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The mechanical properties of red deer antler bone when used in fighting

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SUMMARY

We assessed the hydration state of antlers and its effect on antler mechanical properties compared with wet femur. Red deer antlers were removed from the head at various times, from a few days after velvet shedding till late in the season, and weighed weekly until after casting time. Antlers cut just after losing their velvet lost weight rapidly in the first few weeks, then settled down and changed weight very little, the latter changes correlating with air relative humidity. Antlers cut later showed little weight change at any time. The water content of cortical and trabecular parts of the contralateral antler was assessed after cutting. Most of the weight loss was from the cancellous, not the cortical, part of the antler. Wet and dry specimens from the antlers, and wet specimens from deer femora, were tested mechanically. Compared with wet bone, wet antler had a much lower modulus of elasticity and bending strength, but a higher work to fracture. Compared with wet bone, dry antler showed a somewhat lower Young's modulus, but a considerably higher bending strength and a much higher work to fracture. The impact energy absorption of dry antler was much greater than that of wet bone. In red deer, the antler is effectively dry during its use in fights, at least in southern Spain. In addition, dry antler, compared with ordinary bone, shows mechanical properties that suit it admirably for its fighting function.

Key words: antler, bone, hydration, mechanical properties.

INTRODUCTION

Cervids are the only animals that have antlers, which are made of true bone. Only males grow antlers, except in the genus *Rangifer* where females also have them (Whitehead, 1993). Of true cervid species, only the Chinese water deer lacks antlers. In most species that have antlers the males use them during the rut in dominance battles for access to females (Clutton-Brock et al., 1988; Whitehead, 1993). In the red deer *Cervus elaphus*, and in many other species, these fights consist of an initial clashing of the antlers, followed by a pushing match (Clutton-Brock et al., 1979). These fights are fierce and sometimes result in severe injury and even death of one of the contestants. Deer that break a tine or, worse, break the main beam of an antler in such a fight often (Clutton-Brock et al., 1979), though not always (Johnson et al., 2007), have their chances of reproductive success markedly reduced during that season. It is therefore of considerable selective advantage to have the material properties of the antler, combined with the overall architecture of the antler, such as not to break during a fight. However, building antlers too strong (by means of a thicker cortical layer or beam diameter, for instance) may use up too much material, which is, to a large extent, resorbed from the skeleton (Muir et al., 1987). This may result in a smaller overall antler size and therefore a reduced fighting ability (Clutton-Brock, 1982; Clutton-Brock et al., 1979; Clutton-Brock et al., 1988), as well as making the skeleton weaker.

In *Cervus elaphus* the antlers undergo a yearly cycle. Antlers start to grow from bony pedicles, permanently present on the head of the males, in late winter or early spring (Goss, 1983; Gaspar-López et al., 2008). They grow at the fastest rate known for bone and, in southern Spain (the location for our studies), this can be 1.2 cm per day during the 70 days of fastest growth (Gaspar-López et al., 2008). Growing antlers are covered by a thick 'velvet', the periosteum, with many associated blood vessels. By the middle of summer growth ceases, the antlers mineralise fully, and the velvet dies (Gomez et al., 2006; Gaspar-López et al., 2008). After this, in late July and (mainly) in August, the deer rub their antlers against vegetation in such a way as to remove the dead velvet skin, and the naked antlers appear, ready for fighting. Fighting occurs during the rutting season, lasting in southern Spain from mid-late August until late December (our own observations and those of nearby game managers). In late winter the males grow an abscission layer across the base of the antlers, which are then cast in the last 2 weeks of March (Goss, 1983; Li et al., 2005; Gaspar-López et al., 2008). Shortly thereafter the growth of the next season's antlers starts.

There is disagreement at present, which may partially relate to the species being discussed, as to the state of the antlers after they have completed their mineralisation and shed the velvet. The disagreement concerns whether the antlers are living or dead (Goss, 1995; Rolf and Enderle, 1999). There is certainly evidence in a related species, the roe deer *Capreolus capreolus*, that some mineralisation continues throughout the rutting season (Brockstedt-Rasmussen et al., 1987) and that there is vascular connection between the rest of the body and the central lumen of the antler. Indeed, in the fallow deer *Dama dama*, labelling experiments suggest that some bone remodelling occurs after the antler has completed mineralisation (Rolf and Enderle, 1999), which in turn suggests that water content, at least in the core, might be high. However, such evidence has not been found in red deer and there are several reasons why it is rather unlikely to be of importance for the mechanical properties of red deer antler: (i) antlers from adult red deer males are much larger than those of fallow or roe deer and the large size of the antlers will result in the slow-moving water or plasma taking longer to reach the drying parts of the antler; (ii) the onset of the rut in our region of Spain takes place at a mean maximum temperature of 32.1°C and a mean relative humidity (RH) of 50.8% (mean of minimum RH values 20.8%; see http://crea.uclm.es/~siar/webphp/med_per.php) and such a high temperature is likely to make the cortex, and indeed the whole antler, dry out quickly; (iii) antler is a compact bone tube filled with cancellous bone, and it is the wall of the tube, the cortical layer, which is most important for mechanical properties (Currey, 2002; Davison et al., 2006) this layer is exposed to the air and subjected to ambient weather conditions. Therefore it seems unlikely that the bone in the cortex has significantly more water in it than would be determined by the RH of the air.

Because of its importance for the hunting industry there is an enormous amount of literature about the growth of antlers, the developmental anomalies that can occur, the effects of fracture in one year on the growth of the antlers in the next, the effects of hormones on antler growth, and so on (e.g. Lincoln, 1992; Kierdorf et al., 2007; Price and Allen, 2004). However, little is known about the mechanical properties of the antler when it is used for fighting. We (Currey, 1979a; Zioupos and Currey, 1994) and others (Blob and Snelgrove, 2006) tested the mechanics of antler bone when it was wet, because there were no definitive accounts of how wet it is when it is used in fights. Because all other bones are wet in life, being inside the body, it seemed reasonable to test antler material in the same state as that of all other bones. Dry bone has different mechanical properties from wet bone. It has a somewhat higher stiffness (modulus of elasticity), but undergoes much less post-yield strain (Evans and Lebow, 1951). As a result, in general it absorbs less energy before it fractures. High energy absorption is good in fights that involve the initial clashing of opposing weapons, although the stiffness needs to be reasonably high for the ensuing pushing match.

The aims of this paper concern two interrelated questions. First, to assess how wet an antler is, particularly the cortical layer which is mechanically the most important, when it is being used in fighting. Second, to assess what difference the state of hydration of the antler make to its mechanical properties. Thus, this paper consists of two parts. In the first part we attempt to determine the state of hydration of the antlers during the rut, comparing the amount of water in antler cut at various times during the season and measuring the rate of water loss during the weeks following the cut. We also distinguish water loss from the cortex and water loss from the trabecular medulla. In the second part of the paper we compare the mechanical properties of antlers in the state of hydration found in life with those of other tissues, namely totally wet antler and wet bone. During preparation of this paper, the work by Chen and colleagues (Chen et al., 2009) was published. Apart from being concerned with some matters we do not consider, their work deals with some of the points we cover in the second part of the paper. Chen and colleagues (Chen et al., 2009) obtained results that are in some ways similar to ours, but with less difference between wet and dry antler. We compare our results in the Discussion.

MATERIALS AND METHODS

Animals and handling

The experimental animals were *Cervus elaphus hispanicus* Hilzheimer. The first group of antlers was obtained from 18 animals born and kept in outdoor captivity for research purposes at the Experimental Farm of Universidad de Castilla-La Mancha in Albacete, southeastern Spain (UTM 1 km×1 km coordinates: 30S WJ91, 690 m altitude). They were the offspring of either hinds born in the wild (brought in in 1996) or first generation hinds born on the farm. Animals were kept from birth in a 10,000 m^2 open door enclosure on an irrigated pasture including tall fescue (*Festuca arundinacea*, 50%), cocksfoot (*Dactylis glomerata*, 30%), lucerne (*Medicago sativa*, 15%) and white clover (*Trifolium repens*, 5%). Percentages are approximate seed proportions at planting. Deer were fed *ad libitum* with a diet based on suggestions by Brelurut et al. (Brelurut et al., 1990), using barley straw and meal from barley, alfalfa, oat and sugar beet containing 16% crude protein and 11% water. All animals were adapted to routine management and maintained in good health and body condition during the experiment. Handling procedures and sampling frequency were designed to reduce stress and health risks for the animals, according to European and Spanish law, and current guidelines for the ethical use of animals in research (ASAB, 2008). Mean age (±s.d.) was 5.0±1.4 years, and the range was from 3 to 7 years. On our farm, antlers are ordinarily cut off about 1 cm above the burr for safety reasons. Deer were anaesthetised during antler removal. The cutting took place twice, on 14th August (just after velvet shedding) and 30th August 2007 (Table 1). Left antler beams were kept whole and the cut surface immediately sealed with epoxy paint, and were weighed repeatedly to assess the rate of water loss through the walls of the antler. The right beams were cut open and two sections were taken from each beam to measure water content and create samples for bone mechanical testing as explained below. Seven pairs of antlers were cut on 14th August and used for all procedures, and two additional left beams were weighed whole. Of the antlers cut on 30th August on the farm the nine left antlers were weighed whole, but only one right antler was used for assessing cortical/trabecular water content and mechanical properties, as well as another three right beams from free-ranging deer as explained below.

The second group of antlers was collected from eight animals shot at LM game estate (Abenojar, Ciudad Real, Spain; UTM 1 km × 1 km coordinates: 30S UJ80, 730 m altitude). They came from adult individuals of unknown age but older than 3 years. Antlers

Table 1. Summary of how the various antlers were produced and used for assessment

Origin	Date	Fate	Left antlers dried	Right antlers cort./trab. weight loss	Right antlers mechanical tests	Left antlers unused	Right antlers unused
University farm	14 Aug.	Antlers cut	9	7	7	0	2
University farm	30 Aug.	Antlers cut	9	1	1	0	8
LM estate	30 Aug.	Shot	0	3	3*	3	0
LM estate	20 Sept.	Shot	3	3	3	0	0
LM estate	4 Feb.	Shot	2	0	0	0	2

*Site 3 not tested mechanically.
cort., cortical; trab., trabecular. For further explanation, see text.

were cut on the day animals were shot: three pairs of antlers were cut on 30th August, three on 20th September, and two on 4th February. In all cases they were sent within 24 h to Albacete to be treated like the other antlers.

Antlers from the three deer shot on 30th August had cortical walls too thin for producing specimens for mechanical testing in the upper parts of the antler, although water content in the cortex/trabecular parts was assessed in this section. The weight loss of the left antlers was not measured. Antlers from deer shot on 20th September were used for all procedures explained below. Antlers from deer shot on 4th February were used only for assessing the water content of whole left antlers.

State of hydration experiments

In this paper, we assume that all weight loss and gain is attributable to water loss and gain. This section consisted of three experiments. In the first, we cut and weighed 6 cm antler sections from the right antler of a pair at two heights from the burr (just above the burr and below the crown in the main beam) and separated the cortical layer from the trabecular part. To avoid water loss caused by heating during sawing, we cut the sections with a chisel. In fact, this was the first time we had employed a chisel and it was somewhat surprising to find that in some cases blood oozed from the trabecular part (particularly in antlers cut just after velvet shedding), although in most others the cut surface was totally white and devoid of blood even at the early cutting date. We used a smaller wood-chisel to separate the cortical and trabecular parts. This experiment provided a value for the weight lost from the trabecular and cortical parts after drying. The specimens were dried in a warm oven (DigiHeat, Barcelona, Spain) at 70°C for 72 h, and weighed again to determine the weight loss in the cortical and trabecular parts. The weighing machine was a Gram Precision ST-510 balance (Barcelona, Spain), capable of 0.001 g precision when measuring weights of 0.5 kg.

In the second experimental procedure we sealed the cut surface of the freshly cut left beam with epoxy paint. Then the antlers were put in a laboratory in Albacete at outdoor temperature and RH (although without exposing them to direct sunlight or to rain) and were weighed once a week. The weighing machine was a Scaltec 51 balance (Göttingen, Germany), capable of 0.01 g precision when measuring weights of 4 kg, the approximate weight of the antlers. Antlers were weighed weekly until the end of April the following year; that is, until the casting season in the wild had finished. After that the antlers were completely dried in a warm oven (DigiHeat) at 70°C for 96 h to determine their real ‘dry weight’.

In the third experiment, which was to test not how the antlers lost weight but how quickly the relatively small specimens for mechanical testing lost and gained weight, the 25 antler specimens fractured in mechanical testing (length >40 mm, width 4.5 mm, depth 2.5 mm; see ‘Mechanical experiments’) were immersed in Hanks’ solution for 3 days, taken out, weighed, and allowed to dry in the laboratory at room humidity and temperature. They were weighed, as they dried, every day for 10 days.

The conclusion from the weight loss experiments (see ‘Results’) is that during the rutting season the antlers contain little more water than can be accounted for by assuming that the antlers are in equilibrium with the atmosphere. Therefore mechanical specimens that had been allowed to equilibrate with the atmosphere were probably as near to the natural state of hydration as it was possible to get. The next thing to determine was whether differences in the state of hydration made any difference to the mechanical properties.

Mechanical experiments

For the mechanical experiments specimens of bone and antler were either tested in quasi-static loading in bending, or they were tested in impact. Antler specimens were tested wet, after having been immersed in Hanks’ buffered saline for 7 days, or room-dry. Hanks’ solution, which contains phosphate, was used to obviate the risk of small amounts of mineral leaching out of the bone. All femur samples were tested wet because all long bones are wet in life. No antler specimens were broken wet in impact, because previous observations by us had shown that it is hard to break wet antler in impact unless the shape of the specimen is radically changed. Anatomical provenance of specimens, testing mode and sample size are given in Table 2.

For operational reasons it was not possible to use the femora of the males from which the antlers had been taken, so femora were collected from 12 red deer hinds kept on a natural diet on a 32 Ha plot from the same private deer estate (LM). These were the well-fed control group from an experiment examining how feeding regime affects the skeleton of the hind. All hinds were 3 years old and had been kept under the same conditions their whole life. No hind was allowed to become pregnant during the experiment [a process that might affect mineral mobilisation, as mammals suffer a considerable increase in bone Ca resorption to support lactation (Wysolmerski, 2002)]. The femora were dried for 4 weeks outdoors (but out of any rain); after this period the femur was cut into three parts of similar length with a minidrill (Dremel Series 300; Illinois, USA). Two specimens of each femur (upper and middle parts of the shaft as shown in Fig. 1) were extracted for three-point bending tests on wet specimens. Another specimen was extracted from the lower part of the femur shaft for impact testing. All the specimens were then polished in a Struers machine (Labopol 21, Ballerup, Denmark) until they had dimensions of 4.5 mm width and 2.5 mm depth with a minimum length of 45 mm.

Antler specimens for mechanical testing in three-point bending tests were cut from the two sections mentioned in the previous experiment for assessing water content (Fig. 1). Two bars of the same size as the femur specimens were prepared from each section for the bending tests; one was for testing room-dry, the other for

Table 2. Design for the experiment testing antler and femur bone specimens under two humidity conditions (wet or room-dry)

	Mechanical test	Position	Hydration	*N*
Antler	Bending to fracture	Burr or below crown	Wet	25
Antler	Bending to fracture	Burr or below crown	Room-dry	25
Antler	Impact energy absorption	Mid-point between burr and crown	Room-dry	14
Femur	Bending to fracture	Middle shaft	Wet	12
Femur	Bending to fracture	Distal upper	Wet	12
Femur	Impact energy absorption	Distal lower	Wet	12

There are three sections of antler and of femur (burr or below the crown and the middle section of antler; distal upper/lower part and middle of femur), and two types of mechanical testing (quasi-static three-point bending or impact energy absorption). *N* refers to the number of test specimens.

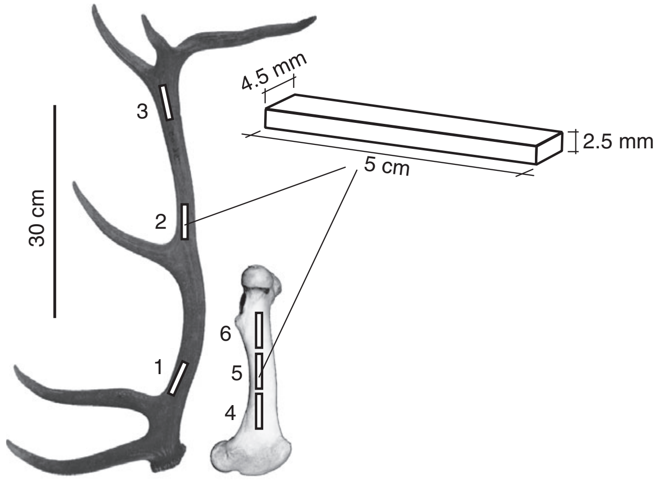

Fig. 1. Sampling positions in deer antler and femur for bars used for mechanical testing. Bars at positions 1 and 3 from antler, and 5 and 6 from femur were used in three-point bending tests. All antler specimens were weighed to enable assessment of their water content within 24 h of detaching the antler from the head of the animal. Bars from position 2 in antler and 4 in femur were tested in impact. Analyses to assess the effect of shaft region on Young's modulus of elasticity, bending strength and normalised work under the curve were carried out in positions 1 and 3 for antler, and 5 and 6 for femur.

testing wet. In addition a specimen for dry impact testing was obtained from a section of antler cut from the middle point between the previous two sections.

All wet specimens had been immersed in Hanks' phosphate-buffered solution for 7 days before testing. The dry specimens had been room dried for 6 months. All tests were carried out at room temperature. Antler specimens were tested as room-dry specimens because, as the results show further below, we found that during the period of active fighting, the antlers, particularly the outer parts, are little wetter than room-dry, and therefore these antler specimens could be considered to be tested in the condition they would be in in life.

For the quasi-static bending to fracture, specimens of both antler and bone, 4.5 mm wide by 2.5 mm deep, with a gauge length of 40 mm, were tested in three-point bending, with the periosteal side in tension, in a Zwick 500 N table model machine (Ulm, Germany). We did not allow for shear deflections because we did not know the shear modulus of our specimens. This ignores the deflection due to shear (Spatz et al., 1996). This, given a gauge length-to-depth ratio of about 16, produced a slight underestimate, of about 10%, of Young's modulus E (manuscript in preparation).

Machine compliance was found to be negligible. The head speed was varied so that all specimens, whatever their Young's modulus, yielded in about 2 s (it was set to 32 mm min^{-1} for wet femur and dry antler, and 112 mm min^{-1} for wet antler). The more brittle specimens broke more quickly after reaching yield than those specimens showing a larger post-yield deformation. The mechanical properties measured were Young's modulus of elasticity (E), bending strength (the maximum stress, calculated from beam theory, at the greatest load borne; BS), and the total work under the load–deformation curve up to the maximum load borne, divided by cross-sectional area (W). Total work normalised like this gives some idea of the toughness of the specimen in quasi-static loading.

The set-up produced no problems with two types of specimen (dry antler, wet bone) but the wet antler specimens deformed into a large bow, and sometimes a maximum load was not reached. The machine stopped automatically when the load decreased sharply. If a maximum load was not reached we considered, arbitrarily, that the specimen had fractured when it bent into a bow so sharp that it fell between the two outer supports. The curve was so nearly flat at this point that it was clear that the value of load thus obtained would be only very slightly less than what would have been found had the maximum load been reached.

We also tested impact energy absorption. The specimens were of the same cross-sectional size and shape as the quasi-static bending specimens. The impact testing method is described in Currey (Currey, 1979b). Essentially it consists of a pendulum falling and breaking an un-notched specimen. The loss of kinetic energy of the pendulum is then measured, and is considered to be the energy required to break the specimen. This energy is normalised by dividing by the cross-sectional area of the specimen. Since the specimens all had the same gauge length, this means that the relative energy absorption could also refer to volume.

After mechanical testing, quasi-static specimens were weighed for their room-dry weight and then heated in the warm oven to drive off the relatively easily lost water, as was done for the weight loss specimens, to produce dry weight. This was also done to make sure that the water content of the antler specimens for mechanical testing was similar to that measured in the cortical layer just after the antler was detached from the animal.

Statistical analysis

General linear models (GLMs) examined differences in weight loss for whole antlers in the first weeks as shown in Table 3, and also that between early and later cutting dates. General linear mixed models examined whether antler section (burr or below crown; the repeated measure) and date of cutting affected the amount of water in cortical or trabecular parts of the antler sections of the shaft (except two antlers cut in February which were included only in the weighing of whole left beams). Cutting date was classified as 1 (early) if cut on 14th August, 2 (start of rut) if cut on 30th August, and 3 (mid-rut) if cut on 20th September. Because GLMs only showed a difference between the first and the rest of the cutting dates, the final model in Results shows the coefficient only for early cutting *vs* rutting period.

For the mechanical experiments a first set of GLMs was investigated to assess whether antlers and femora showed different values for mechanical properties once the effect of hydration state had been removed. After establishing these differences, antler and femur samples were analysed independently for the remaining statistical tests. To assess the effect of region of the shaft in antler and femur, a repeated measure for general linear mixed models was carried out using antler or femur region as a factor in Young's modulus of elasticity E, bending strength BS, and work under the curve W. The regions tested in this case were the burr and below the crown of the beam for antlers, and mid-shaft or upper part for femora. Impact tests were conducted only on a section in the middle of the shaft for antlers, and in the bottom part of the femora, and thus it was not possible to test the effect of region for this variable. Finally, correlations were conducted to assess the three variables obtained in bending tests for each sample (E, BS and W). Again, impact energy could not be included in correlations because it was by necessity tested in other bone specimens.

Table 3. Change in weight and percentage of weight difference compared with completely dry state

	1	2	3	4	
Provenance	Farm	Farm	LM estate	LM estate	
Cutting date	14 Aug.	30 Aug.	20 Sept.	4 Feb.	
N (antlers)	9	9	3	2	
Dry weight (g)	2070±410	860±460	1030±380	690±220	
Weight at cutting (g)	2510±440	990±560	1170±440	800±260	
Water content at cutting (%)	22.2±4.8^{a}	15.5±4.0^{b}	13.2±1.2^{b}	15.5±1.9^{b}	F=5.89, P<0.05
Weight after 4 weeks (g)	2300±150	980±180	1180±250	800±190	
Water content after 4 weeks (%)	11.5±1.1	13.4±1.1	13.4±0.4	15.1±1.4	F=1.14, n.s.
Weight after casting season (g)	2320±150	990±180	1180±250	790±190	
Water content after casting season (%)	12.5±1.1	14.9±1.1	14.1±0.4	14.1±1.4	F=1.00, n.s.

Mean (±s.d.) data for sets of whole antlers (left beam) cut on different dates (1–4) and the cut surface sealed. The antlers were left to open-air temperature and humidity under cover from rainfall and direct sunlight until the following April, after the usual casting date. Antlers were dried at the end of the experiment in an oven to assess final humidity. Most antlers in sets 1 and 3 (and some of those in set 2) also had their right beams used to assess water content in cortical and trabecular parts, and for mechanical testing. Antler cleaning or velvet shedding happens in the experimental farm around the 20th August (Gaspar-López et al., 2008).

Different superscript letters in a row show statistical significance with regard to the last set of antlers assessed in a general linearised model (GLM; *F* statistic and probability shown in last column). n.s., not significant.

RESULTS

Weight loss from whole antlers

Fig. 2 shows the mean weight loss from four sets of whole left antlers compared with the weight the week before. The first set, cut off on 14th August, lost about 8% of their weight in the first 4 weeks. The other three sets lost 1% or less in the first 4 weeks, whenever that might be in the season. There was a greater water content at cutting for whole antlers cut on 14th August compared with the other sets (F=5.89, P<0.05; Table 3). These differences disappeared by 4 weeks after cutting (F=1.14, P>0.1; Table 3). After the first 4 weeks all sets of antlers lost or gained up to at most 0.8% of their weight each week. Most interestingly, all sets gained or lost water simultaneously (Fig. 2), and weight gain correlated with the mean RH of the air for the last 3 or 7 days (R=–0.59 and R=–0.56, P<0.001 for correlation of weight changes of 21 antlers and RH for 29 weeks).

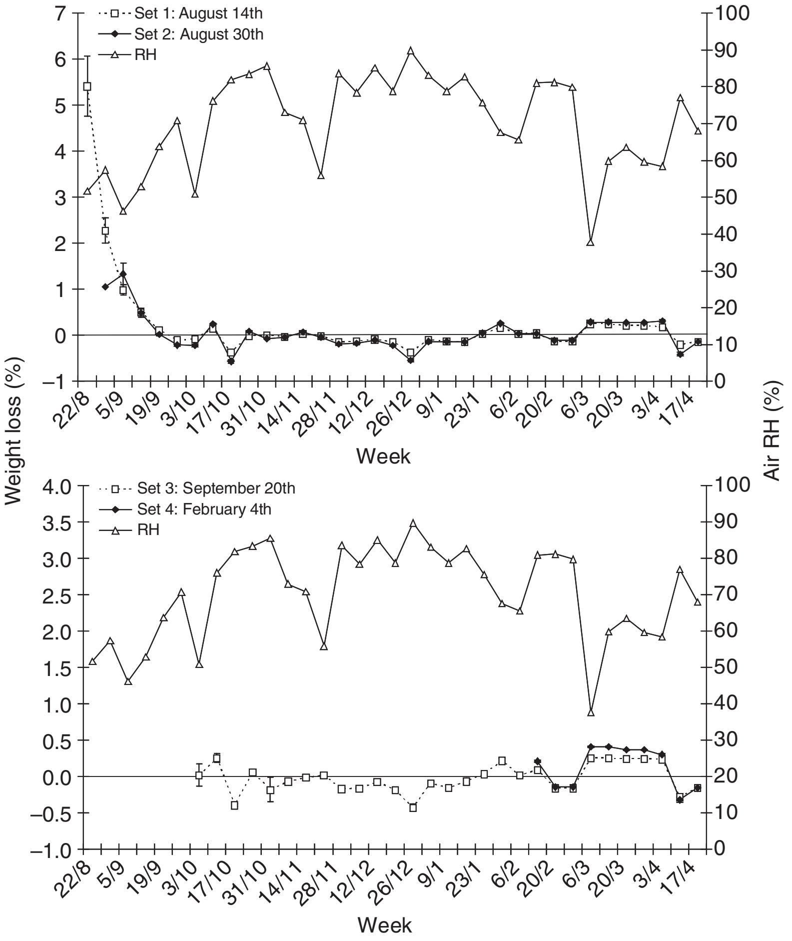

Fig. 2. (A) Mean weight change in two sets of antlers from the experimental farm group, differing in the date of cutting, compared with the weight the week before. Error bars on some values are s.e.m. Air relative humidity (RH) refers to the mean value for the 3 days prior to the weighing date. (B) Mean weight change in two sets of antlers from the LM game estate group, differing in the date of cutting, compared with the weight the week before. Error bars on some values are s.e.m. Air RH refers to the mean value for the 3 days prior to the weighing date.

Weight loss from sections of antlers

The general linear mixed models showed no effect of antler section in terms of weight loss in either cortical or trabecular parts. Similarly, when cutting dates were classified into three groups (early cutting just after cleaning velvet, start of rut and mid-rut), only the antlers cut on 14th August (early cutting date) showed a significant difference from those cut on the other dates. The final model, pooling all the cutting dates except the early one, showed a greater amount of water content for the early cutting dates in both cortical and trabecular parts compared with antlers cut later during the rutting season. No effect of distance to skull (burr or below crown antler sections) was found, nor was the interaction between antler section and cutting date significant.

Weight loss using general linear mixed models was as follows: cortex: intercept 12.66±0.68%, early cutting date 2.91±0.97% mean±s.e.m., P=0.011; trabeculae: intercept 13.80±2.50%, early cutting date 20.22±3.51% mean±s.e.m., P=0.001.

This analysis shows, not surprisingly, a difference in water content between the earliest and later dates that is far greater in the trabecular part (20.2%) than in the cortical layer (2.9%).

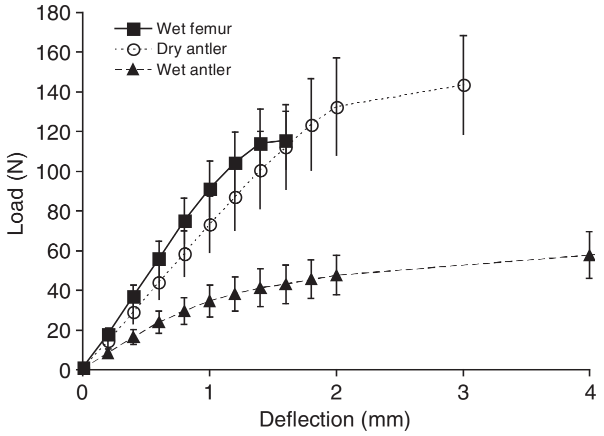

Fig. 3. Load–deformation curves in three-point bending test for wet femur, and wet and dry antler. Error bars represent s.d. Although the deflection is shown up to 4 mm, the wet antler curve remains very nearly flat up to 8 mm. This explains why wet antler has a large work to fracture (Table 4).

Weight loss from mechanical testing specimens

The weight loss in 25 of the specimens used for quasi-static mechanical testing was similar, although somewhat lower than that measured immediately after removing the antlers from the deer's heads (mean±s.e.m. water loss of 10.53±0.26% of the 25 bars from days 2 to 10 inclusive). The specimens contained 24.96±0.43% of water after immersion in Hanks' solution, and the room-dry weight loss was achieved after one day. After the first day the specimens lost on average no more water, simply losing a little or gaining a little weight each day. These small changes over time were well correlated between the 25 specimens (data not shown), presumably being driven by changes in RH.

Mechanical experiments

GLMs showed that antlers and femora had highly significant differences in mechanical properties (Table 4; difference between antler and femur for E, BS and W, respectively, $F_{1,98}$=857, $F_{1,98}$=274 and $F_{1,98}$=372, all $P\ll 0.001$). A similar GLM showed a clearly significant difference in impact energy between antler and femur (antler was only tested dry as it often does not break in impact when tested wet; Table 4; difference between antler and femur for impact energy, $F_{1,38}$=146, $P\ll 0.001$). Fig. 3 shows the load–deformation curves for the three-point quasi-static bending test for wet femur and wet and dry antler. These are not stress–strain curves of course, because stresses and strains vary throughout bending specimens. However, the specimens were very similar in size and shape, and for the same-sized specimens Young's modulus is proportional to the slope of the initial straight part of the curve, bending strength is proportional to the greatest load reached, and work to maximum load per unit cross-sectional area is proportional to the area under the curve. Fig. 3 shows curves in which the slope and maximum load, but not work under the curve, for wet femur and dry antler are more similar than between these and wet antler.

A repeated measures general linear mixed model showed that for the antler the section of the shaft from which the sample was taken was significant in all variables examined in three-point bending, tested wet or dry (except work under the curve tested dry), but not in the femur (Table 5). Specimens of antler taken from near the burr were stiffer, stronger, and showed a greater normalised work under the curve compared with the more distal material from below the crown.

Correlations showed positive relationships between Young's modulus of elasticity, bending strength and normalised work under the curve for all types of testing and bone material except between E and W in antler tested dry (Table 6). The greatest correlation in general was for antler tested wet.

The mechanical values show some striking differences between wet bone and the two types of antler specimen – wet and dry. The differences are summarised in Table 4 and Fig. 3. Wet antler has a very low Young's modulus, and is extremely deformable in bending. Dry antler has a remarkable load–deformation curve. Its Young's modulus is somewhat less than that of bone, but its bending strength is greater, and its deformation at break is much larger than that of wet bone. As a result, the work that it absorbs before fracture in bending is much (*ca*. 2.4 times) greater than that of wet bone.

DISCUSSION

The work described here set out to answer two questions. (1) How wet is antler, particularly the important outer cortical part, when it is being used in fighting? (2) What difference does the state of hydration of the antler make to its mechanical properties?

Table 4. Mechanical properties of wet and dry antler and wet femur tested as shown in Table 2

		E (GPa)	BS (MPa)	W (kJ m^{-2})	U (kJ m^{-2})
Antler	Wet	7.30±0.30	115.7±3.7	31.0±1.3	–
	Dry	17.50±0.45	352.2±8.8	23.4±1.0	47.5±4.0
Femur	Wet	22.39±0.33	263.3±5.5	9.6±0.3	7.2±0.5

Mean (±s.e.m.) data for Young's modulus of elasticity E, bending strength BS, work under the load–deformation curve W, all obtained in three-point bending tests, and impact energy U, tested in a different set of specimens. Antler was not tested wet in impact because it usually did not break. Femur was not tested dry in impact because internal bones are always wet. GLMs or ANOVAs showed that differences within a column are highly significant for all sets (see text).

Table 5. Repeated measures design for general linear mixed models testing the effect of region of shaft for antlers (antler burr or below top branching or palm) and femur (middle or upper part of shaft) on mechanical variables derived from 3-point bending tests

Bone	Hydration	Property	R^2 [a]	AIC[b]	Intercept	Section (burr)[c]
Antler	Wet	*E*	18.7%	84.7	6.43±0.49	1.44±0.42**
		BS	24.8%	195.9	103.2±5.9	20.4±4.8**
		W	16.6%	157.2	28.2±2.4	5.2±2.5†
	Dry	*E*	25.4%	107.0	16.22±0.67	2.26±0.84*
		BS	12.6%	248	336±13	30±16†
		W	2.5%	147	24.3±12.4	–
Femur	Wet	*E*	0.0%	219	22.34±0.48	–
		BS	0.0%	474	263±9	–
		W	0.0%	107.0	9.45±0.45	–

Data for Intercept and Section are shown as mean±s.e.m.

[a] General linear mixed models are based on maximum likelihood and not least squares. Therefore, they do not allow calculation of the variability explained or R^2. However, we have run the same final model shown here in a GLM to obtain a rough idea of R^2 for comparison between models.

[b] AIC stands for Akaike information criterion. It serves for comparison between alternative models and is better the lower its value.

[c] The coefficient shows the increase in the mechanical property for the burr compared with the section in the top below the palm of the antler. In the case of femora, the comparison was between the mid-shaft and upper part of the femur.

We have determined that during the time of year when antlers are being used in earnest they are nearly as dry as they can get, given that they necessarily pick up moisture from the atmosphere, and possibly from vegetation. It may be that for a while there is still a functioning blood supply in the core of part of the antler but our studies show that antlers cut from the deer's head more than about a month after the velvet is gone lose little weight over several months when left lying in a laboratory. Nevertheless there is still a considerable amount of water in this room-dry tissue, as was shown by heating specimens at 70°C to drive off all the readily available water. This produced a loss of weight of 9–11%. Probably, once they had settled down, the antlers were responding by changes in their weight to environmental factors, presumably mainly the RH of the laboratory air. This indicates very strongly that by about the fourth week after being cut off, or sooner, the antlers had lost virtually all the weight that they were going to lose from an 'excess' of water inside the antler. The only set of antlers showing more than a 1% initial loss after being cut off was the first set, cut off in mid-to-late August, fairly soon after losing their velvet. This in turn suggests that there was a reasonable amount of water in the antlers when they lost their velvet, that this water was being lost during early August, and that after the antlers were cut off the process of water loss continued for up to about 4 weeks. After this time they reach a stable hydration state suitable, in life, for their work as a weapon. Most of the extra water found in the first set of antlers initially weighed shortly after losing the velvet is from the unmineralised tissue remaining in the trabecular bone, but not in the cortical bone, which is overwhelmingly more mechanically important.

Table 6. Correlation coefficients between mechanical properties obtained in three-point bending tests

		E		*BS*	
	Specimen	*N*	*R*	*N*	*R*
BS	Wet femur	48	0.50***		
	Wet antler	25	0.95***		
	Dry antler	25	0.87***		
W	Wet femur	48	0.35*	48	0.81***
	Wet antler	25	0.64***	25	0.75***
	Dry antler	25	0.20 n.s.	25	0.61***

$^*P<0.05$, $^{***}P<0.001$; n.s., not significant.

These results indicate that, during the major part of the rutting season the antlers have in them little, if any, more water than could be explained by the antlers being in equilibrium with the atmosphere. This is shown particularly clearly by the second, third and fourth sets of antlers, which were cut off during the rutting season, and lost very little weight during the first 2 weeks after being cut off. This makes it extremely unlikely that in life they had a functioning blood supply sufficient to make even the core of the antler wet.

The fact that when functioning the antlers are 'dry' is perhaps not surprising. What is surprising is how well suited mechanically the dry antler is to its function, which is to absorb the shocks of the original encounter during a fight, yet to have a reasonably high modulus of elasticity and static bending strength to keep the antler from bending too much, or breaking, in the pushing match that follows the first clash of antlers.

The mean Young's modulus of elasticity is, in our dry antler specimens, only 22% lower than that of wet bone specimens. However, the static bending strength of wet bone is 25% lower than that of dry antler. The architectural properties (second moment of area, etc.) are also, of course, of importance, but are not dealt with in this paper. The energy absorption of dry antlers in quasi-static bending is nearly 2.5 times greater than that of wet bone. In impact the difference is even more marked; the energy absorption of dry antler is on average 6.6 times greater than that of wet bone Of course, as we have shown, the material of the antler is necessarily room-dry when used. Were the antlers to be made of 'ordinary' bone, and exposed to the air, they would be dry, and the impact energy absorption of dry bone is only about half that of wet bone, and only 1/13 that of dry antler (Currey et al., 2009).

We found that the specimens taken from the more proximal part of the antler had a somewhat higher value of *E* and of *BS* than the specimens originating more distally. This agrees with the findings of Landete-Castillejos and colleagues (Landete-Castillejos et al., 2007b). The more distal antler is younger than the proximal part, and whether these mechanical differences are related merely to the maturation of the antler, or are adaptive in some way, we do not know.

Many years ago Rajaram and Ramanathan (Rajaram and Ramanathan, 1982) investigated the quasi-static tensile properties of wet and dry antler of *Axis axis* and wet bone. Although their values for tensile strength are perhaps rather low, their results insofar as they can be compared are broadly similar to ours, which were

Table 7. Comparison of the mechanical results of the present work and that of Chen and colleagues

			E (GPa)	BS (MPa)	W (kJ m^{-2})	U (kJ m^{-2})
Antler	Wet	This work	7.3	116	31.0	–
		Chen et al., 2009	7.0	145	–	–
	Dry	This work	17.5	352	23.4	47.5
		Chen et al., 2009	7.6	197	–	–
Femur	Wet	This work	22.4	263	9.6	7.2
		Chen et al., 2009	26.1	238	–	–

Unlike Chen and colleagues, we did not test in compression, or at right angles to the long axis of the antler. They did not assess the work to fracture in quasi-static loading, or impact energy absorption.

measured in bending, of course. They found that the Young's modulus of elasticity of wet antler was about half that of dry antler, as did we, and that the work to fracture of wet antler was 3.6 times greater than that of wet bones; we found a value of 3.2 times, which is remarkably similar. They did not measure impact energy absorption.

The work of Chen and colleagues (Chen et al., 2009) is possibly more relevant to our mechanical work. They tested one cast antler of *Cervus elaphus canadensis* and a number of specimens of femoral bone, taken from 18 month old bovines, and, like us, measured bending properties, both wet and dry. They also tested short bone specimens in compression. They tested the antlers and the bones oriented both longitudinally and transversely. We did not test transversely, or in compression. We do not consider further those of their tests that were not similar to ours. The values obtained by us and by Chen and collegeagues (Chen et al., 2009) are shown in Table 7.

There are marked differences. The Young's modulus of wet bone from cows and wet bone from deer are similar. However, Chen and coworkers (Chen et al., 2009) found that their dry antler specimens were little stiffer than their wet antler specimens. We found a considerable difference, with the dry antler specimens being much stiffer (17.5 GPa *vs* 7.3 GPa). Even more marked were the values for bending strength. Although our values and those of Chen and colleagues for wet bone are fairly similar, they found that the dry bending strength of their antlers was only 35% greater than the wet bending strength, whereas we found a threefold difference. We are at a loss to account for these differences. Chen and colleagues did not test for energy-absorbing capacity; we found that dry antler absorbed 2.5 times more energy in quasi-static loading and 6.5 times more energy in impact than wet femur.

The mechanical properties of all bony materials depend mainly on the mineral content; the higher the mineral content the stiffer and more brittle (less tough) the bone (Currey, 2004). Furthermore, drying the bone has effects in the same direction as increasing mineral content; that is, decreasing the amount of plasticising water, so making the tissue stiffer but less tough. The mineral content of antler, at approximately 60% (Ullrey, 1982; Landete-Castillejos et al., 2007a; Estevez et al., 2008), is such that, when dry, it has a somewhat lower modulus of elasticity than wet bone, though probably it is stiff enough for the pushing match. On the other hand it is much tougher than wet bone. In fact, raising the mineral content of antlers to that of bone would produce a disastrous reduction in impact energy: unpublished results from our group show that a 27% reduction in impact energy and a 10% reduction in work to fracture raises the proportion of seriously damaged antlers (more than two tines broken) from 25% to 55%, and breakage in the main beam from 9% to 33%.

We do not know the optimum mechanical properties of the antler. However, it seems likely to us that it could be advantageous for the antlers to be a little damper than they are. That is, they could be a little less stiff and absorb more energy in impact. In this respect it is interesting that after the velvet is shed the deer tend to rub their antlers in shrubs of Crimson rock rose (*Cistus ladanifer*; Yolanda Fierro, personal observation). This shrub has a sticky liquid covering, and it is possible that this, when transferred to the surface of the antler and dried in the heat, forms a coating that reduces the speed with which water is lost from the surface.

However, fully wet antler would not be a good material for use in fighting because it has such a low modulus of elasticity, which would allow the antler to be distorted by bending in the pushing match that follows the original clash. Also, though probably less important, its quasi-static bending strength (116 MPa) is quite low. Although wet antler has a large work to fracture and a very high impact strength, it achieves these properties, adaptive as they may be in themselves, by extreme distortion after yielding at a low stress. It seems that dry antler material has the best of both worlds; it has a reasonably high Young's modulus of elasticity, a high quasi-static bending strength and a high work to fracture and impact energy absorption. It achieves these last two properties without distorting very much.

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