

SYMPOSIUM

Static Scaling and the Evolution of Extreme Canine Size in a Saber-Toothed Cat (*Smilodon fatalis*)

D. M. O'Brien¹

Department of Biological Sciences, Colby College, 5720 Mayflower Hill Drive, Waterville, ME 04901, USA

From the symposium “Allometry, Scaling and Ontogeny of Form” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2019 at Tampa, Florida.

¹E-mail: devin.m.obrien@gmail.com

Synopsis The canines of saber-toothed cats are a classic example of an extreme morphology, yet important questions pertaining to their evolution remain unanswered. Recent analyses suggest these structures functioned as tools of intra-sexual combat where trait size acts as both a weapon of battle and signal of competitive ability. However, classic skeletal reconstructions suggest saber-tooth canines evolved as specialized hunting tools. Either scenario could have led to the evolution of extreme canine size and distinguishing between these hypotheses is therefore difficult. This is made more challenging by the fact that natural observation of saber-toothed cats is impossible, and biologists must rely on measures of static morphology to study the patterns of selection that favored extreme canine size. Here I analyze the static intraspecific scaling relationship between canine size and body size in the saber-toothed cat, *Smilodon fatalis*, to determine whether or not extreme canine size functioned as a sexually selected signal. I review the literature surrounding the evolution of sexually selected signals and the methods recently established by O'Brien et al. (2018), show how static scaling relationships can be useful, reliable tools for inferring patterns of selection, especially in fossil organisms, and provide evidence that extreme canine size in saber-toothed cats was not the product of selection for effective sexual signals, but instead evolved as either a pure intrasexually selected weapon or a hunting tool.

Introduction

Extreme dentition is a hallmark of sexual selection (Emlen 2008; Rico-Guevara and Hurme 2018). Structures like the canines of non-human primates (Plavcan and van Schaik 1992, 1993) or the tusks of elephants (Chelliah and Sukumar 2013) are among the most recognizable products of sexual competition and are common throughout the animal world (Fig. 1). In this context, extreme dentition typically serves two overlapping roles. First, competitors may use their teeth as weapons in direct, physical altercations over potential mates (walruses, Miller 1975; elephants, Chelliah and Sukumar 2013). Animals with the largest weapons are typically the best competitors and, as a result, have the greatest reproductive success (Emlen 2008; Hardy and Briffa 2013). Second, animals may use enlarged teeth as inter- and/or intrasexual signals (non-human primates, Plavcan and van Schaik 1992; narwhals, Kelley et al. 2015). Here, the signal is the tooth itself and

information encoded in tooth size pertains to the genetic and environmental variation underlying individual fitness (hereafter referred to simply as “quality”). Receivers are either same-sex competitors who use tooth size to determine a rival’s competitive ability (Hardy and Briffa 2013; McCullough et al. 2016; O'Brien et al. 2018; Rico-Guevara and Hurme 2018) or members of the opposite sex who use exaggerated dentition to determine the suitability of potential mates (Andersson 1994; Bradbury and Vehrencamp 2011). Large, conspicuous signals allow for fast, accurate assessment of the bearer. Combined with the high morphological variation that often accompanies extreme structures (Wallace 1987; Alatalo et al. 1988; Petrie 1992; Cuervo and Møller 2001), enlarged dentition can magnify otherwise subtle differences in the quality of competitors (Wallace 1987; Hasson 1991; Tazzyman et al. 2014).

One of the most striking examples of extreme dentition is that of saber-toothed cats (Fig. 1).



Fig. 1 Extreme dental morphology. Clockwise from top left: skull of male western gorilla (*Gorilla gorilla*), enlarged canines; skull of saber-toothed cat (*Smilodon fatalis*), enlarged canines; skull of walrus (*Odobenus rosmarus*), enlarged canines; right tusk of African elephant (*Loxodonta africana*), enlarged incisor. Photo credits in acknowledgments.

Saber-toothed cats (subfamily Machairodontinae) are large, extinct felids that were characterized by elongate canines (i.e., sabers) that extended up to 28 cm in the largest species (Turner and Antón 1997). As one of the most charismatic and abundant representations of extinct megafauna, saber-toothed cats have long attracted the attention of biologists and the general public (Kurtén and Anderson 1980). However, basic questions pertaining to their evolution remain unanswered. In particular, we have yet to determine the selective pressures that led to the evolution of their extreme canine size.

There are currently two well-supported hypotheses regarding the evolution of extreme canine size in saber-toothed cats. First, these structures may have evolved as intrasexual signals that were used to compete with same-sex rivals over access to mates. Previous work suggests canine size displays the type of scaling relationship characteristic of most sexually selected signals (Turner and Antón 1997; Randau et al. 2013) and the presence of saber-shaped lesions on adult saber-tooth skulls suggests canines were used during intraspecific combat (Kurtén and Anderson 1980; Chimento et al. 2019). Alternatively, saber-tooth canines may have evolved as specialized hunting tools. Supported by several of skeletal reconstructions, this hypothesis posits that saber-toothed cats were hypercarnivorous ambush predators that used their canines in isolation to administer killing blows to large prey (Simpson 1941; Anyonge 1996; Biknevicius et al. 1996; Van Valkenburgh 2001; Figueirido et al. 2018). Under both hypotheses, selection could favor the evolution of extreme canine size. Large intrasexual signals allow for fast, reliable assessment of quality and

competitive ability (Wallace 1987; Hasson 1991; Tazzyman et al. 2014) and large predatory structures allow for increased range and speed of attack (Maldonado et al. 1967; Loxton and Nicholls 1979; Vogel 2013; Emlen 2014). Distinguishing between these hypotheses is therefore difficult, especially since natural observation of these animals is impossible. Biologists must instead rely on indirect methods of assessment, such as the study of closely related extant taxa or the analysis of static morphology (i.e., fossils), to infer patterns of selection and/or trait function, practices that, until recently, have been associated with a large degree of uncertainty (Knell and Sampson 2011; Padian and Horner 2011, 2013, 2014; Knell et al. 2013; Hone and Mallon 2017; Mallon 2017).

O'Brien et al. (2018) recently proposed a means to reliably determine trait function using measures of static morphological scaling. These methods leverage the distinct patterns of morphology produced by selection for large, sexually selected signals to identify and ascribe trait function without natural observation. They rely on the fact that when the size of a signal structure is correlated with body size, and body size is tightly correlated with individual quality, then selection for increasingly effective signals should favor the evolution of steep intraspecific scaling relationship slopes and high trait-specific coefficients of variation (CV) (Kodric-Brown and Brown 1984; Green 1992; Petrie 1992; Kodric-Brown et al. 2006; Biernaskie et al. 2014). The end result is that when viewed on a log-log scale, the slope of the scaling relationship between signal trait size and body size is significantly greater than that of other traits within the same organism. It should be noted that these

patterns are not a ubiquitous product of strong sexual selection and that sexually selected structures that do not reflect individual quality, such as genitalia (Hosken and Stockley 2004; Eberhard 2010) and sensory structures (Bertin and Cezilly 2003; O'Brien et al. 2018), do not display steep scaling relationship slopes (Bonduriansky and Day 2003; Bonduriansky 2007; Eberhard et al. 2018). Steep scaling should also be absent whenever body size does not accurately reflect individual quality (e.g., Bolger and Connolly 1989; Cuervo and Møller 2001). In the context of sexually selected *signals*, however, where body size does accurately represent individual quality, steep intraspecific scaling relationships are expected and can be used to reliably distinguish between patterns of selection that produce some extreme structures. Indeed, these methods have been used to identify patterns of selection in fossil species (*Protoceratops andrewsi*, *Rhamphorhynchus muensteri*) and in the context of extreme dental morphology (*Bitis gabonica*, *Cyclommatus metallifer*, *Ursus arctos*) (O'Brien et al. 2018).

Here, using methods adapted from O'Brien et al. (2018), I analyzed the static intraspecific scaling relationship between saber-tooth canine size and body size to determine whether or not these structures functioned as sexually selected signals. I sourced measurements of the saber-toothed cat, *Smilodon fatalis* (Fig. 1), from *Felidae of the Rancho La Brea* by Merriam and Stock (1932) and compared the scaling relationship between canine size and body size with the scaling relationship between reference traits and body size within the same organisms. I predicted that if canine size were the product of strong sexual selection, then the scaling relationship between canine size and body size would be significantly steeper than those of the reference traits and body size. Similarly, trait-specific CV would be higher for canine size than reference trait sizes. Alternately, if extreme canine size were the product of selection for specialized hunting tools, then the scaling relationship between canine size and body size would be no greater than those of the reference traits and body size and the trait-specific CV for canine size should be no greater than those of the reference traits.

Materials and methods

Measurements of *S. fatalis*

Measurements of 25 *S. fatalis* skulls were sourced from *The Felidae of Rancho La Brea* (Merriam and Stock 1932). All specimens were collected from La Brea tar pits in Los Angeles California, USA in

association with the Natural History Museum of Los Angeles County and the Carnegie Institution of Washington (Carnegie Institution of Science). All specimens were adults in which permanent dentition was present.

Measurements of body size, the focal trait (canine size), and reference traits (Table 1) were chosen in accordance with the methods established by O'Brien et al. (2018). The 20 measurements of skull size with the most complete datasets were used to estimate overall body size for each specimen. Skull size offers the most reliable metric of body size in this context, since complete skulls are easily linked with dentition from that same animal (not true for disarticulated skeletons), and skull size is tightly correlated with body mass across mammals (Damuth et al. 1990). Measurements of the focal trait included anterior–posterior canine width and transverse canine width, which were both measured at the base of the canine. Canine width provided a robust and accurate measure of canine size, since canine width (measured at the base) is (a) more resistant than canine length to damage during fossilization or excavation, (b) less susceptible than canine length to wear throughout the animal's life, and (c) scales with body size in a pattern similar to overall canine length, the putative signal trait (Randau et al. 2013).

Reference traits were chosen as five measurements of non-canine dentition that were not expected to be correlated with canine size through development (Michon et al. 2010; Salazar-Ciudad and Jernvall 2010) or selection, regardless of the pattern of selection that favored extreme canine size. If, for example, extreme canine size is the result of sexual selection, then only the conspicuous, protruding canines should experience selection for increased size, not the remaining dentition (Turner and Antón 1997; Maynard Smith and Harper 2003; Bradbury and Vehrenkamp 2011; O'Brien 2018). Similarly, if extreme canine size evolved via selection for effective predation tools, then selection should act on canines in near isolation, since the overwhelming majority of reconstructions suggest saber-toothed cats used their canines independently of the remaining dentition (Butler 1939; Simpson 1941; Akersten 1985; Anyonge 1996). Weak correlations between canine size and the size of non-canine dentition were verified using Pearson correlation coefficients (below).

Statistical analysis

All analyses were performed in R 3.5.2 (R Core Development Team 2018). Mean trait size (μ) and standard error (SE) were calculated for all raw

Table 1 Summary focal, reference, and body size traits including mean trait size and standard error (SE).

Trait	Trait type	n	Mean trait size (mm)	SE
Canine (anterior–posterior diameter)	Focal	24	42.05	0.538
Canine (transverse diameter)	Focal	24	19.675	0.852
Premolar 3 (anterior–posterior diameter)	Reference	17	17.118	0.329
Premolar 4 (anterior–posterior diameter)	Reference	22	40.145	0.538
Premolar 4 (transverse diameter)	Reference	22	16.523	0.33
Premolar 4 (anterior–posterior diameter of base)	Reference	19	12.347	0.183
Premolar 4 (length—base to anterior end)	Reference	18	9.811	0.187
Skull length (anterior end of premaxillary to posterior end of condyles)	Body size	25	308.576	4.793
Basal skull length (anterior end of premaxillary to inferior notch between condyles)	Body size	25	293.884	4.503
Skull length (anterior end of premaxillary to posterior end of inion)	Body size	25	332.368	6.325
Skull length (anterior end of premaxillary to anterior end of posterior nasal opening)	Body size	25	162.552	4.745
Palate length	Body size	24	140.85	2.234
Skull length (posterior end of glenoid cavity to posterior end of condyles)	Body size	24	100.558	2.203
Anterior–posterior diameter of nasals	Body size	24	82.358	1.657
Width of anterior nares	Body size	24	54.938	0.875
Greatest width across muzzle at canines	Body size	24	101.279	4.188
Least width between superior borders of orbit	Body size	25	94.268	1.215
Width across postorbital processes	Body size	23	118.513	1.651
Width across postorbital constriction	Body size	25	60.416	0.75
Greatest width across zygomatic arches	Body size	24	204.625	5.628
Anterior palatal width between superior canines	Body size	24	56.917	0.83
Posterior palatal width between inner roots of superior carnassials	Body size	24	98.371	4.435
Width across palate between posterior alveoli of superior carnassials	Body size	24	127.467	1.462
Greatest transverse diameter across auditory bulla	Body size	24	54.179	1.099
Greatest width across mastoid processes	Body size	24	133.613	2.211
Greatest diameter across condyles	Body size	25	65.02	0.772
Height of anterior zygomatic pedicle	Body size	24	57.225	1.25
Length of anterior zygomatic pedicle	Body size	24	51.904	0.734

measurements of body size, the focal trait, and reference traits.

Data were log transformed prior to the remaining analyses. Mean trait size and the trait-specific CV ($CV = \frac{\sigma}{\mu} * 100$) were calculated for all measurements of the focal trait and reference traits. Mean CV was also calculated for the focal trait and reference traits and compared using a one-tailed Welch's two sample *t*-test.

Focal trait size and reference trait size were regressed on body size in separate models using ordinary least squares (OLS) regression. For this test, principal component analyses (PCA; R package FactoMineR [Le et al. 2008]) were used to estimate overall focal trait size, reference trait size, and body size. In each PCA, PC1 explained the majority of variation in overall trait size (focal trait size: 53%;

reference trait size: 44%; body size: 57%) and was used as an estimate of overall size for that trait. The slopes of these scaling relationships were compared using 95% confidence intervals and analyses of covariance (ANCOVA). PCAs were also used to calculate Pearson correlation coefficients to confirm weak correlations between canine size and the size of non-canine dentition. Correlation coefficients were calculated for focal trait PC1 and reference trait PC1 and separately for focal trait PC1 and each morphological measure that comprised reference trait PC1 (Table 2).

A generalized linear mixed-effects model was also used to assess the effect of trait type (focal/reference) on the scaling relationship slope between trait size and body size [R package lmerTest (Kuznetsova et al. 2017)]. For this test, raw trait measurements were

Table 2 Summary of log-transformed measurements of focal and reference traits, including mean trait size, trait-specific coefficient of variation, and Pearson Correlation Coefficient between canine size (focal trait size) PC1 and each reference trait.

Trait	Trait type	n	Mean trait size	Coefficient of variation	Correlation coefficient
Canine (anterior–posterior diameter)	Focal	24	3.737	1.704	
Canine (transverse diameter)	Focal	23	3.015	2.82	
Premolar 3 (anterior–posterior diameter)	Reference	17	2.229	2.996	0.227
Premolar 4 (anterior–posterior diameter)	Reference	22	3.691	1.738	0.379
Premolar 4 (transverse diameter)	Reference	22	2.801	3.265	0.219
Premolar 4 (anterior–posterior diameter of base)	Reference	19	2.521	2.54	0.261
Premolar 4 (length:base to anterior end)	Reference	18	2.28	3.604	0.341

used rather than estimates from the PCA. The model included trait type (focal/reference) as a fixed effect and trait (i.e., Table 1, Column 1) and specimen number as random effects with random slopes and intercepts.

Results

Mean trait size and standard error for raw measurements of all traits are summarized in Table 1. Mean trait size and trait-specific CV for log-transformed focal and reference traits are summarized in Table 2. Pearson correlation coefficients confirmed relatively weak correlations between focal trait size PC1 and reference trait size PC1 ($r=0.431$) and between focal trait size PC1 and each raw reference trait size measurement (Table 2). Overall, there was no significant difference between the CVs of focal and reference traits (mean $CV_{\text{focal}}=2.262$; mean $CV_{\text{reference}}=2.829$; $t_{1.736}=-0.878$, $P=0.484$; Table 2).

Focal trait size increased as body size increased with a shallow, positive slope ($\beta=0.126\pm0.188$, $F_{1,23}=4.85$, $P=0.038$). Reference trait size also increased as body size increased with a shallow, positive slope ($\beta=0.306\pm0.099$, $F_{1,23}=9.541$, $P<0.01$) (Fig. 2). Overall, the scaling relationship slope between focal trait size and body size was not greater than that of reference trait size and body size. Ninety-five percent confidence intervals surrounding the scaling relationship slopes were overlapping (focal trait [0.008, 0.244]; reference trait [0.101, 0.51]) and the ANCOVA suggested that focal trait size does not scale at a significantly different rate with body size than do the reference traits ($F_{1,46}=3.938$, $P=0.053$). Results from the generalized linear mixed-effects model also indicate that focal trait size does not scale with body size at a different rate than do the reference traits. Here, trait size increased with overall body size ($t_{0.14}=3.01$, $P=0.009$), but there was no significant effect of trait type (focal/reference) on the scaling relationship

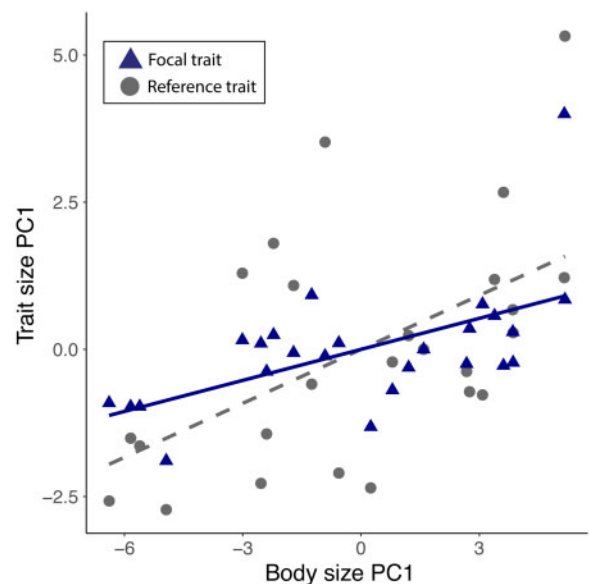


Fig. 2 Static scaling relationship between trait size PC1 and body size PC1 for canines (triangles, solid line) and non-canine dentition (circles, dotted line). Lines represent OLS regressions (focal: $y=0.16x + 3.81e-15$, $F_{1,23}=9.68$, $P<0.01$, $R^2=0.296$; reference: $y=0.31x + 1.4e-14$, $F_{1,23}=9.541$, $P<0.01$, $R^2=0.401$).

slope between trait size and body size (body size || trait type: $t_{5,2}=1.565$, $P=0.18$).

Discussion

The canines of saber-toothed cats represent some of the most extreme dental morphology in the animal world. Such extreme dentition typically functions as a sexually selected signal where the size of the structure displays the quality of the bearer (Emlen 2008; Rico-Guevara and Hurme 2018). Tooth size is correlated with overall body size and body size is correlated with individual quality. Through this connection, tooth size becomes a clear indicator of quality that experiences selection for exceedingly steep scaling relationship slopes and high within-species variation (Andersson 1982; Wallace

1987; Alatalo et al. 1988; Petrie 1992; Cuervo and Møller 2001). These patterns appear true for nearly every sexually selected signal studied to date and, when present, provide compelling evidence for a history of strong sexual selection (Emlen 2008; Eberhard et al. 2018; O'Brien et al. 2018; Rico-Guevara and Hurme 2018). To date, however, it has been unclear whether or not saber-toothed cat canines evolved in response to selection for effective sexual signals and consequently display these patterns of morphology (Simpson 1941; Randau et al. 2013; Figueirido et al. 2018).

Here, the static intraspecific scaling relationship between canine size and body size was analyzed in the saber-toothed cat, *S. fatalis*, to examine whether or not these structures functioned as sexual signals. Overall, the scaling relationship between canine size and body size was not significantly different than that of the reference traits and body size (Fig. 2) and trait-specific CVs were not significantly different between the focal and reference traits (Table 2). This is in contrast to previous work by Randau et al. (2013) where a steep interspecific scaling relationship was clearly identified across saber-toothed feliforms (Nimravidae, Barbourofelidae, Machairodontinae; including *S. fatalis*). Together, these results suggest the canines of *S. fatalis* did not function as signals of quality, since selection for effective sexual signals reliably produces steep intraspecific scaling relationship slopes and high trait-specific CVs (Andersson 1982; Maynard Smith and Harper 2003; Bradbury and Vehrencamp 2011; Eberhard et al. 2018; O'Brien 2018). Instead, these structures likely performed a non-signal function either as "pure weapons" of intrasexual competition or specialized predatory structures where selection favored the evolution of extreme trait size across species but not the evolution of steep scaling relationship slopes within species (McCullough et al. 2016; O'Brien et al. 2018).

Sexually selected structures lie along a continuum that ranges from "pure weapons," which serve no signal function, to "pure signals," which function only to display individual quality (McCullough et al. 2016). The majority of intrasexually selected weapons fall somewhere in between and serve dual function as both tools of combat and signals of quality (Andersson 1982; Bradbury and Vehrencamp 2011; Hardy and Briffa 2013; McCullough et al. 2016; O'Brien et al. 2018; Rico-Guevara and Hurme 2018). The canines of saber-toothed cats, however, may represent a rare case of a pure weapon, where individual quality is not encoded in the relationship between canine size and body size and canine size therefore serves no signal function. If

true, then saber-tooth canines should have neither steep scaling relationship slopes nor high CVs (McCullough et al. 2016; O'Brien et al. 2018). Large teeth may offer a competitive advantage through increased reach and/or faster attack, but this advantage would be experienced by the entire population, regardless of body size. Selection for large pure weapons should therefore favor intraspecific scaling relationships with high intercepts and shallow slopes, which may then manifest as steep interspecific scaling relationships (e.g., Randau et al. 2013). Furthermore, unlike weapon-signals, steep intraspecific scaling relationship slopes and high CVs would likely hinder pure-weapons. In weapon-signal systems, high cost weapons are often maintained by steep scaling relationship slopes that produce large animals with exceedingly large relative weapons sizes (Zeh and Zeh 1988; Green 1992; Petrie 1992; Bonduriansky and Day 2003; Kodric-Brown et al. 2006; Biernaskie et al. 2014). These large weapons come at a justifiable cost, which is essential for signal honesty when weapons indicate quality but provides no benefit for non-signal systems. Selection on pure-weapon systems may therefore mitigate unnecessary cost by reducing the intraspecific scaling relationship slope and decreasing weapon size in the largest animals where absolute cost is greatest (Harvey and Gange 2006; McCullough et al. 2014, 2015; Mills et al. 2016; O'Brien et al. 2017). Non-signal systems also gain no benefit from morphological hypervariation. The magnification of subtle differences in quality is irrelevant in non-signal systems and even subtle variation in weapon size/shape may hinder systems that rely on a particular weapon morphology (Kawano 1997; Dennenmoser and Christy 2013; McCullough et al. 2014, 2015; O'Brien et al. 2017; O'Brien and Boisseau 2018).

Selection for pure hunting tools may also produce extreme trait sizes without increasing the intraspecific scaling relationship slope (O'Brien et al. 2018). Like pure intrasexual weapons, pure hunting tools can benefit from large sizes that increase the range and speed of attack (Maldonado et al. 1967; Loxton and Nicholls 1979; Emlen 2014), but steep scaling relationship slopes and the associated hypervariation may decrease hunting efficacy. This may explain why the scaling relationship between canine and body size in *S. fatalis* was relatively shallow compared with that of the reference traits (Fig. 2). When a particular morphology is required for effective prey capture regardless of body size (e.g., Cresswell 1993; Turingan et al. 1995; Labropoulou and Eleftheriou 1997; Benkman 2003; Snowberg et al. 2015), then shallow

scaling relationships that produce proportional trait sizes across a range of body sizes should be the norm. Indeed, many structures that require particular morphologies for proper function, such as genitalia, tend to display especially shallow scaling relationships (Bonduriansky and Day 2003; Eberhard 2010; Emlen et al. 2012; Eberhard et al. 2018; O'Brien 2018; Rodríguez and Eberhard 2019) and analyses of extant felids suggest that selection for large hunting tools can produce extreme canine sizes without the scaling relationship slopes characteristic of sexually selected signals (Therrien 2005; Christiansen 2006, 2008; Slater and Van Valkenburgh 2008).

Overall, the evidence suggests that extreme canine size in the saber-toothed cat, *S. fatalis*, was not the product strong selection for effective sexual signals. The slope of the static intraspecific scaling relationship between canine size and body size was not different from that of the reference traits and trait-specific CVs were not different between focal and reference traits. Instead, extreme canine size was likely the product of selection for large, pure weapons or pure predation tools since, in both scenarios, selection would have favored the evolution of exceedingly large structures across species, but not steep scaling relationship slopes within species. Future work should be aimed at developing concrete methodology to distinguish between these alternatives, perhaps by assessing patterns of sexual dimorphism within and across species or through behavioral studies of closely related, extant taxa.

Acknowledgments

I would like to thank Ciresse Allen, Melissa Van Kleeck, Dave Hone, Rob Knell, Andrew Knapp, Stuart Christiansen, and Doug Emlen for help in formulating the ideas and methods presented herein and John C. Marriam and Chester Stock for collecting the data published in *The Felidae of the Rancho La Brea*. I would also like to thank Fred Nijhout and Kenneth McKinna for organizing the SICB 2019 symposium that inspired this publication and others, as well my fellow symposium contributors for their valued feedback. Finally, I would like to thank Dave Angelini, Josh Steele, and the remaining Angelini laboratory for feedback on early manuscript drafts. Figure 1 image credit clockwise from top left: Didier Descouens (CC BY-SA 4.0), background removed, Wallace63 (CC BY-SA 3.0), cropped, Mike Peel (CC BY-SA 2.0), background removed, Pawan Sharma (via Unsplash), background removed.

References

- Akersten WA. 1985. Canine function in *Smilodon* (Mammalia; Felidae; Machairodontinae). Los Angeles County: Natural History Museum.
- Alatalo RV, Höglund J, Lundberg A. 1988. Patterns of variation in tail ornament size in birds. *Biol J Linn Soc* 34:363–74.
- Andersson M. 1982. Sexual selection, natural selection and quality advertisement. *Biol J Linn Soc* 17:375–93.
- Andersson MB. 1994. Sexual selection. Princeton, NJ USA: Princeton University Press.
- Anyonge W. 1996. Microwear on canines and killing behavior in large carnivores: saber function in *Smilodon fatalis*. *J Mammal* 77:1059–67.
- Benkman CW. 2003. Divergent selection drives the adaptive radiation of crossbills. *Evolution* 57:1176–81.
- Bertin A, Cezilly F. 2003. Sexual selection, antennae length and the mating advantage of large males in *Asellus aquaticus*. *J Evol Biol* 16:698–707.
- Biernaskie JM, Grafen A, Perry JC. 2014. The evolution of index signals to avoid the cost of dishonesty. *Proc R Soc Lond B Biol Sci* 281:20140876.
- Biknevicius AR, Valkenburgh BV, Walker J. 1996. Incisor size and shape: implications for feeding behaviors in saber-toothed “cats.” *J Vert Paleontol* 16:510–21.
- Bolger T, Connolly PL. 1989. The selection of suitable indices for the measurement and analysis of fish condition. *J Fish Biol* 34:171–82.
- Bonduriansky R. 2007. Sexual selection and allometry: a critical reappraisal of the evidence and ideas. *Evolution* 61:838–49.
- Bonduriansky R, Day T. 2003. The evolution of static allometry in sexually selected traits. *Evolution* 57:2450–8.
- Bradbury JW, Vehrencamp SL. 2011. Principles of animal communication. 2nd ed. Oxford, UK: Oxford University Press.
- Butler PM. 1939. Studies of the mammalian dentition. Differentiation of the post-canine dentition. *Proc Zool Soc Lond* B109:1–36.
- Chelliah K, Sukumar R. 2013. The role of tusks, musth and body size in male–male competition among Asian elephants, *Elephas maximus*. *Anim Behav* 86:1207–14.
- Chimento NR, Agnolin FL, Soibelzon L, Ochoa JG, Buide V. 2019. Evidence of intraspecific agonistic interactions in *Smilodon populator* (Carnivora, Felidae). *Comptes Rendus Palevol* (doi: <https://doi.org/10.1016/j.crpv.2019.02.006>).
- Christiansen P. 2006. Sabertooth characters in the clouded leopard (*Neofelis nebulosa* Griffiths 1821). *J Morphol* 267:1186–98.
- Christiansen P. 2008. Evolutionary convergence of primitive sabertooth craniomandibular morphology: the clouded leopard (*Neofelis nebulosa*) and *Paramachairodus ogygia* compared. *J Mammal Evol* 15:155–79.
- Cresswell JE. 1993. The morphological correlates of prey capture and resource parasitism in pitchers of the carnivorous plant *Sarracenia purpurea*. *Am Midl Nat* 129:35–41.
- Cuervo JJ, Møller AP. 2001. Components of phenotypic variation in avian ornamental and non-ornamental feathers. *Evol Ecol* 15:53–72.
- Damuth JD, Damuth J, MacFadden BJ, John D. 1990. Body size in mammalian paleobiology: estimation and biological implications. Cambridge UK: Cambridge University Press.

- Dennenmoser S, Christy JH. 2013. The design of a beautiful weapon: compensation for opposing sexual selection on a trait with two functions. *Evolution* 67:1181–8.
- Eberhard WG. 2010. Evolution of genitalia: theories, evidence, and new directions. *Genetica* 138:5–18.
- Eberhard WG, Rodríguez RL, Huber BA, Speck B, Miller H, Buzatto BA, Machado G. 2018. Sexual selection and static allometry: the importance of function. *Quart Rev Biol* 93:207–50.
- Emlen DJ. 2008. The evolution of animal weapons. *Annu Rev Ecol Syst* 39:387–413.
- Emlen DJ. 2014. Animal weapons: the evolution of battle. New York, NY: Henry Holt and Company.
- Emlen DJ, Warren IA, Johns A, Dworkin I, Lavine LC. 2012. A mechanism of extreme growth and reliable signaling in sexually selected ornaments and weapons. *Science* 337:860–4.
- Figueirido B, Lautenschlager S, Pérez-Ramos A, Van Valkenburgh B. 2018. Distinct predatory behaviors in scimitar- and dirk-toothed sabertooth cats. *Curr Biol* 28:3260–6.
- Green AJ. 1992. Positive allometry is likely with mate choice, competitive display and other functions. *Anim Behav* 43:170–2.
- Hardy IC, Briffa M. 2013. Animal contests. Cambridge, UK: Cambridge University Press.
- Harvey DJ, Gange AC. 2006. Size variation and mating success in the stag beetle, *Lucanus cervus*. *Physiol Entomol* 31:218–26.
- Hasson O. 1991. Sexual displays as amplifiers: practical examples with an emphasis on feather decorations. *Behav Ecol* 2:189–97.
- Hone DW, Mallon JC. 2017. Protracted growth impedes the detection of sexual dimorphism in non-avian dinosaurs. *Palaeontology* 60:535–45.
- Hosken DJ, Stockley P. 2004. Sexual selection and genital evolution. *Trends Ecol Evol* 19:87–93.
- Kawano K. 1997. Cost of evolving exaggerated mandibles in stag beetles (Coleoptera: Lucanidae). *Ann Entomol Soc Am* 90:453–61.
- Kelley TC, Stewart REA, Yurkowski DJ, Ryan A, Ferguson SH. 2015. Mating ecology of beluga (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*) as estimated by reproductive tract metrics. *Mar Mammal Sci* 31:479–500.
- Knell RJ, Naish D, Tomkins JL, Hone DW. 2013. Is sexual selection defined by dimorphism alone? A reply to Padian and Horner. In: Paul Craze, editor. *Proceedings of the Zoological Society London*, Vol 28, CiteSeer: Trends in Ecology and Evolution (Cell Press). p. 491–562.
- Knell RJ, Sampson S. 2011. Bizarre structures in dinosaurs: species recognition or sexual selection? A response to Padian and Horner. *J Zool* 283:18–22.
- Kodric-Brown A, Brown JH. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *Am Nat* 124:309–23.
- Kodric-Brown A, Sibly RM, Brown JH. 2006. The allometry of ornaments and weapons. *Proc Natl Acad Sci U S A* 103:8733–8.
- Kurtén B, Anderson E. 1980. Pleistocene mammals of North America. New York (NY): Columbia University Press.
- Kuznetsova A, Brockhoff PB, Christensen RHB. 2017. lmerTest package: tests in linear mixed effects models. *J Stat Softw* 82:1–26.
- Labropoulou M, Eleftheriou A. 1997. The foraging ecology of two pairs of congeneric demersal fish species: importance of morphological characteristics in prey selection. *J Fish Biol* 50:324–40.
- Le S, Josse J, Husson F. 2008. FactoMineR: an R package for multivariate analysis. *J Stat Softw* 25:1–18.
- Loxton RG, Nicholls I. 1979. The functional morphology of the praying mantis forelimb (Dictyoptera: Mantodea). *Zool J Linn Soc* 66:185–203.
- Maldonado H, Levin L, Pita J. 1967. Hit distance and the predatory strike of the praying mantis. *Z Vergl Physiol* 56:237–57.
- Mallon JC. 2017. Recognizing sexual dimorphism in the fossil record: lessons from nonavian dinosaurs. *Paleobiology* 43:495–507.
- Maynard Smith J, Harper D. 2003. Animal signals. Oxford: OUP.
- McCullough EL, Ledger KJ, Moore TY. 2015. Variation in cross-sectional horn shape within and among rhinoceros beetle species. *Biol J Linn Soc* 115:810–7.
- McCullough EL, Miller CW, Emlen DJ. 2016. Why sexually selected weapons are not ornaments. *Trends Ecol Evol* 31:742–51.
- McCullough EL, Tobalske BW, Emlen DJ. 2014. Structural adaptations to diverse fighting styles in sexually selected weapons. *Proc Natl Acad Sci U S A* 111:14484–8.
- Merriam JC, Stock C. 1932. The Felidae of Rancho La Brea. Carnegie Institution of Washington.
- Michon F, Tummers M, Kyryönen M, Frilander MJ, Thesleff I. 2010. Tooth morphogenesis and ameloblast differentiation are regulated by micro-RNAs. *Dev Biol* 340:355–68.
- Miller EH. 1975. Walrus ethology. I. The social role of tusks and applications of multidimensional scaling. *Can J Zool* 53:590–613.
- Mills MR, Nemri RS, Carlson EA, Wilde W, Gotoh H, Lavine LC, Swanson BO. 2016. Functional mechanics of beetle mandibles: honest signaling in a sexually selected system. *J Exp Zool* 325:3–12.
- O'Brien DM. 2018. On the evolution of “extreme” morphology: patterns of cost and benefit in sexually selected weapons [PhD thesis].
- O'Brien DM, Allen CE, Van Kleeck MJ, Hone D, Knell R, Knapp A, Christiansen S, Emlen DJ. 2018. On the evolution of extreme structures: static scaling and the function of sexually selected signals. *J Anim Behav* 144:95–108.
- O'Brien DM, Boisseau RP. 2018. Overcoming mechanical adversity in extreme hindleg weapons. *PLoS ONE* 13:e0206997.
- O'Brien DM, Katsuki M, Emlen DJ. 2017. Selection on an extreme weapon in the frog-legged leaf beetle (*Sagra femorata*). *Evolution* 71:2584–98.
- Padian K, Horner JR. 2011. The evolution of ‘bizarre structures’ in dinosaurs: biomechanics, sexual selection, social selection or species recognition? *J Zool* 283:3–17.
- Padian K, Horner JR. 2013. Misconceptions of sexual selection and species recognition: a response to Knell et al. and to Mendelson and Shaw. *Trends Ecol Evol* 28:249–50.

- Padian K, Horner JR. 2014. The species recognition hypothesis explains exaggerated structures in non-avian dinosaurs better than sexual selection does. *Comptes Rendus Palevol* 13:97–107.
- Petrie M. 1992. Are all secondary sexual display structures positively allometric and, if so, why? *Anim Behav* 43:173–5.
- Plavcan JM, van Schaik CP. 1992. Intrasexual competition and canine dimorphism in anthropoid primates. *Am J Phys Anthropol* 87:461–77.
- Plavcan JM, Van Schaik CP. 1993. Canine dimorphism. *Evol Anthropol Issues News Rev* 2:208–14.
- Randau M, Carbone C, Turvey ST. 2013. Canine evolution in sabretoothed carnivores: natural selection or sexual selection? *PLoS ONE* 8:e72868.
- R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rico-Guevara A, Hurme KJ. 2018. Intrsexually selected weapons. *Biol Rev* published online (doi:10.1111/brv.12436).
- Rodríguez RL, Eberhard WG. 2019. Why the static allometry of sexually-selected traits is so variable: the importance of function. *Integr Comp Biol* published online (doi: 10.1093/icb/icz039).
- Salazar-Ciudad I, Jernvall J. 2010. A computational model of teeth and the developmental origins of morphological variation. *Nature* 464:583–6.
- Simpson GG. 1941. The function of saber-like canines in carnivorous mammals. *Am Mus Nat Hist*. 1–12.
- Slater GJ, Van Valkenburgh B. 2008. Long in the tooth: evolution of sabertooth cat cranial shape. *Paleobiology* 34:403–19.
- Snowberg LK, Hendrix KM, Bolnick DI. 2015. Covarying variances: more morphologically variable populations also exhibit more diet variation. *Oecologia* 178:89–101.
- Tazzyman SJ, Iwasa Y, Pomiankowski A. 2014. Signaling efficacy drives the evolution of larger sexual ornaments by sexual selection. *Evolution* 68:216–29.
- Therrien F. 2005. Feeding behaviour and bite force of sabretoothed predators. *Zool J Linn Soc* 145:393–426.
- Turingan RG, Wainwright PC, Hensley DA. 1995. Interpopulation variation in prey use and feeding biomechanics in Caribbean triggerfishes. *Oecologia* 102:296–304.
- Turner A, Antón M. 1997. The big cats and their fossil relatives: an illustrated guide to their evolution and natural history. New York (NY): Columbia University Press.
- Van Valkenburgh B. 2001. Predation in sabre-tooth cats. *Palaeobiology* II:420–3.
- Vogel S. 2013. Comparative biomechanics: life's physical world. Princeton, NJ, USA: Princeton University Press.
- Wallace B. 1987. Ritualistic combat and allometry. *Am Nat* 129:775–6.
- Zeh DW, Zeh JA. 1988. Condition-dependent sex ornaments and field tests of sexual-selection theory. *Am Nat* 132:454–9.