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Original Article

Effects of Extreme Environmental Conditions on White-tailed Deer Antlers

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ABSTRACT Antler size and morphology is the resultant combination of deer age, nutrition, and genetics. Additionally, extreme environmental conditions can affect deer health, which may influence current and future antler metrics. Throughout the antler development season of 2012, the Nebraska, USA, white-tailed deer (*Odocoileus virginianus*) herd experienced a combination of extreme environmental conditions including extreme drought and disease, which we hypothesized would negatively affect antler size and morphology. Our objectives were to evaluate whether 1) age-specific antler metrics differed between deer stressed by an extreme environmental condition year compared with nonextreme condition years, and 2) subsequent age-specific antler metrics of a cohort born during an extreme environmental condition year differed from those born during nonextreme condition years. We measured antler metrics on harvested white-tailed deer from central Nebraska for an 8-year period (2009–2016) that spanned the extreme environmental condition year. Over this same time period, we measured pedicle seal depth on naturally cast antlers. Some trends were apparent for specific antler metrics in particular age groups; but, overall, antler metrics measured from harvested deer were not consistently affected during the extreme environmental condition year. Conversely, pedicle seal depths responded to environmental stressors and were smaller during the extreme environmental condition year compared with nonextreme condition years. We found effects to persist for years following extreme environmental stress—antler metrics of the extreme environmental condition cohort were smaller compared with nonextreme years. These results suggest that stressors caused by extreme environmental conditions can affect deer health and be indexed using sensitive metrics taken on cast antlers. Furthermore, effects on antler metrics can persist, affecting subsequent antler expression for cohorts that experience extreme environmental conditions during their first year of life.

KEY WORDS antler morphology, antler size, cast antler, Cervidae, drought, environmental stress, *Odocoileus virginianus*, pedicle seal, shed, white-tailed deer.

The expression of antler size and morphology in white-tailed deer (*Odocoileus virginianus*) is the resultant combination of age, nutrition, and genetics; therefore, deer antler metrics can be used to index the physical condition of deer populations (Goss 1983, Scribner et al. 1989, Scribner and Smith 1990). Additionally, nuances such as effects from environmental conditions, individual deer health, or large population density may influence antler metrics (Anderson and Medin 1969, Bubenik 1990*a*, Torres-Porras et al. 2009). The pedicle of an antler is essential to normal antler development (Chapman 1975). Similar to antler size and morphology, variation in cast-antler pedicle seal depth can provide insight into an individual deer's health and physical condition because associations have been observed in white-tailed deer between pedicle seal depth and physical condition of the deer at the time of casting (Bubenik et al. 1987, Bubenik 1990*b*). Cast-antler pedicle seal depth represents the manner at which lateral resorption occurs during the process of antler casting, resulting in either a convex or concave antler-seal contour with the magnitude related to individual health and condition (Bubenik 1990*a, b;* Fig. 1). Within experimental white-tailed deer populations, antlers with convex seal depths were cast by healthier males with greater maximum concentrations of blood testosterone at rut while nutritionally deprived males exhibited lower blood testosterone levels and cast antlers with concave seal depths (Bubenik et al. 1987, Bubenik 1990*a, b;* Fig. 1).

Identifying specific environmental conditions that influence antler size and morphology can be difficult given

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[Correction added on November 5, 2019 after first online publication: Changed the unit cm to mm in Table 2].

Figure 1. Freshly cast 1.5-year-old white-tailed deer antlers (collected in Nebraska, USA), representing variation in pedicle seal depth (Left: convex; Right: concave).

the complexity of factors. For example, cooler summer temperature can prolong the availability of high-quality forage, which has been shown to increase mass gain and antler growth (length) in yearling red deer (*Cervus elaphus;* Schmidt et al. 2001). Warm temperatures and increased precipitation have been shown to be positively correlated with antler growth in red deer and elk (*C. canadensis;* Clements et al. 2010, Freeman et al. 2013). Conversely, hot temperatures during the antler-growing season can cause early forage senescence, which is shown to have a negative relationship on antler growth of black-tailed deer (*O. hemionus columbianus;* Thalmann et al. 2015).

Variable climatic conditions such as high temperature and low precipitation are associated with drought and can directly affect vegetation quality and quantity, and thus, subsequently negatively affect deer (Iberian red deer [*Cervus elaphus hispanicus*], roe deer [*Capreolus capreolus*], and white-tailed deer) health and antler size and expression (Azorit et al. 2002, Vanpé et al. 2007, Torres-Porras et al. 2009, Landete-Castillejos et al. 2010, Foley et al. 2012). High population densities can exacerbate the negative effects drought has on antler metrics as found in Iberian red deer (Torres-Porras et al. 2009), while quality nutrition and summer range quality can compensate for high deer densities (Kaji et al. 2004).

Effects of environmental stress may be acute or persist for many years and generations (i.e., lag theory or cohort effect; Anderson and Medin 1969, Monteith et al. 2009, Thalmann et al. 2015). Adverse environmental conditions can affect maternal health and consequently investments in offspring (Festa-Bianchet and Jorgenson 1998, Freeman et al. 2013). In bighorn sheep (*Ovis canadensis*), adult females make energetic trade-offs in times of reduced resources between investments in offspring and individual preservation when the fetus is *in utero* (Festa-Bianchet and Jorgenson 1998). Individual health in ungulates has been linked to conditions experienced early during their year of birth (Hamel et al. 2009), with studies showing that during periods of low spring precipitation, fetus growth can be stunted, resulting in small body size throughout life (Schmidt et al. 2001, Freeman et al. 2013). Mild winter conditions prior to birth in mule deer (*Odocoileus hemionus*) have been shown to positively influence antler size during an individual male's lifetime (Freeman et al. 2013). Conversely, increasing snowfall during the year of birth was correlated with greater antler size in elk throughout life (Freeman et al. 2013). Drought conditions can severely decrease white-tailed deer fawn growth rates, creating long-lasting effects on growth and increased risk of disease transmission throughout life (Wilhite and Glantz 1985, Tosa et al. 2018).

Nebraska, USA, reached extreme drought conditions beginning in August of 2012 that persisted into March of 2013 (NDMC 2019). During this 8-month period, drought severity and coverage index values (DSCI) averaged 462.8 ± 3.9 standard error (SE) DSCI and peaked in September of 2012 (476 DSCI), compared with the average during the 8-year study (96.1 ± 6.9 SE DSCI; NDMC 2019; Table 1). Buffalo County, Nebraska, which encompassed the majority of the study area, was classified within an extreme to exceptional drought from late summer of 2012 through early 2013 as established by the U.S. Drought Monitor and Palmer Drought Severity Index (Fig. 2; NOAA 2018, NDMC 2019). Yearly temperature during 2012 was 14.2% (1.6° C) higher and annual precipitation 45.6% lower (34.8 cm) compared with the study area average (U.S. Climate Data 2018; Table 1). By October 2013, drought classification subsided to "near normal" within Buffalo County (NOAA 2018).

Table 1. Harvested white-tailed deer main beam length (MBL) cut-off values used to differentiate 1.5-year-old deer from those ≥2.5 years old using cast antler samples collected the succeeding spring, drought severity, and coverage index values (DSCI), reported epizootic hemorrhagic disease (EHD) mortalities, growing degree days, and annual precipitation from 2009 to 2016 in Nebraska, USA.

Year	1.5-yr-old MBL cut-off values (mm)	1.5-yr-old casts sampled (*n*)	≥2.5-yr-old casts sampled (*n*)	Nebraska DSCI value		Nebraska EHD mortality	Buffalo Co. EHD mortality	Growing degree days	Annual precipitation (cm)
				$\bar{x}$	SE				
2009	363	27	10	11.9	1.3	10	2	157	56.0
2010	364	50	18	11.6	2.6	8	2	166	79.8
2011	366	36	23	33.1	3.2	6	0	167	80.0
2012	364	50	20	243.8	27.4	5,998	277	152	34.8
2013	363	36	13	318.7	15.5	149	2	157	67.0
2014	357	38	20	93.1	10.8	<5	0	147	63.9
2015	365	33	17	28.5	3.4	<5	3	174	66.2
2016	362	30	26	23.4	3.3	<5	3	183	51.4

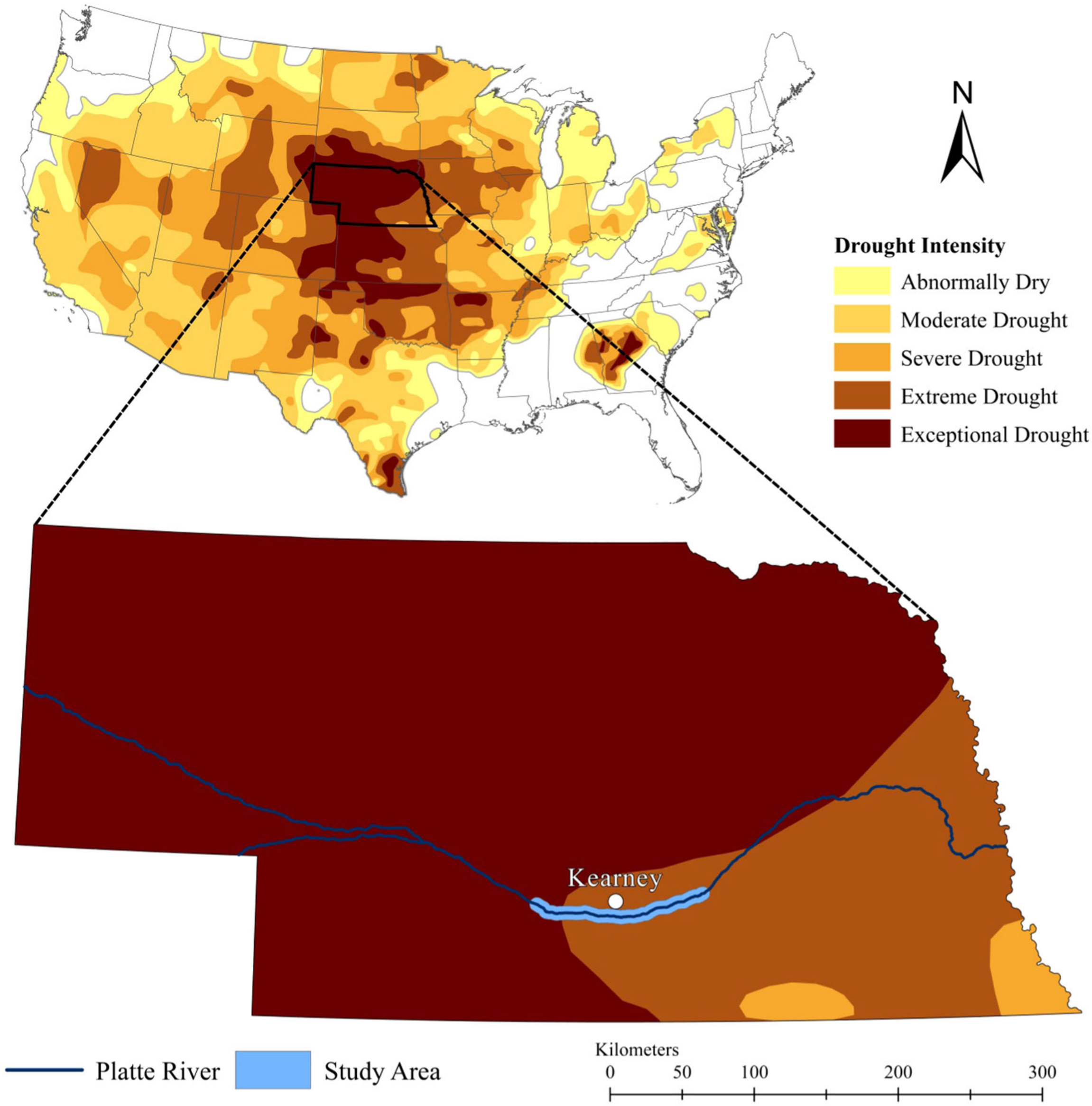

Figure 2. White-tailed deer harvest and cast-antler study area (2009–2016) including peak drought intensity in Nebraska, USA, and the United States during 2012. Map adapted from the U.S. Drought Monitor (NDMC 2019).

With the onset of extreme drought, the Nebraska white-tailed deer population was reduced in 95% of the state as it endured the most severe epizootic hemorrhagic disease (EHD) outbreak recorded since 1976 (Decker 2013, Krausman et al. 2014). Infected males during an EHD outbreak period had lower testosterone levels, which resulted in incomplete antler growth and an increase in antler breakage (Fox et al. 2015). During the 2012 EHD outbreak, 80 times more mortalities (5,998) were reported statewide compared with the 74.3/year average (Decker 2013; Table 1), with Nebraska biologists estimating a 30% decline in the state's white-tailed deer population. Within our study area, 277 EHD mortalities were reported in 2012 compared with an average of 1.7 ± 0.5 during nonextreme condition years (Table 1). All of the EHD mortalities reported during 2012 in our study area consisted of white-tailed deer and were reported between August and October.

Furthermore, a shorter-than-average vegetation growing season may have compounded the stressors of drought and disease. The Nebraska growing season during 2012 (152 days) was 10 days shorter than the defined 162 day normal growing season, and >12 days shorter than the 7-year nonextreme condition average (164.4 ± 4.5; Table 1; UNL 2018). Length of the growing season is based on growing degree days, or the number of days between the last spring freeze and first autumn freeze (>0° C) each year, with fewer days reducing essential vegetation browse. Over the past 15 years (2002–2016), the average first autumn freeze occurred around 8 October, while in 2012, the first autumn freeze occurred on 23 September, which was the earliest during that timeframe. Based on the culmination of all of these factors (drought, disease, and shortened growing season), we defined the 2012 study year as an extreme environmental condition year.

Events of 2012 provided an opportunity to investigate effects of extreme environmental conditions on the metrics of harvested and naturally cast white-tailed deer antlers as part of a long-term study that began in 2009. Studies have detected variation in antler expression associated with environmental changes; however, it is difficult to pinpoint and quantify the specific contributing factors involved (Foley et al. 2012). To date, no known studies have examined the effect of extreme environmental conditions on antler metrics of harvested and naturally cast white-tailed deer antlers. Our objectives were to evaluate whether 1) age-specific antler metrics differed between deer stressed by an extreme environmental condition year compared with nonextreme condition years, and 2) subsequent age-specific antler metrics of a cohort born during an extreme environmental condition year differed from those born during nonextreme condition years.

STUDY AREA

Harvested white-tailed deer during the 2009–2016 9-day November firearm season were brought by hunters to the mandatory check station at the Nebraska Game and Parks Commission (NGPC) Kearney Service Center. White-tailed deer were primarily harvested proximal to the Platte River in south-central Nebraska (Fig. 2; Schoenebeck et al. 2013). No antler restriction regulations were in place within Nebraska during and prior to this 8-year sampling effort. The Nebraska Game and Parks Commission defines antlered deer as having antlers ≥15.2 cm and each hunter may have up to 2 permits/year that allow the take of an antlered deer. Antlered deer permits during the firearm season were reduced from 3,350 to 3,150 within the study area following the 2012 EHD outbreak, and remained at that level through 2016. Antlered deer permits were also available through the unlimited statewide buck, muzzleloader, and archery permits.

Concurrently, we collected naturally cast white-tailed deer antlers February through April 2010–2017 within the same geographical area that deer were harvested (Fig. 2). We collected cast antlers during the successive spring, but we report both the harvest and cast-antler collection year as the antler-growing year for simplicity. The cast-antler search area consisted of multiple land parcels along the Platte River corridor within 60 river-km of Kearney in south-central Nebraska, primarily consisting of riparian habitat bordered by agricultural fields (Fig. 2; Weaver and Bruner 1948, Schoenebeck and Peterson 2014). The majority of casts were collected by B. Peterson and C. Schoenebeck, who systematically searched permissible properties typically once per season. Additionally, the data set was augmented with freshly cast-antlers collected from the study area by cast-antler-collecting hobbyists.

METHODS

The same senior NGPC wildlife biologists aged harvested white-tailed deer using tooth-wear-and-replacement methods similar to those described by Severinghaus (1949), because this is the NGPC standard and accepted method to obtain age class information. We took antler measurements on aged deer using the most accessible antler because antler metrics do not vary between antler sides (Schoenebeck et al. 2013). Measurements taken included antler length (main beam length), antler mass (main beam circumference at smallest point between burr and first point), and number of antler points (total points). We measured main beam length and main beam circumference to the nearest 1 mm using a measuring tape, and counted the number of points ≥25 mm in length as specified by the Boone and Crockett Club (Nesbitt et al. 2009). We compared the extreme environmental condition year to each of the other 7 nonextreme years for 3 age groups (1.5-, 2.5-, and 3.5-yr-old deer) for differences in antler metrics from harvested deer (main beam length, main beam circumference, and total points) using a categorical linear model with normal error structure and 2012 set as the reference year, so model coefficients were contrasts of the 2012 mean with means from all other years ($\alpha = 0.05$).

We identified all white-tailed deer cast antlers as either old or fresh, which we defined as having a skin ring and blood or hair located around the exterior of the pedicle seal just under the base of the burr (Schoenebeck and Peterson 2014). We used only freshly cast antlers defined as typical by the Boone and Crockett Club in data analysis (Nesbitt et al. 2009; we removed 2 nontypical antlers from data analysis). Cast antlers most accurately reflect changes in environmental conditions when accounting for age (Peláez et al. 2018); therefore, we used main beam length to distinguish 1.5-year-old deer cast antlers from those ≥2.5 years old, based on a 364.0-mm main beam length cut-off value previously defined for this region in 2009–2011 (Schoenebeck et al. 2013). The cut-off remained consistent from 2009 to 2016 and was therefore appropriate for all 8 years of this study (363.0 ± 1.0 mm; Table 1).

Using digital calipers, we took pedicle seal depth of cast antlers to the nearest 0.01 mm. We used the measuring blade of the digital calipers to directly measure from the base of the pedicle seal to the center of the pedicle seal's most protruding point, excluding casts containing irregular or broken pedicle bone or an attached portion of skull (MacCracken et al. 1994, Karns and Ditchkoff 2013). We measured cast antlers that exhibited a concave pedicle seal depth by placing the caliper blade tip within the deepest point of the pedicle seal and measuring to the flattest portion of pedicle seal (G. A. Bubenik, University of Guelph, personal communication). In the case of a match set of cast antlers, we included only the first cast collected in the pedicle seal depth analysis. Pedicle seal depths were measured on match sets of antlers to test whether antler sides differed using a paired *t*-test. We compared antler metrics from cast antlers (pedicle seal depth) using a categorical linear model with normal error structure and 2012 set as the reference year, so model coefficients were contrasts of the 2012 mean with the means of all other years ($\alpha = 0.05$).

We evaluated chronic or lasting effects on harvested deer antler metrics using Mann–Whitney *U*-Test Statistic ($\alpha = 0.05$) to compare potential differences in age-specific harvested antler metrics (1.5-, 2.5-, and 3.5-yr-old deer) between the cohort born during the year of extreme environmental conditions (born spring of 2012) with the cohorts born during nonextreme condition years.

RESULTS

Age-specific antler metrics were collected from 1,128 harvested white-tailed deer over the course of the 8-year study (Table 2). The largest percentage of harvested white-tailed deer measured was 1.5 years old (38.0%), followed by 2.5 years old (33.1%), and 3.5 years old (28.8%).

Some trends were apparent for specific antler metrics at particular age groups; however, overall, antler metrics measured from harvested deer were not consistently affected across age groups during the extreme environmental condition year. For example, the average main beam length of 2.5-year-old deer was consistently smaller during the extreme environmental condition year (2012) compared with the other 7 nonextreme years, but the difference was only significant for 2010, 2011, and 2013 (Table 2). The average main beam length was generally larger for 1.5-year-old deer during the extreme environmental condition year than other years, but only significantly larger than 2014 (Table 2). No apparent trend was found for 3.5-year-old deer, but main beam length in 2013 was significantly larger than the extreme environmental condition year (2012; Table 2). The average main beam circumference of 3.5-year-old deer was larger during the extreme environmental condition year (2012) compared with the other 7 nonextreme years, but only significantly larger than during 2015 and 2016 (Table 2). No trends in average main beam circumference were apparent for the other 2 age groups, and only one year (2016) was significantly smaller than the others for 2.5-year-olds (Table 2). The average number of total points of 2.5-year-old deer was greater for 2010 and 2011 compared with other years, including the extreme environmental condition year (2012), but only 2011 was significantly larger (Table 2). No trends in average total points were apparent for the other 2 age groups, though 1.5-year-olds in 2013 had a significantly smaller number of points than the extreme environmental condition year (2012; Table 2).

In contrast to measurements available from harvested deer, antler metrics unique to cast antlers were consistently affected across age categories during the extreme environmental condition year. Antler metrics were taken on 447 freshly cast antlers, of which 300 were classified as 1.5-year-olds and 147 were classified as ≥2.5-year-olds based on the main beam length cut-off value (Table 1). Pedicle seal depths of cast-antler match sets were not different between sides for 1.5 ($t_9 = 0.52$, $P = 0.62$) or ≥2.5-year-olds ($t_{20} = 0.02$, $P = 0.98$). The average pedicle seal depth for both age categories was smaller during the extreme environmental condition year (2012) compared with each of the other 7 nonextreme years (Fig. 3). Average pedicle seal depth of 1.5-year-old deer was significantly smaller during the extreme environmental condition year compared with all 7 of the nonextreme years (year specific P values were <0.01) and significantly smaller for 2 of the 7 nonextreme years for ≥2.5-year-old deer (2011; $P = 0.03$, 2014; $P = 0.02$; Fig. 3). Pedicle seal depth was variable among individuals within each sampling year as 1.5-year-olds ranged from −2.0 to 5.9 mm and −3.5 to 10.7 mm during extreme and nonextreme conditions, respectively; deer ≥2.5 years old ranged from 0.8 to 12.0 mm and −0.9 to 14.7 mm during extreme and nonextreme conditions, respectively.

Linear model error residuals showed slight departures from normality that could affect test size and error rates for small sample sizes. We note that all models in this study had >300 observations (except pedicle seal depth for deer ≥2.5 yr old was 147), and the central limit theorem shows that sample mean estimates converge to normality with sample size >30 regardless of underlying error distribution. Thus, inference from the linear models comparing annual means using t-tests was valid despite the departures from normality in these data.

Antler metrics of harvested white-tailed deer born during the 2012 extreme environmental condition year ($n = 175$) were compared with harvested deer ($n = 953$) born during nonextreme condition years. Antler metrics were consistently smaller for deer born during the extreme environmental condition year compared with deer born during nonextreme conditions. Main beam lengths within the extreme environmental condition cohort were smaller in 2.5-year-olds (1.6%; 6.4 mm) and 3.5-year-olds (3.7%; 15.3 mm), and significantly smaller (Mann–Whitney $U = 7{,}185$ $P = 0.05$) in 1.5-year-olds (2.7%; 13.8 mm;

Table 2. Harvested white-tailed deer (mean ± SE) of main beam length, main beam circumference, and total points represented by age groups (2009–2016) for each antler metric evaluated in Nebraska, USA.

		Main beam length (mm ± SE)						Main beam circumference (mm ± SE)						Total points (± SE)					
	Deer sampled	1.5 yr old		2.5 yr old		3.5 yr old		1.5 yr old		2.5 yr old		3.5 yr old		1.5 yr old		2.5 yr old		3.5 yr old	
Year	(n)	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
2009	107	295.7	7.0	422.5	9.9	449.5	7.9	71.7	1.5	97.0	2.2	102.4	2.2	3.0	0.1	4.1	0.0	4.2	0.1
2010	102	269.9	9.8	425.0[a]	8.7	475.3	7.4	65.8	2.1	96.0	1.6	107.3	2.4	2.7	0.2	4.2	0.1	4.5	0.2
2011	167	270.5	9.9	426.8[a]	5.9	466.8	7.8	67.1	1.7	92.1	1.2	106.9	2.3	3.1	0.1	4.3[a]	0.0	4.5	0.1
2012	142	284.0	10.4	400.0	7.5	455.6	10.7	68.5	1.8	92.6	1.4	108.5	3.0	3.0	0.1	4.1	0.0	4.4	0.1
2013	187	261.8	9.4	422.0[a]	5.9	482.7[a]	6.9	65.2	1.5	92.0	1.2	105.2	2.0	2.6[a]	0.1	4.1	0.0	4.4	0.1
2014	149	253.8[a]	11.0	411.7	8.2	463.5	8.8	64.7	2.0	91.4	1.6	103.5	1.9	2.8	0.2	4.1	0.1	4.2	0.1
2015	170	277.7	6.7	419.8	9.3	448.8	7.1	68.8	1.5	91.1	1.8	100.5[a]	1.6	2.9	0.1	4.1	0.0	4.3	0.1
2016	104	274.8	10.7	401.7	11.0	446.5	7.6	67.5	2.0	87.2[a]	1.9	99.6[a]	2.0	3.1	0.2	4.1	0.1	4.4	0.1

[a] Differences between the extreme environmental condition year (2012) and nonextreme years ($\alpha = 0.05$).

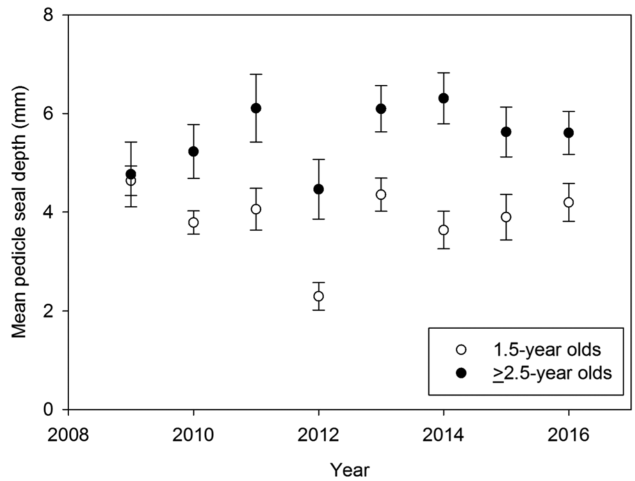

Figure 3. Pedicle seal depth (mean ± standard error) of cast antlers for 1.5- and ≥2.5-year-old white-tailed deer, collected from 2009 to 2016 in Nebraska, USA. We identified 2012 as a year of extreme environmental conditions including extreme drought and disease.

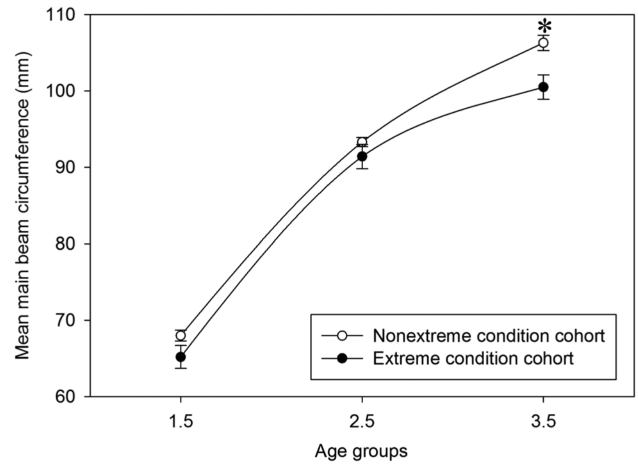

Figure 5. Mean main beam circumference (mm) ± standard error of harvested white-tailed deer antlers, compared between the extreme condition cohort (exposed to extreme drought and disease) and nonextreme condition cohorts of 1.5- through 3.5-year-olds (2009–2016) in Nebraska, USA. Asterisk denotes differences between conditions ($\alpha = 0.05$).

Fig. 4). Main beam circumference was smaller in 2.5- and 1.5-year-olds (1.4–4.1%; 1.3–2.7 mm) and significantly smaller in 3.5-year-olds (4.2%; 4.3 mm; Mann–Whitney $U_1 = 6{,}532$, $P = 0.04$) in the extreme environmental condition cohort (Fig. 5). There were consistently fewer (1.5–1.6%; <0.1) total points for 2.5- and 3.5-year-olds, and significantly fewer total points in 1.5-year-old deer (11.9%; 0.3); Mann–Whitney $U_1 = 6{,}994$, $P = 0.01$) within the extreme environmental condition cohort when compared with those born during nonextreme conditions (Fig. 6).

DISCUSSION

Antler metrics collected from harvested deer antlers were largely not affected by the extreme environmental condition year, although we found a few consistent trends. One consistent trend of harvested deer antler metrics was main beam lengths of 2.5-year-olds were consistently smaller during the extreme environmental condition year compared with all 7 other years. We postulate that in this age group, environmental stress during the extreme environmental condition year may have shifted the investment away from antler building late in the growing season. Antlers grow from the tip and therefore comprise the youngest tissue, with the antler base being the oldest, with growth continuing until antler hardening (Chapman 1975). During the harvest registration process, a greater number of unfinished points or blunted tips were anecdotally observed during the extreme environmental condition year; however, we did not quantify these observations or compare them among years. These findings are supported

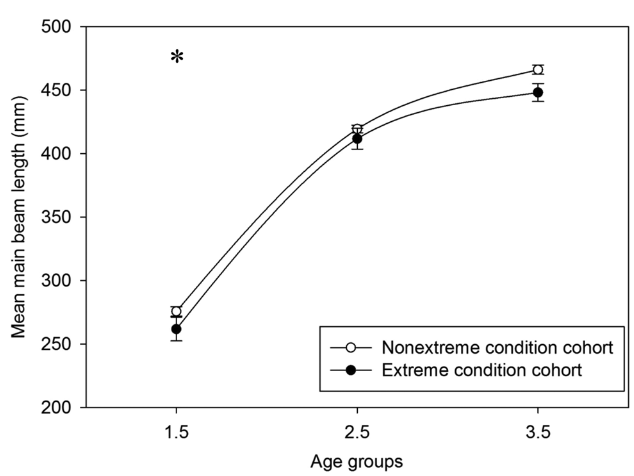

Figure 4. Mean main beam length (mm) ± standard error of harvested white-tailed deer antlers, compared between the extreme condition cohort (exposed to extreme drought and disease) and nonextreme condition cohorts of 1.5- through 3.5-year-olds (2009–2016) in Nebraska, USA. Asterisk denotes differences between conditions ($\alpha = 0.05$).

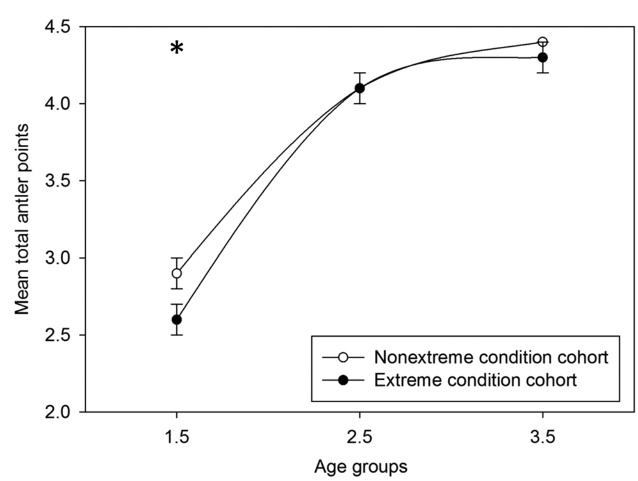

Figure 6. Mean total antler points ± standard error of harvested white-tailed deer, compared between the extreme condition cohort (exposed to extreme drought and disease) and nonextreme condition cohorts of 1.5 through 3.5-year-olds (2009–2016) in Nebraska, USA. Asterisk denotes difference between conditions ($\alpha = 0.05$).

by work describing lower testosterone levels resulting in incomplete antler hardening and increased antler breakage during times of EHD outbreak (Fox et al. 2015), which may explain why we observed a decrease in main beam and point length. Conversely, less antler breakage is common during times of adequate or excess rainfall (McDonald et al. 2005). The onset of extreme environmental conditions late in the antler-growing season likely resulted in the variation we observed between condition types and may represent a trade-off in energetic development of antler tissues. Vegetation browse was noticeably hampered during the extreme environmental year; therefore, essential trace mineral uptake through plant consumption may not have been obtained to reach maximum antler-growth potential. Antler growth, specifically number of antler tines (points) has been found to be greater during years with favorable environmental conditions (Mysterud et al. 2005). Within Nebraska, 4 points/side in ≥2.5-year-olds are common for white-tailed deer making antler points a less sensitive metric to environmental stressors for those age groups. Measurable differences in other additional age groups and antler metrics may have been observed if extreme environmental conditions were initiated at the onset and maintained throughout the antler-growing season (Mar–Sep), as opposed to peaking in the final months.

Pedicle seal depth was negatively affected for both age categories during the extreme environmental conditions representing lower testosterone levels at rut and consequently individual health. We cannot accredit the specific environmental condition or conditions responsible; however, lower testosterone levels have been attributed to EHD infection (Fox et al. 2015). Pedicle seal depths were smaller in 1.5-year-olds than ≥2.5-year-old deer, which is consistent with older deer having larger antlers, but also coincides with testosterone levels typically being lower in 1.5-year-old males (Bubenik and Schams 1986). Pedicle seal depth of 1.5-year-old deer had a greater separation between extreme and nonextreme years compared with deer ≥2.5 years old, suggesting 1.5-year-olds' pedicle seal depth is a good index of environmental stress on deer health because 1.5-year-old deer may be more susceptible to environmental stressors than older age groups. Although we did not document body mass changes by season, we suggest future studies should investigate the effect of extreme environmental conditions on this metric.

Average pedicle seal depths represent a baseline for future comparisons. It is important to note that this study encompassed a regional deer herd, in the central Platte River valley, over the course of an 8-year period. Interestingly, a range of individual deer health as indexed by pedicle seal depth was present during both extreme and nonextreme years, highlighting that this metric is sensitive to the health and physical condition of the individual (Chapman 1975, Bubenik 1990*b*). Our findings support the continued use of cast antlers, and specifically pedicle seal depth of 1.5-year-olds, because they reflect changes in environmental conditions. The gross scores of red deer cast antlers were also affected by environmental conditions (Peláez et al. 2018). Pedicle seal depth may vary by geographical region, so further research should investigate baseline pedicle seal depth values for other geographical areas of interest.

We found no difference in pedicle seal depth between matching cast-antler sides supporting the continued use of cast-antler data because each side equally represents the health of the deer that cast it. Similarly, gross cast-antler score was similar between antler sides for red deer (Peláez et al. 2018), and harvested deer antler morphometry findings in mule deer (Anderson and Medin 1969) and white-tailed deer (Schoenebeck et al. 2013). Cast antlers provide a nonlethal means to gain knowledge of individual deer within the population and can be useful for comparisons between regions and time periods (Ditchkoff et al. 2000, Fierro et al. 2002, Lopez and Beier 2012).

Antler growth represents an expression of an individual's condition and is costly to produce (Zahavi 1975, Ditchkoff et al. 2001). Therefore, healthier individuals can invest more resources toward antler expression, but cannot sustain those investments during times of poor nutritional conditions (Foley et al. 2012). This has been observed in poorly nourished sika deer (*Cervus nippon*), which had smaller antler lengths, mass, and number of points (Kaji et al. 1988). Similarly, we found the cohort born during the extreme environmental condition year had consistently smaller antler metrics when compared with the nonextreme condition cohorts. These findings suggest that fawns were negatively affected during early development and those effects persisted through time. Drought conditions initiated during summer of 2012, with the highest intensity occurring at the end of summer through late winter. This represents the period that male fawns prepare for winter and store nutrients to grow their first set of hard antlers the next spring. These findings may represent a cohort effect and lag time in antler growth, which continued to affect this cohort throughout life. Main beam lengths were consistently smaller within the extreme year cohort, with differences observed between conditions in the 1.5-year-old group. Main beam circumference remained consistently smaller for all age groups similar to poorly nourished sika deer born during an extreme year, with separation peaking with mature, 3.5-year-old males (Kaji et al. 1988). Total point counts showed the greatest separation initially, with 1.5-year-olds having fewer points if born during extreme environmental conditions, which is consistent with observations of sika deer that had fewer points in resource-limiting years (Kaji et al. 1988). Effects observed on 1.5-year-olds for 2 of the 3 tested metrics lend support that the 1.5-year-old age group is the most sensitive age group to environmental stressors (Anderson and Medin 1969).

No aging method is free from error, but tooth wear and replacement methods can introduce variability (Storm et al. 2014). However, this is currently the most time- and cost-efficient method and remains a standard practice for many wildlife agencies including Nebraska. During the course of our 8-year sampling effort, aged deer were classified by the same senior wildlife biologists to minimize aging inaccuracies and standardize age data. However, future studies differentiating age groups may wish to investigate more accurate aging criteria including cementum annuli methods (Storm et al. 2014).

We concluded that deer were healthier during nonextreme condition years based on pedicle seal depth for both age categories. The most indicative sign of stress on white-tailed deer was pedicle seal depth, which was significantly reduced during extreme environmental conditions. A combination of drought, disease, and reduced vegetation growing season resulted in an extreme environmental condition year, which likely contributed to smaller pedicle seal depths in cast antlers. We also observed that deer antlers from the cohort born during drought likely expressed stunted antler growth as a result of lower nutrition when young, with lagging effects persisting through time.

The occurrence of extreme drought and EHD outbreak of this magnitude has never overlapped in recorded Nebraska history, despite incurring similar drought conditions during the antler-growing seasons over the past century. Although this data set represents a case study encompassing only one year of extreme environmental conditions and 7 years of nonextreme conditions, our conclusions aid in understanding the role extreme environmental conditions have on white-tailed deer antler expression and health. We cannot attribute the negative effects on antler metrics to a single underlying environmental condition, but we postulate that a combination of multiple factors likely contributed to the measureable observations in diminutive antler growth. Extreme drought and epizootic outbreaks are difficult to predict; however, when they do occur, reduced pedicle seal depths and lasting effects on antler metrics may occur. Future investigations may be able to elucidate the role individual stressors play on white-tailed deer health during specific years and on specific cohorts.

MANAGEMENT IMPLICATIONS

It is difficult to quantify effects that factors such as birth date (late vs. early), nutrition, habitat condition, and extreme environmental conditions may have on antler size (Demarais and Strickland 2010, Michel et al. 2018); however, this knowledge can be important to various natural resource managers and users as they evaluate population performance and attempt to understand the effect these conditions may have within season as well as potential lag effects on cohorts (McCullough 1982). Results from cast-antler pedicle seal depth measurements provided the best indicator of stress in 1.5-year-olds, supporting cast-antler pedicle seal depth as the most sensitive metric available (Bubenik 1990*b*). With the increased interest in cast-antler collecting and the current push toward citizen science, this source of data may provide wildlife and natural resource managers with an opportunity, albeit delayed, to evaluate the severity of within-year stressors on a population. Pinpointing those stressors or combination of stressors (drought, winter severity, habitat, forage availability) that negatively affect population health may lead to regulations protecting specific cohorts, sexes, harvest quotas or aid in minimizing or reducing disturbance (i.e., time, length of harvest, and cast collecting seasons) during and immediately following extreme environmental condition years. Wildlife managers may be able to use information on antler metrics to make informed decisions if antler restrictions are in effect, but also help interpret important management perceptions such as hunter satisfaction following an extreme environmental condition year. It may also provide management indicators to better interpret changes in male harvest success (i.e., decrease in harvest of male deer) as an extreme environmental condition cohort works its way through the population. Harvested deer antler metrics were not as strong of an index of stress as pedicle seal depth from cast-antler metrics, so we recommend using pedicle seal depth as an index of stress, which also allows managers to be aware of potential decreases in future antler metrics following extreme environmental conditions.

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