



## Biological relevance of antler, horn, and pronghorn size in records programs

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Long-term datasets are becoming increasingly important for assessing population- and species-level responses to a changing environment. Programs that record morphological measurements of horns, antlers, and pronghorns were established in the early- to mid-20th century to collect biological information about animals that possess large horns, antlers, or pronghorns, which could be used to assess the effectiveness of conservation efforts for large mammals in North America. The general relevance of record books has been questioned because of the minimum size requirements for inclusion in a record book, which may mask trends when changes in the population occur. We compared trends in size of antlers, horns, and pronghorns through time using records from three records programs with different minimum size requirements to evaluate the influence of entry requirements on temporal trends. We also investigated whether horn, antler, or pronghorn size affected the probability of specimens being submitted to a records program. Only two of 17 categories exhibited less-pronounced trends in the record book with the highest size requirements for entry, and in two categories trends were more pronounced. Although societal interest in submitting eligible specimens increased slightly over time in one of six categories, the probability of voluntary entry was largely random and not affected by year of harvest or size of specimen. In contrast to previous criticisms, trends in record books should not be expected to represent the size of all males within a population. Instead, our evaluation indicates that the records programs we examined can provide a useful resource for assessing long-term changes in phenotypic characteristics of ungulates, but importantly, they represent the respective range of sizes within which each program collects data.

Key words: antler size, citizen science data, horn size, records programs, selective harvest, temporal trends

Long-term (> 20 years) ecological datasets, although rare, are critically important for understanding ecological and evolutionary responses of animals to environmental change (Odum

1959; Franklin 1989; Lindenmayer et al. 2012). Ecological and evolutionary change in wild populations can take many generations to manifest, and understanding the complex processes

that lead to change at the individual, population, or species level is difficult without access to reliable, long-term datasets (Lindenmayer et al. 2012). Wildlife populations are valued by people around the globe, and sustainable harvest of wildlife is an important management goal. Yet, evolutionary changes resulting from hunting have been documented (Kuparinen and Festa-Bianchet 2017). Despite controversy associated with the evolutionary effects of harvest (Mysterud 2014; Festa-Bianchet 2016; Heffelfinger 2018), harvest strategies that result in evolutionary responses have important conservation and management implications (Kuparinen and Festa-Bianchet 2017). Unfortunately, disentangling the effects of selective harvest from selective pressures imposed by the environment (Berger 2005) is difficult without long-term data (Festa-Bianchet and Mysterud 2018).

Under sufficiently intensive harvest pressure, artificial selection can lead to undesirable evolutionary changes, including reduced reproductive output (Coltman et al. 2003), earlier sexual maturation (Walsh et al. 2006), reduced allele frequencies (Walsh et al. 2006), potentially altered behaviors (Allendorf and Hard 2009), and changes in population structure (McCullough 1979; Conover and Munch 2002; Conover et al. 2009). For wild populations of large-bodied mammals, empirical evidence supporting genetic change through artificial selection remains limited. As humans continue to harvest populations of large mammals around the world, understanding the effects of artificial selection on populations or species over time will become increasingly important (Mysterud 2011; Festa-Bianchet 2016; Heffelfinger 2018).

Among ungulates, the potential evolutionary consequences of harvest by humans can be assessed by evaluating temporal changes in antler, horn, or pronghorn size (hereafter, antlers and horns) because those traits are heritable, linked to reproductive success, and are often the target of selective harvest (Crosmarty et al. 2013; Monteith et al. 2013; Festa-Bianchet et al. 2014; Pigeon et al. 2016). Assessing changes in size over time is difficult in long-lived species because changes in allele frequencies can take decades to manifest as a detectable phenotypic change; moreover, long-term data on phenotypic characteristics are often lacking (Hundertmark et al. 1998).

Measurements from harvested animals may provide a rich source of data for quantifying temporal changes in phenotypic characteristics (Torres et al. 1993; Monteith et al. 2013). For most ungulate species in North America, phenotype of harvested animals is rarely documented by management agencies; one exception is the size of mountain sheep (*Ovis canadensis* ssp. and *O. dalli* ssp.) horns, which have been recorded by most agencies over the past few decades. In contrast, records programs retain measurement records for large specimens harvested from throughout their geographic distribution, and have been doing so for many decades. Records programs were established in the early- to mid-20th century and are managed by conservation organizations that promote ethical hunting and the conservation of large game mammals. Hunters who have harvested an animal that possesses phenotypic characteristics that surpass a minimum size can choose to enter the measurements into a record book (Mogan 2012). Thus, record books represent

one of the longest-running datasets available to wildlife managers, and are potentially useful for answering questions about effects of harvest practices or environmental change on the size of antlers and horns (Monteith et al. 2013). Much like citizen science data, records programs represent an enormous source of information collected across broad temporal and spatial scales (Monteith et al. 2013), and that information may be useful for assessing changes in the size of horns and antlers through time.

Despite the potential relevance of record books to wildlife ecology and management, there has been criticism over the validity of using data maintained in record books to assess trends in sizes (Festa-Bianchet et al. 2015). Data maintained by records programs represent a biased sample, because each specimen must be a certain minimum size to qualify for entry. Specimens documented by records programs only include individuals with large, or in some instances exceptionally large, horns and antlers that may be approaching their maximum attainable size (Festa-Bianchet et al. 2015). Consequently, using data maintained by records programs to identify more general temporal trends may be invalid or dilute changes at the population level (Festa-Bianchet et al. 2015).

Records programs were not designed to document population- or species-level changes, but to record the size and trends of horns, antlers, and pronghorns of large males. If temporal trends detected in record books are not representative of what is occurring among males with large horns or antlers, then they may not be a useful resource for assessing consequences of harvest or environmental change, a result that would undermine one of the primary goals of records programs: to assess the consequences of conservation strategies (Monteith et al. 2013).

Hunters have been particularly interested in males that possess exceptionally large horns or antlers since records programs were established. If that interest varied through time, it could bias temporal trends in size of horns and antlers detected in record books. For example, if interest in submitting specimens that barely meet the minimum requirements of record books increases through time, it could produce a negative trend in horn or antler size (Monteith et al. 2013). If societal interest in entering specimens into a records program has changed through time, or as a function of the size of the specimen, then trends in record books may not represent real biological change among large males.

Our goal was to evaluate if record books provide biologically meaningful data on temporal trends in the size of large horns, antlers, or pronghorns. We: 1) compiled measurement data on horns, antlers, and pronghorns from three records programs and assessed trends in size over time; 2) compared trends across records programs; 3) increased the minimum size requirement for entry in a records program and assessed differences in trends; and 4) assessed changes in societal interest in submitting records to a record book.

## MATERIALS AND METHODS

We evaluated differences in direction and magnitude of trends in size of horns, antlers, and pronghorns for 29 categories of large

mammals across three records programs: Boone and Crockett Club, Pope and Young Club, and Safari Club International. All three records programs maintain records of horn, antler, and pronghorn measurements of free-ranging large mammals that are harvested throughout their native range. Species and geographic region were used to define categories of large mammals for all three records programs; therefore, multiple categories sometimes existed for a single species if there were differences in the size of horns and antlers based on the geographic region. For example, differences in antler size between subspecies of elk (*Cervus canadensis*) located in different geographic regions resulted in three separate categories of elk (i.e., Tule elk, Roosevelt's elk, and American elk). Categories for antlered species were defined as either typical or non-typical; non-typical categories were developed to account for specimens that possessed large antlers but were asymmetrical, and did not penalize for the asymmetry between the two sides of the antlers (Monteith et al. 2013). Eligibility for entry into a record book required that the specimen be legally and ethically harvested or obtained, air-dried for a minimum of 60 days before measured, and recorded by a certified measurer who had been rigorously trained in employing standardized methods. Official measurers used a quarter-inch steel tape, flexible steel cables, or calipers to measure specimens, and measurements were rounded to the nearest 1/8 inch (3.175 mm—Buckner et al. 2009). We used the “gross score,” which is the sum of all measurements of a specimen and gives an approximation of the total volume of those structures, as defined by each records program (Monteith et al. 2013).

In 1932, the Boone and Crockett Club established the first records program in North America and adopted a standardized measurement protocol in 1950 (Buckner et al. 2009; Monteith et al. 2013). The Pope and Young Club was established in 1961 and adopted the same system developed by the Boone and Crockett Club, but with lower size requirements for entry (Fitz 1977; Buckner et al. 2009). In addition, the Pope and Young Club required all entries to have been harvested with archery equipment, whereas the Boone and Crockett Club allowed entry of specimens harvested with any legal method of take (Fitz 1977). The Safari Club International Record Book, founded in 1971 (Schwabland and Barnhard 2016), instituted variable size requirements for entry depending upon the type of award (i.e., there were different awards given for specimens that reached different sizes); for our analysis, we used the lowest minimum size requirements for entry of animals harvested with any weapon. For most categories, minimum size requirements for entry into the Safari Club International Record Book were similar to, or slightly above, the minimum size requirements of the Pope and Young Club Record Book, whereas the Boone and Crockett Club Record Book had the highest size requirements for entry (mean = 19.1% higher than the Pope and Young Club across categories).

The standardized protocol for measurement of horn and antler size used by Safari Club International was mostly analogous to that of the Boone and Crockett and Pope and Young clubs, but with minor deviations that included additional measurements

for some categories (Supplementary Data SD1). Therefore, we compared temporal trends in the relative size of horns, antlers, and pronghorns among the three records programs but did not make direct comparisons of the absolute sizes of horns, antlers, and pronghorns. Minimum entry requirements for some categories in all three books have changed slightly since the establishment of the records programs. Therefore, we used only specimens that met the highest minimum size requirement for entry established for each category (Monteith et al. 2013).

Measurements for most horned categories included total length of horn and four circumference measurements, whereas measurements for most antlered categories included length of main beams, length of tines, four circumference measurements along the main beams, and maximum distance between the main beams (Reneau and Buckner 2005; Buckner et al. 2009; Schwabland and Barnhard 2016; Supplementary Data SD1). Exceptions to these protocols included slight differences in measurement of pronghorn (*Antilocapra americana*), muskox (*Ovibos moschatus*), caribou (*Rangifer tarandus*), moose (*Alces alces*), and some non-typical categories of cervids. Detailed descriptions of measurement criteria are available in Supplementary Data SD1 and elsewhere (Buckner et al. 2009; Monteith et al. 2013).

*Data organization.*—Our aim was to compare the magnitude and direction of temporal trends in size for each category among all three record books (29 total categories; Table 1). We assumed that samples were independent across years, because specimens were obtained at a broad geographic scale (Monteith et al. 2013). In some instances, harvested animals meeting the minimum score could be entered into more than one record book. The number of specimens entered into each book increased through time, so to meet the assumption of homogeneity of variance, we binned data temporally using methods outlined by Monteith et al. (2013). We set the minimum sample size for temporal bins in each category to 20 to produce 95% confidence intervals that bounded the mean by  $\leq 5\%$  (Krebs 1999; Monteith et al. 2013). We created bins by starting with the earliest record and then adding records through time until the minimum sample size was achieved without partitioning data from a single year (Table 2; Monteith et al. 2013). Twelve categories were excluded from our analysis because of an insufficient number of samples ( $< 10$  bins) in at least two record books: Canada moose (*Alces alces americana* and *A. a. andersoni*), Shiras moose (*A. a. shirasi*), non-typical Coues' white-tailed deer (*Odocoileus virginianus couesi*), mountain caribou (*Rangifer tarandus caribou*), Central Canada barren ground caribou (*R. t. groenlandicus*), woodland caribou (*R. t. caribou*), barren ground caribou (*R. t. granti*), Quebec-Labrador caribou (*R. tarandus*), non-typical American elk (*Cervus canadensis nelsoni* and related subspecies), Roosevelt's elk (*C. c. roosevelti*), tule elk (*C. c. nannodes*), and non-typical Columbia black-tailed deer (*O. hemionus columbianus*). For each category, we only compared trends among record books when there was temporal overlap of  $\geq 5$  years for both the first and last bin among all three record books to prevent trends being dictated by data

**Table 1.**—Number of entries for 29 categories of antlered and horned game recorded in the Boone and Crockett Club, Pope and Young Club, and Safari Club International record books from 1907 to 2016 across the geographic range of each category.

Category	Scientific name	Boone and Crockett Club	Pope and Young Club	Safari Club International
Alaska-Yukon moose	<i>Alces alces gigas</i>	576	62	531
Canada moose	<i>Alces alces americana</i> and <i>A. a. andersoni</i>	774	40	0
Shiras moose	<i>Alces alces shirasi</i>	694	33	279
Non-typical Coues' white-tailed deer	<i>Odocoileus virginianus couesi</i>	95	38	58
Typical Coues' white-tailed deer	<i>Odocoileus virginianus couesi</i>	336	577	555
Non-typical white-tailed deer	<i>Odocoileus virginianus virginianus</i> and related subspecies	3,163	4,315	270
Typical white-tailed deer	<i>Odocoileus virginianus virginianus</i> and related subspecies	4,445	53,121	818
Non-typical mule deer	<i>Odocoileus hemionus hemionus</i> and related subspecies	647	660	365
Typical mule deer	<i>Odocoileus hemionus hemionus</i> and related subspecies	803	4,079	1,266
Mountain caribou	<i>Rangifer tarandus caribou</i>	374	0	0
Central Canada barren ground caribou	<i>Rangifer tarandus groenlandicus</i>	280	389	231
Woodland caribou	<i>Rangifer tarandus caribou</i>	210	181	0
Barren ground caribou	<i>Rangifer tarandus granti</i>	852	406	0
Quebec-Labrador caribou	<i>Rangifer tarandus</i>	380	560	219
Non-typical American elk	<i>Cervus canadensis nelsoni</i> and related subspecies	267	232	0
Typical American elk	<i>Cervus canadensis nelsoni</i> and related subspecies	662	8,010	735
Roosevelt's elk	<i>Cervus canadensis roosevelti</i>	347	430	29
Tule elk	<i>Cervus canadensis nannodes</i>	37	50	157
Non-typical Columbia black-tailed deer	<i>Odocoileus hemionus columbianus</i>	29	38	41
Typical Columbia black-tailed deer	<i>Odocoileus hemionus columbianus</i>	943	808	333
Typical Sitka black-tailed deer	<i>Odocoileus hemionus sitkensis</i>	134	416	314
Bison	<i>Bison bison</i>	384	76	595
Muskox	<i>Ovibos moschatus</i>	572	330	202
Pronghorn	<i>Antilocapra americana</i>	2,338	4,775	2,483
Rocky Mountain goat	<i>Oreamnos americanus</i>	741	433	821
Bighorn sheep	<i>Ovis canadensis canadensis</i> and related subspecies	1,191	372	244
Desert sheep	<i>Ovis canadensis nelsoni</i> and related subspecies	768	111	616
Dall's sheep	<i>Ovis dalli dalli</i> and <i>O. d. kenaiensis</i>	323	187	698
Stone's sheep	<i>Ovis dalli stonei</i>	382	104	411

from a different time period. In other words, mean year of the first bin for one book had to be within 5 years of the mean year of the first bin for the other books, and mean year of the last bin for one book had to be within 5 years of the mean year of the last bin for the other books.

**Temporal trends.**—We used simple linear regression to model temporal trends in the size of horns, antlers, and pronghorns recorded in all three record books. We used mean size of horns, antlers, and pronghorns for each category as the dependent variable, and mean year of the samples included in each bin weighted by the inverse of the variance (Kutner et al. 2005; Monteith et al. 2013) as the independent variable. We quantified size of horns, antlers, and pronghorns by summing all measurements used to calculate total score, but without penalizing for asymmetry between the left and right structures for each specimen (analogous to gross score, Supplementary Data SD1). To test for differences in direction and magnitude of trends in size among record books within each category, we used an analysis of covariance (ANCOVA—Dytham 2011). We used size of horns, antlers, and pronghorns for each category as the dependent variable, and an interaction between record book and time (i.e., mean year of each bin) as the independent variable. We used  $\alpha = 0.1$  as our level of statistical significance for all tests to reduce the probability of not detecting minor, but meaningful differences in direction and magnitude of trends that may exist.

**Effect of minimum entry requirements.**—We tested whether trends observed in record books with higher minimum requirements for entry would be weakened compared with those observed in record books with a lower requirement for entry by incrementally increasing minimum entry requirements within a single record book and iteratively reevaluating the trends. For this analysis, we used data from the Pope and Young Club, which had the lowest size requirements for entry among the record books. We iteratively increased the minimum size requirements for entry by 5%, 10%, 20%, and 30% and refit linear regression models in each iteration. Sample size was sufficient to perform this analysis for three categories of large mammal: typical white-tailed deer, typical American elk, and pronghorn. We tested for differences in the direction and magnitude of trends among iterations of the analysis using ANCOVA.

**Changes in societal interest.**—To identify potential bias that could be introduced through shifting societal interest in entering specimens into record books, we modeled the probability of an animal being entered into the Boone and Crockett record book as a function of year of harvest and size for bighorn sheep (*Ovis canadensis canadensis*), desert sheep (*O. c. ssp.*), typical and non-typical mule deer (*Odocoileus hemionus*), and typical and non-typical white-tailed deer (*Odocoileus virginianus*). For sheep, we used harvest records collected by 10 wildlife agencies in the United States. Harvest of mountain sheep was highly regulated, and all harvested individuals must be checked



**Table 2.**—Results of linear regression analyses, weighted by the inverse of the variance in temporal bins, used to evaluate trends of horn and antler size (represented by gross score) for 16 categories in the Boone and Crockett Club, Pope and Young Club, and Safari Club International record books through time. Sample size (*n*) represents the number of temporal bins for each category; bins were comprised of at least 1 year, and a minimum of 20 records.

Category	Boone and Crockett Club					Pope and Young Club					Safari Club International				
	<i>R</i> <sup>2</sup>	<i>n</i>	<i>P</i> -value	Intercept	$\beta$	<i>R</i> <sup>2</sup>	<i>n</i>	<i>P</i> -value	Intercept	$\beta$	<i>R</i> <sup>2</sup>	<i>n</i>	<i>P</i> -value	Intercept	$\beta$
Antlered categories															
Alaska-Yukon moose	0.026	24	0.453	532.815	0.035						0.519	18	0.001	-3235.262	0.535
Typical Coues' white-tailed deer	0.055	11	0.486	441.591	-0.066	0.080	18	0.255	763.937	-0.265	0.006	17	0.766	177.067	0.146
Non-typical white-tailed deer	0.024	30	0.410	703.377	-0.076	0.104	28	0.094	-221.779	0.346	0.239	10	0.152	-1938.191	0.754
Typical white-tailed deer	0.199	60	< 0.001	668.447	-0.097	0.069	41	0.098	579.533	-0.104	0.005	28	0.732	239.089	0.187
Non-typical mule deer	0.215	15	0.082	1157.498	-0.250	0.017	23	0.559	810.946	-0.146	0.281	12	0.076	2034.260	0.383
Typical mule deer	0.013	28	0.569	594.369	-0.032	0.063	33	0.158	187.425	0.121	0.000	36	0.985	446.878	0.115
Typical Columbian black-tailed deer	0.403	32	< 0.001	917.555	-0.269	0.000	26	0.945	280.007	0.013	0.010	13	0.751	202.881	0.155
Typical Sitka black-tailed deer						0.016	14	0.665	309.945	-0.040	0.231	11	0.135	1067.169	0.252
Typical American elk	0.282	23	0.009	414.799	0.297	0.605	31	< 0.001	-1186.706	0.997	0.658	24	< 0.001	-5172.419	0.463
Horned categories															
Muskox	0.028	15	0.552	118.442	0.086	0.116	13	0.255	686.739	-0.211					
Pronghorn	0.425	39	< 0.001	73.270	0.072	0.142	27	0.053	93.241	0.046	0.551	40	< 0.001	-168.788	0.027
Rocky Mountain goat	0.012	18	0.665	113.767	0.009	0.270	15	0.047	-133.421	0.124	0.016	19	0.603	62.039	0.014
Bighorn sheep	0.113	30	0.069	273.086	0.100	0.609	14	0.001	-1164.033	0.791					
Dall's sheep	0.523	13	0.005	620.376	-0.090						0.001	27	0.888	408.374	0.040
Desert sheep	0.086	37	0.077	555.094	-0.056						0.160	21	0.072	127.050	0.079
Stone's sheep	0.153	16	0.134	598.963	-0.080						0.058	17	0.350	574.002	0.082
Bison	0.012	19	0.656	281.392	0.014						0.042	20	0.385	70.885	0.049

by personnel from state or provincial management agencies (Monteith et al. 2018). In addition, some agencies have adopted the Boone and Crockett scoring system to monitor size of harvested males (with no minimum size requirement for an animal to be recorded by the agency). We also used records of large mule deer and white-tailed deer that were collected and reported in books that aimed to collate the stories and background of large specimens that were harvested in individual states (Long et al. 1997; Hatfield 2004, 2006). These books assembled information on size, year of harvest, hunter, and location of animals that either were entered into a record book or were eligible for entry into a record book. We identified specimens that were eligible for entry (i.e., exceeded minimum size for entry) within records of state harvest data, and subsequently determined whether those specimens had been recorded in the Boone and Crockett record book. We determined eligibility for entry based on net score, which penalizes for asymmetry, but is the criterion used to establish eligibility for the Boone and Crockett record book. Because specimens were measured soon after harvest (did not dry for 60 days), we only considered specimens to be eligible if their estimated net score exceeded the minimum requirement for entry by  $\geq 5.1$  cm (2 inches) for both bighorn sheep categories and by  $\geq 7.6$  cm (3 inches) for all four deer categories. We chose these cutoffs to account for potential shrinking during the 60-day drying period and some minor discrepancy in how specimens may have been measured to insure that those classified as eligible would have exceeded the minimum size requirement for entry.

We used logistic regression ( $\alpha = 0.05$ ) to identify whether probability of entry of eligible specimens into a record book has changed through time while controlling for specimen size. The dependent variable indicated whether a specimen was entered into the Boone and Crockett Club Records Program (coded 1) or not (coded 0), and year of harvest, size of the specimen, and an interaction between year of harvest and size of the specimen were the independent variables. We only used Boone and Crockett Club records to assess factors affecting probability of being entered into a record book because we were unable to identify the weapon used to harvest the animal in most instances, a factor that influences entry into other record books.

To further test whether trends in the size of horns, antlers, and pronghorns of males differ based on size requirements for entry, we quantified change in the proportion of each bin that consisted of specimens with exceptionally large horns, antlers, and pronghorns. For each category in the Boone and Crockett record book, we identified all specimens that had horns, antlers, and pronghorns in the largest 25% of the category. We used simple linear regression with proportion of entries in the top 25% as the dependent variable and the mean year of samples in each bin as the independent variable. Finally, we quantified changes in entry rate of all specimens, as well as only those specimens that possessed exceptionally large horns, antlers, or pronghorns, through time. For each category, we used simple linear regression ( $\alpha = 0.05$ ) with number of entries with exceptionally large horns, antlers, or pronghorns (i.e., those in the top 25% of the category) as the dependent variable and year of

entry as the independent variable. We then fit a second set of regression models with total number of entries as the dependent variable and year of entry as the independent variable.

## RESULTS

We evaluated 109,398 records from 17 categories across three record books. Our dataset included 19,506 records from the Boone and Crockett Club Records Program (12,807 for antlered game and 6,669 for horned game; **Table 1**), 78,862 records from the Pope and Young Club Records Program (72,952 for antlered game and 5,910 for horned game; **Table 1**), and 11,030 records from the Safari Club International Records Program (5,406 for antlered game and 5,624 for horned game; **Table 1**).

*Temporal trends.*—The magnitude, direction, or both magnitude and direction of trends in size of horns, antlers, and pronghorns differed among the Boone and Crockett Club, Pope and Young Club, and Safari Club International record books for eight of the 17 categories (**Tables 2 and 3**): Alaska-Yukon moose (*Alces alces gigas*, **Fig. 2I**), non-typical white-tailed deer (*Odocoileus virginianus virginianus*, **Fig. 2H**), typical Columbia black-tailed deer (**Fig. 2E**), typical American elk (**Fig. 2F**), pronghorn (**Fig. 1A**), bighorn sheep (**Fig. 1G**), Dall's sheep (*Ovis dalli dalli* and *O. d. kenaiensis*, **Fig. 1F**), and desert sheep (**Fig. 1H**). Trends in size among the remaining nine categories were similar in magnitude and direction among record books (**Tables 2 and 3**; **Figs. 1 and 2**).

Of the eight categories with differing trends among record books, two categories (non-typical white-tailed deer, **Fig. 2H**; bighorn sheep, **Fig. 1G**) exhibited trends of greater magnitude (but in the same direction) in the record book with the lowest size requirements for entry (Pope and Young). In contrast, for two categories (typical Columbia black-tailed deer, **Fig. 2E**;

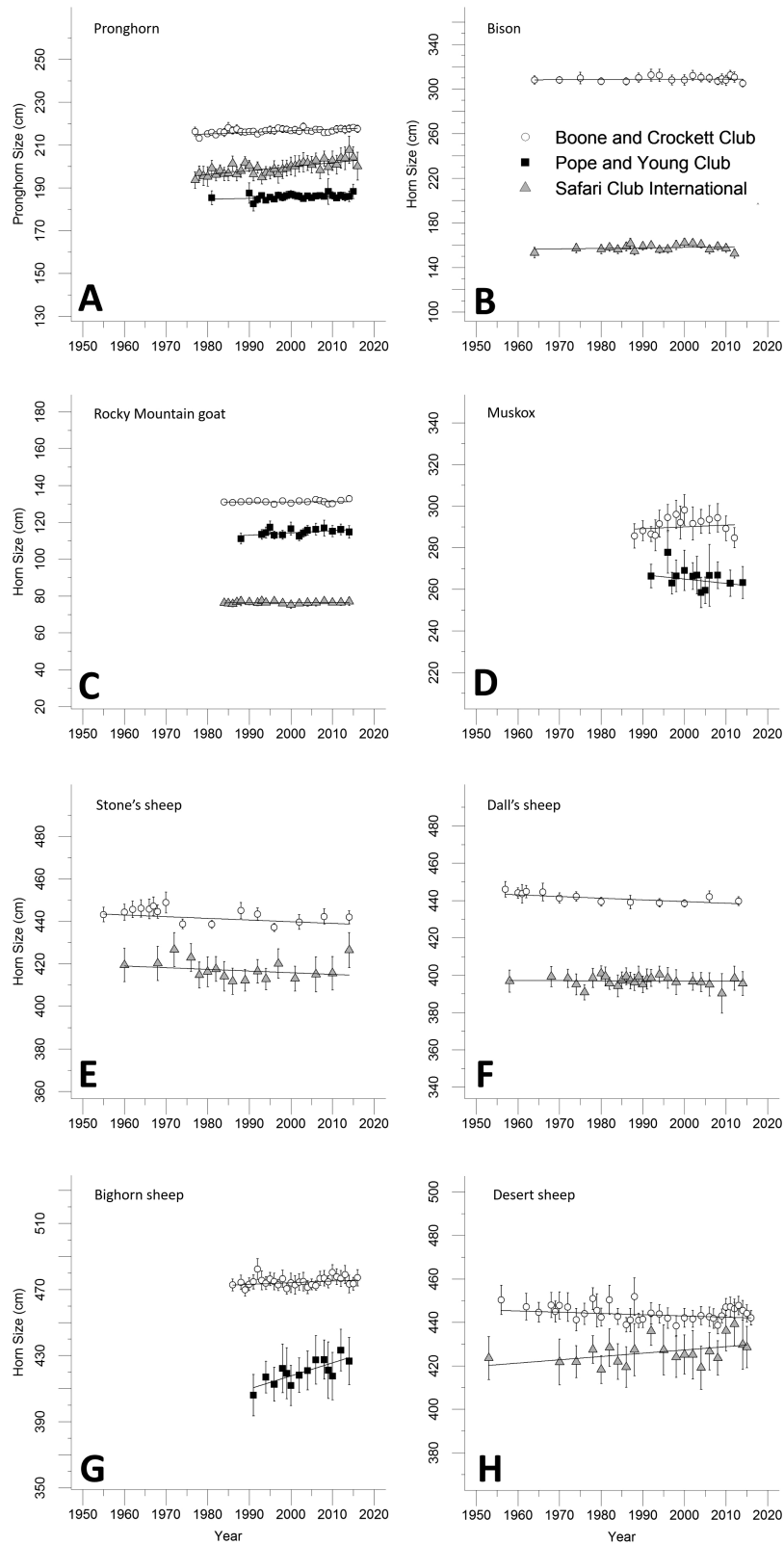
typical Sitka black-tailed deer, **Fig. 2D**), no temporal trend was evident in the Pope and Young data, whereas significant trends were evident in the Boone and Crockett Club and Safari Club International record books, both of which had higher requirements for entry.

*Effect of minimum entry requirements.*—Magnitude and direction of trends in size changed for typical American elk and typical white-tailed deer (but not for pronghorn,  $F_{1,72} = 0.863$ ,  $P = 0.456$ ; **Fig. 3C**) when minimum size for eligibility in the Pope and Young records book was iteratively increased by 5%, 10%, 20%, or 30%. As minimum entry size increased, trends in antler size of typical American elk changed from increasing to stable ( $F_{1,116} = 3.302$ ,  $P = 0.013$ ; **Fig. 3B**), and trends in typical white-tailed deer changed from stable to declining ( $F_{1,147} = 3.696$ ,  $P = 0.007$ ; **Fig. 3A**).

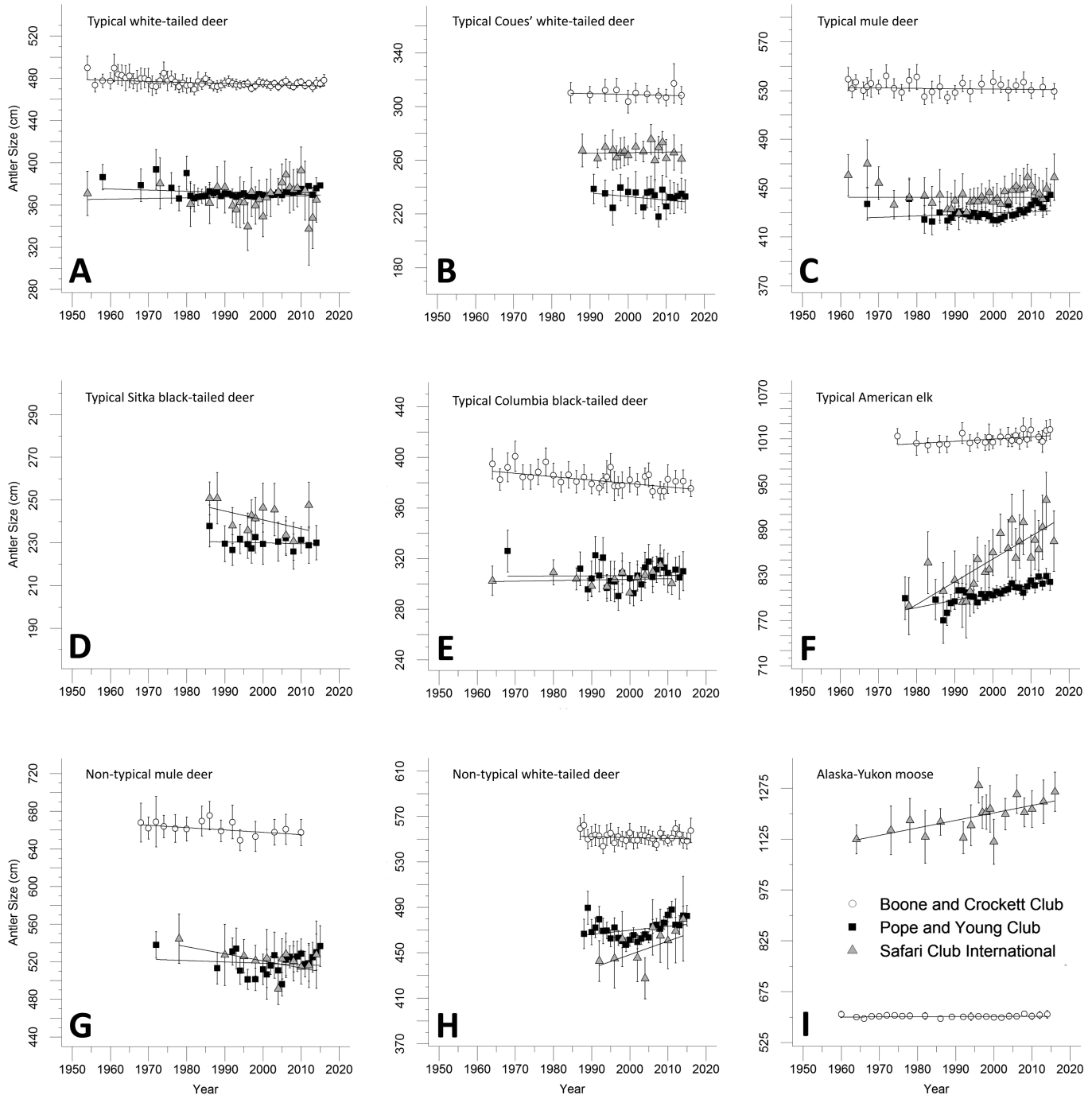
*Identifying changes in societal interest.*—There was a change in societal interest of submitting specimens into a records program in one of six categories. For bighorn sheep harvested in eight states in the United States between 1990 and 2010, probability of entry into the Boone and Crockett record book increased through time, with the size of horns, and by an interaction between year of entry and horn size. For desert sheep, probability of entry was related positively to size ( $P < 0.001$ ) but, unlike bighorn sheep, that relationship did not change over time ( $P = 0.105$ ). Although the influence of size, year, or both, on probability of entry was statistically significant, coefficients of determination for both bighorn sheep and desert sheep were very low (both  $R^2 < 0.07$ ), indicating little functional significance of this effect. There was no change in probability of entry by size, year of harvest, or an interaction between the two variables for typical mule deer (all  $P > 0.16$ ), non-typical mule deer (all  $P > 0.43$ ), typical white-tailed deer (all  $P > 0.30$ ), and non-typical white-tailed deer (all  $P > 0.68$ ).

**Table 3.**—Results of the analysis of covariance to test for differences in the direction, magnitude, or both direction and magnitude of trends in horn or antler size (represented by gross score) among the Boone and Crockett Club, Pope and Young Club, and Safari Club International record books for 17 categories. Significance was determined based on  $P \leq 0.10$  and is highlighted in bold. Sample sizes (number of temporal bins evaluated within each category) are given for each records book.

Category	Type III sum of squares	F	d.f.	P-value	Boone and Crockett	Pope and Young	Safari Club International
<b>Antlered categories</b>							
Alaska-Yukon moose	-6.241	21.585	38	<b>&lt; 0.001</b>	24	0	18
Typical Coues' white-tailed deer	-0.363	0.765	40	0.472	11	18	17
Non-typical white-tailed deer	-1.656	4.057	62	<b>0.022</b>	30	28	10
Typical white-tailed deer	-0.279	0.723	123	0.488	60	41	28
Non-typical mule deer	-0.612	0.722	44	0.491	15	23	12
Typical mule deer	-0.445	0.730	91	0.485	28	33	36
Typical Columbian black-tailed deer	-2.313	2.856	65	<b>0.065</b>	32	26	13
Typical Sitka black-tailed deer	-0.695	2.504	21	0.129	0	14	11
Typical American elk	-12.791	29.854	72	<b>&lt; 0.001</b>	23	31	24
<b>Horned categories</b>							
Muskox	-0.660	1.551	24	0.225	15	13	0
Pronghorn	-2.192	7.384	100	<b>0.001</b>	39	27	40
Rocky Mountain goat	-1.113	2.151	46	0.128	18	15	19
Bighorn sheep	-1.809	9.132	40	<b>0.004</b>	30	14	0
Dall's sheep	-0.913	2.992	36	<b>0.092</b>	13	0	27
Desert sheep	-2.250	5.539	54	<b>0.022</b>	37	0	21
Stone's sheep	< 0.001	< 0.001	29	0.997	16	0	17
Bison	-0.110	0.284	35	0.597	19	0	20



**Fig. 1.**—Trends in the mean horn size of eight categories (A–H) of horned game in the Boone and Crockett, Pope and Young, and Safari Club International record books from 1950 to 2015. Minimum size requirements for entry into a records program results in different distributions of data across the three books. Data points represent mean horn size (represented by gross score) of each bin (minimum bin size was 1 year, comprised of at least 20 records), error bars represent 95% confidence intervals, and trend lines represent fitted least-square regressions weighted by the inverse of the variance in each bin.



**Fig. 2.**—Trends in the mean antler size of nine categories (A–I) of antlered game in the Boone and Crockett, Pope and Young, and Safari Club International records books from 1950 to 2015. Minimum size requirements for entry into a records program results in different distributions of data across the three books. Data points represent mean antler size (represented by gross score) of each bin (minimum bin size was 1 year, comprised of at least 20 records), error bars represent 95% confidence intervals, and trend lines represent fitted least-square regressions weighted by the inverse of the variance in each bin.

The proportion of individuals that were in the largest 25% of all recorded entries in a Boone and Crockett record book decreased through time for 11 of the 19 categories (Supplementary Data SD2). Both total entry rate and entry rate of individuals in the largest 25% of all entries increased through time in 16 of the 19 categories; the magnitude of change in the entry rate of all individuals was greater than the magnitude of change in

the entry rate of individuals in the largest 25% of entries for all categories (Supplementary Data SD2).

**DISCUSSION**

Although rare, long-term datasets are important for detecting patterns of change in wild populations in the face of changing



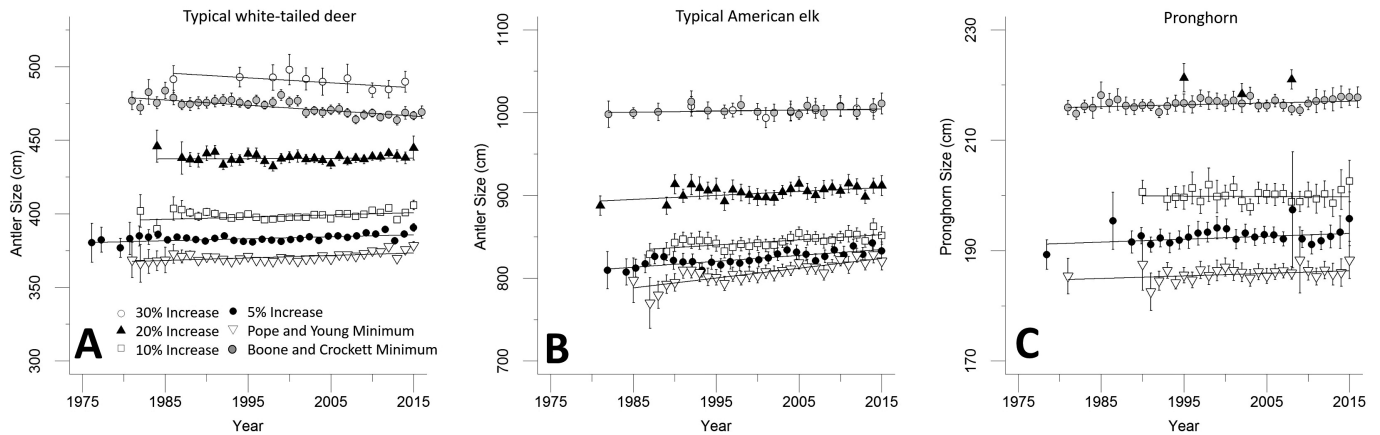


Fig. 3.—Temporal trends in the mean antler or horn size (represented by gross score) for typical white-tailed deer (A), typical American elk (B), and pronghorn (C) from the Boone and Crockett record book and Pope and Young record book, with different minimum size requirements used for truncation (actual Pope and Young minimum, 5% increase in minimum size, 10% increase in minimum size, 20% increase in minimum size, and 30% increase in minimum size).

climates, increased habitat degradation, or unsustainable harvest strategies (Odum 1959; Franklin 1989; Krebs et al. 2001; Lindenmayer et al. 2012). Record books are among the longest-running datasets available for monitoring large mammals across a broad geographic range (Monteith et al. 2013), but their biological relevance has been questioned (Festa-Bianchet et al. 2015). Through comparative analysis of three record books with different minimum entry requirements, we demonstrated that despite some inconsistencies in temporal trends in size, the prediction that higher size requirements (up to 28% higher for some categories) for entry would weaken underlying trends in size of horns or antlers was not supported. Furthermore, we documented minimal potential for bias associated with changing societal interest in voluntary submission of specimens with respect to year of harvest and size. Overall, our analyses indicated that record books likely contain useful, long-term data that can be used to detect and evaluate temporal changes in horn, antler, or pronghorn size of large male ungulates. There are, however, several limitations to the data maintained by records programs that should be carefully considered, and that might affect the ability of researchers to identify and disentangle mechanisms responsible for temporal changes in the size of horns and antlers.

Evolutionary processes are complex and often difficult to detect, and an understanding of population dynamics, demography, and environmental characteristics is necessary to identify the mechanisms of evolutionary change (Urban et al. 2012). Record books lack many of these key pieces of information, and therefore are limited in their ability to address specific questions about the causes of evolutionary change. For example, in most instances, record books do not contain reliable age data for specimens—information that would be necessary to understand whether changes in the size of horns or antlers are a function of shifts in age structure or other factors such as an evolutionary response to harvest (Monteith et al. 2013). Demographic fluctuations can result in changes in the average size of horns or antlers through time (Monteith et al. 2013). For example, an increased proportion of young males could result

in reductions in mean size of horns or antlers independent of evolutionary change. Furthermore, without reliable information on characteristics of populations and habitats where animals were harvested, it is not possible to identify and parse the effects of environmental conditions on changes in the size of horns or antlers. With few exceptions (Jorgenson et al. 1997; Festa-Bianchet et al. 2017), datasets that span a temporal scale necessary to detect evolutionary change in ungulate species are scarce. Nevertheless, our analysis indicates that record books provide useful information about changes in size of horns or antlers of large males.

For data in record books to be representative of trends among males with large horns or antlers in general, the probability of a specimen being entered into a record book should be random or consistently biased through time. Entry of animals into any records program is optional, and if the probability of entry of either large or small specimens changes with societal interest, changes recorded in the data could reflect human behavior rather than an underlying biological phenomenon (Monteith et al. 2013). For only one of the six categories tested (bighorn sheep), interest in entering larger specimens increased through time compared with smaller specimens. Nevertheless, very little (< 10%) of the probability of entry for bighorn sheep was explained by that model, suggesting that temporal trends were not influenced substantially by changes in societal interest. Further, in the remaining five categories we evaluated, probability of entry was not influenced by size or year of harvest. Trends detected in the size of horns and antlers are therefore likely the result of a biological change, not a changing interest in submitting specimens to records programs.

Only two of 17 categories exhibited trends of lesser magnitude in record books with higher size requirements for entry, and in nine categories there was no difference in trends among record books. Furthermore, in contrast to the notion that higher size requirements for entry would weaken the ability to detect negative trends (Festa-Bianchet et al. 2015), we did not observe that pattern. Of the three categories where we iteratively increased the minimum size requirements for entry into the record

book with the lowest entry requirements (Pope and Young Club record book), trends in the one category that was decreasing through time (typical white-tailed deer) became more negative with increasing minimum size requirements (Fig. 3A). Trends did not weaken as predicted, but instead began to more closely resemble that of the record book with the highest requirements for entry (i.e., Boone and Crockett), which indicates that changes detected in record books likely are representative of changes in the size of horns, antlers, and pronghorns of males in the respective range of sizes that each book contains.

Our results both complement and contrast with the results of prior modeling efforts aimed at addressing the relevance of record books (Festa-Bianchet et al. 2015). In a simulated population of bighorn sheep, temporal trends in horn size of males eligible for entry into a hypothetical record book underestimated trends of the total simulated populations over a 50-year period when horn size of males was either artificially increased or decreased through time (Festa-Bianchet et al. 2015). These simulations indicated that record books are simply a weakened representation of trends within a larger range of sizes, and not representative of the average size of the population from which they came. Differences among record books in eight of the 17 categories we evaluated support the idea that truncation makes extrapolating trends from data maintained in record books to a wider population problematic. Nevertheless, data from records programs should be representative of an important subset of the population: males that possess large horns and antlers.

Truncation of sizes of horns or antlers inherent in records programs may result in trends of greater magnitude if males that possess horns or antlers closer to their biotic maxima are the primary driver of temporal patterns of change. Previous work with data from the Boone and Crockett records program demonstrated that patterns in size between the top third (based on size) of a category and the entire category closely resembled each other, whereas patterns in size of the bottom third of a category were less likely to reflect temporal change in the category as a whole (Monteith et al. 2013). When we assessed how the proportion and number of exceptionally large males (i.e., size threshold of the top 25% of each category) changed through time, rate of entry for all specimens and for those exceptionally large specimens increased for most categories, but the number of entries for exceptionally large specimens increased at a slower rate. Further, the direction and magnitude of change in the proportion of exceptionally large specimens in each bin, and in the size of horns or antlers of the entire category, were nearly identical for almost every category (Supplementary Data SD2). This result provides further evidence that males possessing exceptionally large horns or antlers are the underlying driver of temporal patterns across categories (Monteith et al. 2013).

Clear patterns of change can be detected in the data maintained by records programs, which suggests that even at the broad temporal and spatial scale at which records programs maintain data, there may be range-wide mechanisms (i.e., broad-scale harvest regimes or climatic changes) influencing

the size of horns, antlers, or pronghorns of many species of big game. Such patterns may provide a meaningful foundation upon which to build further inquiry into the mechanisms of change in the size of horns and antlers, and further inform managers on which species potentially should be investigated in more detail (Monteith et al. 2013). Horn or antler size can be an important indicator of individual fitness and is related positively to sperm production and reproductive success (Preston et al. 2003; Malo et al. 2005; Mainguy et al. 2008). Males with larger horns or antlers often have greater chances of reproducing than males with smaller horns or antlers (Andersson 1994). Moreover, males that possess large horns or antlers represent a portion of the population that is especially valuable to managers and biologists because the pursuit of large male ungulates is a valued part of the hunting tradition throughout the world (Monteith et al. 2018), and plays an important role in wildlife conservation (Lindsey et al. 2007; Heffelfinger et al. 2013; Hurley et al. 2015; Minin et al. 2016). Interest in harvesting ungulates with large horns or antlers has increased, and the “hornographic” interests of many hunters have contributed to the development of management strategies that emphasize the maintenance of large males within wild populations (Monteith et al. 2018). Records programs were implemented to help evaluate the success of wildlife management programs, and they provide an incredible amount of data collected over long periods of time and across the entire ranges of many species (Monteith et al. 2013). Records programs may improve the relevance of their data for research and conservation by keeping minimum entry requirements low to increase the range in sizes of a category that their data represent and working to garner ages of submitted specimens—an effort already underway by the Boone and Crockett Club. The criticism that trends in the size of horns or antlers detected in record books do not represent trends that are occurring in the entire population is a fallacy of composition; that is, such a critique falls on an inappropriate extension of those data beyond the range of which record book data represent, rather than an actual critique of record book data. Instead, we believe that when used with care, records programs provide valuable data for assessing how broad-scale factors (i.e., harvest regimes or climate) might influence the size of horns, antlers, or pronghorns over time, within the range of sizes that each program represents.

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### SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Differences in the measurement protocol of trophy record categories among the Boone and Crockett Club, Pope and Young Club, and Safari Club International record books.

**Supplementary Data SD2.**—Proportion of entry of exceptionally large trophies in the Boone and Crockett record book through time.

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