In vivo bite and grip forces, morphology and prey-killing behavior of North American accipiters (Accipitridae) and falcons (Falconidae)

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SUMMARY

Raptors exhibit a diversity of strategies to procure their prey but ultimately kill using their beaks and/or talons. Thus, bite and grip forces are ecologically important variables that have direct survival implications. Whereas hawks rely primarily on their feet for killing prey, falcons tend to employ their beaks. Consequently, falcons are expected to achieve relatively greater bite forces, and hawks are expected to generate relatively greater grip forces. Force estimates predicted from musculoskeletal morphology in a previous study indicated that falcons (*Falco* spp.) possess greater jaw force capabilities than accipiters (*Accipiter* spp.) but there were no clear differences in predicted grip-force capacity outside of differences in scaling. The objective of this study was to complement those results with measurements of *in vivo* forces by inducing captive and wild accipiters and falcons to bite and grasp force transducers. Bite force increased isometrically in both groups whereas grip force tended toward positive allometry. After adjusting for body mass, falcons produced greater bite forces, and accipiters produced greater grip forces. Thus, previous anatomical estimates of forces predicted the expected direction and magnitude of differences in bite forces but the overall greater *in vivo* grip forces of accipiters deviated from the pattern obtained from biomechanical estimates. Although the scaling relationships were similar between data sets, forces generated by live birds were consistently lower than those predicted from biomechanics. Estimated and *in vivo* jaw and digital forces were nevertheless correlated, and therefore provide an important link between morphology and killing behavior in these raptors.

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Key words: accipiter, bite force, falcon, feeding behavior, grip force, morphology, performance, prey capture, raptors.

INTRODUCTION

Despite their physical similarities, hawks (Accipitridae) and falcons (Falconidae) differ in their foraging modes. Whereas both hawks and falcons, as groups, feed on similar prey, they employ different hunting strategies (Brown and Amadon, 1968; Cade, 1982). On the one hand, falcons tend to pursue their prey in the open air at high speed, often in long, sustained chases, until they strike it with their feet to immobilize and, in some cases, kill it (Goslow, 1971; Cade, 1982). Most hawks, on the other hand, tend to either ambush their prey or engage in short tail-chases of bursting speed to overcome and forcefully grapple their victims with their feet and talons (Goslow, 1971). In both of these cases the feet play a pivotal role in prey capture but the act of dispatching prey differs. Hawks rely more on their feet for dispatching prey (Brown and Amadon, 1968; Goslow, 1971; Goslow, 1972), predominantly by suffocation resulting from thoracic compression (Csermely et al., 1998). Falcons, however, tend to employ their jaws by delivering powerful bites to the neck to kill their victims by breaking the cervical vertebrae and damaging the spinal cord (Cade, 1982; Hertel, 1995) (but see Csermely et al., 1998). Previous studies have demonstrated how morphological characteristics of the beaks (Bierregaard, 1978; Hull, 1991; Hertel, 1994a; Hertel, 1995; Johansson et al., 1998; Dzerzhinsky and Ladygin, 2004) and hind limbs (Bierregaard, 1978; Hertel, 1994b; Ward et al., 2002; Einoder and Richardson, 2007a) of raptorial birds are related to differences in diet and/or feeding behavior across groups. For instance, Hertel (Hertel, 1995) found suites of

skull, maxillary and mandibular characteristics that served to discriminate among trophic specialists; whereas bird-eaters tend to have wide skulls and beaks with increased mechanical advantage, scavengers tend have narrow beaks with greater curvature. Ward et al. suggested that the greater digit flexor area and grip-force performance of owls relative to similarly sized raptors provides a potential prey-partitioning mechanism between syntopic diurnal and nocturnal birds of prey (Ward et al., 2002). Irrespective of prey type, however, bite- and grip-force capabilities of raptors are fundamentally important for subduing and killing their prey in order to feed (Hertel, 1995).

Bite performance has been employed as an ecologically relevant metric of feeding performance in many vertebrate taxa (reviewed by Anderson et al., 2008) but relatively few groups of birds [flycatchers (Lederer, 1975); Darwin's finches (Herrel et al., 2005a; Herrel et al., 2005b; Herrel et al., 2009); fringilid and estrildid finches (van der Meij and Bout, 2004; van der Meij and Bout, 2006; van der Meij and Bout, 2008); house finches (Badyaev et al., 2008)]. Most pertinently, Hull (Hull, 1993) measured bite forces of Australian peregrine and brown falcons to test hypotheses (Hull, 1991) regarding differences in their skull and jaw musculoskeletal morphology. Grip strength, however, has enjoyed relatively less attention outside the fields of kinesiology and physical anthropology, aside from a few studies of vertebrate locomotion (e.g. Manzano et al., 2008; Abdala et al., 2009). The implications of grip force for feeding have rarely been examined (e.g. Yamada and Boulding, 1998; Schenk and Wainwright, 2001), mostly because the use of gripping (particularly with pedal digits) for

catching and killing prey is relatively rare among vertebrates. In raptors, grip force has clear implications for their abilities to successfully subdue and kill their prey prior to feeding, and consequently has been investigated for some species [e.g. North American owls (Marti, 1974); American kestrels (Yamamoto, 1994); common buzzards and Eurasian kestrels (Csermely et al., 1998; Csermely and Gaibani, 1998); North American *Buteo* hawks, American kestrels and owls (Ward et al., 2002)]. Various characteristics of raptor talons play important roles in grasping, such as claw size and shape (Csermely and Rossi, 2006; Einoder and Richardson, 2007a; Fowler et al., 2009), and the digital flexor tendon-locking mechanism of the feet (Ward et al., 2002; Einoder and Richardson, 2006). Although these features are undoubtedly important for transmitting and maintaining grip forces, in the present study we focus on their abilities to generate them.

Sustaita investigated the mechanistic bases for differences in killing mode, focusing on the physiological cross-sectional areas (PCSAs) and moment arms of the digit flexors and jaw-closing muscles of falcons and *Accipiter* hawks (Sustaita, 2008). These two groups exhibit a similar range of body sizes and tend to specialize on avian prey, although certain members of each group take greater proportions of insect (e.g. American kestrels) or mammalian prey [e.g. northern goshawks and prairie falcons (Johnsgard, 1990)]. The results indicated that falcons tend to have higher estimated bite-force capabilities than do accipiters, as one might anticipate based on the tendency of the former group to use their jaws for dispatching prey. Differences in estimated grip forces between groups, however, were less pronounced due to differences in the scaling of digit flexor PCSA and mechanical advantage between accipiters (positively allometric) and falcons (isometric). Thus, differences in killing modes between accipiters and falcons are primarily reflected in their jaw forces, rather than in their grip forces, which only differ at the smallest and largest body sizes (Sustaita, 2008). The implication is that their feet play similar roles in subduing prey but that their beaks play substantially different roles for dispatching them.

Although these biomechanical differences between groups are consistent with differences in their prey-killing modes in theory, they neglect the potential role of behavior in mediating jaw and foot function (Garland and Losos, 1994; Irschick, 2002). Thus, the primary objective of this study was to quantify *in vivo* bite and grip forces of various North American accipiters (*Accipiter* spp.) and falcons (*Falco* spp.) to determine the extent to which differences in their jaw and digital forces reflect their prey-killing behavior and musculoskeletal morphology. On the basis of their predatory behavior, as well as previous anatomical work (Sustaita, 2008), we expected that falcons would produce greater bite forces than accipiters, which, conversely, we expected to produce greater grip forces than falcons. A secondary goal of this study was to directly compare *in vivo* force measurements with Sustaita's (Sustaita, 2008) biomechanical estimates, both in their magnitudes and scaling relationships with body mass. Because both measurements consist of the same units (Newtons), we anticipated that they would be highly correlated. Finally, we examined relationships between *in vivo* bite and grip forces and key external morphological variables, such as lower jaw and digit lengths. Given their roles as biomechanical out-levers for generating bite and grip forces (Sustaita, 2008), we expected that forces would decrease with increases in their lengths.

MATERIALS AND METHODS
Force transducers

Two separate devices were developed according to designs modified from Hull (Hull, 1993), Binder and Van Valkenburgh (Binder and Van Valkenburgh, 2000), McBrayer and White (McBrayer and White, 2002), and Erickson et al. (Erickson et al., 2003; Erickson et al., 2004) to measure bite and grip forces (Fig. 1A,B). Each device consisted of a thin-beam load cell (LCL-040; 18.4 kgf capacity; 5 Vdc excitation; 2 mV V^{-1} output; Omega Engineering, Inc., Stamford, CT, USA), mounted onto a 25.4 cm or 30.5 cm steel crescent wrench (Husky, Home Depot, Canoga Park, CA, USA), so that the distance between the opposing points of force application could be adjusted easily for different-sized birds. The load cells were connected to an analog/digital converter (MDS-25-S, containing a DP25B series process meter; Omega Engineering, Inc.) set to an input voltage of ±50 mV and 5 Vdc excitation. One end of the load cell was bolted onto the upper surface of a stainless steel crescent wrench and the other to a steel beam. A longitudinally sectioned piece of copper tubing (wrapped in a thin layer of duct tape) was bolted onto the steel beam for the gripping device. The steel beams that formed the lower bars were welded directly onto the lower surfaces of the wrenches.

The digital meter was scaled to the maximum load that we anticipated from birds in the field (~45 N). Gain and amplification settings yielded an input resolution of approximately 0.25% (~0.11 N) at approximately ¼ full-scale range of operation. The devices were calibrated before and after each day of sampling by suspending masses ranging from 55 g to 4544 g (i.e. 0.54–44.6 N, in 0.98 N increments) from the center of the region of the bite beam or grip bar where the birds were induced to apply their bites and grasps. The devices performed consistently, with a grand mean, absolute difference between applied weight and observed readings of 0.63 N, and a mean R^2 of 0.998. Nevertheless, for the sake of accuracy we regressed applied weight on the observed readings from each calibration event preceding each sampling bout separately, and the ordinary least-squares (OLS) regressions were used to obtain more precise force values from the readings obtained in the field (McBrayer and White, 2002; Erickson et al., 2003).
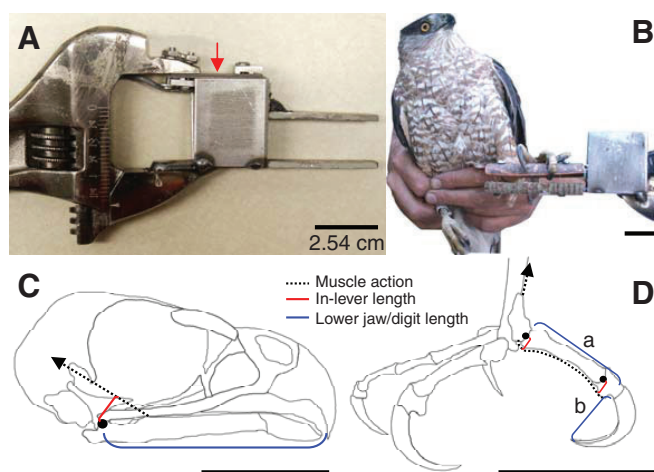

Fig. 1. Upper panels show bite (A) and grip (B, with female Cooper's hawk) force transducers. Strain gauges (indicated by arrow in A) were mounted (upside down) with one end connected to a steel bite plate or grip bar and the other end affixed to the top of an adjustable crescent wrench. Lower panels show lower jaw (C) and digit (D) anatomical in-lever (Sustaita, 2008) and total length measurements (as proxies for out-levers). Measurements in D are shown only for the hallux, and total digit length was calculated as a+b. Black bars represent 2.54 cm in each panel.

Sampling and measurements

Bite and grip force data were gathered opportunistically on wild-caught and captive adult and juvenile raptors: 29 Cooper's hawks (*Accipiter cooperii* Bonaparte), 24 sharp-shinned hawks (*Accipiter striatus* Vieillot), 8 peregrine falcons (*Falco peregrinus* Tunstall), 6 American kestrels (*Falco sparverius* Linnaeus), 3 merlins (*Falco columbarius* Linnaeus) and 4 prairie falcons (*Falco mexicanus* Schlegel) from May 2005 to July 2006. Captive raptors were obtained from raptor rehabilitation facilities and zoos throughout California (see Acknowledgements). Many of these raptors were either wild birds in the final stages of recovery from an injury (to a part of the body other than those tested) intended for release or were kept permanently for educational purposes. All of the wild raptors were obtained from the Manzano Mountains, in the Cibola National Forest, New Mexico, in conjunction with long-term migration monitoring and raptor banding activities conducted by Hawkwatch International, Inc., during late September 2005. Only those in visibly good condition were tested. In addition to the force measurements (detailed below), body mass (to the nearest 1 g, with a spring scale) and several linear measurements were taken (to the nearest 0.01 mm, with digital calipers; Table S1 in supplementary material) on most birds. The most pertinent among these were the lengths of the lower jaw and digits. Lower jaw length was taken from the quadratomandibular joint (approximated by palpating the base of the lower jaw) to the tip of the maxilla (because the tip of the mandible could not be measured accurately with the bill closed; Fig. 1C), and reflects the out-lever of the lower jaw. Digits were measured from the tarsometatarsus–phalangeal joint to the tip of the ungual on each extended toe, and these lengths were added to the lengths of the claw chords (from the distal claw tip to the proximal, ventral base at the ungual; Fig. 1D) to derive the total length of each digit. This length is highly correlated with digit out-lever length as measured previously during an accompanying anatomical study [(Sustaita, 2008) R=0.97, combined over groups and averaged over digits], and was used as a proxy for digit out-lever length in live birds. Body mass values were estimated from total head length (R^2=0.95) for four cases due to missing data, and from head width (R^2=0.87) for a prairie falcon wing amputee.

One of us held each bird vertically, or inclined approximately 45 deg backwards, such that their legs and beaks were free to the front, while the other person took the morphological and force measurements. The force transducers were held steadily in place as they were introduced (one at a time) within reach of one foot or the beak. We attempted both bite- and grip-force measurements on every bird, although some birds refused to either bite or grip the devices. The gripping device was introduced such that vertical axis of strain registration of the grip bars was perpendicular to the striking foot, so as to minimize the impact of the foot on the force reading and to attempt to isolate the force of the grasp itself. Bite and grip bars were adjusted (using the turnstile built into the crescent wrench) for each bird to maintain a constant gape angle (half-maximum) and foot span (complete coverage of lower and upper grip bars by hallux and foredigits, respectively).

Forces were recorded as raptors gripped with all toes contacting the grip bars, or bit the bite plates with the rostral tips of the upper and lower jaws, without exerting any of their body mass onto the transducer. An effort was made to ensure that: (1) the limb (tibiotarsus and tarsometatarsus) was roughly midway between minimum and maximum extension during gripping, and (2) the feet were consistently placed along an area marked in the mid-section of the grip bars, and that the bites were consistently placed along an area marked near the tip of the bite plates, between subjects and trials. Data from bites and grips that were noticeably off-mark were discarded. Each bird was induced to bite and grip the devices 2–5 consecutive times (4.1 trials/individual on average), separated by ~30 s. The maximum value recorded for each bird was used in subsequent analyses (after Herrel et al., 2001; Erickson et al., 2003; van der Meij and Bout, 2004; Herrel et al., 2005a; Herrel et al., 2005b), because (1) force measurements are less likely to be biased by low-motivation performances, and (2) maxima are more likely to approach the true capacity of the animal, which in turn is more likely to be predicted from variation in phenotypic characteristics (Losos et al., 2002). Adolph and Pickering cogently argued the statistical advantages to using means of multiple measurements (Adolph and Pickering, 2008). However, our results did not differ significantly whether trial means or maxima were used in the analyses described below.

Most birds eagerly bit and grasped the devices, although some were encouraged to do so by manually opening the feet or beak, and placing the device between the digits or jaws, and tickling the belly or the corners of the mouth to agitate the birds and elicit a response. We chose this method over more realistic predatory scenarios using transducers disguised as prey lures (e.g. Csermely and Gaibani, 1998), in order to obtain separate measurements of biting and gripping, and because of its general applicability to both captive as well as wild-caught birds (which may be less likely to attack a lure following capture). As such, we acknowledge that this approach may not elicit natural prey-striking behavior and actual killing forces but may be more indicative of their defense capabilities. Nevertheless, these have been argued to reflect maximal effort (Herrel et al., 2004), which ultimately is most important for predicting how phenotypic variation should translate into variation in maximal capabilities (Wainwright, 1994).

Statistical analyses

Group differences and scaling relationships

We used nested analyses of covariance (ANCOVA) to test for differences in maximum bite and grip forces (separately) between accipiters and falcons, after adjusting for differences among species (random factor) within groups (fixed factor) and body mass. Non-significant interactions with body mass were pooled to obtain more powerful tests of main and nested effects (Sokal and Rohlf, 1995). When the effect of the covariate was significant, we computed the reduced major-axis (RMA) slopes (ν; appropriate for randomly varying independent and dependent variables) and 95% confidence intervals (CI) according to Sokal and Rohlf (Sokal and Rohlf, 1995). Slopes that deviated from isometry [i.e. β=0.67, assuming force is proportional to muscle cross-sectional area (Kardong, 2002)] were considered allometric; the significance of deviation was determined according to Clarke's (Clarke, 1980) T statistic and associated degrees of freedom (e.g. Garland, 1985).

We conducted additional analyses to test for overall differences in bite and grip forces (with respect to body mass) between accipiter and falcon clades, using a phylogenetically independent contrasts (PICs) approach described by Garland et al. (Garland et al., 1993). We computed PICs of species (N=6) mean *in vivo* bite and grip forces and body mass, resulting in 5 positivized and standardized contrasts for each variable (Garland et al., 1992). We based the contrasts upon Roulin and Wink's (Roulin and Wink, 2004) phylogenetic topology (trimmed to reflect only the species considered in this study), to which we added the sharp-shinned hawk based on its relationship to other accipiters (Griffiths, 1994), with branch lengths set to unity (Garland et al., 1992). Following fig. 5 in Garland et al. (Garland et al., 1993), we then performed OLS regressions through the origin and calculated 95% prediction limits

[PL; following Sokal and Rohlf (Sokal and Rohlf, 1995)] using only non-basal (N=4) contrasts. A basal contrast falling outside of the 95% PL indicates a significant difference between the clades represented by the basal contrast (i.e. the contrast between accipiters and falcons is greater than expected based on contrasts within them).

Statistical and functional integration of data sets

We took two approaches to compare and integrate *in vivo* data with anatomical data derived from a previous musculoskeletal study of accipiter and falcon jaws and hind limbs (Sustaita, 2008). This data set consists of theoretical estimates of static forces based on muscle PCSA and indices of mechanical advantage for the primary digit-flexing and jaw-closing muscles. Estimates were derived for individual accipiter and falcon specimens of the species represented in this study. Firstly, submaximal bite and grip forces were calculated (respectively) at half-maximum gape, and with the toes partially closed (i.e. phalangeal joints flexed 45 deg from horizontal of proximal phalanges), to mimic the positions of the jaws and toes of live birds during *in vivo* measurements of biting and gripping. We began by testing for overall differences in scaling (slopes) and magnitude (y-intercepts) between *in vivo* force measurements [*in vivo* data set (IV)] and biomechanical estimates [anatomical data set (AN)], while accounting for variation between groups and body mass, using ANCOVA. Secondly, we used OLS regressions to determine the amount of variance in the *in vivo* forces that could be explained by the biomechanical force estimates from the AN data. Because the AN and IV data were obtained from different sets of individuals, we matched cases between data sets based on their multivariate morphological dimensions. We performed a principal component analysis (PCA) on both data sets combined, using a series of linear

beak and hind limb measurements, including body mass and matched cases (uniquely) from opposing data sets by their minimum pairwise nearest-neighbor (Euclidean) distances in two-dimensional PC space (Fig. S1 in supplementary material). We evaluated the significance of the R^2 values by comparing them with null distributions of R^2 values derived from random matches of *in vivo* cases to biomechanical cases, based on group, species and sex. We repeated this analysis using ($\log_{10}$-transformed) species and sex means (N=12), and also PICs of species means (combined over sexes; N=5 contrasts), to determine the overall predictive capabilities of AN bite- and grip-force estimates.

Finally, we performed a series of RMA regressions to reconcile relationships between *in vivo* forces and lower jaw and mean digit length. We anticipated that relative to body mass, force should decrease with increased out-lever length due to the resultant decrease in mechanical advantage, unless there are compensatory changes in the lengths of the in-levers and muscle PCSAs. We restricted this analysis to bite forces in falcons and grip forces in accipiters, because these are the primary killing mechanisms of each group and ought to reveal tighter relationships between morphology and performance. We used residuals from OLS regressions of each morphological and force variable on body mass to produce values that were independent of body size. We then ran complementary analyses using AN data to examine relationships between residual jaw and digit in-lever [i.e. perpendicular distances between lines of muscle action, averaged over muscles (Sustaita, 2008)] and their corresponding (residual) out-lever lengths.

Data treatment and analysis

We screened the data for anomalously high and low maximum force values (asterisks in Fig. 2A,B) prior to analyses (see Appendix), in
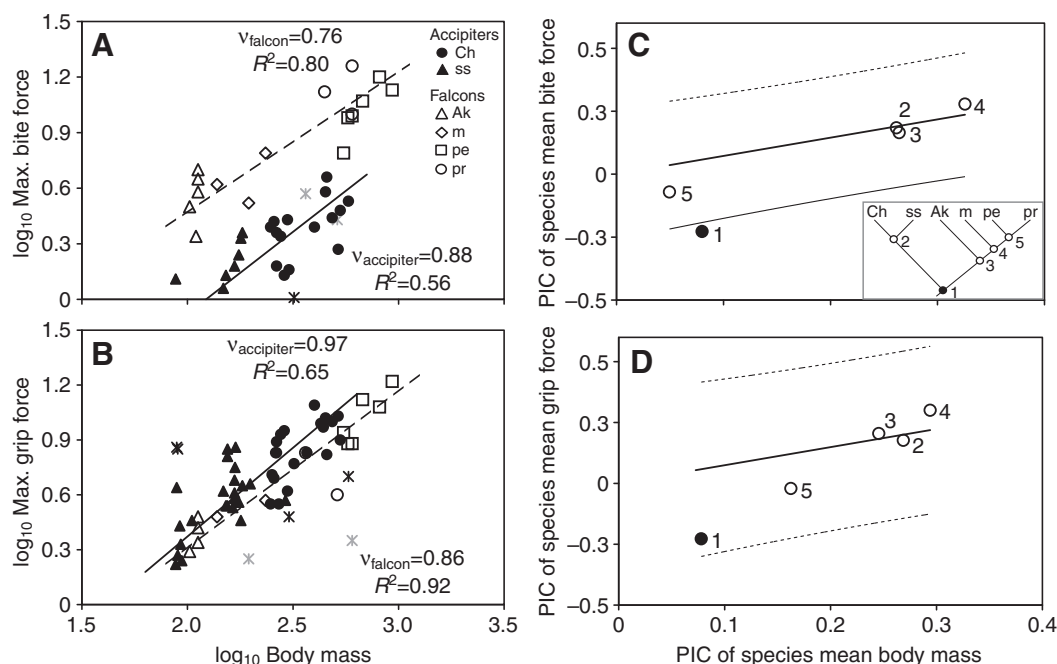

Fig. 2. Reduced major-axis (RMA) regressions of *in vivo* maximum bite (A) and grip (B) forces (in Newtons) on body mass (in grams), for North American accipiters (filled symbols, solid lines) and falcons (open symbols, broken lines). Black and gray asterisks represent extreme values for accipiters and falcons (respectively) that were adjusted or excluded from analysis (Appendix). Panels C and D represent phylogenetically independent contrasts (PICs) of mean maximum bite, C, and grip forces, D. The basal contrasts (filled symbols) were superimposed onto ordinary least-squares (OLS) regressions (solid lines) and 95% prediction limits (broken lines) derived from the other four contrasts (open symbols; labeled by corresponding nodes in C inset). Note that the sister relationship between accipiter (Ch, Cooper's hawk; ss, sharp-shinned hawk) and falcon (Ak, American kestrel; m, merlin; pe, peregrine falcon; pr, prairie falcon) clades is an artifact of our composite topology; some recent phylogenies (e.g. Livezy and Zusi, 2007; Hackett et al., 2008) indicate variable numbers of intervening lineages.

an attempt to reduce the effects of misplaced strikes on the bite and grip bars, systematic errors in measurement or signal processing, errors in resetting the digital meter between trials, and unmotivated attempts [see Losos et al. (Losos et al., 2002) for their discussion on submaximal performance]. We log$_{10}$-transformed all data prior to analyses to improve linearity, and ensure normality and homoscedasticity, which we evaluated by means of Levene's tests and normal probability plots before and after transformation using SPSS 14.0 for Windows (SPSS Inc., Chicago, IL, USA). We used Microsoft Office Excel 2003 (Microsoft Corp., Redmond, WA, USA) to compute repeatabilities [intraclass correlations (Lessells and Boag, 1987)] of bite and grip forces, and to perform the RMA regressions, based on formulae in Sokal and Rohlf (Sokal and Rohlf, 1995). We used SPSS to run the ANCOVAs using the GLM procedure, and the PCA on the correlation matrix. Finally, we used the PDAP:PDTREE package (Midford et al., 2008) for MESQUITE (Maddison and Maddison, 2008) to calculate the PICs.

RESULTS
Bite and grip forces
The force measurements demonstrated considerable intra-individual variation (mean coefficient of variation across individuals was 24% for accipiter bite and grip forces, and 36% for falcon bite and grip forces) but were significantly repeatable (bite force: R_i=0.43, $F_{21,54}$=3.55, P<0.0001 and R_i=0.57, $F_{19,71}$=7.06, P<0.0001 for accipiters and falcons, respectively; grip force: R_i=0.61, $F_{47,164}$=7.94, P<0.0001 and R_i=0.58, $F_{18,57}$=6.56, P<0.0001 for accipiters and falcons, respectively). Forces tended to be greater for females and

for adults (Table 1). After adjusting for body mass, as well as variation among species within genera, falcons produced significantly greater bite forces than did accipiters (nested ANCOVA; $F_{1,4}$=128.04, P=0.0003; Fig. 2A) but accipiters produced significantly greater grip forces than did falcons ($F_{1,4}$=11.84, P=0.026; Fig. 2B; Table 2). In both groups, the 95% CI of the RMA slopes for bite force included the isometric expectation of 0.67 {$\nu_{accipiter\ bite}$=0.88 [0.63–1.14 (95%CI)], R^2=0.56; $\nu_{falcon\ bite}$=0.76 [0.57–0.95], R^2=0.80} whereas both slopes for grip force did not [$\nu_{accipiter\ grip}$=0.97 (0.79–1.15), R^2=0.65; $\nu_{falcon\ grip}$=0.86 (0.71–1.01), R^2=0.92]. Clarke's T statistic, however, demonstrated only marginal grip force allometry in accipiters ($T_{accipiter\ grip,35.2}$=1.81, P=0.079; $T_{accipiter\ grip,21.5}$=2.07, P=0.051 when only adults were considered), and no deviation from isometry in falcons ($T_{falcon\ grip,12.3}$=1.47, P=0.166) (Clarke, 1980). Coupled together, and given the allometry observed in musculoskeletal estimates of accipiter grip forces (Sustaita, 2008), we considered only the scaling of accipiter grip forces significantly allometric. We re-ran these analyses using only adult representatives of accipiters (N=26 out of 43 total), to account for potential biases resulting from age and sample size variation between groups, and the results were qualitatively similar.

When species means were used in the phylogenetically adjusted analyses, OLS regressions based on the non-basal contrasts demonstrated significant, positive relationships between the contrasts of bite (R^2=0.90, $F_{1,3}$=28.0, P=0.013) and grip force (R^2=0.83, $F_{1,3}$=14.6, P=0.032) on body mass. The basal contrast for bite force with regard to body mass deviated significantly from the 95% PL, suggesting a significant, overall difference between accipitrid and

Table 1. Mean ± s.e.m. (N) maximum *in vivo* (untransformed) bite and grip forces and body mass by species, sex and age (adults and juveniles) where applicable

Group	Sex	Bite force (N)	Grip force (N)	Body mass (g)
Accipiters				
Sharp-shinned hawk*				
Adult	Female	1.42±0.30 (4)	4.85±0.45 (8)	165.5±6.1 (8)
	Male	1.19±0.22 (3)	2.99±0.64 (6)	117.0±16.0 (6)
Juvenile	Female	1.60±0.36 (3)	3.99±0.55 (7)	186.0±17.8 (7)
	Male	N/A	3.04±0.73 (3)	94.6±5.2 (3)
Cooper's hawk[†]				
Adult	Female	3.10±0.30 (4)	9.77±0.73 (6)	450.4±25.7 (7)
	Male	1.91±0.23 (6)	6.73±0.67 (7)	283.1±8.14 (8)
Juvenile	Female	3.15±0.78 (3)	8.42±1.21 (3)	501.5±22.5 (3)
	Male	2.54±0.09 (2)	4.69±0.76 (4)	259.4±4.9 (4)
Falcons				
American kestrel	Female	3.33±1.1 (2)	3.01 (1)	110.9±1.3 (2)
	Male	3.99±0.54 (3)	2.26±0.20 (3)	108.9±3.3 (3)
Merlin	Female	4.74±1.43 (2)	3.72 (1)	214.7±19.7 (2)
	Male	4.17 (1)	3.02 (1)	138.0 (1)
Peregrine falcon	Female	12.96±1.84 (3)	12.7±2.60 (3)	773.8±105.1 (3)
	Male	9.23±1.63 (3)	10.11±1.24 (4)	585.3±35.4 (4)
Prairie falcon	Female	N/A	N/A	N/A
	Male	13.79±2.39 (3)	5.37±1.39 (2)	503.7±59.6 (4)

*There were no differences in bite force between sexes and age groups (two-way ANOVA; $F_{1,7}$=0.285, P=0.610 and $F_{1,7}$=0.138, P=0.722, respectively). For grip force, there was no difference between age groups ($F_{1,21}$=0.694, P=0.414) but a significant difference between sexes ($F_{1,21}$=9.49, P=0.006). When mass is included as a covariate, grip force increases with a significantly greater slope in adults than in juveniles ($F_{1,20}$=6.68, P=0.018) and in males than in females ($F_{1,20}$=5.85, P=0.025).

[†]There was no difference in bite force between age groups (two-way ANOVA; $F_{1,12}$=0.710, P=0.416) but there was a significant difference between sexes ($F_{1,12}$=6.18, P=0.029). For grip force, there were significant differences between sexes and age groups ($F_{1,17}$=15.96, P=0.001 and $F_{1,17}$=5.22, P=0.035, respectively).

Table 2. Results of ANCOVAs testing for differences in bite and grip forces between groups, when accounting for differences among species and body mass

Source	d.f.	MS	F-ratio	P
Bite force				
Group	1	0.005	0.005/0.007	0.433
Species (group)	4	0.007	0.007/0.020	0.046
Mass	1	0.056	0.056/0.020	0.088
Group×mass	1	0.011	0.011/0.007*	0.263
Mass×species (group)	4	0.007	0.007/0.020	0.044
Error	30	0.020		
Pooled interactions				
Group	1	2.086	2.086/0.018	<0.001
Species (group)	4	0.016	0.016/0.018	0.465
Mass	1	0.191	0.191/0.018	0.002
Error	35	0.018		
Grip force				
Group	1	0.014	0.014/0.007	0.213
Species (group)	4	0.007	0.007/0.017	0.813
Mass	1	0.082	0.082/0.017	0.032
Group×mass	1	0.012	0.012/0.006*	0.246
Mass×species (group)	4	0.006	0.006/0.017	0.821
Error	47	0.017		
Pooled interactions				
Group	1	0.105	0.105/0.009	0.026
Species (group)	4	0.009	0.009/0.016	0.686
Mass	1	0.536	0.536/0.016	<0.001
Error	52	0.016		

*Test of homogeneity of regression slopes (Quinn and Keough, 2002).
F-ratios are expressed in terms of mean squares (MS) values to illustrate the tests of effects, and P-values were calculated in Excel.

falconid clades represented by this set of species (Fig. 2C). Conversely, the basal contrast for grip force with respect to body mass fell just within the 95% PL (Fig. 2D), suggesting that the difference between clades is not greater than expected based on differences within clades.

Integrated analyses

At mean body mass, IV grip forces were 36% lower than AN estimates [ANCOVA; effect of data set: $F_{1,88}$=119, P<0.001, accounting for variation within and between groups, after pooling data set × body mass term ($F_{1,87}$=0.696, P=0.407)]. Similarly, IV bite forces averaged 25% lower than AN estimates [ANCOVA; effect of data set: $F_{1,67}$=32.2, P<0.001, after pooling data set × body mass term ($F_{1,66}$=0.001, P=0.753)] (Fig. 3A,B). Despite differences in magnitude, there were no differences between slopes (as reflected in the non-significant interaction terms). When cases were matched by their morphological PCA scores, the biomechanical estimates explained significant proportions of variation in *in vivo* grip forces: $R^2_{accipiters}$=0.63, $F_{1,12}$=20.1, P=0.001; $R^2_{falcons}$=0.76, $F_{1,12}$=56.4, P<0.001 (Fig. 3D). With regard to bite force, the variance explained by biomechanics was only significant for falcons ($R^2_{falcon\ bite}$=0.82, $F_{1,12}$=56.4, P<0.001) but not for accipiters ($R^2_{accipiter\ bite}$=0.092±0.21, $F_{1,12}$=1.21, P=0.293) (Fig. 3C). With the exception of bite force in accipiters, the observed R^2 values were greater than those obtained from 1000 permutations of random matches of individuals of the same species and sex, between AN and IV data sets [$R^2_{accipiter\ grip}$= 0.103 (0.095–0.110, 95% CI); $R^2_{falcon\ grip}$=0.037 (0.035–0.040); $R^2_{falcon\ bite}$=0.024 (0.022–0.026); $R^2_{accipiter\ bite}$=0.148 (0.136–0.159)]. The analysis based on species and sex means resulted in more similar proportions of variance explained by AN grip and bite forces (R^2=0.78, $F_{1,9}$=32.4, P<0.001 and R^2=0.84, $F_{1,9}$=49.0, P<0.001, respectively). When averaged over species and adjusted for phylogeny, AN grip and bite force (contrasts) explained 60% (but

only approached significance given the low power of analysis; $F_{1,4}$=6.1, P=0.069) and 83% ($F_{1,4}$=19.1, P=0.012) of the variance in IV grip and bite force (contrasts), respectively.

Residual maximum bite force increased significantly with increased residual lower jaw length in falcons [R^2=0.29, ν=1.58 (0.75–2.42, 95% CI), $F_{1,12}$=4.97, P=0.046; Fig. 4A] but only after removing an extreme low residual bite-force value (asterisk in Fig. 4A). The relationship between residual mean digit length and residual maximum grip force in accipiters was weak, and non-significant (R^2=0.067, $F_{1,40}$=2.87, P=0.098) (Fig. 4D). This pattern was also reflected in the AN data set [R^2=0.37, $F_{1,15}$=8.88, P=0.009 and R^2=0.007, $F_{1,12}$=0.084, P=0.777 for residual falcon bite (Fig. 4B) and accipiter grip force (Fig. 4E), respectively]. Residual muscle PCSA (data not shown) significantly increased with residual out-lever length in falcon jaws [R^2=0.33, ν=2.48 (1.36–3.60), $F_{1,15}$=7.39, P=0.016] but not in accipiter feet [R^2=0.10, ν=0.36 (0.15–0.58), $F_{1,12}$=1.36, P=0.267]. Residual in-lever length increased with residual out-lever length in both groups (R^2=0.48, $F_{1,15}$=13.7, P=0.002 and R^2=0.58, $F_{1,12}$=16.2, P=0.002, for falcon jaws and accipiter feet, respectively; Fig. 4C,F), with an approximately 1:1 relationship [ν$_{falcon\ jaws}$=1.03 (0.62–1.43), ν$_{accipiter\ digits}$=1.40 (0.82–1.97)].

DISCUSSION
Bite and grip forces of accipiters and falcons
Our results demonstrate differences in bite and grip forces between accipiter hawks and falcons that are consistent with their primary prey-killing modes and biomechanical predictions of their capabilities. For a given body size, falcons tended to bite harder than accipiters, consistent with their emphasis on biting for dispatching their prey, as well as with relative enhancements in the mechanical advantage and PCSA of primary jaw-closing muscles (Sustaita, 2008). Conversely, accipiters tended to grip with greater force than did falcons, consistent with their greater
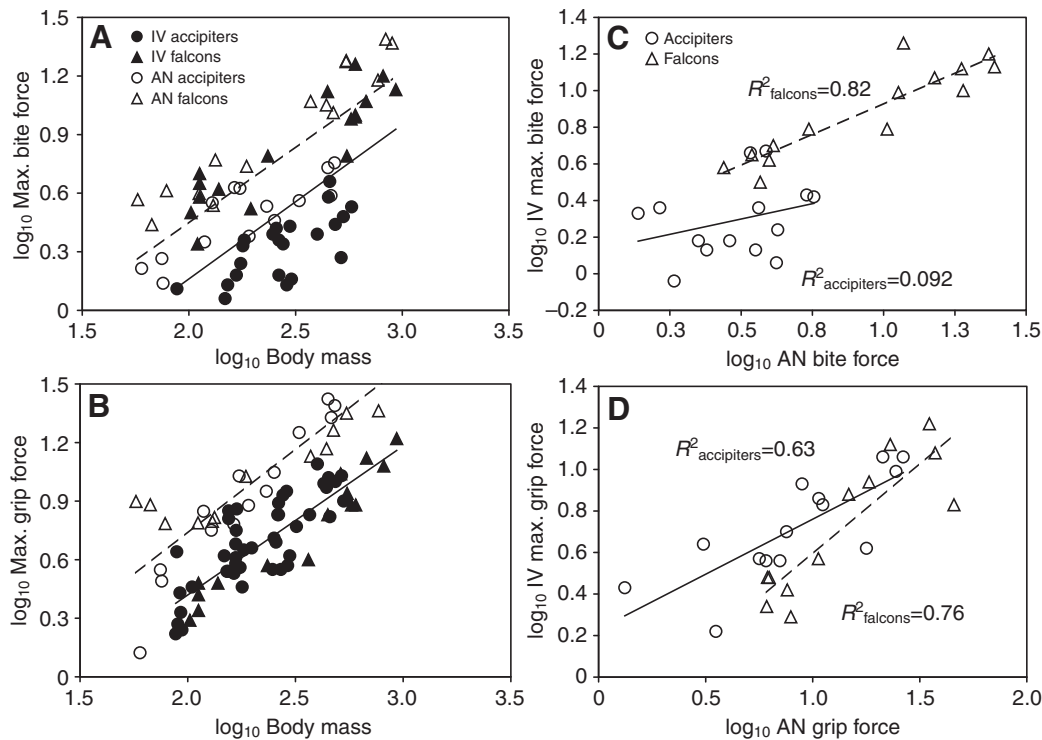
Fig. 3. Relationships between *in vivo* (IV; filled symbols) and anatomical [AN; open symbols; fig. 5A,D from Sustaita (Sustaita, 2008)] bite (A) and grip (B) forces (in Newtons), with respect to body mass (in grams). Panels C and D demonstrate direct relationships between anatomical (AN) and *in vivo* (IV) data sets for bite- (C) and grip-force (D) measurements, after pairing individual AN and IV cases by their morphology (Appendix). Solid (IV data set in A,B; accipiters in C,D) and broken (AN data set in A,B; falcons in C,D) ordinary least-squares (OLS) lines are provided to illustrate the overall differences in magnitude between AN and IV data sets (accipiters and falcons combined; A,B), and the direct relationships between AN and IV data sets for each group (C,D).

reliance on gripping for dispatching prey with their feet. The phylogeny-based analyses partially support these results, in that based on the representatives we studied, there was a difference in bite force between falconid and accipitrid clades but not in grip force. This reflects the small difference in magnitude of grip forces between accipiters and falcons (15% difference at mean body mass), compared with that of bite forces (64% difference). Consequently, a greater diversity of species would ultimately be required to detect a statistical difference when accounting for phylogeny. We acknowledge that the circumstances under which forces were measured may not elicit the actual forces employed by these raptors during prey capture, as well as the importance of measuring performance in its natural context (Irschick, 2003). Nevertheless, we suggest these data lend quantitative support to observed differences in their killing modes, and that the difference in biting and gripping behavior (not necessarily physical capability) explains the observed differences in forces between accipiters and falcons.

We found significantly lower bite and grip forces in juvenile (i.e. hatch year) than adult (i.e. after hatch year) Cooper's hawks (Table 1). Although there were no categorical age differences among sharp-shinned hawks, when body mass was included as a covariate, grip force increased more rapidly with mass in adults than it did in juveniles. Rutz et al. found that as male northern goshawks (*Accipiter gentilis*) age, they take pigeons in greater proportions, presumably because they are more difficult for younger hawks to procure (Rutz et al., 2006). Although it is unclear specifically how young males are limited in their hunting abilities, our results for congeneric Cooper's and sharp-shinned hawks suggest that a deficiency in grip force may be a potential source of reduced predatory performance that restricts them from a portion of the prey resource spectrum. Several other vertebrates exhibit positive allometry of feeding-related morphology and performance throughout ontogeny (Herrel and Gibb, 2006) in accordance with this phenomenon.

Our results are comparable with those of previous studies of force production in raptors. Hull (Hull, 1993) reported bite forces ranging between 3.4–3.9 N for brown (*Falco berigora*) and 3.0–4.6 N for peregrine falcons (*Falco peregrinus*), weighing ~549 g and ~1025 g, respectively (del Hoyo et al., 1994). However, on average, our grip forces tended to be lower than those measured for similar species in other studies. Ward et al.'s (Ward et al., 2002) higher mean (±s.e.m.) grip-force values for American kestrels (7.7±1.6 N for birds weighing a mean of 122.1±6.2 g, compared with our mean of 2.6±0.2 N for 111.8±2.8 g birds) suggest a potential systematic difference between grip-force measurement techniques. However, other species in these studies were comprised of *Buteo* hawks and owls (e.g. Marti, 1974; Csermely and Gaibani, 1998; Ward et al., 2002). These species might be expected to produce greater grip forces than the *Accipiter* hawks and falcons of our study because of their larger body sizes, primarily mammal-eating habits, and, in the case of owls, nocturnal behavior and zygodactylous toe configuration (Ward et al., 2002; Einoder and Richardson, 2007b). Grip forces of accipiters scaled with positive allometry in our study and in Ward et al. (Ward et al., 2002), suggesting that allometric scaling of grip forces (and underlying digit flexor PCSA) may be a general characteristic of accipitrid hawks. Other studies have shown that bite force also scales positively allometric with body mass within and across species (van der Meij and Bout, 2004; Herrel et al., 2005a; Herrel et al., 2005b). Some have suggested that such allometry reflects the increasing demands of larger and/or more difficult prey that larger predators tend towards (e.g. Emerson et al., 1994; van der Meij and Bout, 2004).

The bite forces we recorded were absolutely and relatively (with respect to body mass) lower than those of seed-eating finches (van der Meij and Bout, 2004; Herrel et al., 2005a; Herrel et al., 2005b). In fact, despite the importance of bite and grip forces for subduing and killing prey, compilations of bite forces for a diversity of vertebrates ranging from sharks to hyenas (e.g. Erickson et al., 2003;
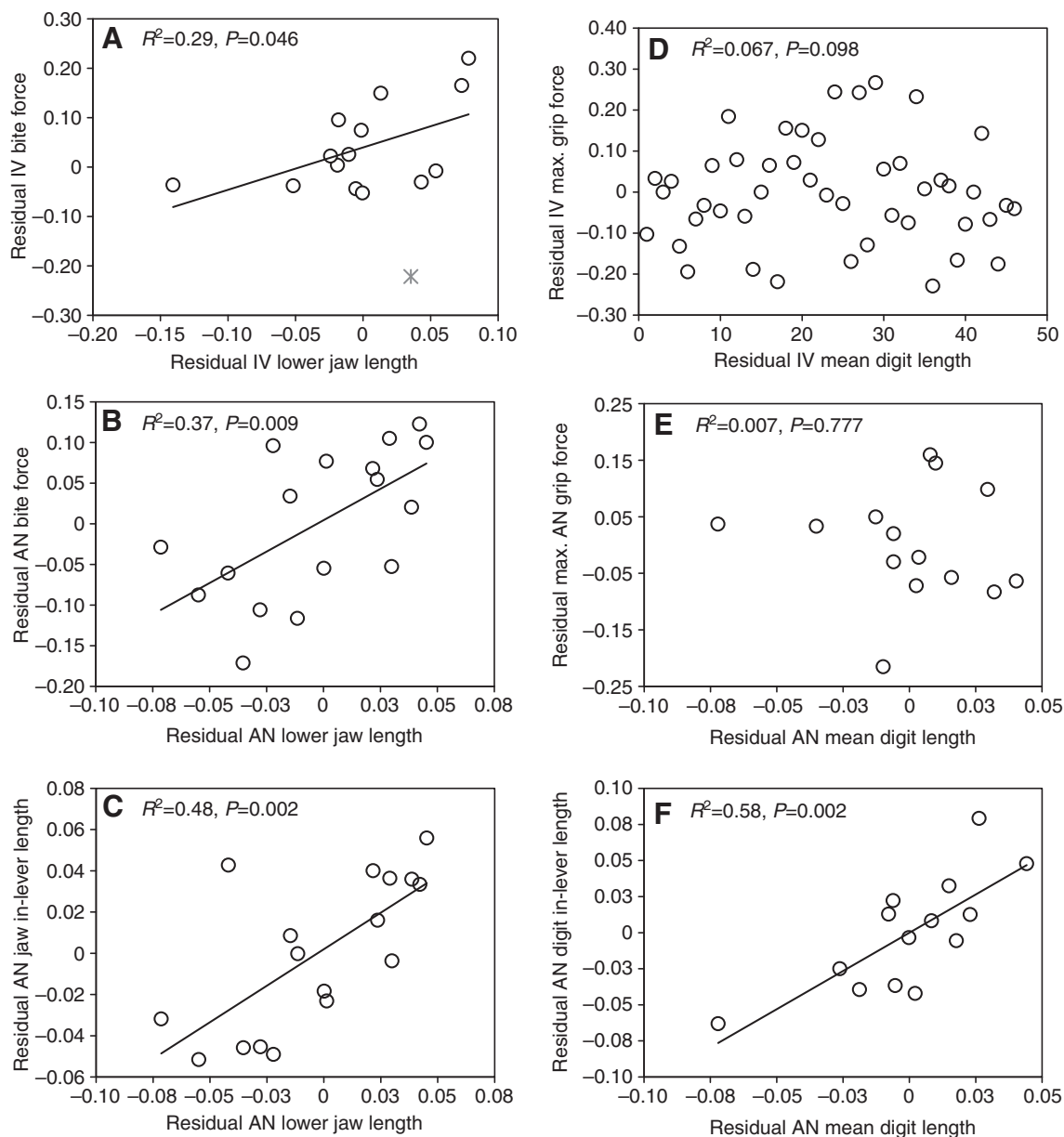
Fig. 4. Relationships between residual *in vivo* (IV) and anatomical (AN) bite and grip forces, and biomechanical attributes: (A) residual IV bite force *vs* lower jaw out-lever length, (B) residual AN bite force *vs* lower jaw out-lever length, (C) residual AN lower jaw in-lever *vs* out-lever length (D) residual IV grip force *vs* digit length (as a proxy for digit out-lever, averaged over digits), (E) residual AN grip force *vs* digit out-lever length, (F) residual AN digit in-lever *vs* out-lever lengths. Observed relationships between forces and out-lever lengths (A,D and B,E) are largely explained by the relationships between in- and out-levers [C and F; see Sustaita (Sustaita, 2008) for methods pertaining to in- and out-lever measurements]. Asterisk in A represents an extreme value excluded from analysis.

Huber et al., 2005; Wroe et al., 2005) suggest that the forces we measured for these raptors are comparatively quite low. This may be explained by differences in the physical characteristics of their primary (birds) and secondary (small mammals) prey (Hertel, 1995), whose pliant and relatively tough (*sensu* Strait and Vincent, 1998) skin and flesh may select less for crushing strength but more for concentrating forces along the tomium and tips of the beak and talons to affect greater shear and normal stresses. Herrel et al. posed a similar argument to explain unexpectedly high bite, and minimized joint, forces of herbivorous, compared with carnivorous lizards, for processing tough plant material (Herrel et al., 1998). Huber and Motta suggested that the relatively low bite-force values they

observed for some sharks might also be explained by the relative importance of other mechanisms, such as cutting teeth and head-shaking behavior during biting (Huber and Motta, 2004).

In falcons, forceful jaw adduction may play a more subsidiary role to powerful upper and lower jaw translation, which would drive the tomial teeth (subterminal ventral maxillary projections) fore and aft to pinch and tear skin, flesh and muscle in the cervical region of their prey. Hull (Hull, 1991) and Sustaita (Sustaita, 2008) have confirmed the relative importance (in terms of mass and PCSA, respectively) of the m. pterygoideus muscle group in falcons, which would play a prominent role in such motion. Additionally, the quadratomandibular joint in some falcons appears to be fortified to

resist stresses incurred by tearing and mandibulating prey carcasses (Dzerzhinsky and Ladygin, 2004), which could have significant antero-posterior components. Furthermore, the morphology of raptor digit flexor tendons and sheaths (Einoder and Richardson, 2006), along with talon size and shape (Einoder and Richardson, 2007a; Fowler et al., 2009), have been suggested to enhance their grasping abilities, and might mitigate any deficiency in force production. Alternatively, perhaps the ability to generate forces rapidly in order to dispatch vigorously struggling prey is paramount, and power (force × velocity), rather than force alone, is the operative metric. In this case, a decrement in jaw or digit force capability may facilitate greater velocities [in accordance with the force–velocity relationship (Hill, 1938; Yamauchi et al., 2007)] that ultimately enhance power output.

Morphological correlates of force

In vivo bite force was positively correlated with beak and head dimensions (Table S1 in supplementary material), just as studies of finches have reported (Herrel et al., 2005a; Herrel et al., 2005b; van der Meij and Bout, 2008), although none was significant after adjusting for body mass (e.g. *via* multiple regression including body mass, or analysis of residuals; results not shown). Similarly, grip force was positively correlated with other hind limb dimensions (Table S1 in supplementary material) such as tarsus length and mid-tibiotarsus circumference (as a proxy for total digit flexor PCSA) but not after controlling for body mass. Overall, body mass was the best predictor of bite and grip forces across groups, suggesting that the most direct route to increasing force is by increasing body size. However, disproportionate increases in underlying musculoskeletal characteristics are also important for determining force-generating capacity. Residual *in vivo* forces tend to increase with increasing residual out-lever length, suggesting that there is a compensatory increase in either (or both) muscle PCSA or in-lever length with increasing out-lever length. Our analyses of the musculoskeletal data indicate that both occur in falcon jaws but only the latter occurs in accipiter feet, and residual in-lever length explains 15% (falcon jaws) and 47% (accipiter feet) more of the variance in residual out-lever length than does muscle PCSA.

Thus, it appears that increases in out-lever lengths incurred by an overall increase in body size are offset by concomitant increases in in-lever lengths (and muscle area, in the jaws) to maintain proportionate (e.g. falcon bite) or increasing (e.g. accipiter grip) force production with increasing body size. Slater and Van Valkenburgh similarly postulated that an increase in the length of the coronoid process of the mandible (as an alternative to increased muscle cross-sectional area) might counteract the loss of leverage resulting from positive allometry of the facial skeleton in larger felids (Slater and Van Valkenburgh, 2009). In-lever length can also be altered by shifting the position of the quadratomandibular joint relative to the line of muscle action. Based on their geometric morphometric analysis, van der Meij and Bout suggested that a caudal shift of the quadrate with increasing body size could have a large impact on bite forces by increasing jaw-closing muscle in-lever length (van der Meij and Bout, 2008). Although this does not appear to have had the greatest impact on differences in bite forces among the finches they studied, it may reasonably apply to falcons, and analysis of skull geometry is certainly warranted. Our results underscore the importance of examining the constituent parts when analyzing gross patterns of whole functional systems and, more practically, the utility of integrating musculoskeletal and performance data sets for developing a better understanding of out-forces.

Anatomical estimates *vs in vivo* forces

Our *in vivo* bite- and grip-force measurements averaged 25–36% lower (in magnitude) than previous biomechanical estimates based on the mechanical advantage and PCSA of the primary digit flexors and jaw-closing muscles (Sustaita, 2008). Although the direction and magnitude of the difference in bite forces between accipiters and falcons were well predicted by the anatomical bite-force estimates, grip-force estimates suggested a difference in scaling between groups, rather than in magnitude as observed *in vivo*. These, we contend, reflect the behavioral tendencies of falcons to impart more effort into biting than gripping, despite the biomechanical capacities of smaller falcons to generate grip forces that meet or exceed those of similarly sized accipiters (Fig. 3B). Analogously, Wroe et al. suggested that the unexpectedly high post-canine bite-force capacity estimated for non-osteophagous mammalian carnivores may be an incidental by-product of the requirement for high force capacity at the canines for capturing prey (Wroe et al., 2005). Perhaps such 'unused' grip-force capacity estimated for falcon feet may be attributable to the relatively high forces estimated for the hallux (Sustaita, 2008), which is often optimally positioned for inflicting damage during high-speed, open-toed glancing strikes at prey (Goslow, 1971; Goslow, 1972).

We found that the amount of variance in the IV data set explained by AN data varied between jaws and feet, and between groups. AN bite force best explained variance in IV bite-force measurements in falcons (R^2=0.82) whereas in accipiters there was little relationship (R^2=0.09). Furthermore, AN grip force explained 13% more variance in IV grip-force measurements in falcons than in accipiters, indicating that the correspondence between anatomical estimates and *in vivo* measurements is generally greater in falcons, and (on average) for grip force. However, the analyses based on species (and sex) means indicated that AN force estimates were generally good predictors of IV measurements but bite forces were better predicted. It is not clear as to why better force estimates were produced for falcons than accipiters, although the 25% higher repeatability of falcon (over accipiter) bite forces may contribute substantially. However, with regard to the generally better performance of the bite-force estimates, perhaps the relatively fewer (biomechanical) degrees of freedom of the jaws compared with the digits allow more of the variance in *in vivo* forces to be captured by the relatively simpler biomechanical jaw model.

There are several potential reasons why our *in vivo* forces failed to match predicted magnitudes based on previous anatomical estimates. This mismatch could be caused by an overestimation of forces from musculoskeletal data and/or a tendency for individuals to under-perform during bite- and grip-force sampling. There were some simplifications in the biomechanical models developed to estimate force-generating capacity (Sustaita, 2008) that may tend to overestimate out-forces. First, the muscle contractile stress of $25\,\mathrm{N\,cm^{-2}}$ used to generate the biomechanical estimates might be overestimated, and when it is varied along the published range of $12.2\,\mathrm{N\,cm^{-2}}$ (Biewener et al., 1992) – $30\,\mathrm{N\,cm^{-2}}$ (Bennett, 1995), estimated out-forces can change by up to 34%. Second, failure to take into account the angles of muscle insertion (particularly in the jaws) would also tend to diminish in-forces. However, there were also simplifications that might tend to underestimate grip force, such as excluding moments of torque of distally inserting tendons on more proximal inter-phalangeal joints. Perhaps *in vivo* muscle stimulation or more detailed cadaveric experiments for estimating moment arms (e.g. Lee et al., 2008) would be useful for determining maximal forces. Studies of other taxa have demonstrated similar levels of discordance between theoretical estimates and actual force measurements (e.g.

Huber and Motta, 2004; Grubich, 2005; Ellis et al., 2008), to which these authors have attributed the simplifying assumptions of the biomechanical models, the effects of unmeasured physiological or biomechanical attributes, and/or the methods used to elicit actual forces. Studies of yet other taxa have demonstrated close to complete concordance between measured and predicted forces (e.g. Osenberg et al., 2004; Herrel et al., 2008), particularly when the 3-D geometry of the skull and mandible are considered (Davis et al., 2010). It appears that biomechanical model performance is influenced by both the complexity of the model, as well as by that of the system being modeled. Nevertheless, even simpler proxies for force (e.g. muscle cross-sectional area) in complex jaw systems have yielded good predictions (van der Meij and Bout, 2004; Osenberg et al., 2004). In our study, total digit flexor and jaw muscle PCSA (alone) generally predicted *in vivo* grip and bite forces (respectively) as well as the biomechanical force estimates.

The most likely explanation is simply a reluctance of live birds to exert their full potential, in part, perhaps, because the force transducers never struggled like live prey. This may be true of many studies of animal performance, for which motivation may vary across individuals, species and contexts (McBrayer and White, 2002; Losos et al., 2002). In general, maximum performance tends to be underestimated because individuals are less likely to achieve their full potential in the course of a few trials (Losos et al., 2002). Furthermore, increased intra-individual variation tends to negatively bias estimates of maximal performance, in some cases by up to 20% (Adolph and Pickering, 2008). It is also possible that these raptors generally use less force than they are physically capable of generating. Studies of other taxa have suggested that individuals rarely perform at their maximal capacities in nature (Wainwright, 1991; Irschick and Garland, 2001). Nevertheless, performance measurements under more contrived conditions need not represent maximal capabilities to illustrate important behavioral differences under natural conditions (Losos et al., 2002).

Another potential source of bias in our study was that most of the accipiters were wild-caught and measured directly in the field whereas most of the falcons may have been originally caught in the wild but had been maintained in captivity for variable amounts of time. Regrettably we did not have sufficient sample sizes to test or otherwise account for this effect. Other studies, however, have demonstrated significant morphological differences between captive and wild animals (reviewed in O'Regan and Kitchener, 2005), some of which may have direct implications for bite force production (e.g. Erickson et al., 2004). Although we cannot rule out potential systematic biases resulting from possible muscle atrophy or obesity due to captive conditions, we feel that they should not compromise our results. First, force estimates from wild specimens (Sustaita, 2008) demonstrate similar patterns to those observed for *in vivo* subjects. Second, such biases would tend to diminish the difference in bite forces, and magnify the difference in grip forces between falcons and accipiters; whereas the latter may be supported, the former is not. Furthermore, the directionality of bias is difficult to predict. One might argue that wild individuals should 'try' harder; Irschick found that *Uma* lizards reach substantially higher speeds in nature than in the lab (Irschick, 2003). However, captive individuals may possess morphological modifications that enhance force production; Erickson et al. found that, when scaled to jaw length, captive American alligators produced greater bite forces than wild ones (Erickson et al., 2004).

Implications

In addition to its utility for understanding the biomechanics of jaw systems, analysis of bite force has played a key role in ecology and evolution for explaining mechanisms of interspecific (Kiltie, 1982; Herrel et al., 2001) and intraspecific (Binder and Van Valkenburgh, 2000; Erickson et al., 2003) resource partitioning, and for elucidating pathways of diversification in feeding form and function (Herrel et al., 2004). Although there exists a voluminous literature on grip force in the fields of kinesiology and physical anthropology, studies in non-primate vertebrates lag considerably behind those of bite force. Studies of grip force in some frogs (Manzano et al., 2008) and lizards (Abdala et al., 2009) have revealed insights into the role of gripping for arboreal locomotion, along with myological and physiological specializations for enhancing grip forces. The few published studies of *in vivo* grip force in raptorial birds have contributed substantially, by revealing mechanisms of prey capture and killing, and their implications for foraging behavior and ecology (e.g. Marti, 1974; Csermely et al., 1998; Csermely and Gaibani, 1998; Ward et al., 2002). We suggest that more comprehensive, phylogenetically explicit studies of grip force among avian taxa, particularly those that depend more heavily on live prey, remain fertile grounds for examining the ecological significance of grip force in birds, and disentangling the selective roles of perching and prey capture.

We support the conclusions of others that combining theoretical and performance analyses provides a better understanding of the role of biomechanics in the functional morphology of feeding (e.g. Huber and Motta, 2004; Huber et al., 2005). Musculoskeletal morphology generally predicted biting and gripping behavior (as quantified by *in vivo* forces) in *Accipiter* hawks and falcons, although the anatomical estimates of grip-force capacity indicated differences in scaling between groups. *In vivo* grip forces, however, appeared to accord better with *a priori* predictions, based on the extent to which accipiters rely on gripping for handling and killing prey. This highlights the importance of complementing biomechanical force estimates with *in vivo* measurements, and *vice versa*, as relying entirely on one source may obfuscate ecologically and evolutionarily relevant differences between 'potential' and 'realized' performance capabilities (Wainwright, 1991).

APPENDIX

Further details regarding statistical analyses and additional results.

Data treatment

Some workers have indicated that body size is often better represented by a composite of structural dimensions (e.g. Piersma and Davidson, 1991) whereas others consider mass the best univariate indicator (e.g. Dunning, 2008). For the sake of consistency with performance studies of other vertebrates, to simplify allometric interpretations and because of its direct relevance for force production (e.g. muscle mass), we used body mass as a covariate. Furthermore, the results of analyses using wing chord as a covariate were consistent with those we report. The body mass value for an additional merlin wing amputee was adjusted by increasing its mass by 6% (determined from the ratio of the mass of the prairie falcon amputee, to its estimated mass based on head width), because no additional morphological measurements were taken on this individual. We screened the original *in vivo* bite- and grip-force data by running separate OLS regressions of each force variable for each group and plotting the 95% prediction intervals (Sokal and Rohlf, 1995) using SPSS 14.0. Cases that fell well below or above these intervals were excluded from further analysis or replaced with the next highest trial value for that individual, respectively. Two anomalously high maximum grip-force trials (for two juvenile sharp-shinned hawks) were replaced with their next highest trial values.

Three anomalously low maximum bite-force values (one Cooper's hawk, one peregrine and one prairie falcon) and four low maximum grip-force values (two Cooper's hawks, one merlin and one prairie falcon) were excluded from the analyses (asterisks in Fig. 2).

Group, sex and age differences

We examined differences between sexes and ages (after hatch year 'adults' *vs* 'hatch year' juveniles) for sharp-shinned and Cooper's hawks, because these were the only species for which we had sufficient sample sizes to do so. We used separate two-way analyses of variance (ANOVAs) (using GLM in SPSS) with 'age' and 'sex' specified as fixed factors. We did not include body mass as a covariate for Cooper's hawks because it is highly collinear with sex (i.e. the effect of sex explains 88% of the variance in body mass, based on one-way ANOVA model R^2 values). However, sex explains 59% of the variance in body mass in sharp-shinned hawks, so in Table 1 we provide results of analyses with and without mass.

Integration of *in vivo* and anatomical data sets

We used a series of linear dimensions (and body mass; see Fig. S1 and Table S1 in supplementary material) measured on carcasses prior to dissection (from Sustaita, 2008), as well as on live subjects (this study) for the PCA to match individuals from AN and IV data sets. We selected these variables to represent morphological size and shape because they were the most consistent and non-redundant measurements taken across data sets. Some individuals were missing a value for one variable or another, in which case a value was derived from the mean of that variable in order to obtain PC scores for every individual. The first two principal components, reflecting overall body size (PC1) and shape (PC2), were used because they explained 87.2% of the variance in the data (supplementary material Fig. S1) and subsequent components contributed minimally (with eigenvalues <1.0; SPSS). We also employed an alternative approach for integrating anatomical and *in vivo* data, by deriving predictions for the values of the dependent variable of one data set (e.g. *in vivo* bite and grip forces of live birds), from the body mass values of the other data set [e.g. specimens used in Sustaita's (Sustaita, 2008) anatomical study], and *vice versa*, using OLS regression parameters generated from each data set. Both approaches produced quantitatively similar results. However, we report the case-matching approach because it incorporates the actual values and variation inherent in each data set.

Phylogenetically adjusted analyses

We calculated standardized, positivized PICs and all relevant diagnostics as described in the PDAP:PDTREE package documentation (Midford et al., 2008). As an alternative to setting branch lengths to 1.0, we derived them according to Grafen's (Grafen, 1989) rho-transformed method [with rho set at 0.5 (Midford et al., 2008)], and the results were qualitatively similar. We chose this method over the phylogenetic ANCOVA also described by Garland et al. (Garland et al., 1993) because we felt that the small number of species considered in our study would be less conducive to the simulation procedures by which it operates. We also performed these analyses including (as presented in the results) and excluding juveniles, and the results were consistent.

LIST OF SYMBOLS AND ABBREVIATIONS

AN	anatomical (data set)
AN(C)OVA	analysis of (co)variance
CI	confidence interval (95%)
IV	*in vivo* (data set)
OLS	ordinary least-squares (regression)
PCA	principal component analysis; PC1 first principle component; PC2 second principle component
PCSA	physiological cross-sectional area
PIC	phylogenetically independent contrast
PL	prediction limit (95%)
R_i	intraclass correlation coefficient
RMA	reduced major axis (regression)
β	hypothesized slope
ν	slope of reduced major-axis regression

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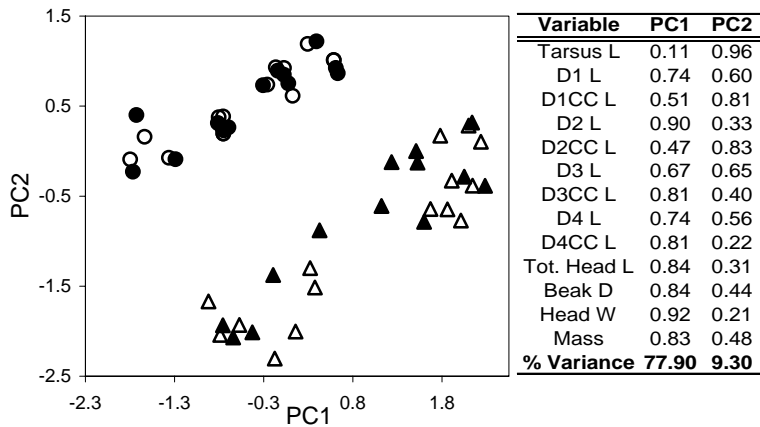| Variable	PC1	PC2
Tarsus L	0.11	0.96
D1 L	0.74	0.60
D1CC L	0.51	0.81
D2 L	0.90	0.33
D2CC L	0.47	0.83
D3 L	0.67	0.65
D3CC L	0.81	0.40
D4 L	0.74	0.56
D4CC L	0.81	0.22
Tot. Head L	0.84	0.31
Beak D	0.84	0.44
Head W	0.92	0.21
Mass	0.83	0.48
% Variance	**77.90**	**9.30**

Table S1. Results of RMA regressions of (log_{10}-transformed) bite and grip forces on selected morphological predictors*

Taxon
  Dependent variable
    Predictor variable
	R^2	v	95% CI	F	d.f.$_{Error}$	P

Accipiters						
Grip force						
Body mass	0.65	0.97	0.79–1.15	79.2	42	<0.001
Wing chord	0.68	4.01	3.30–4.72	88.0	42	<0.001
Tarsus length	0.11	1.41	1.00–1.82	5.5	42	0.024
Mid-crus circumference	0.65	1.59	1.30–1.89	77.8	42	<0.001
Bite force						
Body mass	0.56	0.88	0.63–1.14	28.7	23	<0.001
Wing chord	0.64	3.65	2.62–4.67	29.5	22	<0.001
Total head length	0.47	0.53	0.33–0.74	10.7	22	0.002
Post-orbital head width	0.44	2.22	1.50–2.95	30.9	21	<0.001
Head length	0.43	2.54	1.70–3.37	29.4	21	<0.001
Beak length	0.28	2.61	1.62–3.59	6.5	21	0.019
Beak depth	0.51	2.19	1.50–2.87	18.9	21	<0.001
Beak width	0.51	2.81	1.92–3.71	17.5	21	<0.001
Falcons						
Grip force						
Body mass	0.92	0.86	0.71–1.01	142.1	13	<0.001
Wing chord	0.81	2.61	1.93–3.28	30.7	7	0.001
Tarsus length	0.68	3.50	2.31–4.69	27.3	12	<0.001
Mid-crus circumference	0.89	1.92	1.44–2.39	43.3	9	<0.001
Bite force						
Body mass	0.80	0.76	0.57–0.95	58.6	15	<0.001
Wing chord	0.56	1.78	1.05–2.51	6.7	6	0.041
Total head length	0.83	2.36	1.76–2.97	44.7	10	<0.001
Post-orbital head width	0.83	2.56	1.76–3.36	43.2	11	<0.001
Head length	0.76	2.23	1.56–2.90	38.6	10	<0.001
Beak length	0.74	2.58	1.61–3.55	16.8	11	0.002
Beak depth	0.66	2.08	1.27–2.90	14.9	11	0.003
Beak width	0.79	2.22	1.43–3.01	19.9	11	0.001

*Linear measurements were taken as follows using digital calipers, unless otherwise stated:.

Wing chord=with tape measure, from leading edge of wrist joint to tip of longest primary feather.

Tarsus length=from lateral condyle of tibiotarsus to ventral base of metatarsus I-hallucal joint.

Mid-crus circumference=circumference of ellipse, approximated by: $2\pi\sqrt{((minor^2 + major^2)/2)}$, where antero-posterior depth and medio-lateral width (taken at mid-tibiotarsus length) comprise major and minor axes, respectively.

Total head length=from occipital protuberance to rostral end of culmen curvature.

Post-orbital head width=maximum width just posterior to orbit.

Beak length=cranial edge of cere to tip of maxilla.

Head length=total head length – beak length.

Beak depth=perpendicular to tomium at rictus with bill closed, from cranial edge of cere to ventral surface of mandible.

Beak width=perpendicular to maxilla at cranial edge of cere with bill closed, from one side of gape to the other.