

RESEARCH ARTICLE

Locomotor correlates of the scapholunar of living and extinct carnivorans

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Funding information

NSF EAR-SGP, Grant/Award Number: 1425059; Des Moines University

Abstract

The relationship of carpal morphology to ecology and habitat is under studied in carnivorans and more generally in mammals. Here, we use 3D-scanning techniques to assess the usefulness of a carpal bone, the scapholunar, in carnivorans to reflect ecology and habitat, and to reconstruct the ecology of five extinct carnivorans from two fossil sites: Rancho La Brea and Natural Trap Cave. We 3D-scanned scapholunars and measured articular surface areas and angles between articular facets using GeoMagic and Rhino 3D-software. We analyzed the difference in these metrics using multivariate analysis of variance and discriminant function analysis. Results show that the scapholunar reflects ecological signal, with clear groupings of cursorial carnivorans and grappling/climbing carnivorans; however, phylogenetic signal was also present in the results with hyaenids, canids, and large felids in distinct morphospaces. Extinct species *Miracinonyx trumani* (American cheetah) and *Smilodon fatalis* (sabertooth cat) showed surprising results with *M. trumani* grouping with pantherines instead of *Acinonyx* or *Puma*, suggesting it runs but still retains the ability to grapple prey. *S. fatalis* groups with pantherines, but also shows some unique adaptations, suggesting it had a different range of wrist motion than living cats. Overall, the scapholunar is a good indicator of ecology and functional morphology and can be another tool to use in modern and fossil carnivorans to reconstruct extinct ecologies and locomotor behaviors.

KEYWORDS

carpals, ecometrics, locomotion

1 | INTRODUCTION

Functional morphology is the well-tested idea that body shape is correlated with the forces an animal's body is subjected to each day, for example: running, climbing, or digging. Much work has been done on carnivoran functional morphology, and many studies have shown that carnivoran postcranial morphology correlates well with locomotor mode, habitat use, and prey-killing behavior (e.g., Martín-Serra, Figueirido, &

Palmqvist, 2014a, 2014b; Meachen, Dunn, & Werdelin, 2016; Meachen & Roberts, 2014; Meachen-Samuels & Van Valkenburgh, 2009; Meloro, 2011; Polly, 2010; Samuels, Meachen, & Sakai, 2013; Van Valkenburgh, 1985; Van Valkenburgh, 1987; Walmsley, Elton, Louys, Bishop, & Meloro, 2012). Of all the limb elements, carpals and tarsals are the least developed for reconstructing locomotor modes and environments, since they have been understudied and often overlooked compared with long bones. However, carpals and tarsals are potentially useful as they reflect wrist and ankle mobility, and therefore locomotor mode, substrate use, and overall environment in which

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an animal lives (Polly, 2010). Carpals and tarsals are also useful for paleontological fossil assemblages because they are diagnostic elements and are likely to be fossilized. Higher fossilization probability is due to their hard, compact nature (more cortical and less spongy bone), and because they contain less nutritional value (fat), so are less likely to be destroyed by carnivores preburial (Darwent, Lyman, Haglund, & Sorg, 2001; Marean & Spencer, 1991).

Tarsals have been used with success to capture environmental variables in several groups. Polly (2010) analyzed calcanea using linear measurements and gear ratios in carnivores, and found a strong correlation between temperature, ecoregion, and calcaneal morphology. Panciroli, Janis, Stockdale, and Martín-Serra (2017) also found a clear link between calcanea and locomotor mode in extant and extinct carnivores. Astragali have been analyzed in apes to elucidate locomotor and substrate use differences in gorillas and other primates (Boyer, Yapuncich, Butler, Dunn, & Seiffert, 2015; Dunn, Tocheri, Orr, & Jungers, 2014).

Carpals have also been examined for locomotor traits. Multiple studies have done qualitative examinations of carpal bones to assess their utility in locomotion and phylogeny (Argot, 2001; Lehmann, 1963; Salton & Sargis, 2008; Stafford & Thorington, 1998; Thorington & Darrow, 2000). Many of these studies found morphological correlations between carpal morphology and locomotor mode; however, at least one found no correlation between carpals and locomotor mode (e.g., Swiderski, 1991). Yalden (1970) did a qualitative analysis of carnivore carpals and determined that there are differences in the carpals based on locomotor modes but did not give a quantitative breakdown of these distinctions. Fewer studies have done quantitative analyses on carpal bones (Almécija, Orr, Tocheri, Patel, & Jungers, 2015; Hamrick, 1997; Tocheri et al., 2003), and no quantitative analyses have been done on carnivorous carpals. This may be because these bones are small, rounded, and most of the useful information is from examining surface areas and curvatures, which are difficult to quantify using traditional linear measurements.

The scapholunar bone, a fusion of the ancestral mammalian scaphoid and lunate carpal bones, is found in a few taxonomic groups including tenrecoids, and carnivores, among a few other taxa (Salton & Sargis, 2008). This bone may be a good indicator of substrate use and locomotor mode because it is the largest bone in the carnivore wrist and is one of the bones that make up the major joint of flexion and extension, with the radius being the other. The scapholunar also articulates with the magnum, unciform, trapezoid, and trapezium. Therefore, overall wrist mobility should be reflected in its morphology. Salton and Sargis (2008) found that tenrecoids with arboreal habits had a larger trapezoid/trapezium and unciform, and additionally that they had a larger articular surface of the radius. Yalden (1970) observed that the morphology of the scapholunar bone was correlated with locomotor mode and habitat preference, for example, he noticed that the distal end of a cheetah scapholunar resembles that of canids and hyaenids—all cursors; but that the other felids share affinities with mustelids and ursids—climbers and grapplers. However, Yalden (1970) did not quantify these differences, nor did he examine any extinct species in his study.

Our goal is to assess the scapholunar bone as a proxy for locomotor mode or habitat use in carnivores, using 3D-scans and surface area dimensions. We will compare our results in modern species with known functional morphological and ecological data to determine how well the scapholunar bone reflects functional morphology. Because of its location and articulation with several other carpals, we hypothesize that the scapholunar will be highly indicative of locomotor ecology. Then, using modern species as a baseline, we aim to reconstruct the individual locomotor modes of several extinct species of carnivores from two late Pleistocene fossil sites: Natural Trap Cave, and Rancho La Brea to determine what the scapholunar can teach us about the behavior of these extinct organisms.

2 | MATERIALS AND METHODS

Our sample comprises 34 scapholunars from five extinct species: *Canis dirus*, *Canis lupus* sp., *Panthera atrox*, *Smilodon fatalis*, and *Miracinonyx trumani* from Natural Trap Cave and Rancho La Brea; and 30 scapholunars from six extant species (Table 1). The specimens are housed at the following institutions: Kansas Museum of Natural History (KUM [modern], KUVF [fossil]), American Museum of Natural History (AMNH), University of Wyoming Geological Museum (UW), and Tar Pits Museum (TPM; for a complete list of all specimens with museum catalogue numbers see Supporting Information Table S1). Extant species were chosen either because they represent species most closely related to the extinct species of interest or are thought to be most similar to them in purported locomotor category. For example, for the extinct species *M. trumani*, the American cheetah-like cat, we chose both *Puma concolor* (closest genetic relative; Barnett et al., 2005) and *Acinonyx jubatus* (purported ecomorph; Van Valkenburgh, Grady, & Kurtén, 1990). Care was taken to avoid juveniles whenever possible, although juvenile scapholunars were already ossified in the collections we had access to. We also took care to choose both male and female specimens whenever possible.

TABLE 1 Taxa included in this study

Family	Species	N	Locomotor mode
Extant taxa			
Canidae	<i>Canis lupus</i>	6	Cursorial
Hyaenidae	<i>Crocota crocuta</i>	6	Cursorial
	<i>Hyaena hyaena</i>	2	Cursorial
Felidae	<i>Acinonyx jubatus</i>	4	Cursorial
	<i>Panthera leo</i>	6	Grappler
	<i>Puma concolor</i>	6	Grappler/climber
Extinct taxa			
Canidae	<i>Canis dirus</i>	5	
	<i>Canis lupus</i>	8	
Felidae	<i>Miracinonyx trumani</i>	9	
	<i>Panthera atrox</i>	7	
	<i>Smilodon fatalis</i>	5	

All data were collected from 3D-digital models generated with a NextEngine 3D-Ultra HD-scanner, model 2020i following the methods outlined in Tocheri et al. (2003) and Dunn et al. (2014). Each bone was scanned in two orientations to create two 3D-mesh files using ScanStudioHD software. Each 3D-mesh was exported as a .ply file and imported into Geomagic Wrap 2015 software, which was used to digitally align the two orientations and merge them into a single 3D-model consisting of a triangular mesh. This mesh was then cleaned to remove erroneous triangles and patch small holes. We segmented each cleaned model into articular and nonarticular regions, and each articular surface was separated and exported as a separate .ply file for further analysis (outlined below). In addition, we fit each articular surface with a plane using the “best fit” function in Geomagic Wrap and exported each plane as a .vda file. As the taxa in our sample shows variation in the number of bones that articulate with the scapholunar, the precise homology of segmented units differs among taxa (Figure 1). Compared to felids, hyaenids and canids lack a facet for the trapezium on the scapholunar; however, the distinction

between the articular facets for the trapezium and trapezoid is difficult to discern in felids, so we combined the articular surface for the trapezium and trapezoid into a single surface in felids, hereafter referred to as “trap” for the sake of brevity. Most felids are unique in lacking an articulation for the cuneiform on the scapholunar, whereas this surface is retained by the cheetah, canids, and hyaenids. We segmented the cuneiform facet when present and included it as part of the total articular surface area of the bone but did not include the surface area or angles derived from it in analyses.

Once regions of interest were segmented, the resulting .ply and .vda files were imported into Rhinoceros 5.4.2 for data extraction. We recorded the surface area for the nonarticular area and each articular surface and from these created relative surface areas by dividing the surface area of each segmented surface by the total surface area. We then used the .vda files to calculate angles between pairs of best-fit planes. Angles were calculated between plane normals, resulting in an angle orthogonal to their point of intersection. All angles represent the “internal angle,” or the angle facing the center of the bone, which

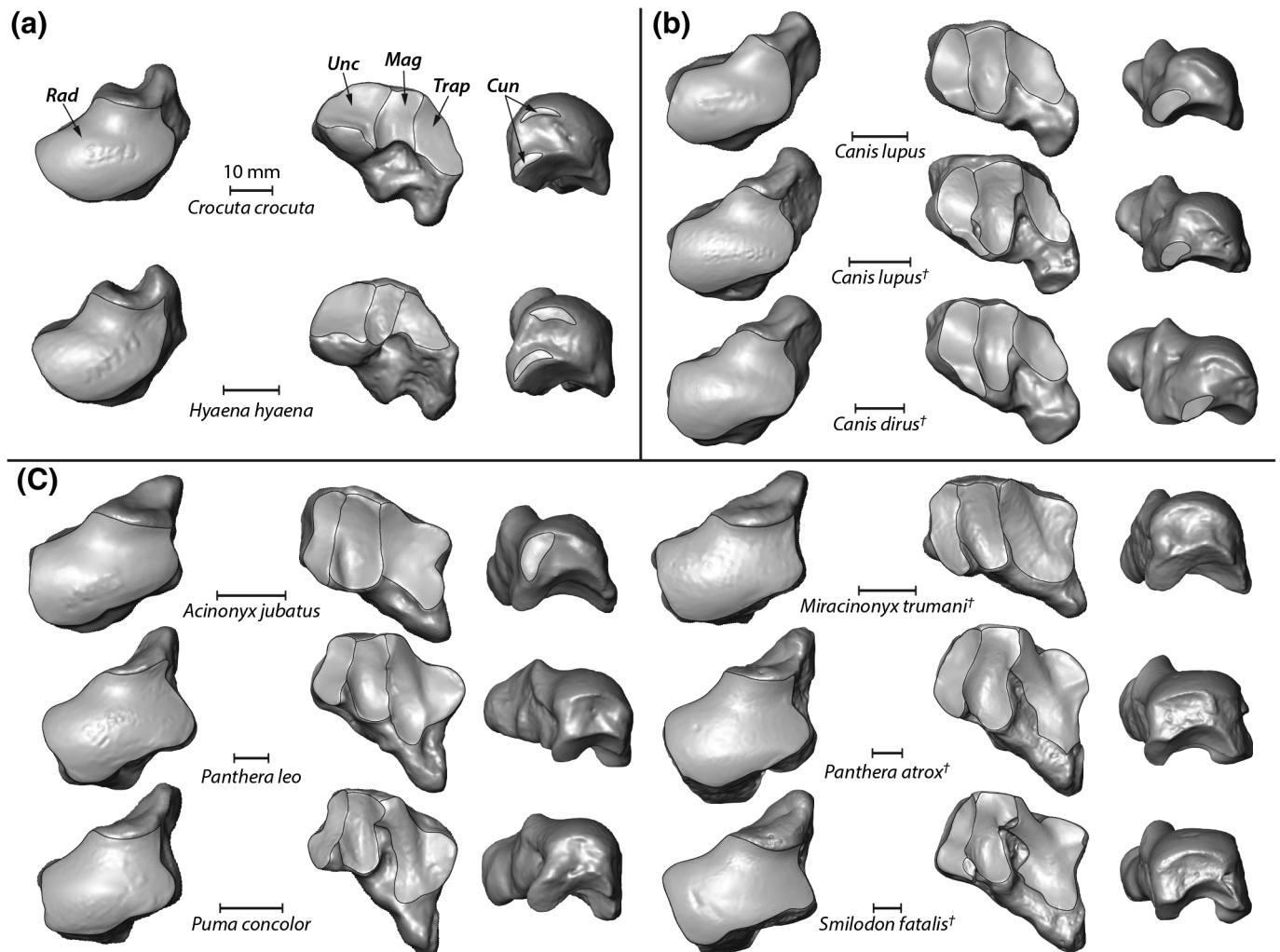


FIGURE 1 Images taken from 3D-laser scans of the scapholunar bone for each taxon in our sample in proximal (left), distal (middle), and ulnar (right) views. (a) Hyaenids, (b) Canids, and (c) felids. Extinct taxa are designated by “†”. Cun, facet for cuneiform; Mag, facet for magnum; Rad, facet for radius; Trap, facet for trapezoid in hyaenids and canids, facet for trapezoid and trapezium in felids; Unc, facet for unciform

is always 180° or less. Our final data set consisted of four relative surface areas and six interarticular angles (Tables 2 and 3). These metrics have been shown to be useful in differentiating locomotor categories in ape carpals and tarsals and are scale-free (Tocheri et al., 2003).

We used discriminant function analyses (DFA) to determine if relative surface areas and angles can be used to differentiate the carnivore species in our sample both by examining canonical structure of the resulting functions and by visual inspections of the DFA graph following Dunn et al. (2014). Variables that contributed most significantly to the DFA axes were examined to infer differences in ecology using a multivariate analysis of variance (MANOVA) with Tukey's post hoc tests for homogenous variance and Tamhane's test for non-homogenous variance, or a Kruskal-Wallis in the case that our data were not normally distributed. The DFA was performed in R version 3.5.1 (R Core Team, 2018) using the "candisc" package (Friendly & Fox, 2017). The MANOVA was performed in SPSS v. 25.

3 | RESULTS

3.1 | Discriminant function analysis

DFA yielded 4 Eigenvalues >1, explaining 97.8% of the variance. The strongest loading variables on DF 1 are the relative surface area of the trap (−0.963) and the angle between the trap and unciform facets (0.958). Other variables loading higher than |0.5| on DF1 include the relative surface areas of the magnum and unciform, and the radius-unciform, and magnum-trap angles (Table 4). DF1 separates felids (negative values) from canids and hyaenids (positive values). Examination of boxplots and mean values for variables included in the DFA

reveals that cats have larger relative surface areas for the trap and a smaller angle (more acute) between the trap and the unciform, and dogs and hyaenids showed the opposite trend. Interestingly, cheetahs hovered around zero for DF1, suggesting they are intermediate in morphology between dogs/hyaenas and other cats (Figure 2).

Two variables were highly loaded on DF2, the angle between the radius and the unciform (0.533) and the relative surface area for the magnum (−0.679). This function separates hyaenas (positive) from dogs (negative), and cats as a group were neutral; however, *P. concolor* was positively loaded relative to other felids (Figure 2). Radius-unciform angle separates canids from hyaenids and felids, with canids having more acute angles than other taxa. Hyaenids have the smallest relative surface areas for the magnum, separating them from the rest of the sample. *P. concolor* diverges from other felids in having a slightly smaller relative surface area from the magnum and in having a more obtuse radius-unciform angle.

DF3 also shows only two highly loaded variables: the angle between the radius and the trap (−0.587), and the angle between the radius and magnum (0.509). DF3 distinguishes *S. fatalis*, with extremely high scores, from all other taxa (Figure 2). *P. concolor* also has relatively high values, but not as extreme as seen in *S. fatalis*.

Only one variable, the angle between the magnum and unciform, loads highly on DF4 (−0.642). DF4 separates modern *C. lupus* and *A. jubatus*—with high negative values, from all other species (Figure 2).

3.2 | Multivariate analysis of variance

Although our variables are not all normally distributed (radius-trap angle, radius-magnum angle, and magnum-unciform angle appear normal; trap relative SA, radius-unciform angle, and trap-unciform angle

TABLE 2 Mean and standard deviation for relative articular surface areas of all taxa in the sample

			Surface areas							
Family	Species	N	Magnum		Radius		Trap ^a		Unciform	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD
Extant taxa										
Canidae	<i>C. lupus</i>	6	6.72 ^H	0.68	22.67 ^{F, Cc}	1.21	5.57 ^F	0.59	6.71 ^{F, CIF}	0.44
Hyaenidae	<i>C. crocuta</i>	5	4.06 ^{C, F}	0.56	27.36 ^{CIM, CIF}	1.54	5.35 ^F	0.38	6.09 ^{Mt, Pa, Pc}	0.26
	<i>H. hyaena</i>	2	3.86 ^{C, F}	0.11	25.48	0.03	4.06 ^F	0.04	5.90 ^{Pc, Sf}	0.16
Felidae	<i>A. jubatus</i>	4	7.70 ^H	0.51	28.27 ^C	2.11	9.34 ^{C, H, Mt, Pa, Pc, Pl}	0.64	5.35 ^{CIM, Sf}	0.59
	<i>P. leo</i>	6	6.94 ^H	0.32	29.38 ^C	0.91	11.63 ^{C, H, Aj, Sf}	0.59	5.03 ^{CIM, Cd}	0.43
	<i>P. concolor</i>	6	6.62 ^H	0.40	26.66 ^{CIM, CIF}	2.37	11.67 ^{C, H, Aj, Sf}	1.50	4.35 ^{C, H}	0.82
Extinct taxa										
Canidae	<i>C. dirus</i>	5	6.91 ^H	0.71	23.71 ^{Aj, Mt, Pa, Pl}	1.32	5.16 ^F	0.70	6.38 ^{Mt, Pa, Pc, Pl, Sf}	0.39
	<i>C. lupus</i>	8	6.89 ^H	0.60	22.59 ^{F, Cc}	1.40	5.32 ^F	0.80	5.72 ^{CIM, Pa, Pc, Sf}	0.72
Felidae	<i>M. trumani</i>	11	7.38 ^H	0.65	26.88 ^C	1.92	12.86 ^{C, H, Aj, Sf}	0.83	5.00 ^{Cc, Cd, CIM}	0.59
	<i>P. atrox</i>	7	7.65 ^H	0.60	27.21 ^C	1.96	11.57 ^{C, H, Aj, Sf}	0.88	4.71 ^{C, Cc}	0.29
	<i>S. fatalis</i>	5	6.94 ^H	0.64	26.32 ^{CIM, CIF}	2.19	9.57 ^{C, H, Mt, Pa, Pc, Pl}	0.76	4.04 ^{C, H, Aj}	0.40

Note. Group differences ($p < .05$) are denoted by superscripts as follows: C = all canids, F = all felids, H = all hyaenids, Aj = *Acinonyx jubatus*, Cc = *Crocota crocuta*, Cd = *Canis dirus*, CIM = *Canis lupus* (modern), CIF = *Canis lupus* (fossil), Hh = *Hyaena hyaena*, Mt = *Miracinonyx trumani*, Pa = *Panthera atrox*, Pc = *Puma concolor*, Pl = *Panthera leo*, Sf = *Smilodon fatalis*. Superscripts denote significant differences ($p < .05$) from MANOVA.

^aTrap = trapezoid + trapezium in all taxa except for canids, which lack a trapezium.

TABLE 3 Mean and standard deviation for angles between articular surfaces of all taxa in the sample

Family		Species	N	Angles				Magnum-trap				Magnum-unciform				Radius-trap				Radius-unciform				Trap-unciform			
				Magnum-radius		SD		Mean		SD		Mean		SD		Mean		SD		Mean		SD		Mean		SD	
Extant taxa																											
Canidae	<i>C. lupus</i>	6	14.14 ^{Pc, Sf}	3.35	160.87 ^{Mt, Pa, Pc, Pl, Sf}	6.04	155.00 ^{Cc, Cd, Mt, Pa, Pc, Pl}	2.82	32.22 ^{Sf}	3.24	29.70 ^{F, H}	1.35	144.72 ^F	3.35													
Hyaenidae	<i>C. crocuta</i>	5	6.99 ^{Aj, Mt, Pc, Sf}	3.80	149.21 ^{Cd, Mt, Pc, Sf}	2.14	141.55 ^{Aj, CIM, CIF}	3.10	30.20 ^{Sf}	3.17	42.16 ^{C, Pc}	5.40	153.86 ^{F, Cd, CIF}	3.80													
	<i>H. hyaena</i>	2	9.24 ^{Pc, Sf}	3.10	153.44 ^{Pc, Sf}	8.26	145.26	3.03	28.31	0.11	41.37 ^{C, Pc}	2.26	148.23 ^F	3.10													
Felidae	<i>A. jubatus</i>	4	18.62 ^{Cc}	3.30	144.84 ^{Cd, Pc}	1.99	151.46 ^{Cc, Pl}	1.81	28.01	2.72	46.99 ^{C, Pc}	2.92	125.86 ^{C, H, Mt, Pc}	3.30													
	<i>P. leo</i>	6	15.46 ^{Pc, Sf}	3.61	145.83 ^{Cd, CIM, Pc, Sf}	14.17	139.52 ^{Aj, CIM, CIF}	4.91	27.33	3.84	43.55 ^{C, Pc}	1.24	121.16 ^{C, H, Pc}	3.61													
	<i>P. concolor</i>	6	27.47 ^{H, CIM, CIF, Mt, Pa, Pl}	4.80	127.27 ^{C, H, Aj, Pl}	4.82	143.17 ^{CIM, CIF}	2.82	27.71	2.74	55.57 ^{C, H, Aj, Mt, Pa, Pl, Sf}	3.50	111.29 ^{C, H, Aj, Pl}	4.80													
Extinct taxa																											
Canidae	<i>C. dirus</i>	5	17.39	5.69	165.71 ^{F, Cc}	3.95	144.73 ^{CIM}	3.35	30.94 ^{Sf}	2.19	29.64 ^{F, H}	2.28	137.51 ^{F, Cc}	5.69													
	<i>C. lupus</i>	8	11.15 ^{Pc, Sf}	4.27	157.42 ^{Mt, Pa, Pc, Sf}	3.71	151.12 ^{Pa, Pc, Pl}	7.64	31.28 ^{Sf}	2.49	28.56 ^{F, H}	3.56	144.25 ^{F, Cc}	4.27													
Felidae	<i>M. trumani</i>	11	18.13 ^{Cc, Pc}	5.43	134.22 ^{C, Cc}	9.50	145.93 ^{CIM}	4.54	31.82 ^{Sf}	2.19	46.96 ^{C, Pc}	3.34	114.37 ^{C, H, Aj}	5.43													
	<i>P. atrox</i>	7	15.99 ^{Pc, Sf}	4.70	135.26 ^C	8.21	143.26 ^{CIM, CIF}	3.16	29.52 ^{Sf}	2.77	45.61 ^{C, Pc}	2.75	116.72 ^{C, H}	4.70													
	<i>S. fatalis</i>	5	27.26 ^{H, CIM, CIF, Pa, Pl}	5.21	129.76 ^{C, H, Pl}	6.11	147.27	2.27	23.63 ^{C, Cc, Mt, Pa}	3.56	42.79 ^{C, Pc}	3.60	118.30 ^{C, H}	5.21													

Note. Superscripts denote significant differences ($p < .05$) from MANOVA. Refer to Table 2 for superscript definitions.

TABLE 4 Correlations between each variable and canonical axis for the DFA

	DF1	DF2	DF3	DF4
% variance	73.4	17.7	4.2	2.5
Eigenvalue	56.061	13.520	3.224	1.926
Relative surface areas				
Magnum.sar	-0.515	-0.679	-0.011	-0.188
Radius.sar	-0.552	0.372	-0.146	0.266
Trapezoid.sar	-0.963	0.008	-0.196	0.069
Unciform.sar	0.730	-0.185	-0.357	-0.122
Angles				
Magnum-radius	-0.559	-0.062	0.509	-0.314
Magnum-trap	0.777	-0.345	-0.124	0.037
Magnum-unciform	0.323	-0.316	0.011	-0.643
Radius-trapezoid	0.248	-0.229	-0.587	-0.093
Radius-unciform	-0.783	0.533	-0.050	-0.105
Trap-unciform	0.958	0.098	-0.100	0.032

Note. Best explanatory variables are emphasized in bold.

are bimodal), we get the same overall results from the MANOVA as from nonparametric tests. Both Kruskal-Wallis and MANOVA show significant differences between species for the 10 variables of interest. The MANOVA indicated that variances were homogenous (via homogeneity of variance test) so Tukey's post hoc tests were used to explore differences between species. See Tables 2 and 3 for all means, standard deviations, and significant differences. Here, we will address the individual variables that helped to differentiate groups in the DFA: relative surface area of the trap and magnum facets, and angles between the trap-unciform, radius-unciform, radius-trap, radius-magnum, and magnum-unciform.

Just as DF1 separates felids from canids and hyaenids, the two highest loading surface areas on DF1 and DF2, relative trap surface area and relative magnum surface area, trap-unciform angle clearly separate the canids and hyaenids from the felids with no overlap between groups (Figure 3). Felids show significantly larger trap surface areas than canids and hyaenids, which are not significantly different from each other (Table 2). Within felids, *Acinonyx* and *Smilodon* were significantly different from all other species in the sample, having relatively smaller trap articular facets, although not as small as canids or hyaenids. Hyaenids show the smallest values for relative surface of the articular facet for the magnum, being significantly smaller than felids and canids; canids and felids have roughly equivalent magnum surface areas, with no differences between or among those groups.

The two highest loading angles on DF2, trap-unciform angle and radius-unciform angle, also differentiate all three families in our sample (Figure 3). Felids demonstrate relatively more acute trap-unciform angles than canids and hyaenids. As a whole, canids and hyaenids are not significantly different from each other; however, *Crocuta* has significantly more obtuse angles than the two fossil canids in our sample, *C. dirus* and *C. lupus* from Natural Trap Cave (Table 3). Among extant

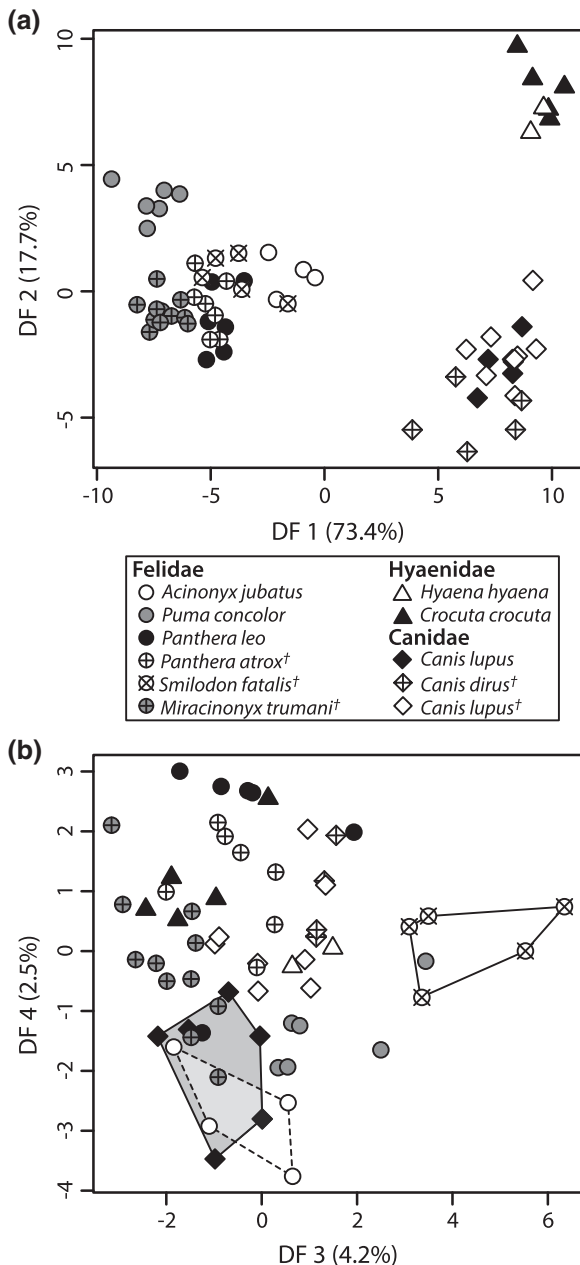


FIGURE 2 Plots of the first four discriminant functions: (a) DF 1 scores versus DF 2 scores and (b) DF 3 scores versus DF 4 scores. (a) Note that the cursorial canids and hyaenids group together with high DF 1 values, whereas the felids are completely separate with low values, and that the most cursorial felid, *Acinonyx jubatus*, has the highest DF 1 scores of all felids. DF 2 primarily separates hyaenids (high) from canids and felids (low). (b) Note that DF 3 separates *Smilodon fatalis* (higher scores) from the rest of the sample and that extant *Canis lupus* and *Acinonyx jubatus* are separated from the rest of the sample in having the lowest DF 4 scores. Extinct taxa are designated by “†”

felids, *Acinonyx* shows the most obtuse angles, whereas *Puma* has the most acute with no overlap between these two species in angle values. *Panthera leo* also has higher values for this angle, showing a significant difference from *Puma*. Considering the fossil felids, *Miracinonyx* diverges from the felid mean by having lower, more acute

values for this angle, being significantly different from *Acinonyx*, but not from *P. leo*. For the angle between the radius and unciform, Canids had significantly lower values (more acute angles) than all other taxa and *Puma* had a significantly more obtuse angle than all other taxa.

The angles between the radius and trap and the radius and magnum are the highest loading variables on DF3, which separated *Smilodon* from the rest of the sample. *Smilodon* exhibits lower (more acute) values for the angle between radius and trap facets than all canids, *Crocota*, and the fossil felids *P. atrox* and *Miracinonyx*. *Puma* and *Smilodon* both show more obtuse angles between the radius and magnum than the other taxa in our sample, being significantly different from hyaenids, extant and fossil *C. lupus*, *P. leo*, and *P. atrox*; *Puma* is significantly more obtuse than *Miracinonyx*, whereas *Smilodon* is not. In addition to differences with *Puma* and *Smilodon*, *Crocota* shows significantly more acute angles than *Acinonyx* and *Miracinonyx*.

Acinonyx, and modern and fossil *C. lupus* show the highest (most obtuse) angle between the magnum and unciform, with *Acinonyx* being significantly different from *Crocota* and *P. leo*. Fossil *C. lupus* differs from *P. atrox*, *P. leo*, and *Puma*, and modern *C. lupus* further differs from *Crocota*, *C. dirus*, and *Miracinonyx*.

4 | DISCUSSION

Our results show a mix of ecological and phylogenetic effects, including distinct differences between the cursorial canids and hyaenids, and the grappling felids (with exception of the cheetah), and differences within the felidae, according to ecological specialization.

The first two discriminant functions separate all three families, with DF1 separating felids, with negative scores, from canids and hyaenids, with positive scores. This function reflects differential supinatory ability, separating grappling/climbing felids from cursorial canids and hyaenids. The most influential variables on DF1 are the relative size of the trap surface area and the angle between the trap and unciform facets. The small facet for the trapezium/trapezoid in canids and hyaenids reflects the reduction of the first digit, and lack of an articular surface for the trapezium in these taxa, a feature related to increased cursoriality. This is in line with the general pattern of reducing the digits, to keep feet lighter, with increasing cursoriality in mammals (e.g., Cooper et al., 2014; Hildebrand, 1985; Lull, 1904).

Cats have a larger area for the trapezium/trapezoid because they retain all five digits on the forepaws and a robust articulation for the trapezium, which allows the felid wrist to move in multiple planes (Hopwood, 1947). These multiple planes of movement may be linked to the animals' ability to pronate and supinate the forelimb, which is related to climbing and prey-killing abilities. This finding in felids seems to be in line with what Salton and Sargis (2008) found in tenrecoids—greater trapezium/trapezoid surface area in arboreal species. Felids are more scansorial in general than canids and use their paws in multiple planes to catch prey as well, this makes functional sense. The cheetah, the definitive cursorial cat, diverges from other felids toward the more cursorial region of the morphospace, reflecting

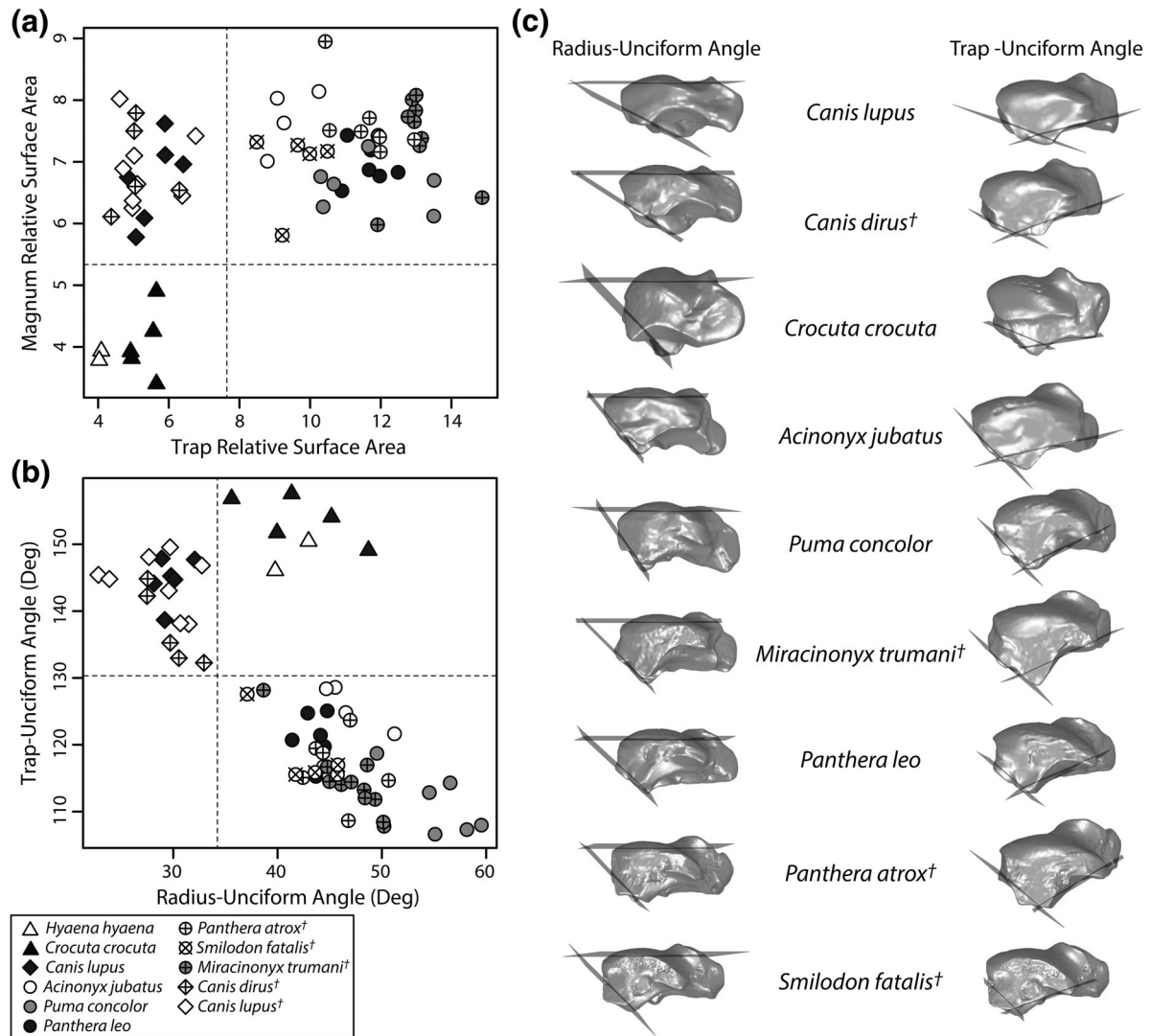


FIGURE 3 Bivariate scatterplots of the four most influential variables on DF 1 and 2 (a and b) and examples of the two most influential angles (c). Dotted lines indicate that each group occupies a separate and nonoverlapping region of morphospace. (a) Note that cursorial canids and hyaenids have the reduced relative trap surface areas compared with felids, with *Acinonyx*, again having among the smallest trap surface areas of the felids, correlating with its more cursorial behavior. Hyaenids are distinguished from canids and felids by having a relatively small surface area for articulation with the magnum. (b) Canids are distinct from felids in having the most acute radius-unciform angles, with hyaenids being intermediate and overlapping with felids. However, hyaenids are distinct from felids in having the most obtuse trap-unciform angles, with canids having intermediate values that overlap with hyaenids. Extinct taxa are designated by “†”

its locomotor ecology and reorientation of the metacarpals—into a more fused, hinge-type joint (Hopwood, 1947). The cheetah does retain the first metacarpal, including retention of a trapezium articulation, for a distinct purpose in prey acquisition; using their dewclaw (or first claw) to hook prey off balance (Londei, 2000), but it does not need to retain the flexibility as in other cats for gripping.

The second discriminant function separates hyaenids (high values) from felids and canids (low values). This reflects the extremely reduced magnum facet in hyaenids, whereas canids and felids are fairly uniform in the size of this articular surface; the only significant difference in this feature is between hyaenids and each of the other groups. We suspect this is a derived feature in hyaenids and may or may not reflect shared functional adaptation in the carpus of this group.

The trap-unciform angle, likely reflects the retention of an articulation between the cuneiform and scapholunar. This change in the orientation of the unciform facet can be explained by the presence of a cuneiform facet. The other influential variable on DF2 is the angle between the radius and unciform facets. We suggest that this angle, like the trap-unciform angle, reflects deviations in the angle of the unciform facet related to presence/absence of the cuneiform. When the cuneiform and the scapholunar are disconnected, this leads to a change in forelimb loading, which is related to the ability to supinate the forelimbs.

With regard to angles, the trap/radius/unciform triangle is where the most important differences occur. Canids and hyaenids have more obtuse trap-unciform angles than felids, which appears to be driven mainly by flattening-out of the unciform facet in the former groups

relative to the articular surface for the trapezium/trapezoid (Figure 3). In contrast, the radius-unciform angle is more acute in canids and more obtuse in felids, which again appears to be driven by changes in the orientation of the unciform facet specifically. This can be partially explained by the carpal morphology of these two groups. Canids and hyaenids both retain contact between the cuneiform and scapholunar, whereas all cats with the exception of cheetahs have lost contact between these two bones. The presence of a cuneiform articulation on the ulnar side of the scapholunar forces the plane of the unciform into a more transverse position. In felids, the lack of a cuneiform facet does not constrain the position of the ulnar border of the unciform facet, facilitating a more oblique orientation. The cheetah acts as a good test for this, as it is the only felid in our sample that shows contact between the scapholunar and cuneiform. In fact, the cheetah has among the highest trap-unciform angles of the felids; however, the radius-unciform angle is not atypical for felids, suggesting that the addition of a cuneiform facet can only partially account for differences in this angle. The end result is that canids have a flatter mid-carpal joint, which is more optimal for wrist fore-aft movement in the sagittal plane, ideal for cursors, whereas cats retain more angular carpal articulations, and a more interlocking mid-carpal joint, allowing more stability across a wider range of motions.

One other morphological feature of note, related to the reorientation of the limbs when the cuneiform and scapholunar are disconnected, is the contact between the carpals and bones of the forearm in grapplers versus cursors. In more cursorial taxa, including canids and *Acinonyx*, most of the force born by the forelimb is transmitted through contact between the scapholunar and radius, with the ulna having little to no contact with the carpals. In grapplers such as large pantherines and *Smilodon*, however, the ulna maintains a connection to the carpal bones through the cuneiform, and thus plays a larger role in the transmission of force through the forelimb. This latter configuration is advantageous when the wrist must maintain stability in a variety of postures, such as when climbing or wrestling with prey. The wrist of *Smilodon* looks more like that of a bear than that of a dog, and in fact Wroe, Lowry, and Anton (2008) made a comparison of *Smilodon* forelimbs to those of a bear. This is also related to the radius being mobile (supination and subsequent pronation) relative to the ulna in grapplers and climbers, which is reduced in the cursorial taxa. See Figure 4 for orientation of radius and ulna relative to carpals and metacarpals in taxa examined here. This figure illustrates how weight is not distributed equally between the radius and ulna in cursors and grapplers.

Our results are consistent with the idea that features associated with cursoriality, or supinatory ability are reflected in the carpal joints, and specifically, scapholunar morphology in extant felids, hyaenids, and canids. Features associated with increased cursoriality are: reduction of the facet for the most radial of the distal carpal bones (the trapezium and trapezoid) associated with a reduction of the first digit, and a more obtuse angle between the trapezoid and unciform, resulting in a flatter mid-carpal articulation. Compared with other extant felids, the cheetah has a reduced facet for the trapezium and trapezoid as well as a more obtuse angle between the trap and unciform facets, which reflects its ecology as the most cursorial extant

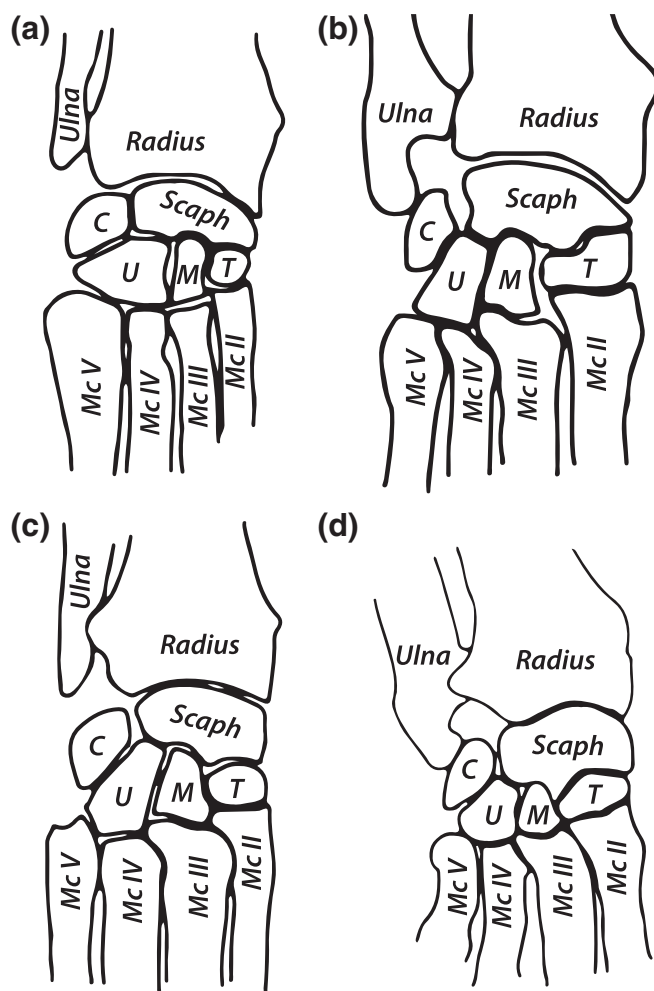


FIGURE 4 Illustrations of radius, ulna, carpal, and metacarpal articulations in (a) *Canis*, (b) *Panthera leo*, (c) *Acinonyx jubatus*, and (d) *Smilodon fatalis* to illustrate bone orientations, and contact with the radius and ulna for weight-bearing assessment. Plots (a–c) were modified from radiograph drawings by Yalden (1970), and plot (d) was created using photos from the articulated *Smilodon* skeleton at the Tar Pits Museum and modified from Merriam and Stock (1932). C, cuneiform; M, magnum; Scaph, scapholunar; T, trapezoid; U, unciform

felid. In grapplers, aka supinators, *Puma* shows a relatively large trap facet and among the smallest trap-unciform angles, reflecting not only prey-killing adaptations in *Puma*, but also its wrist manipulation in climbing, which none of the other extant species in our sample do. This corroborates ecological data on the puma showing it not only grapples prey during killing, but it also uses a wide-variety of substrates, including rocky, mountainous areas, trees, and flat ground (Young & Goldman, 1946). The main feature differentiating hyaenids from all other groups is a reduced facet for the magnum, which is likely of phylogenetic, rather than functional significance.

4.1 | Extinct species

The extinct species *M. trumani* and *S. fatalis* were the most interesting and unexpected results. *M. trumani* is dubbed the American cheetah

because of its cheetah-like morphology in the long bones (Gilbert & Martin, 1984). However, the scapholunar of *M. trumani* is unlike the scapholunar of the modern African cheetah, *A. jubatus*. It also does not resemble the scapholunar of *P. concolor*, its closest living genetic relative (Barnett et al., 2005); all of these taxa inhabit nonoverlapping regions of the morphospace defined by DF1 and DF2. The morphology of *M. trumani*'s scapholunar most closely resembles that of the extant and fossil lions. This unexpected morphology may be the result of an intermediate morphology between the highly cursorial and somewhat dog-like feet of the living cheetah that has foregone prey grappling and manipulation in exchange for increased speed, and the flexible puma that has both scansorial and prey-grappling adaptations. This suggests that *M. trumani* may have chased its prey for long distances, or at high speed, but still retained and used its ability to grapple prey and/or climb. Its dissimilarity with *Acinonyx* suggests *M. trumani* did not use its dewclaw to bring down prey in a similar way.

The position of *Smilodon* on DF1 is surprising as well. Although we would have expected *Smilodon* to hold an extreme position on DF1, it does not. It groups close to the large pantherines and closer to cheetah than expected. This appears to be driven by reduction in the size of the trap facet, which may hold some information about how *Smilodon* used its wrist during prey-killing. Additionally, *Smilodon* resembles *Puma* in radius-magnum angle, and felids generally for several other traits. Interestingly, DF3, which explains 4.2% of overall variance in our sample appears to mainly differentiate *Smilodon* from all other taxa. The two most influential variables on DF3, angles between radius-magnum and radius-trap are difficult to interpret in terms of functional significance, but this does suggest that *Smilodon* has a unique carpal morphology among felids, perhaps suggesting a specialized behavior not seen in modern analogues. These results do not negate the hypothesis that *Smilodon* was an acute grappler; however, they do add another layer to the story. As Wroe et al. (2008) noted, *Smilodon* greatly resembles a bear in forelimb morphology, and this may be reflected in the scapholunar as well. In our next project, we hope to compare *Smilodon* with bears to determine if there are analogous morphological characters in the scapholunar bone of these taxa. Insight from a future study may give us a better idea of the flexibility of *Smilodon*'s wrist.

C. dirus was unremarkable compared with modern *Canis*. It generally grouped with other canids and was not significantly different from them for any measurement except the angle between the magnum-unciform, where it was significantly different from modern *C. lupus*, but not Pleistocene *C. lupus* from Natural Trap Cave. It was likely filling the same ecological role as other canids. Additionally, *C. lupus* sp. (Pleistocene) and *P. atrox* fell into the same morphospace as their modern counterparts (*C. lupus* and *P. leo*, respectively), suggesting no major ecological changes from these extinct species to their modern relatives.

4.2 | Scapholunar as an ecological indicator

The scapholunar appears to be a useful ecological indicator. Like other podials, it conveys information about substrate use as well as phylogeny. For example, canids and hyaenids share a cursorial ecology, but occupy disparate phylogenetic positions from each other, with hyaenids being

more closely related to felids (in Feliformia, Nyakatura & Bininda-Emonds, 2012). Despite these different phylogenetic positions, canids and hyaenids are indistinguishable along DF1 and share several features related to ecology that are discernable in the scapholunar. Likewise, the scapholunar of *Acinonyx*, the most cursorial felid, differs from felids in ways that reflect its ecology and is often differentiated from its closest living relative, *Puma*. Although phylogeny is a confounding factor, it is also difficult to tease phylogeny and function apart. As families arose together in the same habitat, certain adaptations were propagated within lineages for functional reasons.

The sample in the current study is relatively limited, with only three carnivoran families and a handful of genera. In the future, we hope to be able to compare scapholunars from additional carnivoran taxa with a wider variety of locomotor ecologies to assess the usefulness of the scapholunar bone as an ecometric indicator, as in Polly (2010).

ACKNOWLEDGMENTS

We would like to thank K. Bitterman for her assistance with scanning specimens, and L. Werdelin and M. Lewis for discussion and carnivore carpal insight. We would like to thank the following people and collections for access to specimens and loans that made this project possible: E. Westwig and R. MacPhee in Mammalogy at the AMNH; M. Eiffler and R. Timm in Mammalogy at the Kansas Museum of Natural History, and D. Miao and D. Burnham in VP at the Kansas Museum; A. Ferguson and B. Patterson in Mammalogy at the Field Museum; L. Vietti at the U Wyoming Geological Museum; and A. Farrell and G. Takeuchi at the Tar Pits Museum. We also thank B. Breithaupt and G. Hurley (WY BLM) for access to Natural Trap Cave (NTC), and NTC project Co-PI A. Cooper. Additionally, we thank D. Polly and one anonymous reviewer for valuable comments on this manuscript. Funding sources include Des Moines University (student support) and NSF EAR-SGP 1425059 to J.A.M. NTC fieldwork was carried out under BLM permit PA13-WY-207.

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How to cite this article: Dunn RH, Cooper C, Lemert J, Mironov N, Meachen JA. Locomotor correlates of the scapholunar of living and extinct carnivorans. *Journal of Morphology*. 2019;1–10. <https://doi.org/10.1002/jmor.21024>