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Grancel Fitz measuring the circumference of the main beam of an Alaska-Yukon moose. Fitz and Dr. James L. Clark were key members of a committee formed by the Boone and Crockett Club to develop an equitable, objective measurement system for big game of North America. Photo courtesy Boone and Crockett Club.

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Effects of Harvest, Culture, and Climate on Trends in Size of Horn-Like Structures in Trophy Ungulates

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ABSTRACT Hunting remains the cornerstone of the North American model of wildlife conservation and management. Nevertheless, research has indicated the potential for hunting to adversely influence size of horn-like structures of some ungulates. In polygynous ungulates, mating success of males is strongly correlated with body size and size of horn-like structures; consequently, sexual selection has favored the development of large horns and antlers. Horn-like structures are biologically important and are of great cultural interest, both of which highlight the need to identify long-term trends in size of those structures, and understand the underlying mechanisms responsible for such trends. We evaluated trends in horn and antler size of trophy males (individuals exhibiting exceptionally large horns or antlers) recorded from 1900 to 2008 in Records of North American Big Game, which comprised >22,000 records among 25 trophy categories encompassing the geographic extent of species occupying North America. The long-term and broad-scale nature of those data neutralized localized effects of climate and population dynamics, making it possible to detect meaningful changes in size of horn-like structures among trophy males over the past century; however, ages of individual specimens were not available, which prevented us from evaluating age-class specific changes in size. Therefore, we used a weight-of-evidence approach based on differences among trophy categories in life-history characteristics, geographic distribution, morphological attributes, and harvest regimes to discriminate among competing hypotheses for explaining long-term trends in horn and antler size of trophy ungulates, and provide directions for future research. These hypotheses were young male age structure caused by intensive harvest of males (H1), genetic change as a result of selective male harvest (H2), a sociological effect (H3), effects of climate (H4), and habitat alteration (H5). Although the number of entries per decade has increased for most trophy categories, trends in size of horn-like structures were negative and significant for 11 of 17 antlered categories and 3 of 8 horned categories. Mean predicted declines during 1950–2008 were 1.87% and 0.68% for categories of trophy antlers and horns, respectively. Our results were not consistent with a sociological effect (H3), nutritional limitation imposed by climate (H4), or habitat alteration (H5) as potential explanations for long-term trends in size of trophies. In contrast, our results were consistent with a harvest-based explanation. Two of the 3 species that experienced the most conservative harvest regimes in North America (i.e., bighorn sheep [*Ovis canadensis*] and bison [*Bison bison*]) did not exhibit a significant, long-term trend in horn size. In addition, horn size of pronghorn (*Antilocapra americana*), which are capable of attaining peak horn size by 2–3 years of age, increased significantly over the past century. Both of those results provide support for the intensive-harvest hypothesis, which predicts that harvest of males has gradually shifted age structure towards younger, and thus smaller, males. The absence of a significant trend for mountain goats (*Oreamnos americanus*), which are difficult to accurately judge size of horns in the field, provided some support for the selective-harvest hypothesis. One other prediction that followed from the selective-harvest hypothesis was not supported; horned game were not more susceptible to reductions in size. A harvest-induced reduction in age structure can increase the number of males that are harvested prior to attaining peak horn or antler size, whereas genetic change imposed by selective harvest may be less likely to occur in free-ranging populations when other factors, such as age and nutrition, can override genetic potential for size. Long-term trends in the size of trophy horn-like structures provide the incentive to evaluate the appropriateness of the current harvest paradigm, wherein harvest is focused largely on males; although the lack of information on age of specimens prevented us from rigorously differentiating among causal mechanisms. Disentangling potential mechanisms underpinning long-term trends in horn and antler size is a daunting task, but one that is worthy of additional research focused on elucidating the relative influence of nutrition and effects (both demographic and genetic) of harvest. © 2013 The Wildlife Society.

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Los Efectos De La Explotación, La Cultura Y El Clima En El Tamaño De Estructuras Corniformes En Los Ungulados Tipo “Trofeo”

RESUMEN La caza sigue siendo el fundamento del modelo norteamericano de conservación y mantenimiento de la fauna y la flora. Sin embargo, las investigaciones evidencian la posibilidad de que la caza pueda tener un impacto negativo en el tamaño de las estructuras corniformes de algunos ungulados. En el caso de los ungulados poligínicos, el apareamiento exitoso de los machos tiene una estrecha correlación con el tamaño del individuo y de las estructuras corniformes; por lo que la selección sexual ha favorecido el desarrollo de cuernos y de astas de gran tamaño. Las estructuras corniformes tienen importancia desde el punto de vista biológico y cultural, lo que destaca la necesidad de identificar tendencias a largo plazo en el tamaño de dichas estructuras, así como de entender los mecanismos subyacentes responsables de tales tendencias. Hemos evaluado tendencias en tamaño de los cuernos y astas de machos tipo “trofeo” (individuos que presentan cuernos o astas de tamaño excepcional) documentadas desde 1900 hasta 2008, en el Registro sobre la caza mayor en América del Norte (*Records of North American Big Game*), que comprende más de 22.000 registros que abarcan 25 categorías distintas de “trofeos,” comprendiendo el total de las especies que habitan en la extensión geográfica de América del Norte. La circunstancia de que estos datos son de largo plazo y gran escala, neutraliza los efectos localizados del clima y la dinámica demográfica, haciendo posible detectar cambios significativos en el tamaño de las estructuras corniformes entre machos “trofeo” a lo largo del siglo pasado; sin embargo, no tuvimos disponible la edad de cada uno de los especímenes, lo cual nos impidió evaluar cambios en el tamaño de grupos separados por edades. Es por ello que, para discriminar entre las hipótesis alternativas que explican las tendencias en el largo plazo del tamaño de los cuernos y astas de los ungulados tipo “trofeo,” ponderamos la evidencia, basándonos en las diferencias entre categorías de individuos “trofeo” con fundamento en características del ciclo vital, la distribución geográfica, atributos morfológicos y sistemas de explotación, proporcionando así orientación para las investigaciones futuras. Las mencionadas hipótesis son: estructura de edad en los machos jóvenes causada por la explotación intensiva de los mismos (H1), el cambio genético resultante de la explotación selectiva de machos (H2), el efecto sociológico (H3), los efectos del clima (H4) y la modificación del hábitat (H5). Aunque para la mayoría de las categorías “trofeo” ha habido un incremento en el número de registros por década, las tendencias de tamaño en las estructuras corniformes fueron significativamente negativas para 11 de las 17 categorías con astas, y para 3 de las 8 categorías con cuernos. Desde 1950 hasta 2008, la disminución prevista de los promedios para las categorías con astas y las categorías con cuernos fue de 1,87% y de 0,68%, respectivamente. Nuestros resultados no fueron congruentes con el efecto sociológico (H3), la limitación alimenticia impuesta por el clima (H4), ni con la modificación del hábitat (H5), como posibles explicaciones de las tendencias a largo plazo en el tamaño de los trofeos, pero sí concordaron con la explicación basada en la explotación. Dos de las 3 especies en América del Norte que experimentaron los regímenes más conservadores de explotación (a saber, el carnero de las rocosas o muflón montañés, *Ovis canadensis* y el bisonte americano, *Bison bison*) no mostraron una tendencia significativa en el largo plazo en el tamaño de los cuernos. Adicionalmente, el tamaño de los cuernos entre los antílopes americanos (*Antilocapra americana*), cuyos cuernos pueden alcanzar el máximo tamaño a los 2 ó 3 años de edad, aumentó considerablemente a lo largo del siglo pasado. Los resultados anteriores apoyan la hipótesis de la explotación intensiva; lo cual, indica que la explotación cuantiosa de machos a través del tiempo ha desplazado gradualmente las estructuras de edad hacia machos más jóvenes, y en consecuencia, más pequeños. La falta de una tendencia significativa en el caso de la cabra montesa o cabra blanca (*Oreamnos americanus*), el tamaño de cuyos cuernos es difícil de evaluar en su hábitat natural, proporciona apoyo a la hipótesis de la explotación selectiva. Otra proyección que se deriva de la anterior hipótesis no se pudo apoyar. La reducción en estructuras de edad, inducida por la explotación, puede incrementar el número de machos explotados antes de alcanzar el máximo tamaño de cuernos o astas, mientras que el cambio genético impuesto por la explotación selectiva tiene menor probabilidad de ocurrir entre poblaciones silvestres cuando existe la posibilidad de que otros factores, tales como la edad y la nutrición, resten valor al potencial genético de tamaño. Las tendencias a largo plazo en el tamaño de estructuras corniformes tipo “trofeo” son un incentivo para el análisis de la adecuación del patrón de explotación actual, el cual está enfocado principalmente en los machos; no obstante, la falta de información sobre la edad de los ejemplares nos impidió distinguir con precisión entre los mecanismos de causalidad. Dilucidar los posibles mecanismos que respaldan las tendencias a largo plazo en el tamaño de los cuernos y astas es una tarea ardua, pero merecedora de investigación adicional con énfasis en la aclaratoria de la influencia relativa de la alimentación y los efectos (tanto demográficos como genéticos) de la explotación.

Effets de la récolte, de la culture, et du climat sur les tendances de la taille des ornements chez Les ongulés à trophée

RÉSUMÉ La chasse demeure la pierre angulaire des modèles de conservation et d'aménagement de la faune en Amérique du Nord. De récentes recherches ont toutefois révélé que la chasse avait le potentiel d'affecter négativement la structure de la taille des ornements (i.e., cornes ou bois) chez certains ongulés. Chez les ongulés polygynes, le succès d'accouplement des mâles est fortement corrélé à la taille corporelle et à la taille des ornements; par conséquent, la sélection sexuelle tend à favoriser le développement de bois ou de cornes de fortes dimensions. L'importance biologique et le grand intérêt culturel relié aux ornements mettent, tous deux, en évidence la nécessité d'identifier les tendances à long terme dans la taille de ces structures et de comprendre les mécanismes responsables ces tendances. Nous avons évalué les tendances dans la taille des cornes et des bois de mâles trophées (individus présentant des cornes et bois de taille exceptionnelle) enregistrés, entre 1900 et 2008, dans le «Records of North American Big Game» qui comprenait >22,000 enregistrements répartis dans 25 catégories de trophées couvrant la répartition géographique des espèces occupant l'Amérique du Nord. Le fait que les données soient disponibles à long terme et à large échelle spatiale a permis de compenser pour les effets localisés du climat et de la dynamique de population, rendant possible la détection de changements significatifs dans la taille des ornements parmi les mâles trophées récoltés au cours de la dernière décennie; l'âge des individus n'était toutefois pas disponible, ce qui nous a empêché d'évaluer les changements de la taille des ornements entre les classes d'âge. Par conséquent, nous avons utilisé l'approche du poids de la preuve basée sur les différences entre les catégories de trophées au niveau des traits bio-démographiques, de la répartition géographique, des caractéristiques morphologiques, et du taux de récolte afin de discriminer entre les hypothèses concurrentes visant à expliquer les tendances à long terme dans la taille des cornes et des bois des trophées chez les ongulés et d'orienter de futures recherches. Les hypothèses concurrentes étaient que: la jeune structure d'âge des mâles découle de la récolte intensive des mâles (H1), du changement génétique résultant de la sélectivité des mâles récoltés (H2), d'un effet sociologique (H3), et des effets du climat (H4) et d'une altération de l'habitat (H5). Malgré l'augmentation du nombre de données récoltées par décennie pour la plupart des catégories de trophée, les tendances dans la taille des ornements étaient négatives et significatives pour 11 des 17 catégories de bois et 3 des 8 catégories de cornes. Entre 1950–2008, le déclin moyen prédit pour les catégories de trophées de bois et de cornes était, respectivement, de 1.87% et 0.68%. Nos résultats ne concordaient pas avec un effet sociologique (H3), une contrainte nutritionnelle imposée par le climat (H4), ou une altération de l'habitat (H5) comme explications potentielles des tendances à long terme de la taille des trophées. À l'opposé, nos résultats concordaient avec une explication basée sur la récolte. Deux des 3 espèces ayant connu les niveaux de récolte les plus conservateurs en Amérique du Nord (i.e., le mouflon d'Amérique, *Ovis canadensis* et le bison, *Ovis canadensis*) ne présentaient pas de tendance à long terme dans la taille de cornes. De plus, la taille des cornes chez l'antilope d'Amérique (*Antilocapra americana*), qui peut atteindre une taille asymptotique vers l'âge de 2–3 ans, a augmenté significativement au cours du siècle dernier. Ces résultats appuient, tous deux, l'hypothèse d'une récolte intensive prédisant que la forte récolte de mâles peut déplacer graduellement la structure d'âge vers les jeunes et, conséquemment, plus petits individus. L'absence d'une tendance significative pour les chèvres de montagne (*Oreamnos americanus*), dont la taille des cornes est difficile d'évaluer précisément sur le terrain, fourni un certain support à l'hypothèse de la récolte sélective. Une autre prédiction découlant de cette hypothèse n'était pas supportée. Une réduction de la structure d'âge induite par la récolte peut augmenter le nombre de mâles qui sont récoltés avant l'atteinte de la taille asymptotique de leurs bois ou cornes, alors qu'un changement génétique résultant de la sélectivité de la récolte est moins susceptible de se produire chez des populations sauvages lorsque d'autres facteurs, tels que l'âge et la nutrition, prévalent au potentiel génétique pour la taille des ornements. Les tendances à long terme de la taille des trophées incitent à évaluer la pertinence du paradigme actuel suggérant que la récolte cible principalement les mâles; toutefois le manque d'information sur l'âge des individus récoltés nous a empêché de distinguer rigoureusement entre les mécanismes causaux suggérés. Distinguer les mécanismes potentiels sous-jacents aux tendances à long terme de la taille des cornes et des bois est une tâche ardue, mais qui mérite d'être sujette à des efforts de recherche supplémentaires portant sur l'influence relative de la nutrition et des effets, tant démographiques que génétiques, de la récolte.

KEY WORDS antlers, Artiodactyla, Bovidae, Cervidae, climate, exploitation, horns, North America, selective harvest, trophy hunting.

Contents

INTRODUCTION

Horn-like structures of Cervidae and Bovidae are among the most spectacular examples of secondary sexual characteristics (Geist 1966*a*, Gould 1974, Wilson and Mittermeier 2011), and likely evolved primarily for male-male combat, including display related to such interactions (Geist 1966*b*, 1971; Clutton-Brock 1982; Goss 1983; Bubenik and Bubenik 1990). Antlers typically are branched structures composed of bone that are grown and shed on an annual basis, whereas true horns are permanent structures with sheaths composed of cornified epidermal cells usually arranged around a bony core (Goss 1983). Pronghorn (*Antilocapra americana*) are the sole member of Antilocapridae, and possess branched, deciduous horns (Byers 1997, O'Gara and Yoakum 2004).

Size of horn-like structures is influenced by age, nutrition, and genetics (Harmel 1982, Brown 1983, Goss 1983, Bubenik and Bubenik 1990, Hartl et al. 1995). Antler size in cervids typically increases with age, peaks only after asymptotic body mass has been reached, and then often exhibits declines with senescence (Brown 1983, Goss 1983, Stewart et al. 2000, Bowyer et al. 2001, Monteith et al. 2009). In bovids, growth rate of horns declines with age, yet horn size typically continues to increase over the lifetime of an animal (Bergeron et al. 2008). Brooming (i.e., the wearing of horn tips) is an exception to this pattern, because it results in the loss of the distal portion of horns (Geist 1971, Shackleton and Hutton 1971, Bubenik and Bubenik 1990). Annual horn growth in later life may not be adequate to compensate for horn loss associated with brooming. Pronghorn are unique among North American artiodactyls because they exhibit advanced horn development at a young age; peak horn size can occur as early as 2–3 years of age (Mitchell and Maher 2001, 2006).

In contrast to natural sources of mortality, which may affect young-of-the-year and senescent individuals disproportionately, human harvest causes high mortality among prime-aged (after attaining asymptotic body mass, but prior to senescence) and young adults (Gaillard et al. 1998, Festa-Bianchet 2003, Berger 2005). Further, wildlife-management agencies in North America often restrict harvest to mostly males, thereby protecting females that, in polygynous species, represent the primary reproductive component of the population (McCullough 1979); such regimes are possible because a single male can inseminate numerous females (Noyes et al. 1996, 2002; Mysterud et al. 2003; Bowyer et al. 2007). Results of such a harvest regime include sex ratios skewed towards females and a young age structure for males (Ginsberg and Millner-Gulland 1994, Berger and Gompper 1999, Whitten 2001, Jenks et al. 2002, Keyser et al. 2006). Skewed sex ratios and a young male age structure reduces the proportion of prime-aged males, which may cause increased reproductive effort by young males and an associated reduction in their growth (Stevenson and Bancroft 1995, Laurian et al. 2000, Singer and Zeigenfuss 2002, Garel et al. 2006, Milner et al. 2007).

Allocation of resources to size of horn-like structures comes secondary to growth and maintenance of somatic tissues (Jorgenson et al. 1998, Stewart et al. 2000, Kruuk et al. 2002, Festa-Bianchet et al. 2004, Mysterud et al. 2005). Horns and antlers are phenotypic characters that are genetically based but, because they are costly to produce, their growth is influenced strongly by nutrition (Harmel 1982, Geist 1986, Lukefahr and Jacobson 1998, Festa-Bianchet et al. 2004, Monteith et al. 2009). Nutritional effects on growth of horns and antlers may be manifested through mechanisms that are determined by variation in climate and density dependence. For example, large-scale climatic regimes influence local and regional patterns of temperature and precipitation, both of which strongly affect quality and abundance of forage (Post et al. 1997, Post and Stenseth 1999, Marshal et al. 2002, Forchhammer and Post 2004, Forchhammer et al. 2005). As a result, climate-mediated variation in annual forage quality and availability in relation to population density affects net nutritional gain and the capacity of males to allocate resources to growth of horns or antlers (Schmidt et al. 2001, Kruuk et al. 2002, Mysterud et al. 2005, Loehr et al. 2010).

Size and symmetry of horn-like structures are heritable (Hartl et al. 1991, 1995; Williams et al. 1994; Lukefahr and Jacobson 1998; Kruuk et al. 2002), are considered to be honest signals of phenotypic quality (Solberg and Sæther 1993, Ditchkoff et al. 2001, Malo et al. 2005, Vanpé et al. 2007, Bonenfant et al. 2009*b*), including increased sperm production (Preston et al. 2003, Malo et al. 2005, Gomendio et al. 2007) and parasite resistance (Ezenwa and Jolles 2008), and often are positively correlated with body size (Clutton-Brock et al. 1982, Bowyer 1986, Stewart et al. 2000, Monteith et al. 2009). For many species of large herbivores, big males with large horn-like structures frequently enjoy high reproductive success (Clutton-Brock 1982, Coltman et al. 2002, Kruuk et al. 2002, Preston et al. 2003, Mainguy et al. 2008). As a result, sexual selection has favored development of large horn-like structures in many artiodactyls (Vanpé et al. 2010). In harvested populations, however, natural mating systems may be disrupted by the selective removal of large males (Coltman et al. 2003, Garel et al. 2007, Rasmussen et al. 2008, Bonenfant et al. 2009*b*) or heavy harvest of males (Bowyer et al. 1999, Langvatn and Loison 1999, Laurian et al. 2000, Solberg et al. 2000, Milner et al. 2007).

Among polygynous ungulates, large horns and antlers can enhance reproductive success, but they also are favored by trophy hunters (Festa-Bianchet and Lee 2009, Messner 2011). Although effects of hunting on demographics of ungulate populations are well recognized (Bowyer et al. 1999, Langvatn and Loison 1999, Solberg et al. 2000, Milner et al. 2007, Hengeveld and Festa-Bianchet 2011), the consequence of selection against heritable traits remain a contentious issue (Darimont et al. 2009, Festa-Bianchet and Lee 2009). The primary empirical evidence supporting effects of trophy hunting on growth of secondary sexual characters is for wild sheep (*Ovis* spp.), wherein intensive harvest of males with superior secondary sexual characteristics has led to decreased size or altered conformation of horns (Coltman et al. 2003, Garel et al. 2007). Long-term consequences of human harvest on targeted phenotypes continue to be debated (Mysterud and Bischof 2010, Hedrick 2011, Mysterud 2011, Pérez et al. 2011), in part because the applicability of these unique studies to other populations occupying a variety of habitats with wide geographic ranges, and different harvest pressure, is uncertain.

Despite the importance of hunting as a tool for conservation and management (Whitfield 2003, Lindsey et al. 2007, Festa-Bianchet and Lee 2009, Groves and Leslie 2011, Becker et al. 2013), heavy harvest of males could reduce mean size of horn-like structures through changes in age at harvest (Stewart et al. 2000, Loehr et al. 2007, Bonenfant et al. 2009*b*, Monteith et al. 2009, Servanty et al. 2011), sex ratios (Laurian et al. 2000, Garel et al. 2006, Milner et al. 2007), or via genetic changes caused by selective removal of large or rapidly growing males (Coltman et al. 2003, Garel et al. 2007). As a result, questions related to effects of harvest on size of horn-like structures remain controversial (Fenberg and Roy 2008). A major difficulty in addressing those questions is the near absence of data that span a sufficiently long time frame for harvested populations (Proaktor et al. 2007, Tiilikainen et al. 2010, Servanty et al. 2011). Effects of harvest may require decades to manifest themselves (Hundertmark et al. 1998), and studies conducted at the population level must account for effects of nutritional limitation via density dependence, habitat loss, or other factors, which are more likely to be diluted and less influential when analyses are conducted at a broad geographic scale, such as the geographic range of a species.

The importance of trophy hunting as an economic activity and conservation tool for multiple species in many countries (Harris and Pletscher 2002, Whitfield 2003, Lindsey et al. 2007, Groves and Leslie 2011, Becker et al. 2013) reinforces the need to understand long-term relationships between harvest regimes and horn and antler size. The Records of North American Big Game, which was established by the Boone and Crockett Club in 1932, contains data on horn and antler size of trophy ungulates spanning more than a century and includes the entire geographic range of most native species (Reneau and Buckner 2005). Data available in Records of North American Big Game represent a unique resource for evaluating long-term patterns of horn and antler size among trophy ungulates in North America. Although these data do not represent a random sample of ungulates across North America, they should be representative of the size of large, trophy ungulates, most of which will already have attained asymptotic body mass (Monteith et al. 2009). Moreover, if changes in the size of large, horn-like structures occur, they should be manifested in the size of these trophy males.

Weight-of-Evidence Approach

The broad-scale nature of Records of North American Big Game precluded testing some hypotheses that could explain temporal trends in those data at a smaller spatial scale (i.e., regional). In addition, ages of individual specimens were not available, which prevented us from evaluating age-class specific changes in size of horns and antlers. Consequently, after identifying temporal trends in size of horn-like structures, we used a weight-of-evidence approach (Bowyer et al. 2003, Pierce et al. 2012) that was based on a series of category-specific predictions for explaining those trends that followed directly from 5 primary hypotheses. We identified differences among trophy categories in life-history characteristics, geographic distribution, morphological attributes, harvest regimes, and anthropogenic disturbance that helped to infer potential mechanisms underpinning observed trends.

Intensive-harvest hypothesis (H1).—The intensive-harvest hypothesis is based on the premise that as harvest intensity increases, age distribution shifts towards younger age classes (Jenks et al. 2002). Harvest intensity of large ungulates varies greatly both among and within species across their geographic ranges (Demarais and Krausman 2000). Given the difficulty in estimating population size and harvest rates of large ungulates accurately, reliable estimates of harvest intensity generally were not available (Walker 2011). Consequently, we limited our interpretation of relationships between harvest intensity and trends in horn or antler size to a categorical comparison of bighorn sheep (*Ovis canadensis canadensis*), desert sheep (*Ovis canadensis nelsoni*), and bison (*Bison bison*) with all other trophy categories. Although harvest of some populations of wild sheep are still regulated by size restrictions, most populations of bighorn sheep, desert sheep, and bison are harvested based on very conservative quotas compared with other species where males are more heavily exploited (Winkler 1987, Douglas and Leslie 1999, Krausman and Shackleton 2000, Festa-Bianchet and Lee 2009). Among jurisdictions responsible for managing bighorn and desert sheep in North America, harvest rates of male sheep as of 2007 averaged 2.5 males per 100 sheep (range 1.3–3.5), which represented an estimated 7–12% of all males within the population, with 51% of the harvest ≥8 years old (Wild Sheep Foundation Professional Biologist Meeting Attendees 2008). Similarly, because of their restricted range, which often is limited to national and state parks or preserves, bison were not typically managed to provide a sustained harvest, but were harvested by small opportunistic hunts with limited trophy harvest (Shaw and Meagher 2000). Although, for other trophy categories, some hunt units are more conservatively managed to allow for increased trophy potential, the more common management scenario increases hunter opportunity by allowing harvest of a much larger proportion of the male segment of the population (Jenks et al. 2002). For example, an estimated 14.3% of deer (*Odocoileus* spp.) and 15.5% of elk (*Cervus* spp.) across 19 western states and provinces were harvested in 2009 (Walker 2011), which typically results in a lower age distribution of the male harvest. Indeed, for 26 states with available age data, 68% of male white-tailed deer harvested in 2010 were ≤2.5 years old (Adams et al. 2012).

Conservative male harvest yields a higher relative abundance of prime-aged males with large horns or antlers (Milner et al. 2007, Fenberg and Roy 2008), compared with other species where males are more heavily exploited. If intensive harvest of males has progressively shifted age structure toward younger males with fewer individuals surviving to old ages and reaching large sizes, then horn size of bighorn sheep, desert sheep, and bison should be less likely to decline through time, because male harvest regimes for those trophy categories generally were highly conservative (i.e., limited harvest of males; P1a). Additionally, pronghorn should be less prone to declines in horn size caused by a downward shift in age structure by heavy harvest (P1b), because pronghorn can attain peak horn size by 2–3 years old (Mitchell and Maher 2001, 2006).

Selective-harvest hypothesis (H2).—We assessed 2 predictions that were based on the hypothesis that trophy hunting has selected against genes for large horn-like structures. Species that are difficult to field judge should be less likely to exhibit a negative trend than species for which hunters can more easily assess size in the field, and thus selectively remove the largest individuals (P2a). For example, mountain goats (*Oreamnos americanus*) should be less prone to selective harvest because size of their small, cylindrical horns is difficult to assess in the field (Festa-Bianchet and Côté 2008).

Once a horned animal becomes large enough to be considered a trophy, it will remain a trophy throughout its lifetime regardless of environmental conditions or age, unless substantial brooming occurs. In contrast, antlers are cast and regrown each year, and size varies as a curvilinear function of age and can be influenced strongly by interannual variation in environmental conditions. Consequently, an individual cervid may be a trophy in 1 year and not in subsequent years. Based on those differential patterns of growth and morphology, we predicted that if selective harvest was the primary cause of declines in size of horn-like structures, then declines would be more apparent for horned than antlered game (P2b); trophy hunters may be more effective at removing trophy males with large horns, because those phenotypic characters are expressed more consistently through time than are those of antlers.

Sociological effect hypothesis (H3).—We evaluated 2 specific predictions that followed from the hypothesis that an increased desire to submit smaller, yet eligible, trophies to the Boone and Crockett Club record book (i.e., sociological hypothesis; Messner 2011) has biased observed trends in size of horn-like structures downward through time. First, assuming that annual number of entries recorded partially reflects interest in submitting trophies, number of entries (number of trophies entered per year for each trophy category) should be negatively related to size of horn-like structures (P3a). Second, negative trends in size of trophy horn-like structures should be less apparent among the largest specimens compared with the entire dataset, because the sociological hypothesis is based on the premise that a disproportionately larger increase in entry of smaller eligible trophies is influencing observed trends (P3b).

Climate (H4) and habitat (H5) hypotheses.—We also evaluated predictions that followed from hypotheses related to climate and habitat alteration. First, although effects of global changes in climate are difficult to separate from density dependence (Bonenfant et al. 2009*a*), if climatic changes have affected the ability of males to grow large horn-like structures, then broad-scale climatic indices should be related to the underlying trends in size of antlers at the continent-wide scale of this analysis (P4a). Climatic patterns can affect growth of antlers and horns similarly, but effects of climate on antler size are realized annually, whereas effects of climate on horn size are cumulative because horns grow continuously throughout the life of the animal. Because most horn growth occurs during numerous years prior to harvest, the absence of age data prevented an evaluation of potential climate effects on size of horns (Loehr et al. 2010). Therefore, we assessed effects of climate on trends in size of deciduous horn-like structures (i.e., antlers and pronghorns).

Most large mammal species in North America have experienced some degree of both habitat improvement and degradation over the past century (Demarais and Krausman 2000). Quantifying these changes, however, is nearly impossible, and thus we used examples that occurred at one extreme of the continuum of habitat change to evaluate the hypothesis that loss of habitat has negatively influenced size of horn-like structures. If loss or degradation of habitat has affected growth of horn-like structures, then horn size of Dall's sheep (*Ovis dalli dalli* and *O. d. kenaiensis*), Stone's sheep (*Ovis dalli stonei*), and muskox (*Ovibos moschatus*) should be least likely to show a negative trend in horn size, because most of the range of those species is pristine and intact (Bowyer et al. 2000; P5a) and muskox have expanded into high-quality habitat in recent years (Klein 2000).

METHODS

We evaluated patterns in horn and antler size of trophy animals recorded in Records of North American Big Game by the Boone and Crockett Club. We used trophy categories defined by the Boone and Crocket Club, including typical and non-typical categories (Table 1). For cervids, non-typical categories were developed to facilitate recognition of large, asymmetrical specimens, the scores of which would otherwise be severely penalized for exhibiting excessive abnormal characteristics. In addition, because we were interested only in total size of horn-like structures, we used the sum of all measured components of size (defined as gross score by the Boone and Crockett Club). Gross score, or some derivative of that metric, has been used

Table 1. Trophy categories of native, North American big game recorded in Records of North American Big Game. We provide scientific names of all taxa included in each category, along with sample sizes of trophies within categories included in our analyses (1900–2008).

Trophy category	Scientific name	*n*
Antlered game		
Alaska-Yukon moose	*Alces alces gigas*	576
Canada moose	*Alces alces americana* and *A. a. andersoni*	774
Shiras moose	*Alces alces shirasi*	694
Non-typical Coues' white-tailed deer	*Odocoileus virginianus couesi*	95
Typical Coues' white-tailed deer	*Odocoileus virginianus couesi*	335
Non-typical white-tailed deer	*Odocoileus virginianus virginianus* and related subspecies	3,182
Typical white-tailed deer	*Odocoileus virginianus virginianus* and related subspecies	4,443
Non-typical mule deer	*Odocoileus hemionus hemionus* and related subspecies	656
Typical mule deer	*Odocoileus hemionus hemionus* and related subspecies	803
Mountain caribou	*Rangifer tarandus caribou*	374
Central Canada barren ground caribou	*Rangifer tarandus groenlandicus*	280
Woodland caribou	*Rangifer tarandus caribou*	210
Barren ground caribou	*Rangifer tarandus granti*	852
Quebec-Labrador caribou	*Rangifer tarandus*	380
Non-typical American elk	*Cervus elaphus nelsoni* and related subspecies	267
Typical American elk	*Cervus elaphus nelsoni* and related subspecies	662
Roosevelt's elk	*Cervus elaphus roosevelti*	347
Non-typical Columbia black-tailed deer	*Odocoileus hemionus columbianus*	29
Typical Columbia black-tailed deer	*Odocoileus hemionus columbianus*	943
Typical Sitka black-tailed deer	*Odocoileus hemionus sitkensis*	134
Horned game		
Bison	*Bison bison*	384
Muskox	*Ovibos moschatus*	399
Pronghorn	*Antilocapra americana*	2,338
Rocky Mountain goat	*Oreamnos americanus*	741
Bighorn sheep	*Ovis canadensis canadensis* and related subspecies	1,191
Desert sheep	*Ovis canadensis nelsoni* and related subspecies	768
Dall's sheep	*Ovis dalli dalli* and *O. d. kenaiensis*	323
Stone's sheep	*Ovis dalli stonei*	382

frequently to quantify size of horn-like structures (Jorgenson et al. 1998, Ditchkoff et al. 2001, Festa-Bianchet et al. 2004, Garel et al. 2007, Lockwood et al. 2007), and is strongly correlated with other metrics of size for horns and antlers (Stewart et al. 2000; Strickland and Demarais, 2000, 2008; Bowyer et al. 2001, 2002; Monteith et al. 2009).

Records of North American Big Game

Following the unregulated exploitation of most populations of large, hoofed mammals across North America in the late 19th and early 20th centuries, conservationists recognized the need for laws to protect wildlife. Laws and regulations promulgated at the beginning of the conservation movement in North America sharply curtailed the harvest of large mammals, which allowed for their recovery (Allen 1954, Posewitz 1994, Dunlap 1998, Rattenbury 2008). At the forefront of that conservation movement was President Theodore Roosevelt, who founded the Boone and Crocket Club in 1887. Advocating for conservation of large mammals in the late 19th century, the Boone and Crockett Club was the first to deal with issues of national prominence (Reiger 1975, Williamson 1987). Indeed, 1 of the 5 objectives of that organization was, "To work for the preservation of the large game of this country, and, so far as possible, to further legislation for that purpose, and to assist in enforcing the existing laws" (Reiger 1975:119). In accordance with that objective, the Records of North American Big Game was established in 1932 to collect biological, harvest, and location data for trophy specimens of large mammals in North America. The Boone and Crockett Club posited that such information would aid in the preservation of large mammals, and further legislation for that purpose (Reiger 1975). The Boone and Crockett Club has since compiled a database of horn, antler, and skull sizes for 38 categories of native, North American big game that spans more than a century and includes >40,000 records.

The primary goal of the Boone and Crockett Records Program at its inception was to establish a baseline against which future trends in size of trophy animals could be compared (Gray 1932). Initially, measurements were quite simple, and included only length of the skull or the longer antler or horn. In 1949, a committee was formed to develop an objective and standardized system of measurement for large mammals in North America. An approved measuring system was adopted in 1950, and has become the universally accepted standard for quantifying size of antlers and horns in North American big game. Following adoption of that standardized system of measurement, an attempt was made to re-measure all specimens recorded before 1950 using the new system. Those data were first published in the Records of North American Big Game in 1952 (The Committee on Records of the Boone and Crockett Club 1952), and included trophies collected as early as the late 19th century.

All specimens must be air-dried for a minimum of 60 days before official measurement to eliminate the effects of shrinkage over time on the total score. To be eligible for inclusion in Records of North American Big Game, hunter-harvested specimens must be taken under "fair chase" conditions, which specify ethical conduct as defined by the Boone and Crockett Club

(Buckner et al. 2009). In addition to legally harvested animals, the Boone and Crockett Club recognizes trophies possessed by state or federal agencies and those legally collected from the field following natural mortality (Buckner et al. 2009).

All measurements of antlers and horns were obtained according to strict methods and guidelines that are specific for each category of game recognized by the Boone and Crockett Club (Buckner et al. 2009). The standardized system placed emphasis on symmetry by reducing the total score based on the amount of asymmetry between the left and right antlers or horns. Eligibility of submitted specimens for the record book was determined by whether this adjusted score exceeded minimums established by the Boone and Crockett Club. Although minimum entry requirements have varied slightly for some species over the past century, we avoided this potential source of bias (i.e., an increased number of smaller specimens submitted following reduction of the minimum entry requirement) by using the highest minimum for each trophy category in our analyses.

Records of North American Big Game only incorporates data from large mammals native to North America (Table 1; Reneau and Buckner 2005, Buckner et al. 2009). The Boone and Crockett Club defines a trophy category based primarily on species, but many large mammals exhibit geographic variation in morphology; thus, some species have been divided into ≥2 categories for record-keeping purposes. For example, moose occupying the intermountain West (Shiras category; *Alces alces shirasi*) are markedly smaller than those in the remainder of North America. Moose occupying Alaska and the Yukon and Northwest Territories (Alaska-Yukon category; *Alces alces gigas*) are the largest category, and moose distributed across other areas of North America (Canada category; *Alces alces americana* and *A. a. andersoni*) are intermediate in size. As a general rule, the geographic boundaries of a category are established to reduce the probability of a specimen belonging to a category characterized by larger individuals being obtained within the boundary of a category designated for smaller geographical variants. Categories recognized by the Boone and Crockett Club do not necessarily correspond with subspecies designations (Table 1; Wilson and Reeder 2005). For instance, Hundertmark et al. (2003) delineated 4 subspecies of moose for North America based on genetic markers, but the Boone and Crockett Club recognizes only 3 categories.

Antler and horn measurements were collected with a quarter-inch (6.35 mm) steel tape; however, main-beam lengths of antlers were measured with flexible steel cables, and the width of boss and horn of muskox were measured with a caliper. Measurements for antlers and horns were rounded to the nearest eighth inch (3.18 mm). To be considered a "measurable tine" (a branch emanating from the main antler beam or from another tine), a projection must have been at least 1 inch (25.4 mm) in length, with length exceeding the width at 1 inch or more of length (Buckner et al. 2009). For caribou (*Rangifer tarandus*), however, a tine was defined as a projection that was at least 0.5 inches (12.7 mm) in length, with length exceeding the width at 0.5 inches or more of length (Buckner et al. 2009).

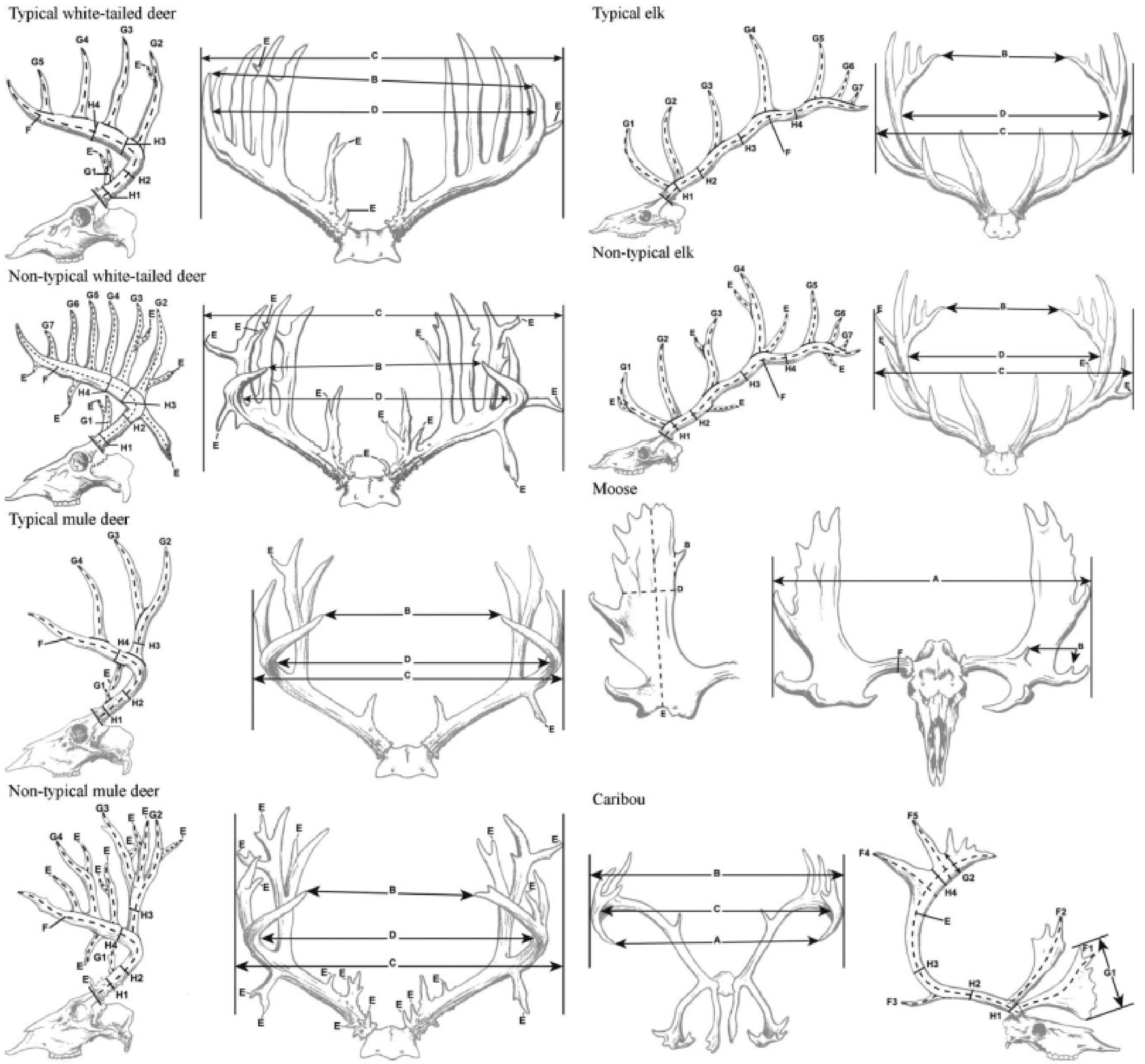
For most antlered species, 4 types of measurements composed the total score: 1) length of tines as they arise from the main beam or from other tines; 2) 4 circumference measurements; 3) length of the main beams; and 4) inside spread (distance between the main beams; Fig. 1). For moose and caribou, however, number of tines was added to the total score. In addition, for moose, the length and width of the palm were included, greatest outside rather than inside spread was measured, and only 1 circumference measurement was obtained at the smallest point along each main beam (Fig. 1). Additional exceptions for caribou included measurement of only 4 tines (i.e., brow palm, rear tine, and the 2 longest top tines), and measurement of width of the brow palm and top palm (Fig. 1).

For most horned species, 2 types of measurements comprised the total score: length of the outer edge of the horn and 4 circumference measurements equally spaced along each horn (Fig. 2). Two exceptions to this general approach existed: pronghorn, in which the length of the prong was added to the total score, and muskox, in which the width of the boss was substituted for the first 2 circumference measurements.

When the Boone and Crockett measuring system was adopted in the 1950s, the individuals that developed the scoring system and those that received direct training and were appointed by the Club were responsible for measuring trophies. Beginning in the 1970s, a training program for Official Measurers was developed to minimize variance in data acquisition and ensure repeatability in measuring trophies. Official Measurers appointed by the Boone and Crocket Club are certified only after completing a rigorous 5-day workshop during which they receive the training necessary to ensure that all species of North American big game are measured precisely and consistently (Buckner et al. 2009). Official measurers receive no compensation for their services and perform their duties under strict ethical and technical guidelines (Buckner et al. 2009). To date, these Official Measurers have voluntarily measured >40,000 specimens that are recorded in the Records of North American Big Game, a subset of which constituted the basis for our analyses.

Statistical Analysis

We used simple linear regression (Neter et al. 1996) to identify time trends in size of horns and antlers of trophy categories recognized by the Boone and Crockett Club. We assumed that samples between years were independent, which is reasonable given the broad geographic scale at which samples were obtained. For nearly all categories, the number of specimens recorded annually has increased through time; consequently, to meet the assumption of homogeneity of variance, we binned data temporally based on year of harvest and used the mean and associated variance from each bin in a weighted least-squares regression (Neter et al. 1996, Zar 1999). We used the method of Krebs (1999:231) to determine the minimum number of samples per bin necessary to produce 95% confidence intervals that bounded the mean by no more than ±5%. This analysis indicated that ≥20 samples per bin were sufficient for producing the desired level of precision across all categories; therefore, we used 20 as the minimum sample size per bin. To produce these temporal bins within each category, we began with the year of the earliest recorded specimen and added samples from subsequent years until the minimum sample size was achieved; we never partitioned data from a single year. Sample sizes for non-typical Columbian black-tailed deer (*Odocoileus hemionus columbianus*;



Typical white-tailed deer

Typical elk

Non-typical white-tailed deer

Non-typical elk

Typical mule deer

Moose

Non-typical mule deer

Caribou

Figure 1. Illustrations of measurements of antlered game according to the Boone and Crockett scoring system. For all antlered categories except moose and caribou, total antler size comprised the sum of all D, E, F, G, and H measurements. Total antler size comprised the sum of measurements A, D, E, F, and total number of tines for moose, and the sum of measurements C, E, F, G, H, and total number of tines for caribou.

$n = 29$), non-typical Coues' white-tailed deer (*Odocoileus virginianus couesi*; $n = 95$), and typical Sitka black-tailed deer (*Odocoileus hemionus sitkensis*; $n = 134$; Fig. 3) were insufficient to produce an adequate number of bins for regression analyses.

Mean size of horns or antlers in each bin was the dependent variable in our analyses. Likewise, we used mean year of all samples in each bin as the independent variable, and weighted regressions by the inverse of the variance in size (Neter et al. 1996). We used the inverse of the variance, rather than sample size, for weighting to ensure that means from more variable bins did not receive undue weight (Neter et al. 1996). As a result, number of bins and their temporal width differed among trophy categories, but binning criteria remained consistent. Moreover, the temporal position (i.e., the value of the independent variable) of each bin was inherently weighted by the distribution of samples within that bin. Consequently, bins were representative of temporal patterns in size for each trophy category. In addition, because the official records program did not begin until the early 1950s, a potential bias existed in those data because there may have been a higher probability of only the most exceptional trophies collected prior to 1950 being "retroactively" entered. To address this potential bias, we conducted an identical series of simple linear regression analyses using only post-1950 data and compared results of this analysis with results of analyses based on the full dataset.

We used multiple linear regression weighted by the inverse of the intra-bin variance in size to determine whether time trends could be explained by broad-scale indices of climate or changes in number of entries over time within each trophy category. Broad-scale climatic patterns influence ecological processes;

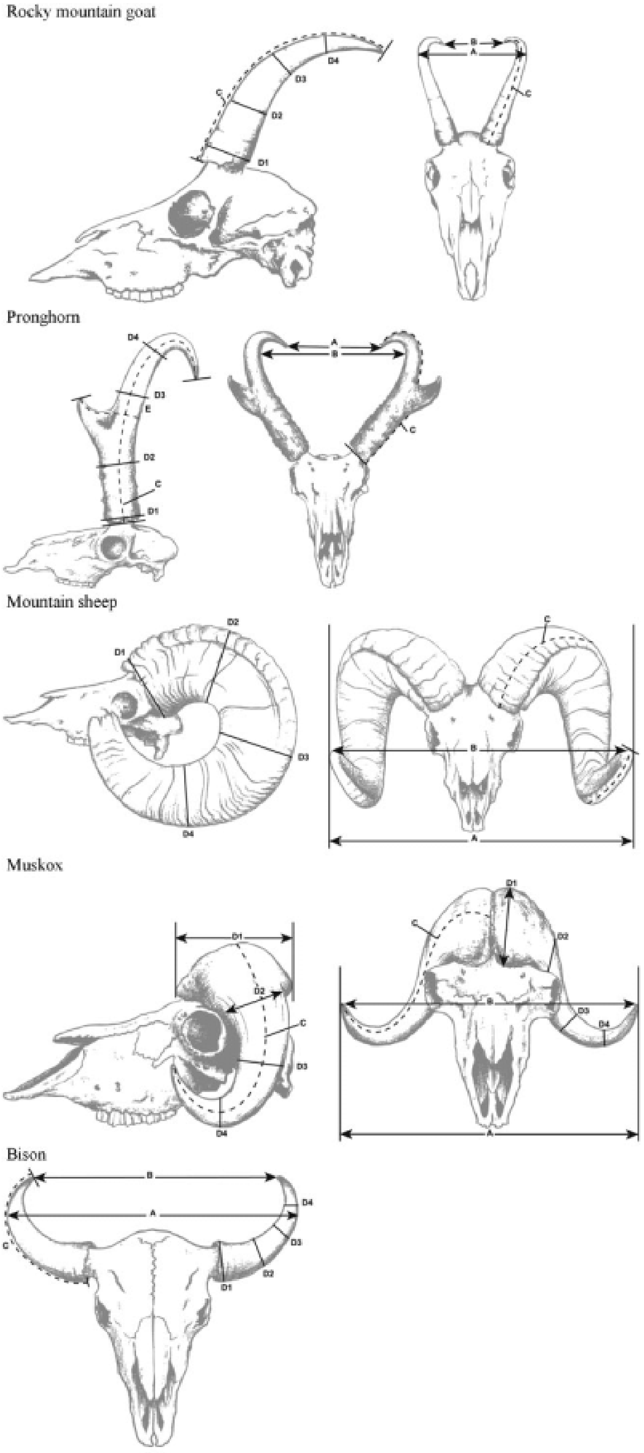


Figure 2. Illustrations of measurements of horned game according to the Boone and Crockett scoring system. Horn size comprised the sum of C and D measurements for all horned game with the exception of pronghorn, where measurement E (length of prong) was added.

such large-scale measures, rather than local weather conditions, could provide insight into ecological responses at a continental scale (Stenseth et al. 2003, Forchhammer and Post 2004, Hallett et al. 2004). Although there is no universally accepted index to describe climatic phenomena, most indices are highly correlated (Stenseth et al. 2003). Thus, we selected 2 commonly used indices of large-scale climate likely to influence large mammals in North America, the first of which was the North Atlantic Oscillation (NAO; Hurrell 1995). Effects of the NAO are manifested strongly across terrestrial ecosystems throughout much of the northern hemisphere (Hurrell et al. 2001; Ottersen et al. 2001; Stenseth et al. 2002, 2003), and are related to population dynamics of large mammals (Post and Stenseth 1999, Patterson and Power 2001, Forchhammer et al. 2002, Mysterud et al. 2003). Biological effects of the NAO are not as evident in western North America (Stenseth et al. 1999), possibly a result of the dominance of Pacific climate effects (Trenberth and Hurrell 1994). Consequently, we also included an index of the North Pacific Oscillation (NPO) in our analyses (Rogers 1981, Trenberth and Hurrell 1994, Forchhammer and Post 2004). The NPO can influence population dynamics of large mammals in North America (Forchhammer and Post 2004, Hebblewhite 2005). Values of both indices obtained during winter (Nov–Apr) are most closely related to a multitude of ecological processes (Hurrell 1995, Forchhammer and Post 2004, Hebblewhite 2005, Mysterud et al. 2005), so we used mean values of each index during that period in our analyses.

We included climatic indices as predictor variables in models only for species with deciduous horn-like structures, because those structures are re-grown every year and are more likely to reflect interannual variability in climate (Schmidt et al. 2001, Mysterud et al. 2005). We assigned values of each climatic index from the previous winter to each specimen in Records of North American Big Game based on the year it was collected. Mean values of each climatic index for all specimens included in a bin served as the climatic predictor variables in the multiple regressions.

The number of specimens meeting the minimum requirements for inclusion in Records of North American Big Game has increased markedly in recent decades for nearly all categories (Buckner et al. 2009). This increase likely is related to additional availability of trophy animals; however, we posited that it also may be influenced by a sociological effect, wherein desire to enter smaller, yet eligible, trophies has increased over time. Such an effect might bias observed trends in size of trophy horn-like structures downward. To test this hypothesis, we calculated an intra-bin measure of entry rate (mean number of entries per year for years included in each bin) for inclusion as a predictor variable in multiple regression analyses.

We used residual and sequential regression (Graham 2003) to evaluate the effects of year and submission rate, which often were correlated, on size of trophy horn-like structures. We assigned priority to the year effect, because we were most interested in investigating temporal trends in size. Consequently, we regressed submission rate against year and extracted the residuals from that analysis, which yielded a metric that was independent of the year effect and represented the unique contribution of submission rate (Graham 2003). We then included the residuals from that analysis in a multiple regression with year and climate. The goal of the multiple regression analyses was to determine whether the temporal trend represented by the effect of year was altered by the inclusion of climate or submission rate. Therefore, we used forward stepwise selection with year as the base model to assess

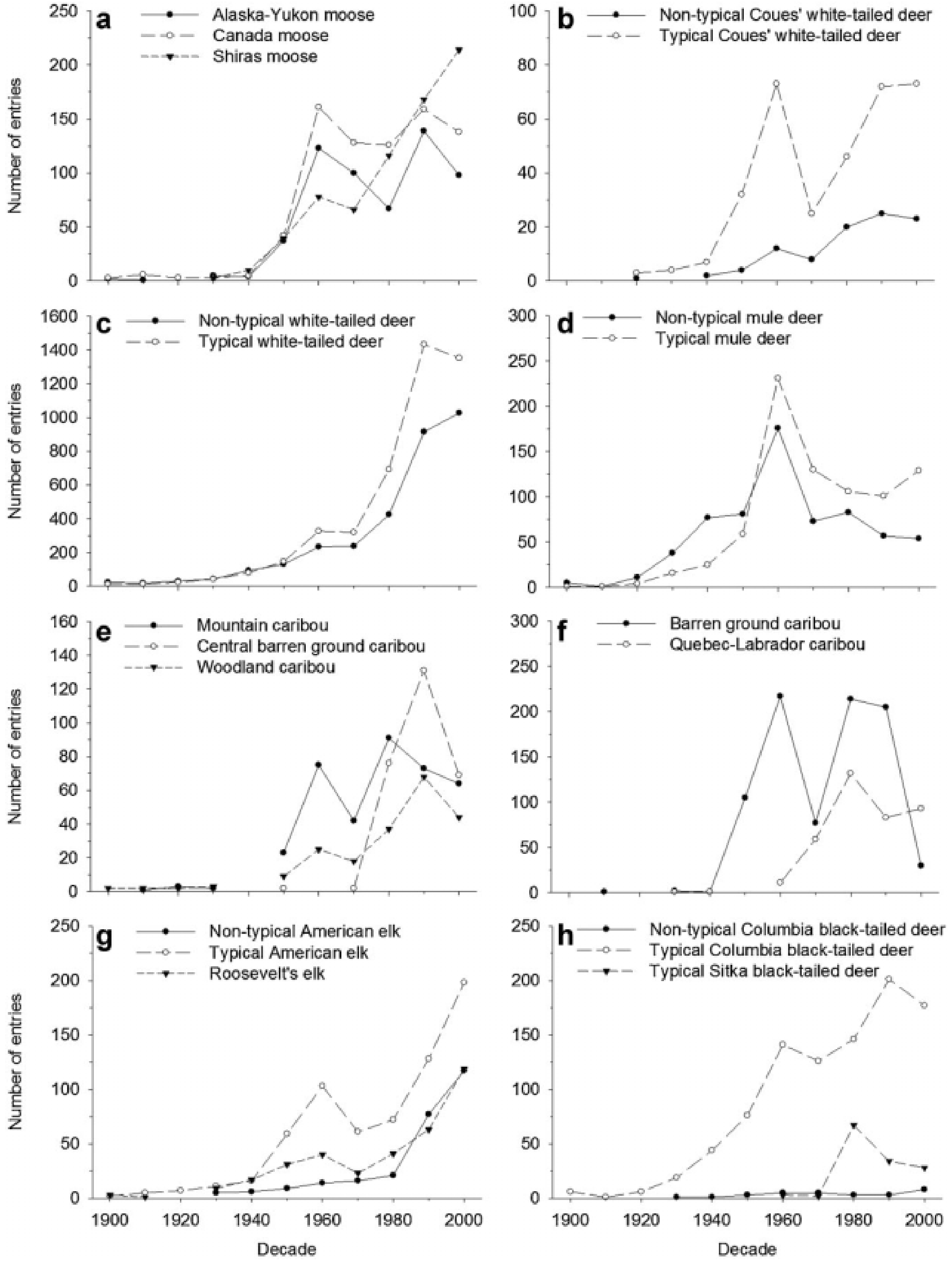


Figure 3. Decadal entries of antlered trophies recorded in Records of North American Big Game. Data points represent total number of entries for each trophy category that exceeded the highest minimum size requirement for eligibility established by the Boone and Crockett Club during the past century.

the influence of climate and submission rate on trends in size (Neter et al. 1996). We used a *P*-value of 0.10 to enter the model and 0.05 to remain.

We used an additional approach to evaluate the potential for a sociological effect on size of trophies. A prediction of the sociological hypothesis is that temporal patterns in size of horn-like structures result largely from an increase in the number of smaller, but eligible, specimens entered in the record book through time. Accordingly, temporal patterns observed in the full dataset should be less apparent when only the largest trophies are considered, because the largest specimens should be less affected by an increase in the number of smaller individuals. We tested this prediction by comparing results of weighted multiple regression analyses (Neter et al. 1996) using the full dataset with the same analyses using only the top and bottom thirds (based on size) of the dataset for each category. Partitioning the dataset resulted in intra-bin sample sizes that no longer met our criteria for sample size. Variance in size among samples in the top and bottom third of the dataset was lower, and we determined (using the method of Krebs 1999:231) that a minimum intra-bin sample size of 13 was sufficient for this analysis. We re-binned data for each trophy category to include a minimum of 40 samples per bin, and then extracted the top and bottom third of specimens from each bin for analysis.

We also tested for a specific directional trend across similar categories by combining probabilities from category-specific analyses into a single statistical test. We combined probabilities for the time trend (*P*-values for year) obtained from simple regression analyses based on the full dataset in a meta-analysis using the method of Sokal and Rolf (1995:795) for horned and antlered game separately. We also evaluated the influence of each trophy category on results of the meta-analysis by performing a series of meta-analyses in which a single category was withheld during each iteration. We recorded the minimum and maximum *P*-values, and the respective categories that were withheld to produce them, for horned and antlered game, to determine if any single category would cause results of the meta-analyses to shift from significant to non-significant (or vice-versa). For all such meta-analyses, we adopted an alpha of ≤ 0.02 to account for a potential lack of independence among tests (Bowyer et al. 2007, Monteith et al. 2009) that resulted from some species being represented by >1 category (i.e., typical and non-typical categories). For all other tests, we used an alpha of 0.05.

RESULTS

After truncating the Boone and Crockett data based on the highest recorded minimum entry score (based on net score) for each trophy category, we included 22,304 trophies obtained from 1900 to 2008 in our analyses: 15,778 for antlered game, and 6,526 for horned game. Number of trophies recorded in Records of North American Big Game per decade increased for nearly all trophy categories (Figs. 3 and 4). Decadal increases in recorded trophies were pronounced following the inception of the Boone and Crockett Records Program in the early 1950s. In contrast to this upward trend, a few categories exhibited peaks in decadal entries in the 1960s and declined thereafter, including non-typical and typical mule deer (*Odocoileus hemionus*), Dall's sheep, Stone's sheep, and Rocky Mountain goats (Figs. 3 and 4).

Temporal Trends in Size

Temporal trends in mean antler size of trophy specimens generally were negative over the last century (Fig. 5). Alaska-Yukon and Canada moose (Fig. 5a), non-typical and typical American elk (*Cervus elaphus*; Fig. 5g), and central Canada barren ground (*Rangifer tarandus groenlandicus*) and woodland caribou (*Rangifer tarandus caribou*; Fig. 5e), however, did not exhibit a significant temporal trend (Table 2). In addition, trends in antler size typically were linear, with Quebec-Labrador caribou (*Rangifer tarandus*; Fig. 5f) and Roosevelt elk (*Cervus elaphus roosevelti*; Fig. 5g) representing possible exceptions. Percent change in antler size of trophies during the past 58 years (1950–2008), predicted by simple linear regression models, was negative ($\bar{x} = -1.87\%$, SD = 1.40) for all but 1 category, and ranged from −4.93% for typical Columbia black-tailed deer to 0.18% for Canada moose (Table 2).

Temporal trends in mean horn size of trophy specimens were less consistent than patterns for antlered categories (Fig. 6). Horn size of trophy mountain sheep declined significantly over much of the past century (Table 2), with the exception of bighorn sheep, in which horn size leveled out or increased in recent decades (Fig. 6c,d). Bison and mountain goats did not exhibit a significant temporal trend in horn size of trophies (Table 2), whereas trophy

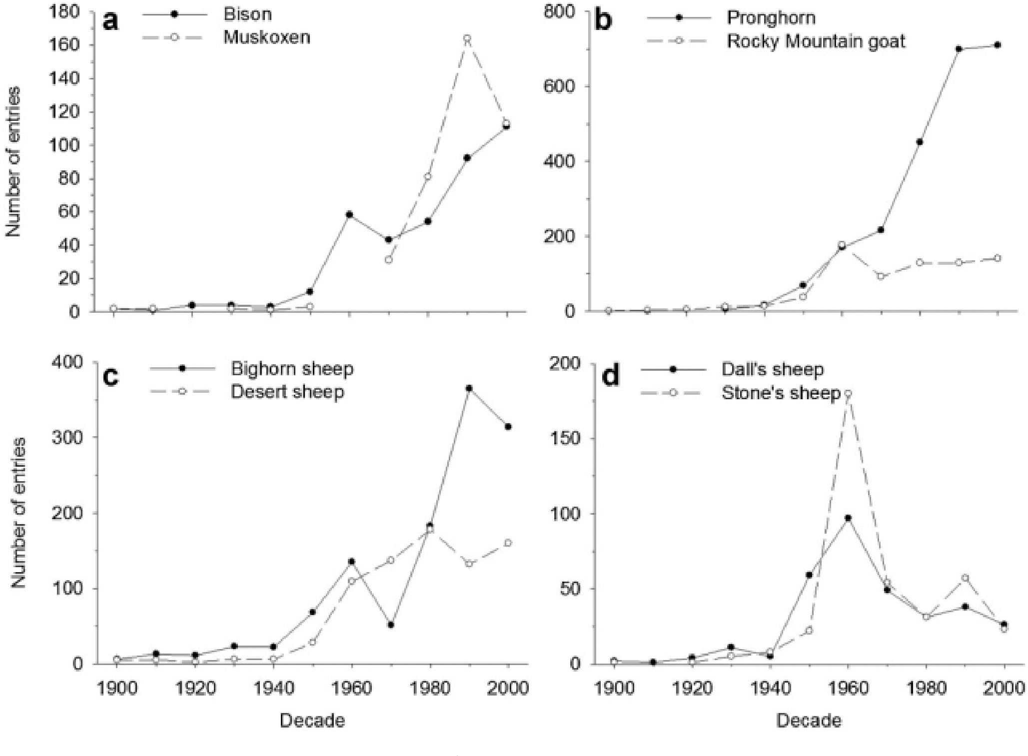


Figure 4. Decadal entries of horned trophies recorded in Records of North American Big Game. Data points represent total number of entries for each trophy category that exceeded the highest minimum size requirement for eligibility established by the Boone and Crockett Club during the past century.

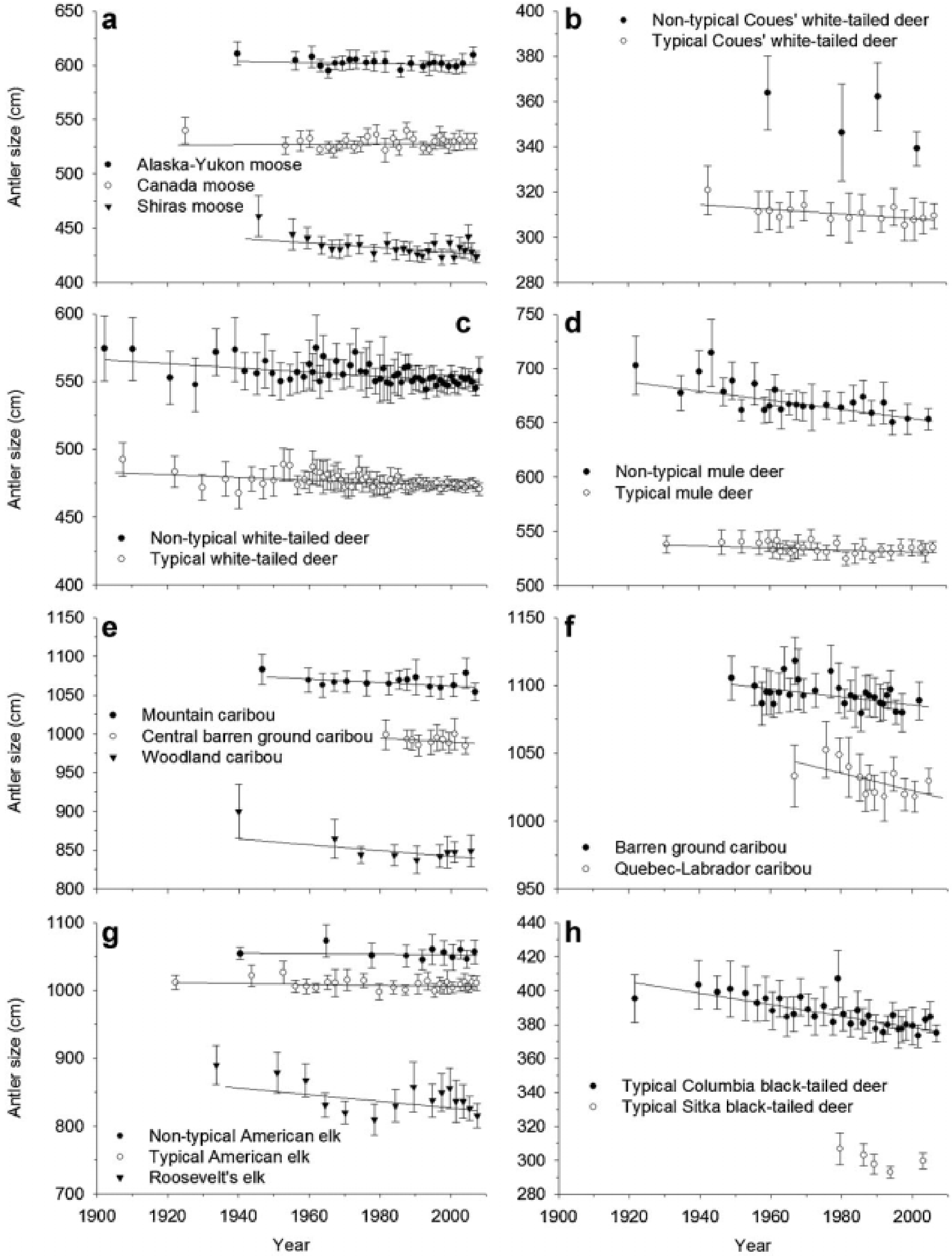


Figure 5. Temporal trends in antler size of trophies recorded in Records of North American Big Game during the past century. Data points represent mean (±95% CI) antler size (cm) of temporal bins containing a minimum of 20 samples; minimum bin size was 1 year. Lines represent fitted least-squares regressions weighted by the inverse of the variance associated with each bin.

pronghorn exhibited a slight, but significant, increase in size (Table 2). In contrast, mean horn size of muskox increased markedly since the 1970s (Fig. 6a), with a 7.12% increase predicted over the last 58 years (Table 2). For other horned game, mean predicted change in horn size of trophies was −0.68% (SD = 1.02), and ranged from −1.82% for desert sheep to 0.57% for pronghorn (Table 2).

A significant effect of climate or submission rate on size of trophy horn-like structures occurred for only 3 of 17 antlered categories, and 2 of 8 horned categories (Table 3). The addition of climate or submission rate, however, did not qualitatively alter the temporal trend for any of those 5 categories. The NPO was negatively related to antler size for Canada moose, and positively related to antler size for typical American elk (Table 3). The NAO was related negatively to antler size for central Canada barren ground caribou (Table 3). Submission rate was not related to size for any antlered category, but was related positively to horn size of bighorn sheep and Stone's sheep (Table 3).

To determine whether retroactive entry of specimens collected prior to the 1950s might bias observed trends in size of trophies during the past century, we conducted the same simple linear regression analyses for each trophy category using only post-1950

Table 2. Results of simple linear regression analyses used to evaluate trends in size of antlers and horns of trophy big game in North America during the past century. Sample size represents the number of bins for each trophy category, and % change represents the predicted change in size from 1950 to 2008 based on results of the linear regression using the full dataset for each trophy category.

Trophy category	r^2	*n*	*P*-value	Intercept	β	% change
Antlered game						
Alaska-Yukon moose	0.05	22	0.33	605.51	−0.05	−0.48
Canada moose	0.00	28	0.79	526.24	0.02	0.18
Shiras moose	0.28	25	0.01	449.27	−0.22	−2.87
Typical Coues' white-tailed deer	0.35	15	0.02	318.45	−0.10	−1.89
Non-typical white-tailed deer	0.28	57	<0.01	566.39	−0.16	−1.65
Typical white-tailed deer	0.23	61	<0.01	483.40	−0.10	−1.24
Non-typical mule deer	0.47	25	<0.01	696.21	−0.42	−3.62
Typical mule deer	0.14	28	0.05	540.30	−0.09	−1.00
Mountain caribou	0.32	15	0.03	1,084.50	−0.23	−1.23
Central Canada barren ground caribou	0.12	10	0.32	1,014.91	−0.25	−1.47
Woodland caribou	0.27	9	0.16	879.09	−0.37	−2.51
Barren ground caribou	0.25	29	0.01	1,115.17	−0.30	−1.55
Quebec-Labrador caribou	0.31	13	0.05	1,086.64	−0.64	−3.53
Non-typical American elk	0.04	11	0.55	1,057.29	−0.05	−0.26
Typical American elk	0.08	25	0.19	1,013.19	−0.07	−0.41
Roosevelt's elk	0.23	15	0.07	875.56	−0.49	−3.33
Typical Columbia black-tailed deer	0.67	34	<0.01	411.89	−0.34	−4.93
Horned game						
Bison	0.00	15	0.84	310.07	−0.01	−0.17
Muskox	0.56	17	<0.01	257.01	0.49	7.12
Pronghorn	0.08	46	0.05	214.19	0.02	0.57
Rocky Mountain goat	0.01	28	0.62	130.61	0.01	0.22
Bighorn sheep	0.01	38	0.63	473.74	−0.01	−0.17
Desert sheep	0.44	29	<0.01	455.45	−0.14	−1.82
Dall's sheep	0.79	13	<0.01	452.31	−0.14	−1.80
Stone's sheep	0.29	15	0.04	451.71	−0.12	−1.60

data. Among antlered game, the time trend changed from negative and significant to not significant for mountain caribou, typical Coues' white-tailed deer, and typical mule deer, but did not change for any of the other 14 categories (Table 4). Among horned game, the time trend changed from not significant to positive and significant for bighorn sheep, and negative and significant to not significant for Stone's sheep, but did not change for any of the other 6 categories (Table 4).

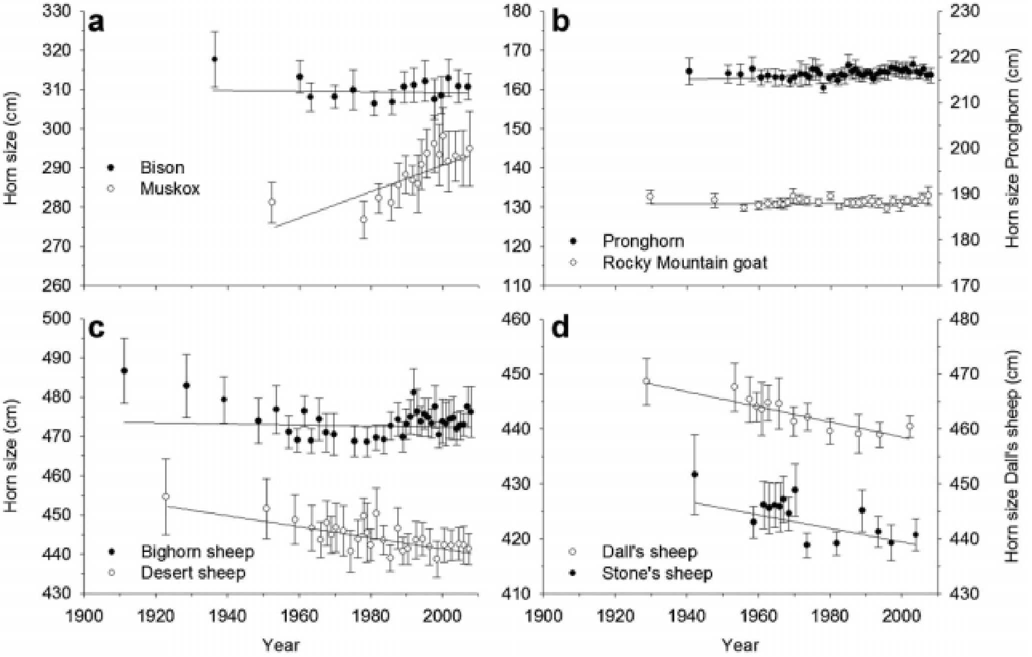


Figure 6. Temporal trends in horn size of trophies recorded in Records of North American Big Game during the past century. Data points represent mean (±95% CI) horn size (cm) of temporal bins containing a minimum of 20 samples; minimum bin size was 1 year. Lines represent fitted least-squares regressions weighted by the inverse of the variance associated with each bin.

Table 3. Results of step-wise, multiple linear regression analyses to evaluate the influence of climate and submission rate on temporal trends in size of antlers and horns of trophy big game in North America during the past century. We binned samples temporally based on a minimum sample size of 20, and weighted regressions by the inverse of the variance within each bin; sample size represents the number of bins for each trophy category. We show only trophy categories with a significant effect of climate (North Atlantic Oscillation [NAO] or North Pacific Oscillation [NPO]) or submission rate (SubRate). We did not include climate variables for horned game (na) and indicated non-significant variables with "ns."

				Parameter estimates and *P* values								
Trophy category	**Adj. R^2**	***n***	***P*-value**	**Intercept**	**Year**	***P*-value**	**NAO**	***P*-value**	**NPO**	***P*-value**	**SubRate**	***P*-value**
Antlered game												
Canada moose	0.31	28	<0.01	557.92	−0.08	0.17	ns	ns	−2.39	<0.01	ns	ns
Central Canada barren ground caribou	0.43	10	0.06	1,027.57	−0.38	0.09	−4.06	0.04	ns	ns	ns	ns
Typical American elk	0.17	25	0.05	987.88	−0.02	0.67	ns	ns	2.25	0.04	ns	ns
Horned game												
Bighorn sheep	0.13	38	0.04	474.73	−0.03	0.37	na	na	na	na	0.17	0.01
Stone's sheep	0.44	15	0.01	451.20	−0.11	0.03	na	na	na	na	0.25	0.04

Size-Specific Trends

Sample size was sufficient to partition data into upper and lower thirds for 10 categories of antlered game and 4 categories of horned game. Based on regression analyses, the temporal trend in size of trophies was similar (i.e., significance and direction) between the largest third and the full data set for all but 2 antlered categories (i.e., Shiras moose and typical mule deer), and all horned categories (Table 5). Similarly, the trend for the smallest third was the same as that observed in the full dataset for 8 of 10 antlered categories (typical mule deer and barren ground caribou were the exceptions), and all horned categories except pronghorn (Table 5).

Although we expected less variation within the smallest third of specimens, because their inclusion in the dataset was bounded by a minimum net score, patterns in size among bins for the largest individuals closely resembled patterns observed in the full dataset, whereas trends in size among the smallest individuals often were less apparent and did not reflect temporal patterns in the full dataset (Figs. 7 and 8). Parameter estimates for the smallest and largest thirds were highly correlated with those of the full dataset ($r > 0.84$), but a post hoc, paired *t*-test indicated that parameter estimates from the full dataset did not differ from those of the largest third ($t_{13} = 1.80$, $P = 0.09$), whereas parameter estimates differed between the full dataset and the smallest third ($t_{13} = 3.67$, $P = 0.003$). Thus, temporal trends in size of trophies observed in the full dataset were influenced primarily by specimens in the largest third of the entries.

Meta-Analysis

Results of the meta-analysis indicated a significant, negative trend in antler ($\chi^2_{34} = 104.84$, $P < 0.001$) and horn ($\chi^2_{14} = 37.53$, $P = 0.0017$) sizes of trophy North American

Table 4. Results of simple linear regression analyses used to evaluate trends in size of antlers and horns of trophy big game in North America during 1950–2008. Sample size represents the number of bins for each trophy category based on results of the linear regression using post-1950 data for each trophy category.

Trophy category	**r^2**	***n***	***P*-value**	**Intercept**	**β**
Antlered game					
Alaska-Yukon moose	0.00	21	0.83	601.55	−0.01
Canada moose	0.04	27	0.30	525.28	0.07
Shiras moose	0.22	24	0.02	436.70	−0.18
Typical Coues' white-tailed deer	0.21	14	0.10	311.93	−0.07
Non-typical white-tailed deer	0.16	48	<0.01	557.73	−0.14
Typical white-tailed deer	0.28	54	<0.01	479.66	−0.14
Non-typical mule deer	0.31	20	0.01	670.98	−0.29
Typical mule deer	0.08	26	0.17	535.19	−0.08
Mountain caribou	0.17	14	0.14	1,070.27	−0.16
Central Canada barren ground caribou	0.12	10	0.32	1,002.21	−0.25
Woodland caribou	0.01	8	0.81	847.02	−0.05
Barren ground caribou	0.25	29	0.01	1,100.39	−0.30
Quebec-Labrador caribou	0.31	13	0.05	1,054.56	−0.64
Non-typical American elk	0.12	10	0.33	1,063.03	−0.23
Typical American elk	0.01	23	0.68	1,007.88	−0.03
Roosevelt's elk	0.07	14	0.35	842.03	−0.27
Typical Columbia black-tailed deer	0.55	30	<0.01	394.93	−0.33
Horned game					
Bison	0.07	14	0.37	307.80	0.04
Muskox	0.56	17	<0.01	273.81	0.34
Pronghorn	0.11	45	0.02	215.07	0.03
Rocky Mountain goat	0.09	26	0.14	130.46	0.02
Bighorn sheep	0.17	34	0.01	469.64	0.07
Desert sheep	0.37	28	<0.01	448.08	−0.13
Dall's sheep	0.71	12	<0.01	445.33	−0.14
Stone's sheep	0.23	14	0.09	444.97	−0.11

Table 5. Results of linear regression analyses used to evaluate differences in temporal trends in size of antlers and horns of the largest and smallest third of trophy big game in North America during the past century, while controlling for effects of climate and submission rate if they were significant in the previous analysis. We binned samples temporally based on a minimum sample size of 13, and weighted regressions by the inverse of the variance associated with each bin; sample size represents the number of bins for each trophy category. The last 3 columns present the direction of the temporal trend in size for statistically significant time trends based on regression analyses, negative (−), positive (+), or non-significant (ns).

	Largest third of specimens					Smallest third of specimens					Summary		
				Time-trend					Time-trend				
Trophy category	**Adj. R^2**	***n***	**Intercept**	**β**	***P*-value**	**Adj. R^2**	***n***	**Intercept**	**β**	***P*-value**	**Largest**	**Smallest**	**All**
Antlered game													
Alaska-Yukon moose	0.17	12	636.96	−0.15	0.18	0.10	12	586.95	−0.04	0.32	ns	ns	ns
Canada moose	0.00	16	542.76	0.09	0.61	0.00	16	511.76	−0.02	0.65	ns	ns	ns
Shiras moose	0.26	14	478.77	−0.27	0.06	0.28	14	416.13	−0.08	0.05	ns	−	−
Non-typical white-tailed deer	0.20	43	616.13	−0.23	<0.01	0.42	43	526.96	−0.09	<0.01	−	−	−
Typical white-tailed deer	0.41	45	521.00	−0.22	<0.01	0.18	45	454.76	−0.04	<0.01	−	−	−
Non-typical mule deer	0.49	14	758.41	−0.68	0.01	0.61	14	650.47	−0.22	<0.01	−	−	−
Typical mule deer	0.15	17	568.11	−0.15	0.12	0.07	17	516.65	−0.04	0.32	ns	ns	−
Barren ground caribou	0.26	16	1,173.73	−0.46	0.04	0.00	16	1,056.55	−0.01	0.91	−	ns	−
Typical American elk	0.00	14	1,010.49	−0.01	0.97	0.19	14	967.44	0.00	0.91	ns	ns	ns
Typical Columbia black-tailed deer	0.74	19	455.54	−0.52	<0.01	0.49	19	372.52	−0.14	<0.01	−	−	−
Horned game													
Pronghorn	0.14	36	218.42	0.05	0.02	0.05	36	210.85	0.01	0.17	+	ns	+
Rocky Mountain goat	0.02	16	133.89	0.01	0.62	0.10	16	128.54	0.00	0.24	ns	ns	ns
Bighorn sheep	0.03	22	485.60	0.05	0.55	0.26	22	461.66	0.01	0.64	ns	ns	ns
Desert sheep	0.63	15	478.44	−0.23	<0.01	0.40	15	435.99	−0.05	0.01	−	−	−

big game. Iteratively withholding any single trophy category did not alter the results of the meta-analysis for antlered (maximum $P < 0.001$) or horned (maximum $P = 0.05$) game, indicating robustness of the overall negative trend in size of trophy horn-like structures among North American big game.

DISCUSSION

Although some variability existed among trophy categories, trends in horn and antler size of trophy big game harvested or collected in North America were predominantly negative over the past 50–100 years. The absence of age data precluded us from directly evaluating age-class specific changes in size. Nevertheless, our analyses revealed clear patterns of change among trophy horn-like structures, and knowledge of such patterns is important for management of large ungulates. We used a weight-of-evidence approach that was based on differences among trophy categories in life-history characteristics, geographic distribution, morphological attributes, harvest regimes, and anthropogenic disturbance to test predictions that followed directly from the aforementioned hypotheses for explaining negative trends in size and, thereby, evaluated the relative amount of support for each hypothesis (Table 6). Our results provided no support for a sociological effect (H3), effects of large-scale climate (H4), or broad-scale habitat change (H5) as the primary explanations for downward trends in size (Table 6). In contrast, our results provided moderate support for the hypothesis that intensive harvest may have resulted in a gradual shift in male age structure towards younger males (H1), and limited support for genetic effects as a result of selective male harvest (H2), as potential explanations for observed trends in size of horn-like structures.

Based on the intensive-harvest hypothesis, we expected that trophy categories with conservative harvest regimes would be less likely to exhibit a decline in horn or antler size than those experiencing heavy harvest of males, which shifts age structures toward young males that have relatively smaller horns and antlers (Noyes et al. 1996, Langvatn and Loison 1999, Solberg et al. 2000, Jenks et al. 2002, Milner et al. 2007). Although we did not have data on temporal patterns in age structure, several of our results support that prediction. First, 2 of the 3 species that arguably experience the most conservative harvest regimes in North America (bighorn sheep, desert sheep, and bison) did not exhibit a significant, long-term trend in horn size. In particular, horn size of trophy bighorn sheep declined steadily from the early to mid-20th century, but leveled out and has increased during the last few decades. Coincident with that shift in trend, harvest regimes for bighorn sheep became increasingly conservative and reintroduction efforts were well underway (Douglas and Leslie 1999, Toweill and Geist 1999, Krausman and Shackleton 2000, Festa-Bianchet and Lee 2009), which likely resulted in older males in superb nutritional condition with larger horns (Geist 1986). Secondly, if intensive harvest of males was at least partially responsible for the observed trends in horn and antler size, then pronghorn should be less prone to that effect because they develop large horns at an early age (Table 6; Mitchell and Maher 2001, 2006). The positive, significant trend in horn size of trophy pronghorn is consistent with this prediction, providing additional support for the intensive-harvest hypothesis.

In the southwestern United States, conservative harvest strategies were adopted for desert bighorn sheep with reopening of recreational harvest in the 1950s (Festa-Bianchet and Lee 2009). Nevertheless, horn size of trophy, desert bighorn sheep continued to decline during 1950–2008 (Fig. 6c). Horn size of desert sheep harvested in Arizona indicated a similar negative trend during 1980–2009; however, mean winter rainfall experienced during the lifetime of individual males was positively related to their horn size when harvested (Hedrick 2011). Therefore, persistent drought and declines in winter snowfall and snowpack during

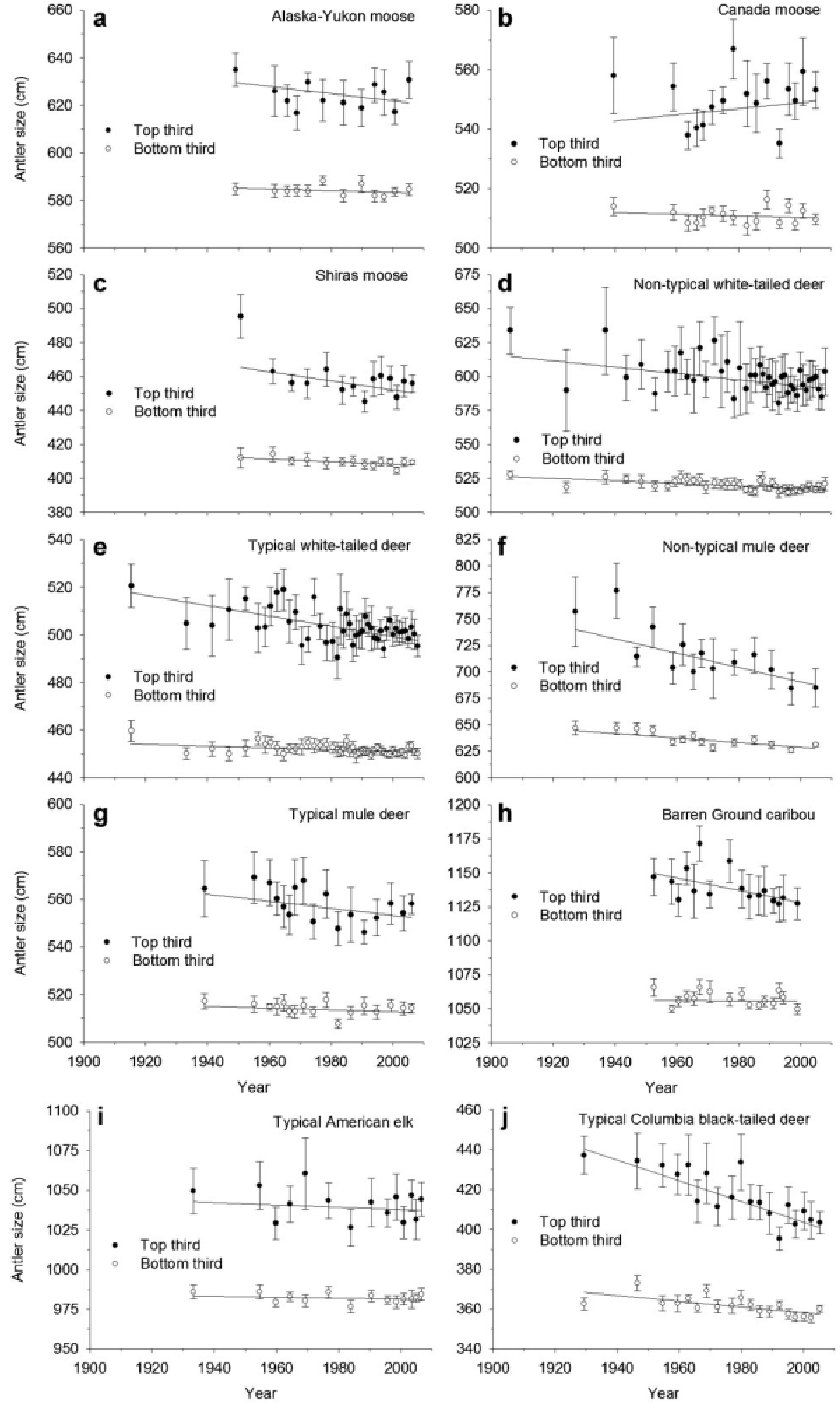


Figure 7. Temporal trends in antler size of the largest and smallest third of trophies recorded in Records of North American Big Game during the past century. Data points represent mean (±95% CI) antler size (cm) of temporal bins containing a minimum of 13 samples; minimum bin size was 1 year. Lines represent fitted least-squares regressions weighted by the inverse of the variance associated with each bin.

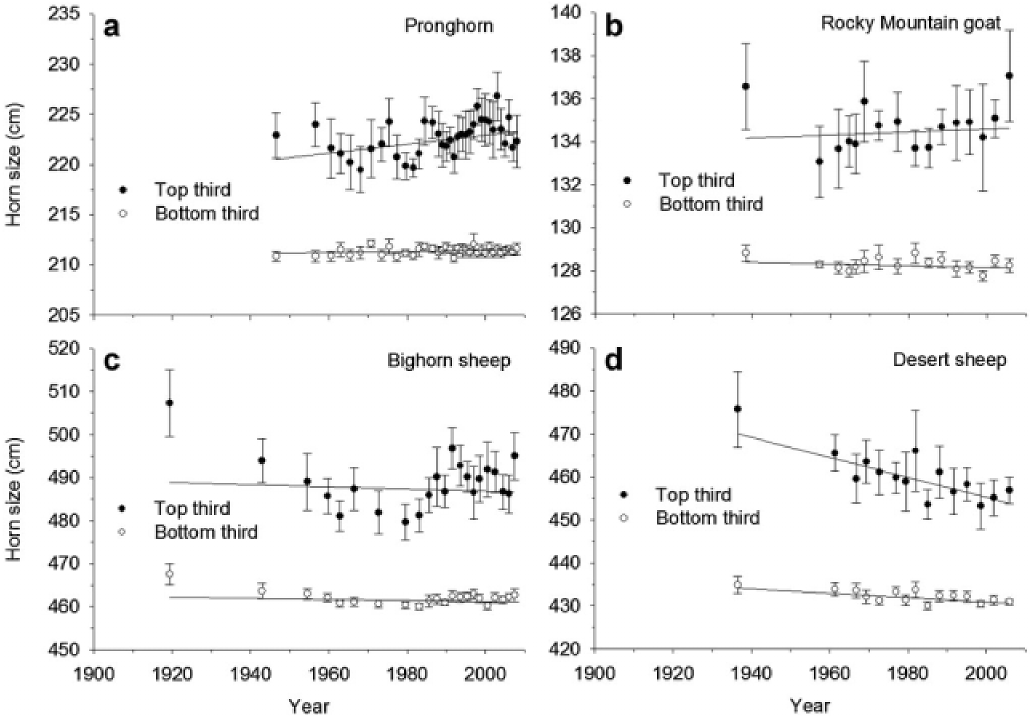


Figure 8. Temporal trends in horn size of the largest and smallest third of trophies recorded in Records of North American Big Game during the past century. Data points represent mean (±95% CI) horn size (cm) of temporal bins containing a minimum of 13 samples; minimum bin size was 1 year. Lines represent fitted least-squares regressions weighted by the inverse of the variance associated with each bin.

recent decades in the western United States (Hamlet et al. 2005, Knowles et al. 2005, Barnett et al. 2008) may be partially responsible for the negative trends in horn size observed for desert bighorn sheep, conservative harvests notwithstanding.

Under the selective-harvest hypothesis, we expected that ability to accurately assess size of males in the field would influence the amount of selective pressure imposed on the targeted trait. Accordingly, horn size of trophy Rocky Mountain goats, which are difficult to accurately judge in the field, should be less likely to exhibit long-term declines than other trophies that can be easily field judged (Table 6). Consistent with that prediction, mountain goats did not exhibit a significant trend in horn size over the past century. From the selective-harvest hypothesis, we also predicted that trophy horned game would be more susceptible to negative effects of selective harvest because once those bovids attain trophy size, they express that characteristic throughout the remainder of their lifetime. In contrast to horns, antlers are cast and regrown each year, and antler growth can be influenced by environmental

Table 6. Hypotheses for explaining long-term trends in horn and antler size of trophy big game in North America. Each hypothesis is followed by specific predictions evaluated using data from Records of North American Big Game (1900–2008) and the relative of amount support for each prediction based on results of our analyses.

Hypothesis	Mechanism	Predicted outcome	Empirical support
Intensive harvest	Intensive harvest of males has shifted age structure towards young males	1a) Trophy categories experiencing heavy harvest of males should exhibit steeper, negative slopes than those with a conservative harvest regime	Limited support
		1b) Trophy categories with early maturation in horns and antlers should be less prone to a reduction in size of those structures caused by a premature age distribution	Supported
Selective harvest	Trophy hunting has selected against genes for large horn-like structures	2a) Trophy categories for which horn or antler size is difficult to assess in the field will be less prone to selection against large horn-like structures and thus, less likely to exhibit a negative trend	Supported
		2b) Horned game should be more prone to a reduction in size of horn-like structures than antlered game, because size of horns is expressed consistently through time	No support
Sociological effect	Increased desire to submit smaller, yet eligible trophies to the Boone and Crockett record book has negatively biased observed size of hornlike structures	3a) Submission rate should be negatively related to size of horn-like structures	No support
		3b) Negative trend in hornlike structures should be less apparent in the largest third of samples than in the entire dataset	No support
Climate	Global changes in climatic regime have limited the ability of males to grow large horn-like structures	4a) Size of antlers should be negatively related to large-scale climatic indices and be largely responsible for the underlying trend	No support
Habitat	Loss and degradation of habitat has limited growth of horn-like structures	5a) Trophy categories that have experienced minimal loss or degradation of habitat should not exhibit a negative trend over time	No support

conditions and age in any particular year. Contrary to our prediction, declines in size of cranial appendages were nearly ubiquitous among antlered game, but were less consistent among horned game, which does not support the selective-harvest hypothesis.

Several factors could have confounded interpretation of temporal trends identified in our analyses, many of which related directly to the potential for a sociological effect (H3). During the past century, the appeal of animals with large antlers or horns has increased dramatically (Sudbeck 1993, Festa-Bianchet 2008, Messner 2011), resulting in a concomitant increase in the desire among individuals to harvest and receive recognition for those trophies. If changes in the desire to receive recognition are dependent upon trophy size, then observed trends in size of trophy horns and antlers could be a function of this sociological effect (H3).

We evaluated several specific predictions that followed from the sociological-effect hypothesis. The first such prediction was that entry rate should be negatively related to size of horn-like structures. With only 2 exceptions (bighorn sheep and Stone's sheep), entry rate was not a significant predictor of size for any trophy category (Table 3). In the 2 instances in which entry rate was significant, the relationship with size was positive (Table 3), contrary to the prediction of the sociological effect hypothesis. Because a sociological effect would depend upon increased rate of entry of smaller eligible trophies through time, then those trends should be less apparent in the largest samples than in the entire dataset. Once again, our results did not support that prediction because negative trends in size were most apparent among the largest specimens (Figs. 7 and 8). Our results were inconsistent with the sociological-effect hypothesis and often were contradictory to predictions of that hypothesis. We conclude that the long-term trends in size of trophy horn-like structures identified in our analyses were not a sociological artifact. Moreover, the relative declines in size of the largest animals in the dataset were consistent with predictions of the intensive-harvest hypothesis (H1).

In addition to having strong heritable and age-dependent components, patterns of growth in horns and antlers have nutritional underpinnings that are influenced by climate (Schmidt et al. 2001, Kruuk et al. 2002, Mysterud et al. 2005, Loehr et al. 2010) and habitat conditions (Strickland and Demarais 2000, 2008; Monteith et al. 2009; Mahoney et al. 2011). We evaluated the potential influence of climate and habitat on long-term patterns of horn and antler size of trophy big game in North America using 2 separate approaches. Ample evidence indicates nutritionally mediated effects of climate on interannual growth of horn-like structures (Schmidt et al. 2001, Kruuk et al. 2002, Mysterud et al. 2005, Loehr et al. 2010); however, our results did not support an effect of the climate indices that we assessed for explaining long-term patterns in size of deciduous horn-like structures of trophy ungulates. Likewise, declines in number of antler points for harvested caribou in Newfoundland, Canada during 1986–2005 were not related strongly to climate (Mahoney et al. 2011). Although we were unable to test for a climate effect directly for horned game, climate affects horn and antler growth via the same nutritional mechanisms (Goss 1983, Bubenik and Bubenik 1990, Mysterud et al. 2005, Loehr et al. 2010).

At the continent-wide scale of our analysis, we could not quantify changes in the quality, abundance, or distribution of habitat available to the various trophy categories included in our analyses. In addition, the scale of our analysis precluded incorporating information on population size, which is highly variable spatially and temporally across North America. Indeed, most ungulate populations have increased markedly in the recent century following the cessation of commercial hunting and adoption of regulated-harvest regimes (Demarais and Krausman 2000), which may have led to density-dependent effects on horn and antler size. Nevertheless, the degree of spatial and temporal heterogeneity in population size and habitat change across North America is precisely the reason why these factors are unlikely explanations for the near ubiquitous declines we observed, particularly among antlered game. If habitat change was the underlying reason for those trends, Dall's sheep, Stone's sheep, and muskox should have been the least likely to exhibit a decline, given that nearly all of their range remains both intact and pristine (Bowyer et al. 2000). In contrast to this expectation, trophy Dall's and Stone's sheep exhibited one of the steepest declines in horn size (Table 2); however, trophy muskox exhibited a substantial increase in horn size (Fig. 6a). Muskox have experienced nutritional and demographic benefits from range expansions that occurred throughout the Arctic (Klein 2000). Such range expansions led to increased hunting opportunity in recently established populations that likely contained abundant, prime-aged males, yielding greater potential for harvest of trophy males.

Potential Weaknesses of the Selective-Harvest Hypothesis

Hunting influences populations of ungulates by altering social structure, age structure, sex ratios, and population dynamics (Milner et al. 2007, Mysterud 2010). Furthermore, mortality as a result of hunting is not always functionally redundant with natural causes of mortality. For example, individuals most susceptible to natural mortality (i.e., young, senescent, nutritionally compromised, diseased) often are not the most susceptible to hunting mortality, and the temporal patterns of mortality between the 2 causes often differ (Berger 2005, Bischof et al. 2008). Under intensive harvest regimes that are regulated solely by size criteria, fast-growing males are more susceptible to harvest at a younger age than slow-growing males (Bonenfant et al. 2009*b*, Hengeveld and Festa-Bianchet 2011). The only example in North America demonstrating negative genetic effects of selective harvest on size of horn-like structures of ungulates was published by Coltman et al. (2003), who reported significant declines in horn size and body mass in bighorn sheep in a selectively and intensively hunted population. This sheep population at Ram Mountain, Alberta, Canada, was a small, isolated population where harvest was restricted to individuals having horns with a 4/5 curl, but with an unlimited number of hunters. Consequently, about 40% of males that attained legal size were harvested each year, allowing males with slow-growing horns to reach older age classes (Bonenfant et al. 2009*b*) and, thus, do a disproportionate amount of mating (Coltman et al. 2003). Such heavy harvest resulted in selection against males with fast-growing horns before their reproductive peak, and thereby reduced their genetic contribution to the population

(Coltman et al. 2003), although declining horn size may have been confounded by increasing population density (Coltman 2008).

Other factors decreasing the potential influence of trophy hunting on selection for horn and antler size among artiodactyls are skewed sex ratios, and age structures of young males that are biased downward as a result of heavy harvest (Laurian et al. 2000, Jenks et al. 2002, Webb et al. 2012). One potential effect common to a skewed sex ratio and an altered age distribution is disruption of the structure of the mating system, which is characterized by intense intraspecific competition among males (Geist 1966*a*, Andersson 1994, Mysterud 2010). Indeed, mating systems of sexually dimorphic ungulates typically are polygynous (Weckerly 1998, Loison et al. 1999), wherein mature, dominant males limit the mating opportunities of younger subordinates (Bowyer 1986, Maher and Byers 1987, Mysterud et al. 2003, Bergeron et al. 2010, Bowyer et al. 2011). The degree of participation in mating by young males, however, is related to the proportion of young relative to prime-age males in the population (Komers et al. 1994, Noyes et al. 1996, Mysterud et al. 2003, DeYoung et al. 2006, Bowyer et al. 2007), and heavy harvest may increase mating opportunities and reproductive effort among young, subordinate males (Stevenson and Bancroft 1995; Laurian et al. 2000; Mysterud et al. 2004, 2008; Garel et al. 2006). As a result, increased reproduction by young males holds consequences for the evolution of life-history strategies, in particular age at first reproduction (Festa-Bianchet 2003, Garel et al. 2006, Proaktor et al. 2007). In addition, because growth of horn-like structures increases until prime age in cervids and bovids, a harvest-induced reduction in age structure will yield a disproportionate increase in the number of young males that are harvested prior to attaining asymptotic body mass and, thus, peak horn or antler size (Monteith et al. 2009, Loehr et al. 2010).

The nutritional consequences of density dependence and habitat quality directly influence size of secondary sexual characters of large ungulates, and both have the potential to override demographic or selective effects of harvest (McCullough 1982, Geist 1986, Mysterud et al. 2005, Schmidt et al. 2007, Monteith et al. 2009). For example, based on standard genetic theory and heritability of antler size, Kruuk et al. (2002) predicted that antler size should have increased by 0.146 standard deviations per generation in a wild population of red deer (*Cervus elaphus*). Despite the positive genetic contribution to antler size, however, antlers actually declined in size during the 30-year study because of nutritional limitation in response to rising population density (Kruuk et al. 2002). Current simulations of the effects of various harvest regimes on frequency of genes for growing large antlers or horns indicate the potential for selective harvest to result in genetic change, but those responses are highly variable relative to harvest criteria and may take decades to be expressed (Thelen 1991, Hundertmark et al. 1998, Sæther et al. 2009). Such examples highlight the importance of considering effects of nutrition on patterns of horn and antler growth before assuming that selective harvest was responsible for observed trends (Kruuk et al. 2002, Schmidt et al. 2007). Indeed, maternal effects can have life-lasting consequences on growth and development, regardless of environmental conditions later in life or genetic potential for growth (Monteith et al. 2009). In contrast, compensatory growth in horn or antler size in response to slow development early in life may limit the potential for selective harvest to affect size of horn-like structures, because size of those structures in early life may not be indicative of the genetic potential of an individual for growth and maximum size (Bunnell 1978, Côté et al. 1988, Rughetti and Festa-Bianchet 2010).

Additional Considerations

We also considered incorporating an additional hypothesis. The size-distribution hypothesis is based on the distribution of horn and antler size, specifically the right-hand tail of the distribution in size. Trophy categories that have a strongly skewed distribution with a long right-hand tail should: 1) exhibit increases in trophy size as ungulate populations grow and expand because of a potential increase in the number of large males in the tail of the distribution and, consequently, 2) would be more sensitive to harvest pressure because removal of individuals in the right-hand tail would have a dramatic effect on average size compared with a trophy category with a truncated distribution (i.e., short right-hand skew). We were already dealing solely with what likely were the largest recorded specimens in each trophy category and, in essence, our data represent the tail of the tail of the distribution in size. As a result, the predictions, although elegant given a more broadly representative dataset, would not be expected to be supported by the Boone and Crockett dataset even if the size-distribution hypothesis was correct. To effectively test that hypothesis, we would need to quantify skewness of the entire distribution in horn or antler size of each trophy category—a worthwhile consideration for future research with other datasets.

We chose 2 indices of climate that are known to influence important ecological patterns and processes at a broad geographic scale (Stenseth et al. 2003). Although other indices exist (e.g., Southern Oscillation Index), they are generally more regional in nature, which was not consistent with the scale of our dataset. Ecological processes are sometimes more strongly associated with broad-scale climate metrics, because such metrics may better capture complex associations between local climate and ecological processes (Hallett et al. 2004). Our ability to detect nutritionally mediated effects of climate on size of horn-like structures was hindered by the absence of age-specific data. Nutritional effects on growth can be most influential during ontogeny, which may render individuals unable to garner considerable benefit from enhanced nutrition later in life (Kruuk et al. 2002, Monteith et al. 2009). Furthermore, we were unable to evaluate climate indices for bovids directly, because size of permanent horn structures is an accumulation over the life of an individual, and climate has much less of an effect once an individual has attained trophy size (Geist 1986, Hedrick 2011). Data on age of specimens would have allowed for a more rigorous evaluation of the nutritionally mediated effects of climate on trends in horn and antler size, even though our data likely consisted of mostly prime age, or older, animals in which the largest horn-like structures occur.

Our analyses and interpretations were based on horn and antler sizes that were biased towards exceptionally large individuals, which may bring into question how such data reflect ungulate populations in general, or even trophy ungulates. Although these data were heavily biased towards one end of the phenotypic range, we find no reason to believe that such individuals are in any way inherently devoid of meaningful biological information, or that the Boone and Crockett dataset is not representative of the size of trophy ungulates in North America. Because Records of North American Big Game contains data on horn and antler sizes for 38 categories of native, North American big game that span more than a century and includes >40,000 records, it is difficult to imagine that these data are not meaningful with respect to trophy animals. In addition, we took a number of methodological steps to identify and account for potential biases in our evaluation of predictions that stemmed from the sociological effect hypothesis—none of which were supported.

We used a weight-of-evidence approach to evaluate potential explanations for observed trends in size, mainly because of an absence of age data and the broad geographic and temporal scale of the dataset. Nonetheless, those very characteristics should make it difficult to detect temporal trends; that we detected near-ubiquitous patterns in size supports the existence of a meaningful biological signal in those data. The likelihood of this pattern occurring by chance alone is negligible. Although we were unable to unequivocally extricate the specific mechanisms that potentially underlie the trends in horn-like structures that we observed, we believe our efforts invite discussion on the long-term sustainability of harvest strategies for ungulates and will help foster and guide future research. Elucidating how well data recorded by conservation organizations, such as the Boone and Crockett Club, reflect morphological patterns within ungulate populations is warranted, especially because such data-rich sources are an under-appreciated resource for promoting conservation and management.

MANAGEMENT IMPLICATIONS

We documented significant declines in size of trophy horns and antlers among most categories recorded in Records of North American Big Game during much of the past century. Whether such declines predicate the need for a change in management strategies is uncertain. Indeed, a mean of 1.87% and 0.68% reduction in size of trophy antlers and horns, respectively, during 1950–2008 may be inconsequential relative to the benefits that accrue from recreational hunting opportunities and resultant overall benefits to conservation (Singer and Zeigenfuss 2002, Whitfield 2003, Lindsey et al. 2007, Groves and Leslie 2011, Heffelfinger 2013). The dramatic increases in entries of trophies for most categories during the last few decades (Figs. 3 and 4) also are a testament to the success of management programs for these North American species. If reductions in size of trophy horns and antlers represent concerns for social or biological reasons, managers may want to reevaluate the current harvest paradigm, wherein harvest is focused largely on males. Our weight-of-evidence approach indicated that such male-biased harvest may have gradually reduced male age structure, which in turn has resulted in smaller average horns and antlers among trophy animals. If intensive harvest of males was the underlying reason for the observed declines in size of horn-like structures among trophy males, then a reduction in harvest pressure on males could simultaneously increase male age structure, yield a more balanced sex ratio, and lessen harvest of large, fast-growing males, all of which may help reverse the negative trends we observed (Webb et al. 2007; Hengeveld and Festa-Bianchet 2011; Mysterud 2010, 2011).

In addition to reducing harvest pressure on males, the most effective means of lowering density to enhance nutritional condition and stimulate recruitment when resources are limited is through female harvest (McCullough 1979, McCullough et al. 1990, Jorgenson et al. 1993). Density of males has a limited effect on recruitment patterns of young (McCullough 1979), largely because sexually dimorphic ruminants sexually segregate and, thus, partition use of resources throughout much of the year (Bleich et al. 1997, Kie and Bowyer 1999, McCullough 1999, Bowyer 2004). Moreover, large males likely are most susceptible to resource limitation as a result of density dependence because they often enter the most nutritionally challenging time of year (i.e., winter) after nutritional reserves have been depleted during the mating season. Density dependence may have a greater influence on size of males than that of females (Verme and Ozoga 1980, Clutton-Brock et al. 1982, Ashley et al. 1998, Keyser et al. 2005) because nutritional limitation affects body mass (and size of horn-like structures) in males, as opposed to reproductive status of females (Clutton-Brock et al. 1982, Stewart et al. 2005, Monteith et al. 2009). Achieving desirable female harvest, however, can be difficult given public perception of harvesting females and the growing emphasis on trophy size (Festa-Bianchet and Lee 2009, Messner 2011).

Disentangling effects of selective harvest, demographic responses to harvest, and nutritional effects on size of horn-like structures is a daunting task, but one worthy of further investigation. We documented statistically significant changes in trophy horn and antler sizes of numerous North American ungulates during the past century that may be harvest-related, although we were unable to completely unravel causal mechanisms. Monitoring programs, such as the Records of North American Big Game, that rely on characteristics of harvested animals have been invaluable for assessing long-term trends in morphological characteristics. Nonetheless, collecting information on age, in addition to size, would help clarify mechanisms of potential change. To increase the relevance of their data to conservation and management of wildlife, the Boone and Crockett Club recently initiated efforts to obtain ages of all trophy submissions; such efforts help to dispel the notion that Records of North American Big Game is merely a records book (Spring 2012). Quantitative genetics is a powerful alternative approach, but such investigations require knowledge of phenotypes and pedigrees among known individuals (Garant and Kruuk 2005), which precludes their application in most situations for large free-ranging ungulates. Data from long-term field studies that monitor horn or antler size of individuals and their influence on probability of survival likely will provide the most effective means of differentiating between demographic and selective effects of harvest (e.g., Bonenfant et al. 2009*b*). Those data must be corroborated with data on population density in relation to carrying capacity, climate, and forage quality, although measures of nutritional condition will likely provide an integrated measure of current nutritional status of the population (Parker et al. 2009).

SUMMARY

- We evaluated long-term trends in size of trophy horn-like structures of native, North American ungulates during the past century using data recorded in Records of North American Big Game. Trophy specimens that were harvested, collected, or possessed by agencies were included in our analyses.
- We used a weight-of-evidence approach to evaluate the relative merit of several competing hypotheses for explaining long-term trends in size of horns and antlers at a continental scale. Hypotheses included intensive harvest, selective harvest, sociological effect, broad-scale climate, and habitat alteration.
- The number of entries per decade increased for most trophy categories. Trends in size of horn-like structures were negative and significant for 11 of 17 antlered categories and 3 of 8 horned categories. Muskox and pronghorn were the only trophy categories that exhibited a significant, positive trend in size of horn-like structures.
- Our results provided support for harvest-based hypotheses for explaining long-term trends in size, but no support for sociological, climatic, or habitat-based explanations.
- The intensive-harvest hypothesis is based on the premise that heavy harvest of males has gradually shifted age structure toward younger males, resulting in smaller average size of trophy horn-like structures. The absence of a significant decline in horn size for 2 of the 3 species that experience the most conservative harvest regimes in North America, and a significant increase in horn size among pronghorn (which exhibit an early peak in horn size) both support the intensive-harvest hypothesis.
- The selective-harvest hypothesis is based on the premise that trophy hunting has selected against genes for large horn-like structures. One of 2 specific predictions that followed from that hypothesis was supported by our results.
- Although we documented significant declines in size of trophy horns and antlers recorded in Records of North American Big Game, average predicted declines of 0.68% and 1.87% in size of trophy horns and antlers, respectively, may be less important relative to the benefits that have accrued from recreational opportunities and resultant overall contributions to conservation.
- Our results provided some support for a potential effect of harvest on size of trophy horn-like structures; however, we were unable to directly assess causal mechanisms because of the nature of the dataset. Disentangling those mechanisms is an important pursuit for the conservation of large ungulates; thus, additional research should focus on elucidating the relative influence of harvest and nutrition on horn and antler size.

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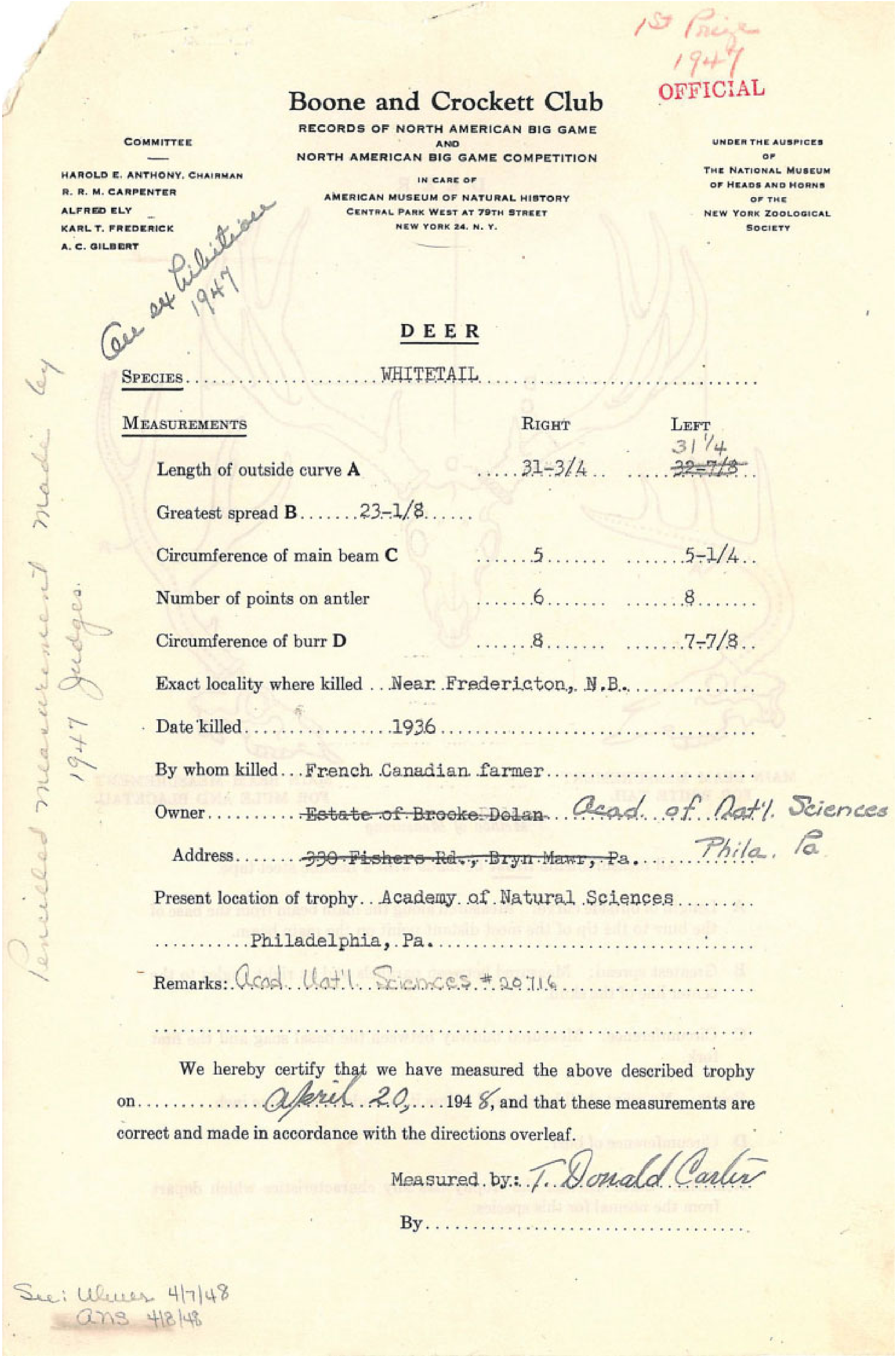

1st Prize 1947

OFFICIAL

Boone and Crockett Club

RECORDS OF NORTH AMERICAN BIG GAME
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UNDER THE AUSPICES
OF
THE NATIONAL MUSEUM
OF HEADS AND HORNS
OF THE
NEW YORK ZOOLOGICAL
SOCIETY

Case at Exhibition 1947

Pencilled measurement made by 1947 Judges.

DEER

SPECIES WHITETAIL

MEASUREMENTS	RIGHT	LEFT
Length of outside curve **A**	31-3/4	~~32-7/8~~ 31 1/4
Greatest spread **B** 23-1/8		
Circumference of main beam **C**	5	5-1/4
Number of points on antler	6	8
Circumference of burr **D**	8	7-7/8

Exact locality where killed Near Fredericton, N.B.

Date killed 1936

By whom killed French Canadian farmer

Owner ~~Estate of Brooke Dolan~~ Acad. of Nat'l. Sciences

Address ~~330 Fishers Rd., Bryn Mawr, Pa.~~ Phila. Pa

Present location of trophy Academy of Natural Sciences Philadelphia, Pa.

Remarks: Acad. Nat'l. Sciences #20716

We hereby certify that we have measured the above described trophy on April 20, 1948, and that these measurements are correct and made in accordance with the directions overleaf.

Measured by: T. Donald Carter

By

See: Ulmer 4/7/48
ans 4/8/48

Score chart for white-tailed deer in 1947 before the adoption of the standardized measuring system in 1950. Photo courtesy Boone and Crockett Club.