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Effects of antler breakage on mating behavior in male tule elk (*Cervus elaphus nannodes*)

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Abstract Although antler size has been identified as a primary determinant of dominance, fighting success, and reproductive success in male cervids, >80% of the male tule elk (*Cervus elaphus nannodes*) in the Owens Valley, California, experience antler breakage. To determine the effect of antler breakage on male mating success, we recorded antler morphology, body size, and mating behavior of male elk throughout the rut. Antler breakage, regardless of severity, had no effect on male–male assessment, fighting success, or harem-holding status. The factor consistently associated with our indices of male mating success was not antler size but body size. Although antler size is frequently emphasized as a key factor in male dominance and social rank, this association may reflect the correlation between antler size and body size. In the Owens Valley, it appears that male elk are not assessing competitors based on antler morphology but on other characteristics.

Keywords Antler breakage · Fighting success · Male assessment · Mating behavior · Owens Valley

Introduction

Elaborate weapons, such as horns, tusks, and antlers, have evolved as secondary sexual characteristics in males of

numerous species (Andersson 1994). Weaponry is typically used in intraspecific male competition, as individuals fight over the acquisition and defense of females (Geist 1966; Andersson 1994; Katsikaros and Shine 1997). Due to the high energetic costs of developing and maintaining elaborate weaponry (Bobek et al. 1990), such traits are assumed to convey a significant fitness advantage (Darwin 1871). Among competing males, weapon size has been frequently correlated with body size, dominance, and reproductive success (Geist 1966; Brown and Siegfried 1983; Sneddon et al. 1997).

Most cervid species maintain a polygynous mating system, where only a few males obtain a majority of the reproductive opportunities (Gibson and Guinness 1980a). The reproductive success of an individual is determined by a social hierarchy, where males must physically assess and compete with one another for dominance that results in access to females (McCullough 1969; Lincoln et al. 1970; Clutton-Brock 1987). Except for Chinese water deer, all male cervids develop antlers, and these are used during the rut to strike opponents, guard against incoming blows, and push competitors during sparring matches. Typically, males with the largest antlers are observed to have the highest social ranking, increased fighting success, and have gained the greatest number of mating opportunities (Lincoln 1972; Clutton-Brock et al. 1979; Gibson and Guinness 1980b; Bowyer 1986; Barrette and Vandal 1990).

Because combat between male cervids carries a high risk of injury, it is advantageous for individuals to accurately assess their competitors before fighting (Maynard Smith and Price 1973; Clutton-Brock et al. 1979). During the rutting period, males frequently display antlers to potential competitors, vigorously thrashing their heads during male–male interactions (McCullough 1969). As a result, antlers may serve as a representation of a male's physical status, size, health, and, perhaps, fighting ability (Geist 1971; Lincoln 1972; Bowyer 1986; Barrette and Vandal 1986, 1990). Moreover, antlers may allow males to advertise their social status while conducting noncontact, low-risk assessments of opponents (McElligott et al. 1998; Mattiangeli et al. 1999).

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While antler size has been correlated with dominance, fighting, and reproductive success, the specific influence of antler morphology on these factors is confounded by body size. As a male increases in body size, his antlers increase in length, weight, and number of tines (Hyvarinen et al. 1977; Bowyer 1986). Most studies evaluating the importance of antler size in male contests have not adequately accounted for the influence of body size. As a result, researchers have questioned whether the relationship between antler size and dominance is just a by-product of the relationship between body size and dominance (Clutton-Brock et al. 1979; Clutton-Brock 1982).

Investigations conducted on the effect of antler breakage and removals on male dominance have yielded equivocal results. In some studies, males with altered antlers were challenged immediately by smaller, subordinate males. The altered males eventually lost social rank, became less effective in their fighting ability, and were incapable of securing females (Espmark 1964; Lincoln et al. 1970; Lincoln 1972). Conversely, Appleby (1982) reported that social rank in mature males, or males within the same size class, was not affected by antler size and concluded that antler breakage had no effect on the social status of a male. Clutton-Brock et al. (1979) observed red deer with broken antler tines and also concluded that such damage had no effect on male fighting capabilities or reproductive success.

It remains unclear how high rates of antler breakage affect male behavior and mating success. If male assessment, fighting success, and reproductive success are based primarily on antler morphology, we would expect males with the most severe antler breakage to be least successful during rut. Such individuals may receive challenges from males with larger antlers, be more likely to lose challenges, be less likely to initiate challenges, be incapable of securing harems, or be of less appeal to females. Conversely, if antler morphology is not an important determinant of male mating success, then breakage should have little effect on male reproductive behavior.

Tule elk (*Cervus elaphus nannodes*) in the Owens Valley, California, exhibit a high rate of antler breakage (McCullough 1969; Fig. 1). In 2002 and 2003, >80% of the males in the Owens Valley ($n=112$) had broken antler tines, and 35% had broken main beams (Johnson et al. 2005). Antler breakage is suspected to result from a mineral deficiency in the diet, with a vast majority of males exhibiting broken antlers after the rut. The high rate of antler breakage observed in the Owens Valley currently is undocumented elsewhere; estimates for rates of antler breakage among males in other cervid populations are typically <5% (Henshaw 1971). To determine the role of antler morphology in the mating success of tule elk in the Owens Valley, we monitored antler breakage, body size, and behavior of males throughout the rutting period. Specifically, we evaluated the effect of antler breakage on male–male assessment, fighting success, and harem-holding status.

Materials and methods

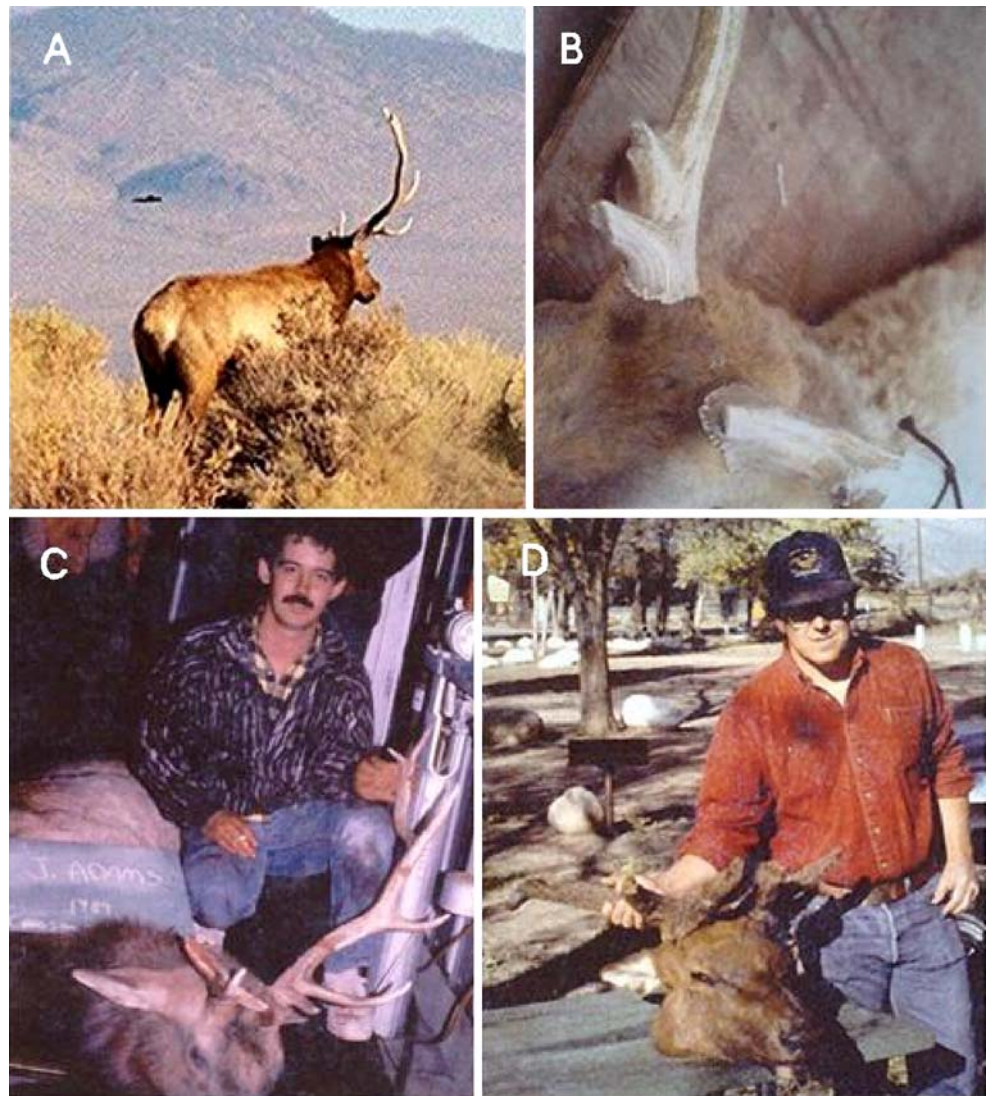
Study area The Owens Valley is located in Inyo County, California. The valley is oriented in a north–south direction, approximately 195 km long and 26 km wide, with an elevation at the north end of 1,335 m and at the south end of 1,160 m (Bleich et al. 2001). The Sierra Nevada is on the western side of the Owens Valley, and the White Mountains are on the eastern side; both ranges reach elevations of 4,200 m. The valley lies in the rain shadow of the Sierra Nevada, receiving approximately 13 cm of rainfall/year (National Oceanic and Atmospheric Administration 2003). Winter temperatures frequently fall below freezing, while summer temperatures are often >37°C.

Vegetation consists of Great Basin and Mohave Desert shrub communities (McCullough 1969). Saltbush (*Atriplex* spp.), rabbitbrush (*Chrysothamnus nauseosum*), and sagebrush (*Artemisia* spp.) dominate uplands, while greasewood (*Sarcobatus vermiculatus*), saltgrass (*Distichlis spicata*), and shadescale (*Atriplex confertifolia*) dominate lowlands (Bleich et al. 2001). The Owens River flows south through the valley creating a riparian area that consists of willow (*Salix* spp.) and cottonwood (*Populus fremontii*) forests and cattail (*Typha domingensis*) marshes. Cattle ranching occurs throughout the valley, but crop agriculture is limited to a few alfalfa fields. Tule elk inhabit the valley bottom, which is primarily owned by the Los Angeles Department of Water and Power (McCullough 1969).

Field methods We observed males in the largest three herds of tule elk in the Owens Valley: Bishop, Tinnemaha, and Lone Pine (A. Pauli. 2001 Owens Valley Tule Elk Surveys, California Department of Fish and Game [CDFG], Bishop, California). We used radiocollared animals in each herd to locate groups of elk in the field. The relatively flat terrain and sparse vegetation in the Owens Valley provided a unique opportunity to observe nearly all individuals in the population. Because vegetation typically does not exceed 1 m in height, elk were easily visible. We conducted field observations from approximately sunrise to 1100 and from 1500 to sunset. Observations began 15 July, before the onset of the rut and any antler breakage had occurred, and ended 30 September, when rutting activity had ceased. Each herd was monitored at least 2 times/week. We used 10×40 binoculars and a 15–40× spotting scope for field observations.

We recorded antler morphology, body size, and harem-holding status of all male elk observed. Antler morphology included the number of tines a male had originally developed on the right and left antlers (before any breakage), the number of remaining intact tines, and the number and location of broken tines and main beams. We used the number of antler tines as an indicator of antler size, a measure that was easily obtained from field observations. We diagrammed the antler morphology of each male to track changes among individuals over time. If an antler, or part of an antler, was missing due to a break in a main beam, we assumed that the original number of tines on the broken antler was equal to the original number of tines on the intact contralateral antler. Five males broke

Fig. 1 Photos of antler breakage on male tule elk, Owens Valley, California



both main beams during the study; however, we were able to determine their original antler morphology through individual antler diagrams. We visually categorized body size of males as small, medium, or large; we used antler morphology before any breakage, development of the dewlap and mane, girth of chest, and the definition of the withers to place each male in a size category (William 1955; Page 1959). We classified males as harem holders or non-harem holders, and we recorded the number of females for each harem-holding male. Because these males achieve the vast majority of mating opportunities, we used harem-holding status as an indicator of reproductive success (Gibson and Guinness 1980b; Bartos and Perner 1998).

We used focal-animal sampling (Altmann 1974) to record agonistic interactions among male elk. To conduct a focal-animal sample, at least two active (non-bedded) males had to be present and within 50 m of each other (Bowyer 1981). We selected males at random for focal observations and continually observed them for 10 to 20 min (Weckerly 2001). During the sampling period, we recorded each aggressive behavior that involved the focal

animal and any other male. Aggressive behaviors were identified when one male initiated a ritualized aggressive act toward another (McCullough 1969; Weckerly 2001) and terminated when one male turned, walked, or ran away. For each aggressive behavior we recorded the antler morphology, body size, and harem status (holder or nonholder) of both males involved in the dyad. In addition, we recorded the identity of the male that initiated the aggressive behavior, and which male received the behavior. We recorded the winner and loser of all interactions having a decisive outcome, where one male clearly turned, walked, or ran away from the other to end an aggressive interaction.

Analysis To evaluate the effect of antler breakage on male behavior, we used two indicators of antler morphology: the original number of antler tines and the remaining number of antler tines. We used the original number of antler tines as a measure of pre-breakage antler size, expressed as the total number of tines on both antlers before breakage. The remaining number of antler tines was used as the post-breakage measure: the total number of

tines on both antlers at the time of an observation. For all males that were uniquely identifiable from the beginning of rut to the end, we used a paired *t* test to compare the original number of antler tines to the remaining number of antler tines.

To determine the effect of antler breakage on male assessment, we conducted separate pre- and post-breakage analyses. Antler breakage was first observed on 12 and 3 August in 2002 and 2003, respectively. Aggressive behaviors observed before these dates were used in pre-breakage analyses, and behaviors observed on or after these dates were used in post-breakage analyses.

To assess whether males were evaluating each other based on antler morphology, male–male assessment, we compared the relative antler characteristics of males initiating and receiving aggressive behaviors. In the pre-breakage analysis, we used logistic regression to determine whether the original number of antler tines was associated with initiating or receiving an aggressive behavior. In the post-breakage analysis, we used logistic regression to determine whether the original or remaining number of antler tines was associated with initiating or receiving an aggressive behavior. To control for differences in body size among males, we included size class as a covariate in both regression analyses.

To examine the effect of antler breakage on male fighting success, we also conducted a pre- and post-breakage analysis. Aggressive behaviors observed before any antler breakage were used in the pre-breakage analysis, and behaviors after antler breakage were used in the post-breakage analysis. We included only aggressive interactions where a definitive winner and loser could be determined. To evaluate fighting success pre-breakage, we used logistic regression to determine whether the original number of antler tines was associated with winning an aggressive interaction. In the post-breakage analysis, we used logistic regression to determine whether the original, or remaining, number of antler tines was associated with winning an aggressive interaction. To control for the effect of body size, we again included size as a covariate in the regression models.

We determined whether antler morphology was associated with harem-holding status and, thus, access to females. For the analysis, we included the antler characteristics of males observed in groups containing a harem holder and at least one non-harem male. Because data were insufficient to conduct a separate pre-breakage analysis, we examined harem-holding status only post-antler breakage. We used logistic regression to determine whether the original or remaining number of antler tines was associated with being a harem holder. Body size class again was included in the regression model as a covariate.

Results

During the 2002 and 2003 field seasons, we obtained 398 focal observations with a mean duration of 12.22 min. Sixty focal observations occurred before the onset of antler

breakage, and 338 occurred after the onset of antler breakage. In 4,340 min of focal observations, we observed 446 aggressive interactions, 59 before and 387 after the onset of antler breakage. Before antler breakage, 53 aggressive interactions yielded decisive outcomes, while 346 aggressive interactions yielded decisive outcomes post-antler breakage. The mean number of antler tines a male possessed declined as rut progressed (Fig. 2), differing at the beginning of rut (pre-breakage) when compared to the end of rut (post-breakage) ($t_{111}=-11.85$, $P<0.001$). On average, males had a total of 11.1 ± 2.0 antler tines when the rut began, and they had only 7.7 ± 3.1 antler tines when the rut had ended.

After accounting for the effects of body size ($\chi^2=6.91$, $df=2$, $P=0.032$), males initiating aggressive interactions before the onset of antler breakage did not have a greater number of original antler tines than males receiving the aggressive behaviors (Table 1; $\chi^2=0.24$, $df=1$, $P=0.62$). Post-antler breakage and after accounting for the effects of body size (Table 1; $\chi^2=41.09$, $df=2$, $P<0.001$), males that initiated aggressive acts were characterized by having a greater number of original antler tines ($\chi^2=4.93$, $df=1$, $P=0.026$) but not a greater number of remaining antler tines ($\chi^2=0.61$, $df=1$, $P=0.44$) than recipients. On average, males initiating aggressive interactions had 1.18 times (95% C.I.= 1.02–1.34) the original number of antler tines as the receiving males. Of the males that initiated aggressive acts, 87% won the encounter, with the other male turning, walking, or running away.

Before antler breakage and after accounting for the effects of body size ($\chi^2=10.53$, $df=2$, $P=0.005$), the winners of aggressive interactions had a greater number of original antler tines than losers (Table 1; $\chi^2=7.50$, $df=1$, $P=0.006$). After antler breakage, neither the number of original antlers nor the number of remaining antler tines was associated with winning (Table 1; body size $\chi^2=46.79$, $df=2$, $P<0.001$; original tines $\chi^2=0.02$, $df=1$, $P=0.90$; remaining tines $\chi^2=0.12$, $df=1$, $P=0.73$).

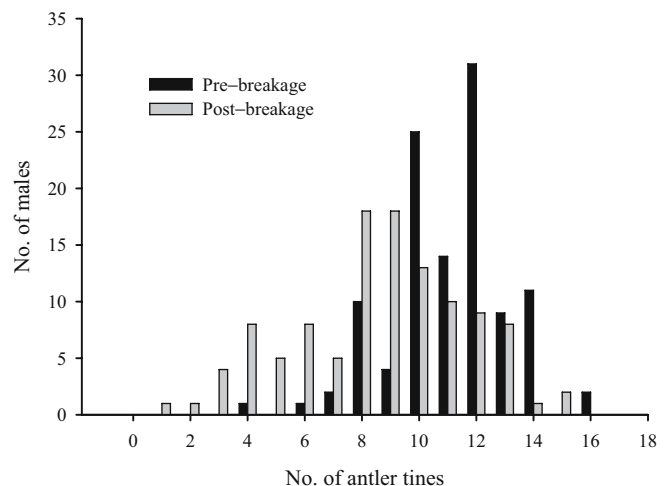


Fig. 2 Number of antler tines of uniquely identifiable male tule elk ($n=112$) possessed at the beginning of rut (pre-breakage) and at the end of rut (post-breakage), Owens Valley, California, 2002–2003

We observed 85 groups of elk that contained a harem male and a greater than or equal to one nonharem male. From these groups, we used 492 males to determine whether antler morphology differed between harem and nonharem holders. After accounting for body size ($\chi^2=31.59$, $df=2$, $P<0.001$), we found that harem males had a greater number of original antler tines than nonharem males ($\chi^2=11.31$, $df=1$, $P<0.001$). On average, harem males originally had 1.36 times (95% C.I.=1.11–1.58) the number of antler tines as nonharem males. The number of remaining antler tines a male possessed had no effect on whether he was a harem holder ($\chi^2=0.23$, $df=1$, $P=0.63$).

Discussions

Although antler size has been identified as a primary determinant of mating success in male cervids, we found no evidence to suggest that post-breakage antler morphology influenced male–male assessment, fighting ability, or harem-holding status in male tute elk in Owens Valley. In several taxa where males possess weaponry for intraspecific competition, weapon size has been traditionally correlated with dominance, fighting, and reproductive success (Miller 1975; Katsikaros and Shine 1997; Sneddon et al. 1997; Styrsky and Van Rhein 1999) and is assumed to be a primary determinant of these qualities. This assumption may not be warranted in all cases. Appleby (1982) reported that antler length did not determine social rank in male red deer of the same size class. In a study of European earwigs, the fighting success of males that had intact forceps was compared to males that had their forceps reduced by 50% (Styrsky and Van Rhein 1999). Fighting success was not influenced by reduced forceps length but, instead, by the original (pre-manipulated) length of the forceps. Similarly, in male tute elk, assessment and harem-holding status did not appear to be influenced by the number of antler tines a male possessed after antler breakage but, instead, by the number of antler tines a male possessed before breakage.

The importance of weapon size in male mating success of some species may be confounded by the influence of body size. Because weapon size generally increases with male body size (Andersson 1994), it has been difficult for

investigators to assess these variables independently of each other. We considered the body size of males as a covariate in our analyses and found that it was significant in all cases. In addition, the importance of the “original” number of antler tines is probably also a reflection of body size, as investigators have shown that the number of antler tines on male cervids is directly related to body size (Hyvarinen et al. 1977; Bowyer 1986). As a result, the number of tines a male originally developed is probably a much more sensitive indicator of body size than reflected by our size categories (i.e., small, medium, and large). Because it was the number of original antler tines, not remaining antler tines, that was significant in male assessment and harem-holding status, it appears that body size may be more important than antler morphology in the determination of mating success in Owens Valley tute elk.

A discrepancy existed between factors associated with male assessment before the onset of antler breakage and after the onset of antler breakage. In the pre-breakage analysis, initiators of aggressive behaviors were not associated with a greater number of original antler tines, while in the post-breakage analysis, initiators were associated with a greater number of original antler tines. This difference may be attributed to a “learning” period at the beginning of rut. Barrette and Vandal (1990) suggested that sparring matches allow male caribou to physically assess their competitors, an experience which they may use when visually assessing other opponents. Similarly, wild boars and some fish use wrestling techniques to assess their fighting ability relative to competitors (Barrette 1986; Enquist and Jakobsson 1986). Tute elk males may ascertain their physical capabilities early in rut, when the costs and benefits of fighting are relatively low, learning to better assess their opponents as the rut progresses.

Unlike other indicators of post-breakage male mating success, fighting ability did not appear to be influenced by the number of original antler tines. While antler morphology influenced fighting success before antler breakage, it appeared to have no effect on fighting success after the onset of antler breakage. This difference may reflect a change in aggressive behavior between pre- and post-breakage observations. In the Owens Valley, pre-breakage male aggressive interactions occurred only for 1 or 2 weeks at the start of rut. Almost all of these aggressive interactions

Table 1 The number of male tute elk having greater than, less than, or the same number of antler tines as a male competitor during an aggressive interaction, Owens Valley, California, 2002–2003

	Number of antler tines relative to a competitor			
	<i>n</i>	Greater than	Less than	Equal to
Initiators of aggressive interactions				
Pre-antler breakage	59	28	20	11
Post-antler breakage				
Original number of tines	387	228	92	67
Remaining number of tines	387	201	128	57
Winners of aggressive interactions				
Pre-antler breakage	53	31	4	18
Post-antler breakage				
Original number of tines	346	201	79	66
Remaining number of tines	346	177	119	50

involved nonharem males in bachelor groups where there were no immediate reproductive benefits. The majority of rutting activity occurred after the onset of antler breakage, when potential benefits of fighting had increased (Clutton-Brock et al. 1979). Incentives for participating in aggressive behaviors may vary among individuals depending on harem-holding status, reproductive history, number of estrous females, and the capabilities of a particular competitor, with these factors being more influential in fighting success than antler size. Male tule elk were observed to fight and defend harems even if they had only one antler or if they had broken both main beams and had only brow tines. It appeared that a primary function of antlers, no matter what size, was as weapons to obtain or defend mating opportunities.

Because male mating success in Owens Valley tule elk did not appear to be dependent on antler size, these males may use other characteristics to evaluate the strength and social status of their competitors. Even in cervid populations devoid of antler breakage, researchers have suggested that antler size is an unreliable indicator of mating success (Clutton-Brock and Albon 1979). Due to high energetic demands, the body condition of male elk deteriorates throughout the rut. Males reduce food intake and increase activity, resulting in loss of mass and body fat (Bobek et al. 1990). In a cervid population experiencing low levels of antler breakage, the antler morphology of a male will remain unchanged throughout the rut, while the male's fighting abilities will likely change. Because antlers are insensitive to changes in a male's physical condition, it is advantageous for elk to have other means of evaluating competitors. Roaring frequency and lateral body displays have been hypothesized to serve as such indicators (Clutton-Brock and Albon 1979; McComb 1991; Reby et al. 2001) and may be important for competitor assessment in male tule elk.

Although antler breakage did not significantly affect male mating success in Owens Valley tule elk, we do not imply that antlers are not important in the behavior of male cervids. Clearly, antler removal has had consequences, as males that suffered complete antler removal in other studies subsequently lost social rank and failed to participate in normal rutting behavior (Espmark 1964; Lincoln et al. 1970; Lincoln 1972; Bubenik 1983). In addition, experiments where male cervids were exposed to dummies with different sized antlers have elicited behaviorally appropriate responses, indicating that males do perceive variation in antler size (Bubenik 1983).

The lack of importance of antler size in mating behavior of male tule elk may reflect the unusually high rates of antler breakage in the Owens Valley. Unlike experimental studies of antler removal, almost all males enter the rut with an intact set of antlers, only gradually breaking tines and main beams as they participate in fights and sparring matches. It is possible that male tule elk use antler morphology to assess their competitors early in the rutting season, before the onset of antler breakage, and apply this knowledge to intraspecific interactions after breakage has occurred.

The high energetic cost of antler regeneration implies that for antlers to persist in cervid species, they must convey fitness advantages (Geist 1966; Clutton-Brock 1982). Although poorly understood, antler size may play a role in female choice (Bubenik 1983; Small 1992; Geist 1998). Because antler growth requires an excess of resources, antlers may serve as a representation of male quality for reproductive females (Geist 1998). While we used harem-holding status as an indicator of potential reproductive success (Bartos and Perner 1998), we were not able to count the number of matings each harem holder obtained. Because elk reproduction requires female cooperation, a harem holder can mate successfully only with females that are behaviorally receptive (Geist 1982). Bubenik (1983) reported that female cervids were more attracted to head mounts of males with larger antlers. If antler size is important for female choice, males with severe antler breakage may be able to secure harems but may be less able to gain mating opportunities.

After accounting for body size, we found no evidence to suggest that antler morphology influenced male–male assessment, fighting ability, or harem-holding status in male tule elk in the Owens Valley. In cervid populations devoid of antler breakage, antler size, body size, and mating success are all highly correlated. It is important to recognize, however, that even though antler size is often correlated with male mating success, it may not necessarily dictate male mating success. The use of antler size in the assessment of male cervids may be more widely used by hunters and field biologists than by elk. Because antler breakage had no effect on the mating behavior of male tule elk in the Owens Valley, elk in this population may be using factors other than antler morphology to assess competitors and determine dominance.

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References

- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–267
- Andersson M (1994) Sexual selection. Princeton University Press, New Jersey
- Appleby MC (1982) The consequences and causes of high social rank in red deer stags. *Behaviour* 80:259–273
- Barrette C (1986) Fighting behavior of wild *Sus scrofa*. *J Mammal* 67:177–179
- Barrette C, Vandal D (1986) Social rank, dominance, antler size, and access to food in snow-bound wild woodland caribou. *Behaviour* 97:118–146
- Barrette C, Vandal D (1990) Sparring, relative antler size and assessment in male caribou. *Behav Ecol Sociobiol* 26:383–387

- Bartos L, Perner V (1998) Distribution of mating across season and reproductive success according to dominance in male red deer. *Folia Zool* 47:7–12
- Bleich VC, Chun CSY, Anthes RW, Evans TE, Fischer JK (2001) Visibility bias and development of a sightability model for tule elk. *Alces* 37:315–327
- Bobek B, Perzanowski K, Weiner J (1990) Energy expenditure for reproduction in male red deer. *J Mammal* 71:230–232
- Bowyer RT (1981) Activity, movement, and distribution of Roosevelt elk during rut. *J Mammal* 62:574–582
- Bowyer RT (1986) Antler characteristics as related to social status of male southern mule deer. *Southwest Nat* 31:289–298
- Brown L, Siegfried BD (1983) Effects of male horn size on courtship activity in the forked fungus beetle *Bolitotherus cornutus* (Coleoptera Tenebrionidae). *Ann Entomol Soc Am* 76:253–255
- Bubenik AB (1983) The behavioral aspects of antlerogenesis. In: Brown RD (ed) *Antler development in Cervidae*. Caesar Kleberg Wildlife Research Institute, Texas, pp 389–449
- Clutton-Brock TH (1982) The functions of antlers. *Behaviour* 79:108–125
- Clutton-Brock TH (1987) Sexual selection in the Cervidae. In: Wemmer CM (ed) *The biology and management of the Cervidae*. Smithsonian Institution Press, Washington, DC, pp 110–122
- Clutton-Brock TH, Albon SD (1979) The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69:145–170
- Clutton-Brock TH, Albon SD, Gibson RM, Guinness FE (1979) The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim Behav* 27:211–225
- Darwin C (1871) *The descent of man, and selection in relation to sex*. Murray, England
- Enquist M, Jakobsson S (1986) Decision making and assessment in the fighting behaviour of *Nannacara anomala* (Cichlidae, Pisces). *Ethology* 72:143–153
- Espmark Y (1964) Studies in dominance-subordination relationship in a group of semi-domestic reindeer (*Rangifer tarandus* L.). *Anim Behav* 12:420–426
- Geist V (1966) The evolution of horn-like organs. *Behaviour* 27:175–214
- Geist V (1971) *Mountain sheep: a study in behavior and evolution*. University of Chicago Press, Illinois
- Geist V (1982) Behavior. In: Thomas JW, Toweill DE (eds) *Elk of North America: ecology and management*. Stackpole Books, Pennsylvania, pp 219–277
- Geist V (1998) *Deer of the world: their evolution, behavior, and ecology*. Stackpole Books, Pennsylvania
- Gibson RM, Guinness FE (1980a) Differential reproduction among red deer (*Cervus elaphus*) stags on Rhum. *J Anim Ecol* 49:199–208
- Gibson RM, Guinness FE (1980b) Behavioral factors affecting male reproductive success in red deer (*Cervus elaphus*). *Anim Behav* 28:1163–1174
- Henshaw J (1971) Antlers—the unbrittle bones of contention. *Nature* 231:469
- Hyvarinen H, Helle T, Nieminen M, Vayrynen P, Vayrynen R (1977) The influence of nutrition and seasonal conditions on mineral status in the reindeer. *Can J Zool* 55:638–655
- Johnson HE, Bleich VC, Krausman PR (2005) Antler breakage in tule elk, Owens Valley, California. *J Wildl Manage* 69:1747–1752
- Katsikaros K, Shine R (1997) Sexual dimorphism in the tusked frog, *Adelotus brevis* (Anura: Myobatrachidae): the roles of natural and sexual selection. *Biol J Linn Soc* 60:39–51
- Lincoln GA (1972) The role of antlers in the behaviour of red deer. *J Exp Zool* 182:233–250
- Lincoln GA, Youngson RW, Short RV (1970) The social and sexual behavior of the red deer stag. *J Reprod Fertil Suppl* 11:71–103
- Mattiangeli V, Mattiello S, Verga M (1999) The fighting technique of male fallow deer (*Dama dama*): an analysis of agonistic interactions during the rut. *J Zool* 249:339–346
- Maynard Smith JM, Price GR (1973) The logic of animal conflict. *Nature* 246:15–18
- McComb KE (1991) Female choice for high roaring rates in red deer, *Cervus elaphus*. *Anim Behav* 41:79–88
- McCullough DR (1969) *The tule elk: its history, behavior, and ecology*, vol 88. University of California Publications in Zoology, California
- McElligott AG, Mattiangeli V, Mattiello S, Verga M, Reynolds CA, Hayden TJ (1998) Fighting tactics of fallow bucks (*Dama dama*, Cervidae): reducing the risks of serious conflict. *Ethology* 104:789–803
- Miller EH (1975) Walrus ethology part I. The social role of tusks and applications of multidimensional scaling. *Can J Zool* 53:590–613
- National Oceanic and Atmospheric Administration (2003) *Climatological data annual summary, monthly surface data, California*. National Climate Data Center, North Carolina
- Page TFJ (1959) *Field guide to British deer*. The Mammal Society of the British Isles, Cox and Wyman Ltd. England
- Reby D, Hewison M, Izquierdo M, Pepin D (2001) Red deer (*Cervus elaphus*) hinds discriminate between the roars of their current harem-holder stag and those of neighboring stags. *Ethology* 107:951–959
- Small MF (1992) Female choice in mating. *Am Sci* 80:142–151
- Sneddon LU, Huntingford FA, Taylor AC (1997) Weapon size versus body size as a predictor of winning in fights between shore crabs, *Carcinus maenas* (L.). *Behav Ecol Sociobiol* 41:237–242
- Styrsky JD, Van Rhein S (1999) Forceps size does not determine fighting success in European earwigs. *J Insect Behav* 12:475–482
- Weckerly FW (2001) Are large male Roosevelt elk less social because of aggression? *J Mammal* 82:414–421
- William G (1955) *The Roosevelt elk*. Port Angeles Evening News, Washington