatively supported.

Finally, to provide a more closely matched frame of reference to our parrots, we compared our measured grip forces with previously published data from single limbs of other taxa (Fig. 5), all of which were measured under similar experimental conditions to our own. Both parrot species registered a grip-to-body mass ratio of 150%

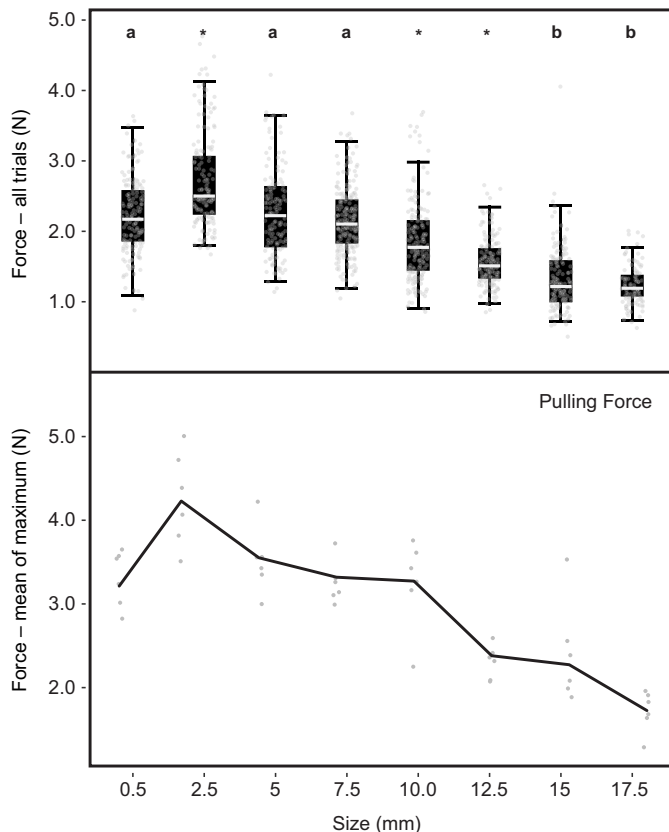


Fig. 2. Box-and-whisker plots of pulling forces in *Agapornis roseicollis*, measured across a range of perch diameters. (Top) Force across all trials. (Bottom) Mean of maximum force, calculated by taking the average of each bird's highest trial within each experimental condition, to control for the influence of low motivation cycles. Box plots show median (horizontal line) values, upper and lower quartiles (box), 1.5× interquartile range (whiskers) and outliers (dots). Asterisks indicate perch sizes that were statistically significantly different from all others ($P<0.05$); matching letters indicate sizes that did not differ from one another, but did differ from all other perch sizes.

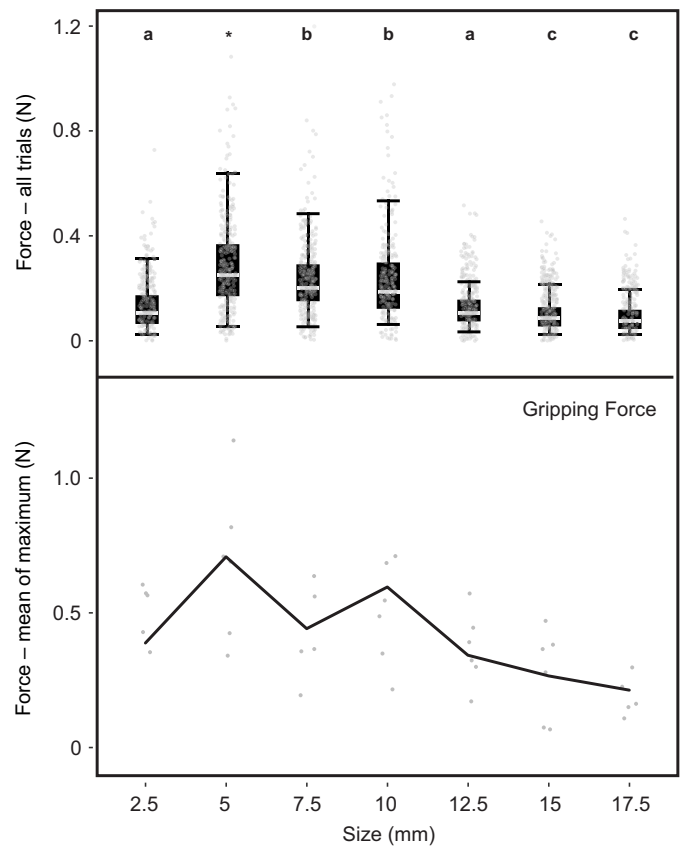


Fig. 3. Box-and-whisker plots of gripping forces in *A. roseicollis*, measured across a range of perch diameters. (Top) Force across all trials. (Bottom) Mean of maximum force. Asterisks indicate perch sizes that were statistically significantly different from all others ($P<0.05$); matching letters indicate sizes that did not differ from one another, but did differ from all other perch sizes.

BW (Fig. 5), which fell towards the lower end of the range occupied by raptors; indeed, only a single species (prairie falcon; 110% BW) exhibited a relatively weaker grip force for its body size. The relatively strongest gripping forces were observed in hawks and in the American kestrel, all of which registered ratios in excess

Table 3. Statistical parameters derived from linear mixed effect models demonstrating the statistical importance of various fixed effects with the response variable pulling force

Fixed effect	Estimate	s.e.	d.f.	t-value	P-value
(Intercept)	1028.19	23.81	58.75	–	–
Substrate diameter (mm)					
0.5	–187.98	28.23	1249.25	–6.66	<0.001
5	–178.73	28.90	1249.53	–6.18	<0.001
7.5	–219.91	26.57	1249.16	–8.28	<0.001
10	–425.86	27.62	1249.25	–15.42	<0.001
12.5	–582.72	28.58	1248.68	–20.39	<0.001
15	–732.83	28.42	1250.44	–25.79	<0.001
17.5	–799.59	31.97	1252.05	–25.01	<0.001
Foot (versus right)	–70.19	14.17	1249.80	–4.95	<0.001

Significant P -values are in bold. Substrate diameter 2.5 mm is not listed because inclusion within least squares regressions would be a statistical redundancy and violate assumptions of collinearity; 2.5 mm was selected as the reference substrate diameter because it was the size at which the birds generated the largest pull force.

Table 4. Statistical parameters derived from linear mixed effect models demonstrating the statistical importance of various fixed effects with the response variable gripping force

Fixed effect	Estimate	s.e.	d.f.	t-value	P-value
(Intercept)	1459.59	57.05	8.82	–	–
Substrate diameter (mm)					
2.5	–694.00	36.30	1936.92	–19.12	<0.001
7.5	–137.51	34.77	1936.11	–3.96	<0.001
10	–223.75	36.03	1936.33	–6.21	<0.001
12.5	–682.85	34.44	1936.42	–19.83	<0.001
15	–852.60	33.33	1936.49	–25.58	<0.001
17.5	–941.28	35.81	1936.15	–26.28	<0.001
Foot (versus right)	22.34	18.99	1936.40	1.177	0.24

Significant *P*-values are in bold. Substrate diameter 5 mm is not listed because inclusion within least squares regressions would be a statistical redundancy and violate assumptions of collinearity; 5 mm was selected as the reference substrate diameter because it was the size at which the birds generated the largest pull force.

of 2:1. All birds exhibited stronger gripping forces than any non-avian taxon.

DISCUSSION

Perch size and grasping performance in parrots

Pulling and gripping forces in parrots peaked at 2.5 and 5 mm perch diameter, respectively, suggesting that these birds do indeed exhibit maximal performance when grasping perches commensurate in size to those most frequently used within a free-ranging setting (Granatosky et al., 2022). However, in both instances, these forces were significantly greater than those registered at the smallest perch diameter (0.5 mm for pulling, 2.5 mm for grasping). Thus, despite a seeming adaptation towards grip force on small substrates, there would appear to be very small sizes at which forces begin to diminish (Figs 2 and 3) which correspond to excessive ‘overwrapping’ of the toes in which the digits wrap multiple times around the support (Fig. 6). However, some overwrapping is clearly beneficial to gripping forces, as one full foot span is equivalent to a perch with a circumference of 10.38 mm, higher than the size at which maximal forces can be generated (Fig. 6). This relationship likely reflects the length–tension properties of the digital flexor musculature (and in the case of pulling force, perhaps the hindlimb musculature more generally), in which muscle fibers are reduced in efficiency while their constituent sarcomeres occupy less effective regions of the length–tension curve (Gans and Bock, 1965; Edman, 1966; Gordon et al., 1966; Lieber, 1986; Kaufman et al., 1989; Herzog et al., 1992). Indeed, both pulling forces and gripping forces appear to tightly correspond to a Hill-type model of muscle tension, in which peak tension is generated when fibers are stretched slightly beyond resting length but not yet overextended into regions of diminishing contractile potential (Hill, 1938; Van

Eijden et al., 1997; Blümel et al., 2012). Thus, the trends captured within our data likely reflect this fundamental property of muscle physiology, though further experimental data in other avian taxa are necessary to determine how this relationship between substrate size and grasping forces varies across lineages, as well as the scaling of optimal perch size to foot or body size across avians.

Secondarily, the extent to which pulling forces dwarf gripping forces at any given perch size is also noteworthy, especially given these two terms have been historically conflated or interchangeably applied to measures of grasping performance (e.g. Herrel et al., 2013; Hämäläinen et al., 2015). While it was anticipated that pulling forces would – by definition – exceed grasping forces, the magnitude of this difference (which registered 5–10 times between diameters) exceeded our initial expectations. Some of this difference can certainly be ascribed to the frictional forces of the talons themselves, when resisting removal from the perch. However, we also suggest a potentially important contribution to the incredible pulling capabilities of parrots may derive from their ability to activate a tendon-locking mechanism within the digital flexor musculature (Quinn and Baumel, 1990; Einoder and Richardson, 2006; Trbojević Vukičević et al., 2018). This mechanism presents anatomically as a series of ridges upon the plantar surfaces of the digital flexors that interact with corresponding folds on the adjacent tendon sheath (Quinn and Baumel, 1990). When the digits are flexed around a substrate, and pressure is placed upon the flexor tendons via the podothecal pads, these two structures form an effective anchor which provides passive force to maintain a firm digital grasp. This interlocking system not only relieves the need for constant muscular contraction to maintain flexion but also provides a secondary interlocking mechanism via which the bird can resist being pulled away from its perch. While this mechanism is widespread among non-ratite avians (Einoder and Richardson, 2006, 2007; Tsang et al., 2019), it has been noted via histological analysis that the inner surface of the tendon sheath as well as the ridges located on the ventral surface of the tendons themselves are strongly developed in parrots (Trbojević Vukičević et al., 2018). However, the development of this system within parrots is still reduced relative to that in raptorial birds (Einoder and Richardson, 2006), and the extent to which specific ecologies or modes of locomotion may drive morphological differences in this system remains unclear.

Arboreality and grasping

Initial analysis of pulling forces in arboreal taxa tentatively suggests that highly arboreal animals tend to exhibit strong forces for their respective body sizes (Fig. 4). While the low number of sampled species makes it tenuous to draw any conclusions within an adaptive evolutionary framework, it is suggestive that, for example, mouse lemurs have a relative pull force more than 2 times that of a mouse (Nevins et al., 1993; Thomas et al., 2016). Further, considering that

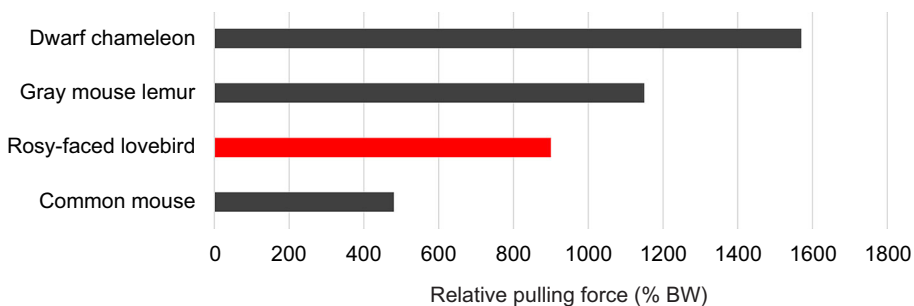


Fig. 4. Relative pulling force (adjusted for body size) in other tetrapods. Data are given as a percentage of body weight (BW). Dwarf chameleon data from da Silva et al. (2014); mouse lemur data from Thomas et al. (2016); mouse data from Nevins et al. (1993). Note that data from the rosy-faced lovebird (present study, highlighted in red) are from the hindlimb and single-sided (i.e. unipedal) whereas other data points represent dual-sided, forelimb (i.e. bimanual) forces.

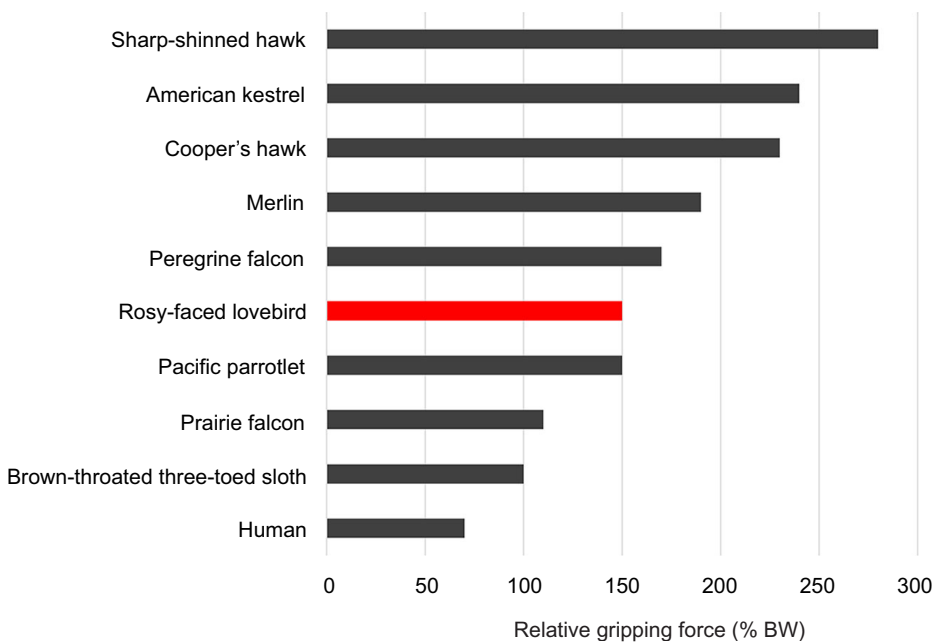


Fig. 5. Relative gripping force (adjusted for body size) in other tetrapods. Data are given as a percentage of body weight (BW). Rosy-faced lovebird (this study) data are highlighted in red; human data from Bardo et al. (2021); pacific parrotlet data from Roderick et al. (2019); other avian data from Sustaita and Hertel (2010); sloth data from current authors (M. W. Young, M. C. Granatosky, J. A. Avey-Arroyo, M. T. Butcher and E. Dickinson, unpublished data).

pulling forces in parrots were measured from a single limb, their bipedal pulling capacity would likely fall somewhere between that of mouse lemurs and chameleons in terms of pull-force-to-body mass ratio (Fig. 4). However, the major conclusion from these data is the necessity for broader taxonomic sampling of pulling forces in terrestrial mammals and lizards, as well as from both perching and terrestrial birds. Such comparative data are necessary before trends reported in pulling forces between taxa can confidently be evaluated within a functional or ecological framework. Thus, a clear future objective from this study is to apply this methodological framework of pull and grip force sampling across a broader sample of vertebrates and thus permit more a more informed interpretation of trends in performance.

Grip forces in birds

Prior to this study, it was anticipated that parrots – as an arboreally specialized lineage with several anatomical adaptations towards climbing and grasping – would exhibit high grip forces for their relative size. Our data closely match those presented by Roderick et al. (2019) on Pacific parrotlets, whose grip-to-body mass ratio (~150% BW) is similar to that of lovebirds. Thus, while parrots do appear to show commensurate relative forces to those of arboreal specialists in other lineages, they do not exhibit a particularly strong grasp within the context of other birds (Figs 4 and 5). While a clear caveat exists with regards to taxonomic sampling (as grasping forces had previously only been measured within a single parrot and a handful of raptorial taxa), it is potentially noteworthy that the grip-force-to-body mass ratio of parrots outperforms that of only a single non-parrot taxon (the prairie falcon, *Falco mexicanus*). Meanwhile, the highest performing bird (the sharp-shinned hawk, *Accipiter striatus*) exhibits a relative grip force 2 times that of parrots.

This observation may be ascribed to several, non-exclusive factors. Firstly, as observed by Ward et al. (2002) in an analysis of pulling forces between owls and hawks, forces increase with positive allometry relative to body size, such that larger-bodied birds produce relatively higher forces. A similar conclusion was also reported from a comparison of relative grip forces in falcons and hawks (Sustaita and Hertel, 2010). Thus, it is possible that larger-bodied parrots would produce relative gripping forces more in line

with those of hawks and falcons, a hypothesis that future taxonomic sampling will be able to test.

A second explanation, however, may be found when considering anatomical specializations inherent to the feet of raptorial birds. Owls and hawks both demonstrate a dual-closing mechanism within their talons, a convergent adaptation between these lineages that is not shared by their closer relatives (Conroy et al., 1997; Ward et al., 2002). This mechanism allows these birds to first grasp using the digital flexor musculature in the typical manner, and subsequently flex the joint between the tibiotarsus and the tarsometatarsus via contraction of the tibialis cranialis, a muscle that primarily flexes the intertarsal joint and pulls the tarsometatarsus towards the body (Goslow, 1972; Conroy et al., 1997; Ward et al., 2002). This action drives the talons into the prey or substrate, further increasing gripping ability (Ward et al., 2002). Thus, it is further possible that both parrots (as arboreal specialists) and raptors (as aerial predation specialists) exhibit anatomically distinct adaptations that each serve to increase relative grip forces, with the latter producing a greater relative increase in force potential. However, more rigorous experimental testing and broader taxonomic sampling are necessary both to isolate the potential role of these mechanisms and to understand their roles within a comparative ecological framework.

Conclusions

The gripping and pulling forces of parrots peaks at substrates 2.5–5.0 mm in diameter, a range that also describes their preferred branch diameter within a free-ranging setting. Analyzing the relationship between forces and perch size reveals that this behavior follows a generalized Hill-type length–tension model, in which peak tension is generated slightly beyond resting length but declines as the flexor musculature becomes overstretched. Relative grasping performance (adjusted for body size) in parrots is roughly equivalent to that of other arboreal specialists from other tetrapod lineages (e.g. mammals and lizards). However, grip force in parrots is relatively low compared with that of raptorial birds, which may reflect additional specializations within the feet of aerial predators towards maximizing grasping performance. Further taxonomic sampling across a range of body sizes and ecological niches is

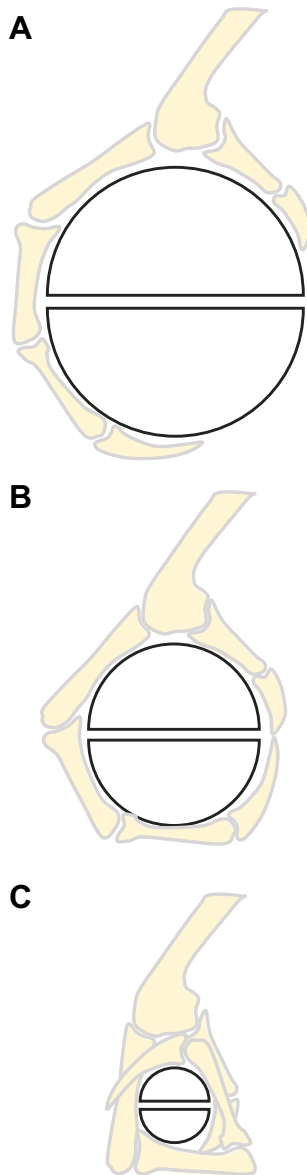


Fig. 6. Configuration of the digits during grasping in *A. roseicollis*, measured across different perch diameters. (A) 15 mm diameter perch (toes span ~60% circumference); (B) 10 mm diameter perch (toes span 90% of perch circumference); (C) 5 mm diameter perch (toes span 140% of perch circumference, resulting in 'overlapping').

paramount to understanding how grasping performance varies in an adaptive evolutionary context.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: E.D., M.C.G.; Methodology: E.D., M.Y., C.J.K., M.C.G.; Formal analysis: E.D., M.Y., M.C.G.; Investigation: E.D., M.Y., C.J.K., M.C.G.; Data curation: E.D., M.C.G.; Writing - original draft: E.D.; Writing - review & editing: M.Y., C.J.K., M.H., M.C.G.; Visualization: E.D., M.Y.; Supervision: M.C.G.; Project administration: M.C.G.; Funding acquisition: M.H., M.C.G.

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Table S1.

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