Sizing Up Swords: Correlated Evolution of Antlers and Tusks in Ungulates

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Abstract

Most sexual weapons in sexual combat and visual displays of dominance (e.g., antlers, horns) show positively allometry with body size for both growth during development and evolution across species, but allometry in species with more than one sexual weapon is unstudied. We examined the allometric relationships between body size and tusks (pure combat weapons) and/or antlers (both a visual signal and combat weapon) from forty-three artiodactyl species including the muntjaks (Muntiacinae), which uniquely have both antlers and tusks. We found that in Muntiacinae antler length scales positively allometrically with skull length, whereas tusk size scales isometrically suggesting greater energy investment in antlers as signals over tusks as combative weapons when both are present. Interspecifically, we found that species who possess only one weapon (either solely tusked or solely antlered) scaled positively allometrically with body mass, and the latter relationship levels off at larger body sizes. In our tusk analysis, when we included Muntiacinae species the positive allometric trend was not conserved resulting in an isometric relationship suggesting the possession of antlers negatively affect the energy investment in tusks as weapons. Overall, our findings show that species that possess dual weapons unproportionally invest energy in the development and maintenance of their multiple weapons.

Introduction

Sexual weapons are used in physical combat to secure mating opportunities; victorious males typically have larger body size and larger sexual weapons as a direct result of intrasexual selection (Geist 1999; Emlen 2008; McCullough et al. 2016; Sol et al. 2020). Structures that serve as intrasexual signals and weapons (e.g., ungulate antlers and horns) typically exhibit positive allometry in both developmental growth and evolution: As individuals grow and species evolve larger body sizes, they grow and evolve disproportionately larger ornaments than smaller individuals and species (Gould 1974; McCullough et al. 2015; Rico-Guevara and Hurme 2018; Somjee et al. 2021). Larger, stronger individuals invest more energy into these presumably honest signals of strength in order to avoid costly or injurious fights (Barrette 1977; Emlen 2008). Pure sexual weapons (e.g., tusks, claws, rhinoceros beetle horns), however, have evolved to provide advantages during intrasexual fights, are only used in combat, and thus provide little signaling value (McCullough et al. 2016; Rico-Guevara and Hurme 2018; Sol et al. 2020). Few studies, though, have examined static allometric growth or allometric evolution of these pure, non-signaling, sexual weapons, and even fewer examine these allometric relationships in species with multiple sexual weapons. In this study, we investigate the allometric relationships that influence the growth and evolution of tusks and antlers as sexual weapons within and among the artiodactyl families Tragulidae, Moschidae, and Cervidae, and among the Muntiacinae, the only ungulate group with both sexual weapons.

Sexual weaponry is a result of intrasexual selection (Emlen 2008), and weapons can vary in size, shape, and purpose across several classes of animals (McCullough et al. 2016). Sexual ornaments range between pure sexual weapons (e.g. beetle horns and mandibles) to pure sexual signals (e.g. eye stalks in flies). Weapons that fall in the middle of this continuum, such as ungulate antlers and fiddler crab claws, can serve both functions (McCullough et al. 2016). Beetle horns, for example, increase with body size and usually become the stronger strategy for attaining mates through physical combat rather than other non-combat sexual mating strategies (Moczek and Emlen 2000; McCullough et al. 2015). Some sexual weapons, though, can serve dual functions, as they are very often used as visual signals of dominance (McCullough et al. 2016; Rico-Guevara and Hurme 2018) and/or fighting ability (Mills et al. 2016) to other males. The large complex antler racks of male deer, for example, are critical fighting weapons of combat, are honest signals of their bearer's strength and size, and may be used in

female assessment of males (Vanpe et al. 2007). While antlers (and horns in bovids) are the more common sexual weapon among artiodactyls, tusks are the sole weapon in several groups and grow along with antlers in the Muntiacinae (muntjaks and tufted deer). This presence of dual weaponry in ungulates provides an opportunity to understand how selection may prioritize growth and maintenance of one weapon over the other and whether there are constraints on the size of such structures.

Possession of tusk-like canine teeth is the ancestral state for all Artiodactyls, with antlers, horns, and pronghorns evolving later in the cervids, bovids, and antilocaprids, respectively (Cabrera & Stankowich, 2018). Tusks were retained in the mouse deer and chevrotains (Tragulidae: three genera *Moschiola*, *Hyemoschus*, and *Tragulus*; Wilson and Mittermeier 2011), which are nocturnal and live in dense forests (Prothero 2007). Adult males use their large upper canines to attack in a sideways slashing motion targeting the neck and head of their opponent (Matsubayashi et al. 2003); these fights are likely often fatal (Prothero 2007). As ungulates evolved larger body sizes and moved into more open habitats, large tusks were lost with the evolution of antlers, horns, and pronghorns, but were re-evolved as the sole combat weapon in the Chinese water deer (Cervidae: *Hydropotes*; Fig. 1C) and musk deer (Moschidae: *Moschus*; Fig. 1D), both of which lack antlers but possess very large upper canines that reach 10 cm in length (Aitchison 1946; Fennessy 1984; Cabrera and Stankowich 2018). Living a “slinker” lifestyle in closed, forested environments favors the evolution of smaller “duiker”-like bodies for easier maneuverability (Geist 1999; Cabrera and Stankowich 2018), makes close-range combat essential for territory maintenance (Wilson and Mittermeier 2011), and favors the evolution and retention of tusks as the primary combat weapon in Artiodactyls (Cabrera and Stankowich 2018), where larger tusked males hold the best territories (Cooke, 2019). This lifestyle also likely results in minimal sexual selective pressure favoring an additional visual signal of dominance (i.e., antlers; Cabrera & Stankowich 2018). Open grassland habitats, on the other hand, favor visual displays of dominance rather than physical combat, which should result in larger ornamental weapons like antlers and horns and shorter tusks, which are limited in their ability to signal dominance from longer distances (Emlen 2008).

Within the cervids, the Muntiacinae (*Muntiacus* (Fig. 1A) and *Elaphodus* (Fig. 1B)) are very primitive deer that possess both tusks and antlers, and their antlers may have evolved in parallel with other cervids rather than being shared by their common ancestor (Groves and Grubb 1990). Males use large 2–4 cm upper canines, which begin emerging as early as five months and reach their maximum length around year five (Cooke, 2019), in physical combat to maintain control of access to mates (Fennessy 1984; Geist 1999). Tusks. In muntjaks, tusks are their main weapon; thus, damage to them can result in loss of territory and reduced mating opportunities (Cooke 2019). *Elaphodus* have the smallest antlers of all deer; they do not shed annually, and are so small that they can only be seen by parting the long tufts of hair on the pedicles (Fennessy 1984; Groves and Grubb 1990). Muntjaks have very long, permanent antler pedicels with short deciduous antlers (Fig. 1A; Fig. 2B; Cooke 2019). Muntjaks perform a “dominance display” before potential fights to deter the weaker opponent from engagement, which results in a reduction in frequency of fights (Barrette 1977) similar to other antlered deer. Because the Muntiacinae possess both versions of combat weaponry, they provide an opportunity to compare the allometric developmental and evolutionary relationships for species with two distinct types of sexual weapons: one pure weapon (tusks) and one signal/weapon (antlers).

The allometric relationships (static and evolutionary) between sexual ornaments/weapons and body size have been studied for several types of weapons in different taxa. Previously, it was assumed that most sexually selected traits scale positively allometrically with body size (Kodric-Brown et al. 2006; O'Brien et al. 2018), and

there are plenty studies that support positive static allometric relationships between sexually selected traits and body size (Simmons and Tomkins 1996; Kodric-Brown et al. 2006; Ñoñiguez et al. 2019; Graham et al. 2020; Powell et al. 2020). Evolutionarily, however, there has been recent support that positive allometry, while common, is not a universal rule in sexually selected traits (Bonduriansky and Day 2003; Pomfret and Knell 2006; Eberhard et al. 2018; O'Brien et al. 2018; Somjee et al. 2021). For example, Bonduriansky (2007) summarized that some weapons and ornaments can scale isometrically or negatively allometrically, and O'Brien and colleagues (2018) suggested that the positive allometry hypothesis for sexually selected traits should only be applied to visual signals of body size or quality and be tested against a reference trait without signaling function. Cranial weapons in bovids, cervids, and beetle species, indeed, have a positively allometric relationship with body mass in smaller species, but it levels off in larger species (i.e., weapons stop increasing in length with body mass in larger species), suggesting that there are physical constraints on growing and maintaining bigger weapons at very large body masses (Emlen 1996; Lemaitre et al. 2009; McCullough et al. 2015; Romiti et al. 2015; Tidière et al. 2017; Chen et al. 2020). Although, recent evidence suggests that, intraspecifically, continued positively allometrically scaling weapons at extreme sizes may be possible through lower metabolic rates (Somjee et al. 2021). Gould (1974) found that the massive extinct Irish Elk (*Megaloceros giganteus*) violates this physical constraint explanation in cervids as their antlers are on the same positively allometric trajectory as smaller cervids. Whereas the equally large moose (*Alces* spp) fall well below this trajectory and likely drive the appearance of physical constraints on larger antlers in large extant cervids (Gould 1974). Tusks have evolved independently across multiple mammalian taxa (e.g., whales, elephants, ungulates), but their static and evolutionary allometric growth patterns are not well understood. Tusk girth, weight, and length in male narwhals (*Monodon monoceros*) all had positively allometric relationships with body length (Gerson and Hickie 2011). It is unknown how the presence of both a pure weapon and a weapon/ornament in the same species will alter allometric relationships.

Here, we analyze the relationship between overall body size (shoulder height, body mass, and skull length) and sexual weaponry among only tusked, both tusked and antlered, and only antlered ungulates. In our static allometry tests, we hypothesized that the growth of larger body sizes favors the growth of disproportionately longer antlers and longer tusks when they are the sole sexual weapon available (i.e., positively allometric), however tusks are not generally visual signals of size (i.e., pure weapons) and may not scale positively allometrically. When both types of weapons are present, however, we hypothesized that larger body sizes favor disproportionately larger antlers but not tusks as larger antlers make for stronger signals and may be advantageous in fights. Evolutionarily, we hypothesized that evolving larger body sizes favors disproportionately larger weapons, regardless of whether one or two types of weapons are present, but that dual-weapon species may invest less in each weapon relative to single-weapon species of similar size. We examined these relationships both within several species of tusked adult ungulates, and between species of tusked and antlered deer using linear regression and phylogenetic generalized least squares (PGLS) analyses respectively.

Methods

Data Collection

Two-hundred and ninety-seven adult male skull specimens were measured from four museums: National Museum of Natural History (NMNH), Natural History Museum of London (NHML), American Museum of Natural History (AMNH), and the Field Museum of Natural History (FMNH) (All data and specimen catalog numbers available in Online Data Supplement). We measured twenty-eight species from seven genera of tusk-bearing cervids:

Muntiacus (110), *Elaphodus* (21), *Hydropotes* (16), *Hyemoshus* (5), *Tragulus* (127), *Moschus* (12), and *Moschiola* (6). Skulls varied in completeness, with some missing premaxilla or tusks, and others were just skullcaps with antlers (i.e., most of the skull was missing).

We used digital calipers to measure skull, antler, and canine features to the nearest 0.01 mm. If available, both the right and left values of all measurements were collected, and measurements were not taken on tusks, antlers, or skull lengths if that feature was broken. We measured Skull Length from the anterior tip of the premaxilla to the most posterior point of the skull (typically the occipital crest) (Fig. 2). Because tusk-like canine teeth are mesially-distally curved structures, two measurements of the longest intact tusk were averaged to obtain Canine Length (1) from the most mesial point on the buccal surface where the tooth emerges from the skull to the tooth tip, and (2) from the most distal point on the buccal surface where the tooth emerges from the skull to the tooth tip (Fig. 2A). For Muntiacinae species, which have substantial bony pedicels that are often more than half of the total weapon length, we calculated Total Cranial Weapon Length as the sum of the pedicel length and antler length of the longest antler on the skull (used in intraspecific analyses only). Pedicel length was measured along the medial surface of the antler bone from the coronal suture (between the frontal and parietal bones) in the notch between the antler bone and cranium to a nodule on the medial midline of the burr (antler/bone complex). True Antler length was then measured from this same nodule to the most distal tip of the antler (Fig. 2B).

We took photographs of each skull from the dorsal view and both lateral views using a Nikon D3100 camera. Because many skulls were broken or missing teeth, we had many missing measurements for individual specimens, especially Skull Length. In order to estimate the missing skull lengths, we used a combination of morphometrics and Bayesian methods. We first used ImageJ (Schneider 2012) to plot 20 universal landmarks on all photographed skulls (7 from the dorsal view and 13 from the lateral view; Fig. 2C,D). We calculated 23 euclidean distances (mm) between these points. We separated our dataset into three groups: 1) smaller-tusked tragulids, 2) larger tusked cervids (*Hydropotes inermis* and *Moschus moschiferus*), and 3) the dual-weaponed Muntiacinae (*Muntiacus* species and *Elaphodus cephalophus*). For each group, we created an additional data subset that contained 10 of the 23 distances that were complete for most of the specimens (i.e. the fewest NA's). We then used the "pcaMethods" package (Stacklies W 2007) in R (R_Core_Team 2019) to conduct a principal components analysis using Bayesian methods to use these known values to estimate missing skull length values in both datasets (full and reduced) for each of the three groups.

All data were centered prior to the estimation analyses, then were uncentered after estimation to reflect original measurements. We ran Pearson correlation analyses between the full 23-distance dataset and the limited 10-distance dataset for each group and found estimated values were highly correlated ($R > 0.9$ for all three groups), suggesting the estimates were robust and consistent. We used the 10-distance estimations of skull length for specimens with missing skull lengths in subsequent analyses.

We obtained antler lengths and male body masses for thirty-one other species of cervids from Plard and colleagues (2011) and antler length data of the extinct Irish Elk (*Megaloceros giganteus*) from Gould (1974). For these species, Antler Length was measured as the main beam without the pedicel, which is typically very short and makes up less than 10% of overall weapon length. We obtained most body masses and shoulder heights from (Wilson and Mittermeier 2011). Other shoulder heights were obtained for: *Megaloceros giganteus* (Ward 1910), *Moschus berezovskii* (Xiaolun 1982), *Hyemoschus aquaticus*, *Moschiola memmima* (Zhao 2015), *Tragulus javanicus* (Agungpriyono et al. 1992) and *Tragulus kanchil* (Francis and Barrett 2008). Body mass of *Tragulus nigricans* was not available in the literature and was estimated by running a regression of the body masses of

Tragulus napu, *T. kanchil*, and *T. javanicus* on our measurements of their skull lengths (Body Mass = $0.2723 \times \text{Skull Length} - 24.719$). We then used our measured skull length of *Tragulus nigricans* to estimate a body mass of 5 kg. Our final analyses included data from 46 ungulate species.

Static Allometric Analyses

Following Gould (1974), for all static (intraspecific) allometric tests of Canine Length and Total Cranial Weapon Length, Skull Length (mm) was used as our measure of body size. The literature is divided on whether to use ordinary least squares (OLS) or reduced major axis (RMA) regression tests for allometric studies (Green 1999; Al-Wathiqui and Rodríguez 2011; Kilmer and Rodríguez 2017). As most past studies of weapon allometry have used OLS (Plard et al. 2011; Lemaitre et al. 2014; Dalosto et al. 2019; Somjee et al. 2021), and because RMA usually produces slope estimates that are far greater (inflated) than what the data appear to suggest, we relied on OLS methods here, but report the results of all the same tests using RMA methods in the Online Supplement. All variables were natural log (ln) transformed prior to regression analyses. We conducted linear and quadratic regression models for Canine Length on Skull Length for each tusked species for which we had at least 10 samples (Tables 1, 2) using the “lm” function (Wickham et al. 2019) in R (R_Core_Team 2019). We conducted linear and quadratic regression models for Total Cranial Weapon Length on Skull Length individually for *Elaphodus cephalopus*, *Muntiacus muntjak*, *M. reevesi*, and *M. vaginalis*. For all static tests of weapon length on skull length, a slope (β) of 1 indicated isometry, we used 95% confidence intervals of the slope estimates to assess deviation from isometry, and we deemed either linear or quadratic models as the best fit if the difference in AIC values was greater than 2 (Burnham and Anderson 2004)

Table 1

Summary of intraspecific allometric analyses for Muntiacinae. SkL = total skull length; CL = maximum canine length; CWL = maximum pedicel + antler length. For all tests, isometry is predicted as $\beta = 1$. For quadratic tests, results for the quadratic (x^2) and linear (x) terms of the model are separated by a "/". Skull sample size (N), regression slope (β), t-statistic (t), p-values (p), AIC scores. Statistically significant allometric relationships are indicated: Isometry (I) and Positive Allometry (+).

	<i>Elaphodus cephalophus</i>	<i>Muntiacus muntjak</i>	<i>Muntiacus reevesi</i>	<i>Muntiacus vaginalis</i>
N	21	38	37	20
Linear CL vs SkL				
β	0.032	1.03 (I)	1.85 (+)	-0.085
Standard Error	0.909	0.37	0.91	0.22
t	0.036	2.79	2.04	-0.379
p	0.972	0.01	0.04	0.71
AIC	-58.44	-85.19	-81.62	-85.74
Quadratic CL vs SkL				
β	-114.94/11.03	30.43/-2.796	289.90/-28.4	8.86/-0.84
Standard Error	120.21/11.54	60.09/5.72	114.6/11.31	24.41/2.29
t	-0.95/0.95	0.51/-0.49	2.53/-2.51	0.36/-0.37
p	0.35/0.35	0.62/0.63	0.01/0.01	0.722/0.719
AIC	-57.48	-83.46	-85.93	-83.903
Linear CWL vs SkL				
β	1.825	2.32 (+)	1.44 (+)	0.62
Standard Error	1.6	0.408	0.63	0.42
t	1.141	5.707	2.26	1.47
p	0.292	p < 0.01	0.04	0.16
AIC	-23.65	-98.06	-92.04	-70.79
Quadratic CWL vs SkL				
β	-228.95/22.06	57.8/-5.27	158.9/-15.5	40.3/-3.7
Standard Error	309.19/29.55	46.23/4.39	82.09/8.10	55.8/5.24
t	-0.740/0.746	1.25/-1.2	1.93/-1.91	0.72/-0.71
p	0.487/0.484	0.22/0.23	0.06/0.006	0.48/0.48
AIC	-22.45	-97.6	-93.88	-69.39

Table 2

Summary of intraspecific allometric results solely tusked species. SkL = total skull length; CL = maximum canine length. For all tests, isometry is predicted as $\beta = 1$. For quadratic tests, results for the quadratic (x^2) and linear (x) terms of the model are separated by a "/". Skull sample size (N), regression slope (β), t-statistic (t), p-values (p), AIC scores. Statistically significant allometric relationships are indicated: Isometry (I) and Positive Allometry (+).

	<i>Hydropotes inermis</i>	<i>Moschus moschiferus</i>	<i>Tragulus napu</i>	<i>Tragulus kanchil</i>	<i>Tragulus nigricans</i>	<i>Tragulus javanicus</i>
N	16	12	75	27	10	14
Linear CL VS SkL						
β	0.262	1.138	0.664	2.09 (+)	0.7914	1.82 (+)
Standard Error	0.502	1.213	0.418	0.39	0.993	0.91
t	0.522	0.938	1.588	5.32	0.797	2.01
p	0.61	0.370	0.117	< 0.01	0.449	0.06
AIC	-71.48	-43.12	-236.05	-103.66	-30.6	-34.32
Quadratic CL VS SkL						
β	83.39/-8.19	-11.57/1.26	9.23/-0.928	176.42/-18.91	-82.12/8.98	116.97/-12.55
Standard Error	90.71/8.94	438.4/43.528	38.34/4.15	27.71/3.01	135.26/14.65	71.71/7.82
t	0.919/-0.916	-0.026/0.029	0.241/-0.22	6.36/-6.29	-0.61/0.61	1.63/-1.61
p	0.375/0.376	0.980/0.977	0.810/0.824	< 0.01/<0.01	0.563/0.559	0.13/0.13
AIC	-70.48	-41.12	-234.11	-127.9761	-29.18	-35.27

Recently, O'Brien and colleagues (O'Brien et al. 2018) showed that comparing allometric relationships of sexually selected traits with a trait that should not possess any signaling power (reference trait) confirms positive allometric relationships of signaling traits. Similarly, we natural log transformed all tusk and antler lengths of the species described above, standardized them, and ran OLS analyses. We then used the length of M² molar measured from lateral images in ImageJ as the reference trait and conducted identical allometric analyses with skull length. We found that amongst tusked species, generally all weapons (tusks and/or antlers), scaled qualitatively higher than the reference trait, M², except in *Muntiacus muntjak* (both weapons) and *Elaphodus* (tusks). Due to limited sample sizes, however, there were no statistically significant differences between any weapon and its corresponding reference trait; we therefore focus our results and discussion on traditional static OLS analyses. Full results from these tests, including 95% confidence intervals of regression slopes, can be found in the Online Supplement.

Evolutionary Allometric Analyses

We were interested in how tusks and antlers evolve with body size across many taxa. We grouped species in several ways to compare relative allometric relationships of tusks and antlers depending on the presence/absence of the other type of weapon. These included "Only Tusked" (*Tragulus*, *Moschus*, *Hydropotes*), "All Tusked"

(*Tragulus*, *Moschus*, *Hydropotes*, *Elaphodus*, and *Muntiacus*), “Only Antlered” (all cervid species except *Hydropotes*, *Elaphodus*, and *Muntiacus*), and “All Antlered” (all cervid species except *Hydropotes*). For our “All Antlered” analyses, we used our own measured Antler Lengths (i.e., not including the pedicel length) for Muntiacinae species, when available to match the data available. To facilitate direct comparisons of allometric slopes with previous studies, we first ran linear and quadratic regression analyses (uncorrected for phylogeny) on Canine Length vs. Skull Length, Shoulder Height, and Body Mass for Only Tusked, All Tusked, and Muntiacinae; and on Antler Length vs. Shoulder Height and Body Mass for Only Antlered and All Antlered (we did not have skull length measures for non-tusked antlered species). For both weapon types, isometry with Skull Length and Shoulder Height would be $\beta = 1$, but isometry with Body Mass would be $\beta = 0.33$. We deemed either linear or quadratic models as the best fit if the difference in AIC values was greater than 2 (Burnham and Anderson 2004). Full results from these tests, including 95% confidence intervals of regression slopes, can be found in the Online Supplement.

Following recent allometric research (Duncan et al. 2007; Plard et al. 2010; Lovegrove et al. 2011; Tidière et al. 2017), we used phylogenetic generalized least squares (PGLS) analyses (Martins and Hansen 1997) across the DNA-only consensus tree from Upham and colleagues (Upham et al. 2019). First, we pruned the tree for each of the four groupings of species: Only Tusked, All Tusked, Only Antlered, and All Antlered. We then ran PGLS analyses on both linear and quadratic equations using “caper” (Orme D 2012) in R (R_Core_Team 2019). We present the slope (β), standard error, t-statistics, p-values, and phylogenetic signals (λ) for each test (Table 4) and provide the AIC scores for each model. In addition, we also report Phyla RMA (Revell 2012) results in the Online Supplement

Table 4: Summary of interspecific allometric analyses from All Tusked species. SkL=total skull length; CL = maximum canine length, SH=shoulder height; MASS=body mass. For tests of skull length and shoulder height, isometry is predicted as $\beta = 1$; for tests of body mass, isometry is predicted as $\beta = 0.33$. For quadratic tests, results for the quadratic (x^2) and linear (x) terms of the model are separated by a “/”. Skull sample size $N = 14$, regression slope (β), standard error of β , t-statistic (t), p-values (p), lambdas (λ), AIC scores. Statistically significant allometric relationships are indicated: Isometry (I) and Positive Allometry (+).

ALL TUSKS			
N=14	LINEAR	QUADRATIC	
		χ^2	X
CL vs SkL			
$\bar{x}$	0.107	-161.13	15.62
St. Error	1.759	588.68	57.063
t	0.061	-0.273	0.273
p	0.956	0.829	0.829
λ	0	0	
AIC	1.746	3.456	
CL vs SH			
$\bar{x}$	0.545	13.51	-1.722
St. Error	0.3742	13.92	1.848
t	1.457	0.970	-0.932
p	0.282	0.509	0.522
λ	0	0	
AIC	-1.140	-1.641	
CL vs MASS			
$\bar{x}$	-0.426	7.144	-1.230
St. Error	0.210	3.143	0.510
t	-2.029	2.272	-2.409
p	0.1794	0.264	0.250
λ	0	0	
AIC	-2.720	-8.392	

Results

Intraspecific Allometric Relationships

We had sufficient sample sizes to test allometric relationships in four species of Muntiacinae: *Elaphodus cephalophus*, *Muntiacus muntjak*, *M. reevesi*, and *M. vaginalis* (Table 1). In *Elaphodus* canine length was unrelated to skull length; there was a trend towards a positively allometric relationship between antler length and skull length, but this effect was not statistically significant ($p = 0.292$). For *M. muntjak*, the quadratic and linear

models of canine length on skull length were equally fit, and the linear model showed an isometric relationship (Table 1, Fig. 3). The quadratic model for canine length in *M. reevesi* was the best fit. This model showed a positively allometric relationship for smaller skull sizes, before leveling off at large sizes (Table 1, Fig. 4). For cranial weapon length on skull length, the linear and quadratic models performed equally well in both *M. muntjak* and *M. reevesi*, and both showed positively allometric relationships (Table 1, Figs. 3,4). In *Muntiacus vaginalis*, however, we found no relationship between either canine or cranial weapon length and skull length (Table 1).

The allometric relationship between canine length and skull length were analyzed in six species of tragulids (Table 2). Datasets for *Hyemoschus* and *Moschiola* were insufficient to run species-level analyses. Among the four tragulid species examined, only *Tragulus kanchil* showed a positively allometric relationship between canine length and skull length with quadratic regression model as the best fit (Table 2; Fig. 5). We also found a trend towards a positively allometric relationship in *T. javanicus*, and the fits of the two models were similar, but the effects in neither model reached statistical significance (linear: $p\text{-value} = 0.067$; quadratic: $p\text{-value} = 0.13$; Table 2; Fig. 4). Non-significant relationships in *T. nigricans* and *T. javanicus* (N = 14) may have stemmed from low sample sizes, but *T. napu* showed no indication of an allometric relationship despite a large sample size (N = 75).

Hydropotes and *Moschus* did not show any statistically significant allometric relationships between canine length and skull length (Table 2). While *Moschus* may not have shown any significant trends due to the low sample size (N = 12) despite a slope resembling isometry (linear $\beta = 1.137$), the slope of the relationship in *Hydropotes* (N = 16) was indeed near zero (linear $\beta = 0.262$).

Evolutionary Allometric Relationships

To examine interspecific allometric relationships, although we conducted non-phylogenetic linear and quadratic regressions for comparisons with older studies (Table 3), we base our main conclusions on the results of phylogenetically corrected models (Table 4). Phylogenetic signal (λ) was mostly weak and near zero in tusk analyses and variable (but greater than zero) in antler analyses (Table 4).

Table 3: Summary of interspecific allometric analyses from Only Tusked species. SkL=total skull length; CL = maximum canine length. For tests of skull length and shoulder height, isometry is predicted as $\beta = 1$; for tests of body mass, isometry is predicted as $\beta = 0.33$. For quadratic tests, results for the quadratic (x^2) and linear (x) terms of the model are separated by a "/". Skull sample size N = 9, regression slope (β), standard error of β , t-statistic (t), p-values (p), lambdas (λ), AIC scores. Statistically significant allometric relationships are indicated: Isometry (I) and Positive Allometry (+).

ONLY TUSKS			
N=9	LINEAR	QUADRATIC	
		X^2	X
CL vs SkL			
$\bar{y}$	2.902 (+)	-15.696	1.933
St. Error	0.323	31.027	3.224
t	8.974	-0.505	0.599
p	<0.01	0.634	0.575
λ	0	0	
AIC	-1.484	-0.7055	
CL vs SH			
$\bar{y}$	1.58 (+)	-13.67	2.13
St. Error	0.332	6.456	0.90
t	4.76	-2.11	2.36
p	<0.01	0.08	0.06
λ	0	0	
AIC	5.789	2.90	
CL vs MASS			
$\bar{y}$	0.123	-0.51	0.203
St. Error	0.193	0.75	0.23
t	0.637	-0.68	0.88
p	0.547	0.52	0.41
λ	1	1	
AIC	4.958	6.9	

Only Tusks

First, we tested how canine length scaled against skull length, body mass, and shoulder height within solely tusked species (i.e., lacking antlers; N = 9; “Only Tusks”; Table 3). Our PGLS linear regression analyses support a significant positively allometric relationship between tusk length and skull length (Fig. 7). The quadratic model was the best fit model to support significant relationships between canine length with shoulder height in “Only Tusked”, and it was supported by the PGLS linear regression model. The linear model was the best fit model

supporting a positively allometric relationship between canine length and body mass, but this relationship was not statistically significant in the PGLS analysis.

All Tusks

Second, we analyzed how canine length scaled across all tusked genera (i.e., “All Tusks” = “Only Tusks” plus Muntiacinae; N = 14; Table 4, Fig. 7). Though our OLS models across all tusked species indicated that canine length scaled isometrically with skull length and shoulder height, they were not supported after controlling for phylogeny in the PGLS analyses (Table 3)

All Antlers

Next, we tested how antler length in “All Antlered” species (N = 29), including Muntiacinae, scales with body mass and shoulder height. In our PGLS, we found that antler length scaled positively allometrically with both shoulder height and body mass (Table 5). The linear models provided the best fit with shoulder height, and the quadratic models provided the best fit for body mass. The latter suggests that antler length scales positively allometrically with body mass at small to moderate body masses, before leveling off in the largest species (Fig. 8).

Table 5: Summary of phylogenetic interspecific allometric analyses from All Antlered species. SH=shoulder height; MASS= body mass; AL= antler length. For tests of shoulder height, isometry is predicted as $\lambda = 1$; for tests of body mass, isometry is predicted as $\lambda = 0.33$. For quadratic tests, results for the quadratic (x^2) and linear (x) terms of the model are separated by a “/”. Skull sample size N = 29, regression slope (β), standard error of β , t-statistic (t), p-values (p), lambdas (λ), AIC scores. Statistically significant allometric relationships are indicated: Isometry (I) and Positive Allometry (+).

ALL ANTLERS			
N=29	LINEAR	QUADRATIC	
		x^2	x
AL vs SH			
β	2.022 (+)	3.075	-0.118
St. Error	0.347	5.170	0.581
t-value	5.813	0.594	-0.203
p-value	<0.01	0.557	0.840
λ	0.634	0.631	
AIC	56.691	58.644	
AL vs MASS			
β	0.744 (+)	2.360	-0.18
St. Error	0.084	0.548	0.062
t-value	8.854	4.3	-2.970
p-value	<0.01	<0.01	<0.01
λ	1	1	
AIC	40.974	34.518	

Only Antlers

Lastly, we tested how antler length in “Only Antlered” (N = 23) species, excluding Muntiacinae, scales with body mass and shoulder height. In our PGLS analysis, we found that antler length scaled positively allometrically with both shoulder height and body mass (Table 6). The linear models provided the best fit with shoulder height. For body mass, the quadratic PGLS model provided the best fit, suggesting that antler length scales positively allometrically with body mass at small to moderate body masses, before leveling off in the largest species.

Table 6: Summary of interspecific phylogenetic analyses from Only Antlered species. SH=shoulder height; MASS= body mass; AL= antler length. For tests of shoulder height, isometry is predicted as $\beta = 1$; for tests of body mass, isometry is predicted as $\beta = 0.33$. For quadratic tests, results for the quadratic (x^2) and linear (x) terms of the model are separated by a “/”. Skull sample size N = 23, regression slope (β), standard error of β , t-statistic (t), p-values (p), lambdas (λ), AIC scores. Statistically significant allometric relationships are indicated: Isometry (I) and Positive Allometry (+).

ONLY ANTLERS		
N=23	LINEAR	QUADRATIC
AL VS SH		
$\bar{x}$	1.711 (+)	2.7/-0.1101
St. Error	0.279	4.087/0.454
t-value	6.116	0.66/-0.24
p-value	<0.01	0.516/0.810
λ	0.223	0.221
AIC	33.474	35.407
AL VS MASS		
$\bar{x}$	0.657 (+)	2.165/-0.169
St. Error	0.0714	0.388/0.043
t-value	9.203	5.573/-3.924
p-value	<0.01	<0.01/<0.01
λ	0.626	0.7327
AIC	18.866	7.794

Discussion

Intraspecific Static Allometric Relationships

Intraspecifically, amongst the dual weapon-bearing genera, there were different results for each species. *Muntiacus muntjak* tusks scaled isometrically with skull length (Fig. 3), while *M. reevesi* showed a positively allometric relationship (Fig. 4). We found positively allometric relationships between antler length and skull length in both *M. muntjak* and *M. reevesi* (Fig. 3, 4), with the latter also showing this relationship levels off in larger individuals. *Elaphodus* and *M. vaginalis* showed no significant relationships between skull length and tusk or antler length. Within solely tusked species (*Tragulus*, *Moschus*, and *Hydropotes*) we found no static allometric relationships, except we found positively allometric relationships between tusk length and skull length in both *T. javanicus* and *T. kanchil* (Fig. 5, 6), with the latter also showing this relationship levels off in larger individuals. These inconclusive results may be due to lack of sufficient sample size, issues with tusk preservation, or possible physical constraints on weapon size as body mass increases. Together the data suggest that (1) antler length in Muntiacinae predictably scales with body size up to a certain point before leveling off, and (2) there might be an upper limit on selection favoring longer tusks: i.e., tusks grow with age up to a point, but having longer tusks at larger sizes either provides no advantage or makes the tusks physically weaker.

Contrary to the predicted positive static allometric relationship between tusk length and skull size (Geist 1999) within solely tusked species, only two of the six species showed positive allometry (although three of these species suffered from low sample sizes; $N = 10-16$). The mixed results in this group are difficult to interpret. Tragulids are small and similar in ecology and behavior, but the allometric slopes varied from 0.5–2.1. Reference trait analyses (see Methods, O'Brien et al 2018) also showed that the allometric slopes of tusks were greater than those of the second molar but did not reach statistical significance. The taxonomy of this family is unclear, and species and subspecies names are frequently being revised, suggesting that some specimen identification labels may be incorrect and the individual belongs in another group, contributing to the varied results. There was no relationship between canine growth and skull size in *Hydropotes* and *Moschus*. Compared to the Tragulids (1–3 kg), *Moschus* and *Hydropotes* are considerably larger in body size (~ 15 kg) and tusk length (Wilson and Mittermeier 2011). Though tragulids are far smaller than any cervid and *Moschus* and *Hydropotes* are small relative to most cervids, their tusks may reach a maximum size and stop growing, even while body size continues to increase. There are six potential *post hoc* explanations for these results. First, *Hydropotes* are known to keep their upper canines sharp by wearing them down using friction with their lower lip, which may limit further significant growth (Cooke, 2019). Second, much longer, positively allometrically scaling tusks could become too large to maintain or use for the animal to benefit from directly and/or prone to breakage, putting the bearer at a huge competitive disadvantage in fights (tusks are their only sexual weapon and can't regrow like antlers), reducing reproductive fitness. Third, after tusks reach some critical length, investment in larger body sizes may be more important than longer tusks and improve fighting success. Fourth, tusks may not function as a visual signal of body size or quality and not meet the requirements for the positive allometry hypothesis (O'Brien et al 2018). Therefore, it is unsurprising that we failed to find strong positive allometric growth of this pure weapon, contrary to the findings of Kodric-Brown and colleagues (2006) that allometric exponents for sexual weapons are "almost invariably" positive (typically 1.5–2.5). There are also two alternative, non-biological explanations. Fifth, the canine teeth of these larger genera are typically loose or separate from the skull in museum collections (especially *Hydropotes*), and after placing them back into the skulls, their relative positional depths during measurement may not have been consistent, confounding the results. Sixth, museum collections emphasize adult specimens and we may have seen allometric growth if our samples included smaller and juvenile members of each species.

Our intraspecific allometric analyses for the Muntiacinae provided contradicting results when it came to canine length. In *Elaphodus*, there was no detectable relationship between canine length or antler length with skull size. The antlers are rudimentary, however, and tusks likely remain as the primary sexual weapons. Like the solely tusked species, there may be little positive selection favoring (or even negative selection disfavoring) tusks above a certain size due to risks of breakage; although their tusks are noticeably thicker and more robust than any other tusked species we measured. Unlike *Elaphodus*, *Muntiacus muntjak* tusks grew isometrically, and cranial weapons (antler + pedicel) grew positively allometrically with body size, similar to other intraspecific studies of antler allometry in cervids (Gould 1974; Vanpe et al. 2007). *M. reevesi* tusks and antlers both scaled positively allometrically with skull length; although the former did level off with increased size (quadratic relationship: Fig. 4). A hint of the same trend is visible in *M. muntjak* tusks (Fig. 7), but the linear model was the best fit. Behaviorally antlers in muntjacs are used to knock an opponent off balance before stabbing the neck, face, and ears with their sharp tusks (Barrette 1977). This suggests that both weapons are critical to victory but that (1) strong, long antlers are more critical for generating opportunities to quickly stab with the tusks, which don't need to be great in size to do significant damage, and (2) antlers do stop increasing in length with greater body sizes. Interestingly, the permanent bony pedicel in Muntiacinae makes up most of the cranial weapon length (much more than other cervids), and the deciduous antler tip is very short compared to other cervids. Limiting the energy

required to regrow the full length of the antler every year may allow these species to divert more energy to growing and maintaining their tusks, which other cervids don't have (except the antlerless *Hydropotes*). Comparison of the allometric growth rates of two sexual weapons in the same species provides great insight into (1) the relative energetic investment into the two weapons and (2) why progressively longer antlers might be more important to winning fights and provide greater fitness benefits than progressively longer tusks.

Kodric-Brown and colleagues (2006) outline a number of important biological points regarding positive allometry of sexual weapons that inform our finding of non-positive allometric growth relationships of tusks. First, growing small non-deciduous tusks is not especially expensive, but it is possible to have steep positive allometries even when the weapon is cheap. Second, tusks are not “exaggerated traits” like antlers and horns, which also function as signals; given that females and rival males don't pay attention to their size, there is no need for exaggeration, and we may not see positive allometry (O'Brien et al 2018). Finally, exponentially larger tusks may not provide greater fitness benefits.

Signaling weapons are commonly elaborate, exaggerated structures that can deter rival males through visual assessment of the weapon (McCullough et al. 2016). For signaling weapons, combat is uncommon, instead their signals are presented through visual displays of threatening behaviors (Barrette 1977; Wilkinson et al. 1998). These structures are likely honest signals of fighting quality since the cost of cheating would be too risky if a stronger rival engaged them in combat (Simmons et al. 2007; Emlen et al. 2012). In most cases, these sexually selected traits evolutionarily scale positively allometrically with body size (Gould 1974; Kodric-Brown et al. 2006; Somjee et al. 2021), and our findings for solely antlered species produce similar results (Table 5,6; Fig. 8). However, that is not always the case, as some studies have found sexual selected traits can evolve isometrically or negatively allometrically (Eberhard et al., 2018, Bonduriansky & Day, 2003, Pomfret & Knell, 2006, O'Brien et al., 2018). To confirm our findings of positive allometry, we compared our sexually selected traits allometric trends to a non-signaling control trait, the length of the upper molar M^2 (O'Brien et al. 2018). In nearly all comparisons, the sexually selected traits, tusks or antlers, scaled more positively with body size than the reference trait, supporting positive allometry of ungulate sexual weapons (Table S5).

Interspecifically, among solely tusked species (excluding Muntiacinae) we found that tusk size scaled positively allometrically with head size (Fig. 7) and shoulder height. These relationships appeared isometric in when including all tusked species (including Muntiacinae), but no relationship at all was detected using phylogenetically corrected analyses. This difference in scaling relationship between solely tusked and all tusked species suggests a decreased investment in larger tusks in the antler-bearing Muntiacinae. As has been found previously (Gould 1974; Vanpe et al. 2007), antler length scaled linearly positively allometrically with both shoulder height and body mass but levels off in larger species (Fig. 8). Interestingly, the Muntiacinae all showed smaller than predicted antler lengths for their body size (Fig. 8), suggesting investment in antlers is reduced when tusks are still used in sexual combat. Overall, as deer-like Artiodactyls evolved larger body sizes, their primary weapon shifted from tusks to antlers (Cabrera & Stankowich 2019), and the primary weapon increased in size disproportionately faster than the body (this study).

Evolutionary Allometric Relationships

We generally saw that tusks have a positively allometric relationship among solely tusked species. This positively allometric evolutionary relationship between relative body size and one sexual combat weapon is seen in weapons in other taxa, such as the mandibles of Stag beetles (*Odontolabis*) (Kawano 2009), weevil rostrums (Somjee et al.

2021), bovid horns (Gould 1974), and antlers of cervids (Gould 1974; Lemaitre et al. 2014; This study). In addition, rhinoceros beetle horn length is strongly correlated with fighting ability; therefore smaller horned males resort to other behavioral methods, such as sneaking behavior, suggesting smaller horns possess weaker signaling power (McCullough et al. 2015). Within solely tusked species, tusks serve as their only form of sexual weaponry, thus maintaining the size and effectiveness of their enlarged canines requires large energy investment resulting in their positive allometric relationship with body size.

The positively allometric evolutionary relationship between tusks and body size is not preserved when dual-weaponed Muntiacinae are included, suggesting a trade-off in energy investment in the presence of two weapons. That a sexual weapon (tusks) does not evolve positively allometrically with body size within a taxon is unique. But Muntiacinae species are unique because they possess two sexual weapons, whereas most evolutionary allometric studies focus on the relationships of species that possess only one sexual weapon. So, drawing any conclusions about the evolutionary allometry of tusks while including the Muntiacinae may be like comparing apples and oranges. We did not have sufficient data from enough species to conduct meaningful evolutionary allometric analyses strictly within the Muntiacinae (5 out of 13 species). But the fact that, when compared to other single-weapon artiodactyls, they had shorter-than-predicted tusks (Fig. 7) and antlers (Fig. 8), suggests that neither weapon follows the same energetic allometric relationship when both are present and that solely tusked species and solely antlered species follow predicted positively allometric relationships, as shown in other taxa (Kodric-Brown et al. 2006).

During Barrette's (1977) observations of muntjacs fighting, the main role of antlers was not to lock up with the other male and wrestle as it is in other deer, but instead shove and twist the opponent into a position where a tusk blow can be delivered. Sexual selection favoring larger antlers may be weaker in Muntiacinae compared to other cervids, where the role of sexual signaling from afar in open habitats (Cabrera and Stankowich 2018) favors a more exaggerated trait. Also, species with greater breeding group sizes (i.e., more polygynous with greater male-male competition) have larger antlers for a given body size compared to species with smaller breeding group sizes (Plard et al. 2010). This greater signaling opportunity and stronger sexual selection on males favored antlers to grow to immense size, which led to increased efficiency of honest signaling from longer distances between opposing males and possibly with females assessing male body condition (Vanpe et al. 2007).

Our finding that antler length evolutionarily scales positively allometrically with both shoulder height and body mass confirms that antlers are both weapons and exaggerated sexual signals that are expensive to grow and regrow annually. As body mass increases, there is a general transition from tusks to antlers in ungulates, commonly accompanied with the transition from dense forested habitats to more open habitats (Cabrera and Stankowich 2018). Antler growth amongst solely antler-bearing species, including the enormous Irish Elk had previously been shown to scale positively with shoulder height with $\beta = 1.74$ in non-phylogenetic studies (Gould 1974). We found slightly higher values for this relationship in our corresponding supplemental, non-phylogenetic analyses (Table S6; S7) regardless of whether the Muntiacinae were included (without Muntiacinae $\beta = 1.88$; including Muntiacinae: $\beta = 2.43$).

Pure combative weapons serve little to no signaling power as they are solely used in combat to determine access to mating (McCullough et al. 2016; Sol et al. 2020), and fights between weapon-bearing individuals are frequent and could result in injury or death (Barrette 1977; Matsubayashi et al. 2003; Emlen et al. 2012). In some species, large weapons are not found on all individuals of the same sex. For example, in *Onthophagus taurus*, major males fight with large horns, while minor males have smaller horns and use alternative mating strategies and

physiological compensation to enhance reproductive success (Simmons et al. 2007). In our study, tusks showed positively allometric relationships with body size in solely tusked species (Table 3; Fig. 5). This positive relationship was not conserved, however, when we included Muntiacinae in our analyses (Table 4) suggesting that the presence of a second sexual selected trait (antlers) diminished the investment in and need for longer tusks.

Selection favoring positive allometry in a sexual weapon may or may not have compensatory effects on other allometric relationships, depending on the nature of the second trait (O'Brien et al. 2018). When the secondary trait is another part of the same weapon, both traits may show positive allometric growth and evolution. For example, in fiddler crabs, the enlarged claw possesses both strong signaling power through claw width and combative power through gripping forces in the claw fingers with little compensation in either strategy (Dennenmoser and Christy 2013). However, other non-combat traits may suffer compensatory losses (Husak and Swallow 2011). In dung beetles and eye stalked flies, males with exaggerated weapon lengths suffered compensation in secondary traits for flight performance through reduced wing traits (Swallow et al. 2000). In the present study, we uniquely examined static and evolutionary allometric relationships in two independent weapons in Muntiacinae and found that antlers nearly always grew and evolved with positive allometry with body size, while tusks showed mixed static allometric relationships and no evolutionary allometric growth. This finding, combined with the stronger evidence for positive evolutionary allometry in solely tusked species, suggests moderate secondary sexual trait compensation whereas dual-weapon species increase in size, they invest more in their signaling weapon than their combat weapon (Tomkins et al. 2005).

Our dataset did suffer from two major limitations. First, many of the skulls available were broken or incomplete. These imperfections limited our ability to take direct skull measurements of skull length, and we relied on digital imaging, morphometrics, and principal component analyses to generate predicted skull length values when missing, based on existing skull landmarks. While this does generate some uncertainty in the skull length data, the same analyses were able to predict the skull lengths of the complete skulls to a high degree of precision. Second, we were unable to collect enough data to analyze allometric relationships from many other tusked species not reported here; these data would have strengthened our findings. In all, we took measurements from 14 tusked species, but we had measurements from fewer than 10 skulls for *Hyemoschus aquaticus*, *Moschiola memmina*, *Moschus berezovskii*, *Muntiacus truongsongensis*, and *Muntiacus vuquangensis*. This particularly affected our interspecific Muntiacinae analyses, as we only had six species with at least 10 measurements to generate species averages to use in the interspecific analyses. A greater sampling of the rarer species of muntjacs might have allowed us to make stronger conclusions about the evolution of tusk and antler allometry within this unique clade.

Declarations

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Figures

Figure 1

Taxidermy mounts of several tusked deer. A) Muntiacus; B) Elaphodus; C) Hydropotes; D) Moschus.

Figure 2

Physical skull measurements (A,B) showing skull length (blue), two measurements of canine length (green, red), pedicel length (yellow), and antler length (orange). Digitized landmarks (red dots; N=7) and distances measured (yellow lines; N=13) on the dorsal surface (C) and lateral surface (D) used in the morphometric analyses to estimate missing skull lengths.

Figure 3

The scaling relationships of (A) antler length and (B) canine length with skull length in *Muntiacus muntjak*. The filled circles (●) represent natural log transformed canine measurements and the red triangles represent natural log transformed antler measurements (▲). The black dashed line represents the isometric relationship between tusks and skull length ($\lambda=1.03$). The red solid line represents the positive allometric relationship between antler length and skull length ($\lambda=2.32$).

Figure 4

The scaling relationships of (A) antler length and (B) canine length with skull length in *Muntiacus reevesi*. The filled circles (●) represent natural log transformed canine measurements and the red triangles represent natural log transformed antler measurements (▲). The black curved line represents the quadratic relationship between tusks and skull length. The red solid line represents the positive linear relationship between antler length and skull length ($\beta=1.44$).

Figure 5

The scaling relationship of canine length with skull length in *Tragulus kanchil*. The filled circles (●) represent natural log transformed canine measurements. The black curve represents the quadratic regression model of canine length and skull length.

Figure 6

The scaling relationship of canine length with skull length in *Tragulus javanicus*. The filled circles (●) represent natural log transformed canine measurements. The black dashed line represents the suggestive positive linear relationship between canine length and skull length. The black curve represents the quadratic regression model of canine length and skull length.

Figure 7

The scaling relationship between skull length and canine length amongst tusked species. Open circles (○) represent solely tusked species (Just Tusks) and filled circles (●) represent dual weapon wearing species (Muntiacinae). The solid black line describes the positive linear relationship found amongst just tusk-bearing species ($\alpha = 2.9$).

Figure 8

The scaling relationship between body mass and antler length amongst all antler-bearing species. Red triangles (▲) represent Muntiacinae species (dual weapon bearing), filled circles (●) represent extant solely antler bearing species, and the filled diamond (◆) represents the extinct Irish Elk. The solid black curve presents the PGLS quadratic regression model of antler length with body mass.

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