Predation shapes the evolutionary traits of cervid weapons

Matthew C. Metz [1,2]*, Douglas J. Emlen[3], Daniel R. Stahler[2], Daniel R. MacNulty[4], Douglas W. Smith[2] and Mark Hebblewhite [1]

Sexually selected weapons evolved to maximize the individual reproductive success of males in many polygynous breeding species. Many weapons are also retained outside of reproductive periods for secondary reasons, but the importance of these secondary functions is poorly understood. Here we leveraged a unique opportunity from the predator–prey system in northern Yellowstone National Park, WY, USA to evaluate whether predation by a widespread, coursing predator (wolves) has influenced a specific weapon trait (antler retention time) in their primary cervid prey (elk). Male elk face a trade-off: individuals casting antlers early begin regrowth before other males, resulting in relatively larger antlers the following year, and thus greater reproductive success, as indicated by research with red deer. We show, however, that male elk that cast their antlers early are preferentially hunted and killed by wolves, despite early casters being in better nutritional condition than antlered individuals. Our results run counter to classic expectations of coursing predators preferring poorer-conditioned individuals, and in so doing, reveal an important secondary function for an exaggerated sexually selected weapon—predatory deterrence. We suggest this secondary function played a key evolutionary role in elk; uniquely among North American cervids, they retain their antlers long after they fulfil their primary role in reproduction.

Intense competition for mates drives the evolution of sexually selected traits that maximize individual reproductive success[1,2]. The associated arms race produced striking ornaments in some species, while in others it resulted in traits that provide tools (for example, increased appendage size) to physically outcompete conspecifics for access to mates[3,4]. Developing and wielding such elaborate traits often carries a considerable cost; more conspicuous individuals may be preferentially killed by predators[5–7] and individuals with large weapons may suffer from awkward and metabolically expensive locomotion[8]. Conversely, developing relatively more pronounced sexually selected traits can provide secondary benefits to individuals. Larger claw size in fiddler crabs (genus *Uca*) also reduces predation risk[9,10], for example. The associated costs and benefits of sexually selected traits highlight that selection also acts on these traits outside the context of reproduction. However, only a limited understanding exists of how benefits provided through secondary functions have affected the evolution of sexually selected traits.

Among the most impressive sexually selected traits are ungulate weapons (horns or antlers). These weapons differ in that horns are permanent structures, whereas antlers, unique to and nearly ubiquitous among cervids, are annually cast and regrown. In many species with horns, both sexes have this weapon. By contrast, antlers are confined to males in all cervids except caribou/reindeer (*Rangifer tarandus*). Regardless, for both horns and antlers, competition for mates is the primary driver of weapon evolution in males. This is evidenced by larger weapon size among ungulate species with bigger breeding group sizes[11,12], and higher within-population annual reproductive success for males with larger weapons[13,14].

The timing of antler casting and regrowth is tied to the reproductive cycle of species and is triggered by changes in hormone levels and, for individuals living in temperate climates, photoperiod[15–17]. By annually regrowing antlers, males develop honest signals of fighting ability that track age-specific changes in quality and status[18–20]. Every adult male within a population casts its antlers each year, but they do not all do so at the same time, even in temperate climates where casting is generally synchronous. Some of this variation occurs at the population level—all individuals may cast their antlers earlier when environmental conditions are less severe, for example[21]. However, marked variation also exists between individual males within a population. Across cervid species, older, dominant males are the first to cast their antlers over the period of antler casting[21–24], which often spans multiple months[25]. For instance, like our study population of North American elk (*Cervus canadensis*), red deer (*Cervus elaphus*) cast their antlers over a 2–3 month period[21] (Fig. 1a). Elk and red deer, species so similar that whether their taxonomy differs is still debated[26,27], begin growing their next set of antlers immediately following casting. Individuals that start growth earlier benefit by growing larger antlers, as evidenced by research on red deer[21].

Why all individuals within a population do not cast their antlers as early as possible is unclear because weapons such as antlers are heavy and expensive to carry[28] and casting them sooner would minimize these costs. That some males within populations retain their antlers for months longer than others hints at considerable benefits that accrue after the rut. One obvious possible benefit is protection from large carnivores[29]. Many adult males emerge from the rut exhausted, starved and injured[18,30–32], and therefore especially vulnerable to predation[33]. Horns are a known predatory deterrent[34,35], and if antlers function similarly, then males should benefit from retaining their antlers longer following their breeding season, especially for species most preferred by predators.

Predator preference for various prey species, and individuals within each prey species, is generally driven by factors (such as,

[1]Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W. A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, USA. [2]Yellowstone Wolf Project, Yellowstone Center for Resources, Yellowstone National Park, WY, USA. [3]Division of Biological Sciences, University of Montana, Missoula, MT, USA. [4]Department of Wildland Resources and Ecology Center, Utah State University, Logan, UT, USA. *e-mail: matthew.metz@umontana.edu

body size, age and nutritional condition) that affect a prey's vulnerability to predators[36-41]. Here, we tested whether antlers functioned as a predatory deterrent using data from the wolf (*Canis lupus*)–prey system of northern Yellowstone National Park, WY, USA, 2004–2016. We focused our analysis on wolf predation on adult male elk during March when individuals begin to cast their antlers (Fig. 1a). Eight ungulate species (all bearing horns or antlers) are available for wolves to kill, but elk are wolves' most used and preferred prey, especially during winter[42,43] (Supplementary Fig. 1). We expected wolf predation to have been a strong evolutionary source of selection on adult male elk because wolves preferentially kill adult males during winter months[44,45] (Supplementary Fig. 2a). Moreover, relative to other age–sex classes of elk, adult males often experience the highest per capita risk of dying due to wolf predation during winter months, especially in comparison to adult females (Supplementary Fig. 2b). If antlers deter wolves, then wolves should prefer pedicled (that is, individuals who have cast their antlers) to antlered individuals when they hunt adult males.

To test this prediction, we analysed data about wolves hunting adult male elk (2005–2015), the composition (that is, antlered or pedicled) of wolf-killed adult male elk (2004–2016) and the composition of the adult male elk population (2005–2008). Our results revealed that wolves strongly preferred to kill pedicled individuals despite these individuals often being in better nutritional condition, and thereby highlight that antlers are indeed an important predatory deterrent for elk. In fact, we now suspect that predation may help to explain variation in post-rut antler retention time across cervid species living in temperate climates.

Results and discussion

Hunting encounters of wolves on adult male elk. We first used data from 55 observations of wolves encountering adult male elk individuals and groups (≥2 male elk), characterizing each individual or group as 'antlered', 'pedicled' or 'mixed' (consisting of both antlered and pedicled individuals; Supplementary Table 1 for model selection; Supplementary Fig. 3 for beta coefficients; Supplementary Fig. 4 for predictions). Individuals or groups that included pedicled individuals were 3.6 times more likely to be attacked by wolves (odds ratio (OR): 3.6; 85% confidence interval (CI): 1.2–11.7). However, the presence of at least one pedicled individual appeared more influential on whether wolves attacked male elk when wolves encountered groups of ≥2 male elk (*n* = 37 groups; Fig. 1b). For these encounters, wolves were almost ten times more likely to attack the group if a pedicled individual was present (OR: 9.7; 85% CI: 2.2–60.3). Additionally, wolves tended to specifically target these pedicled individuals as encounters escalated in their predatory intensity (Fig. 1b).

Wolf preference for pedicled and antlered adult male elk. Our observations of wolf–male elk encounters suggested that wolves tended to preferentially attack male elk groups when they included pedicled individuals, although our ability to fully evaluate the effect of pedicled individuals being present was limited by our relatively small sample size (see Methods). But if wolves preferentially attacked pedicled males, then this choice should be reflected in the characteristics of male elk killed by wolves. Therefore, we leveraged a much larger sample of wolf-killed adult (≥2 years old) male elk and compared the frequency of pedicled males in this sample with that in the male elk population at large. We evaluated wolves' preference for pedicled or antlered elk when pedicled individuals were rare (early March: 1–15 March) and increasingly common (late March: 16–30 March) in the population (Supplementary Fig. 5). We measured use (that is, killed) and availability (that is, classified during surveys) of adult male elk with 216 detected wolf kills (*n*$_{early}$ = 103, *n*$_{late}$ = 113; Supplementary Fig. 6; Supplementary Table 2) and 460 classified individuals (*n*$_{early}$ = 194, *n*$_{late}$ = 266; Supplementary Figs. 5, 6).

We used these data to calculate preference ratios for pedicled and antlered elk. In both March periods, wolves preferred pedicled individuals (Fig. 2). That wolves strongly preferred to kill pedicled individuals indicates that antlers are indeed an important predatory deterrent for male elk.

Characteristics of wolf-killed adult male elk. Given that pedicled males are at higher risk of predation from wolves, why are some males then casting their antlers earlier than others? The timing of antler casting in red deer is known to be affected by an animal's age[21,46], and is thought to be influenced by their nutritional condition. We used generalized linear mixed-effect models (including a random effect for wolf pack) on our sample of wolf-killed male elk to evaluate the effect of these characteristics (age and femur marrow fat percentage (a measure of nutritional condition[47,48])) on whether a male had cast its antlers. We also included population-level factors known to affect the timing of casting (elk abundance, winter severity[21,46,49]) and the day in March when the animal died. We only included males that were at least 5 years old (*n* = 139) because there were no pedicled individuals younger than age 5 in our data (Supplementary Fig. 7).

Whether a wolf-killed male elk had cast its antlers or not was affected by the individual's nutritional condition, how long into the antler-casting season it was when the animal was killed by wolves and how many elk were in the population (Fig. 3a; Supplementary Table 3; Supplementary Fig. 8). Other than date—males continue to drop their antlers as the antler-casting season progresses (Fig. 2b; Supplementary Fig. 5), so wolf-killed males were more likely to be antlerless at the end of March than they were at the beginning of the month (Fig. 3a; Supplementary Fig. 8)—the animal's nutritional condition most influenced the likelihood that an individual had cast its antlers (Supplementary Fig. 8). Specifically, wolf-killed pedicled males tended to be in better nutritional condition than antlered males (Fig. 3; Supplementary Fig. 8).

Male elk (≥5 years old) were more likely to get an early start on growing their antlers when they were in better nutritional condition. The odds of an individual having cast its antlers were 2.1 (85% CI: 1.6–2.7) times greater for every 20% increase in femur marrow fat percentage, equivalent to an ~1% increase in total fat (for elk with femur marrow fat ≤ 90%[48]). Previous work on red deer showed that males casting their antlers earliest grew new antlers that were relatively heavier, leading to increased reproductive success during the subsequent breeding season[21]. Our research suggests that early casters can grow these heavier antlers because these individuals begin antler growth sooner due to their relatively better nutritional condition during the early portion of the antler-casting season. Presumably, for these individuals the benefits of an early onset to antler growth outweigh the increased risk of predation.

Young male elk (that is, ages 2–4) did not cast their antlers early (that is, during March) in our study (Supplementary Fig. 7), despite usually being in similar, or better, nutritional condition than old individuals that had cast their antlers (Fig. 3b). If these young individuals rarely successfully reproduce during the upcoming breeding season anyway, then delaying casting as long as possible makes sense (for example, the mating strategy–effort hypothesis[50]). Studies of mating success in the Isle of Rum red deer population indicate that young males are unlikely to successfully defend a harem[18], and these young males delay antler casting until later than older males[21]. Interestingly, this introduced red deer population has not lived with wolves for centuries[51,52] (although red deer are often preferred by wolves in parts of their range where they overlap[53,54]), suggesting that there may be additional benefits to retaining one's antlers. For example, delaying the onset of new antler growth to better match the period when forage conditions are improving may be one such benefit. But other cervid species cast their antlers at times when forage is clearly not improving (that is, in winter); young males in
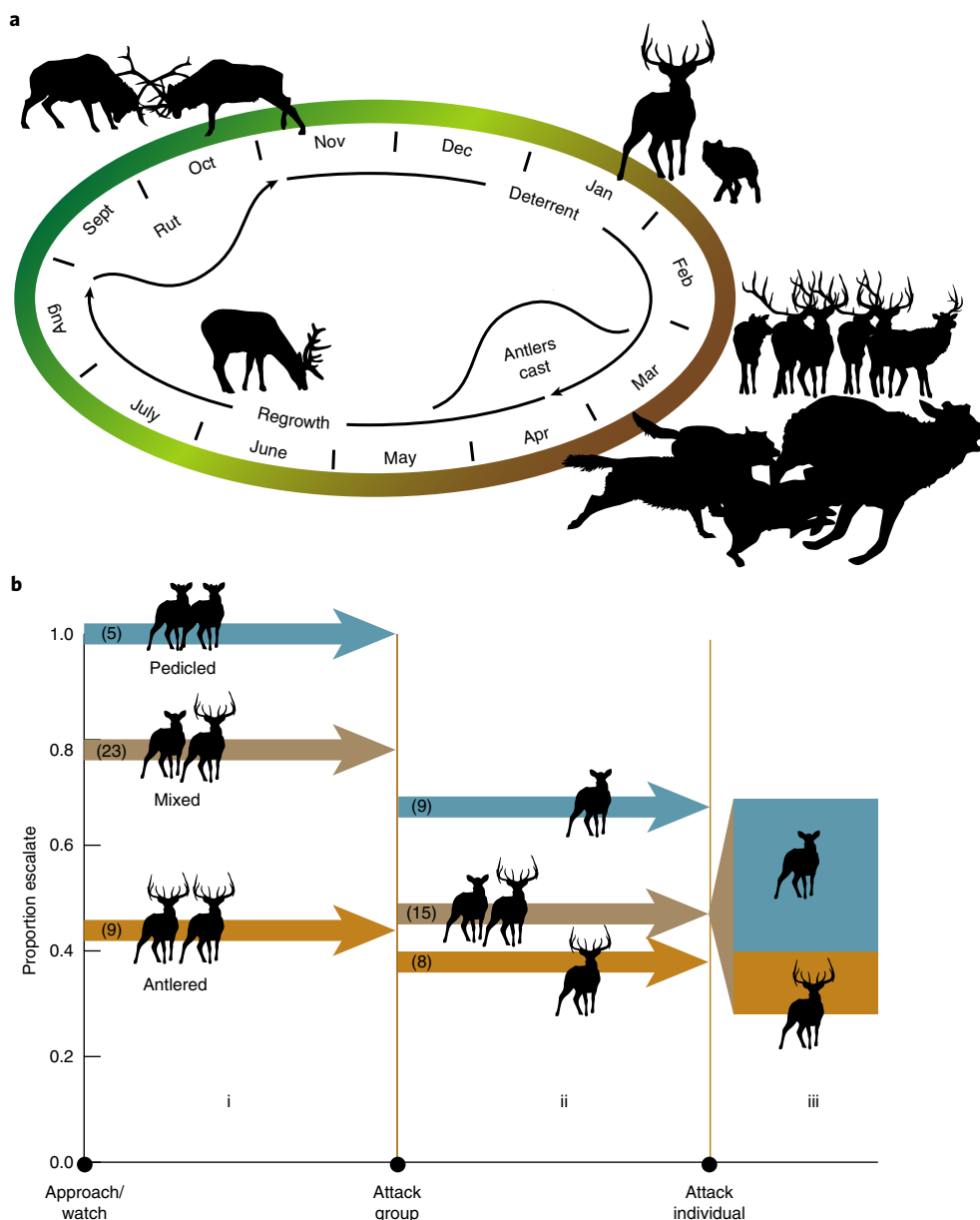
Fig. 1 | The function of antlers and wolf–adult male elk encounters. a, Adult male elk cast their antlers each spring (over a 2–3 month period at the population level) to grow new antlers to use in competition for mates during the rut. Early casters trade the benefit of increased reproductive success[21] for the cost of losing a predatory deterrent. The shading of the circle depicts elk nutritional condition (dark green, best; dark brown, poorest), which begins to decline during autumn and improve during spring. **b**, Raw data from observations of wolf–adult male elk encounters (only for groups of ≥2 individuals) highlight the potential cost of being an early caster. The arrows represent the proportion of observations for pedicled, mixed and antlered male elk that escalated from wolves (i) encountering the group to attacking (for example, pursuing) it and (ii) attacking an individual, with the type of individual attacked for 'mixed' also displayed (iii). Note that the antler condition above (ii) represents the antler condition for the group (or individual) being attacked (for example, pursued) during (ii), and is not necessarily the same as (i). Also note that multiple attacks can occur during an encounter[63]. The numbers in parentheses indicate the total number of observations. Credit: illustration by E. Harrington, Missoula, MT, USA.

these other species such as moose (*Alces alces*) and caribou also cast their antlers relatively later than older individuals[15]. Our study highlights a secondary function of antlers that could help to explain why these young individuals evolved to retain their antlers for an extended period of time.

Comparing antler retention across ungulate species. At the end of winter in Yellowstone National Park, wolves frequently encounter male elk within the population that are antlered and antlerless (pedicled). Wolves prefer to kill pedicled individuals (Fig. 2c), despite these individuals being in better nutritional condition than

antlered males (Fig. 3). That these preferred individuals tend to be in better nutritional condition highlights that a prey's vulnerability to predators is affected by multiple factors, and often cannot be simply defined by a single characteristic such as nutritional condition. Nonetheless, this behaviour runs counter to theory and numerous studies worldwide that demonstrate that coursing predators prefer to kill poorer-conditioned individuals, especially during periods of the year when prey are nutritionally constrained[37–39,55,56]. This striking finding is consistent with antlers being a formidable anti-predator weapon and may help to explain why elk retain their antlers for ≥5 months post-rut. Predation risk is greatest post-rut
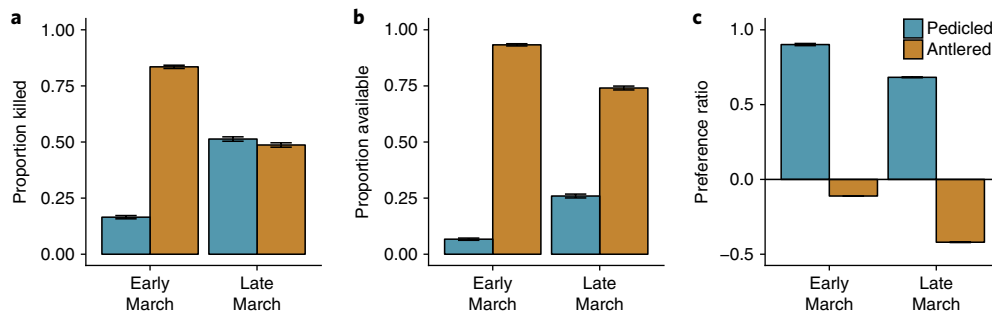
Fig. 2 | Adult male elk antler condition and preference by wolves. a, Use of adult male elk for each antler condition. **b**, Availability of male elk for each antler condition. **c**, Wolf preference for adult male elk, dependent on antler condition. Error bars represent 95% CIs.

through early spring for male elk, when individuals are in declining or poor nutritional condition (Fig. 1a); this period coincides with their unusually long antler retention time.

In fact, considering the post-rut function of antlers as a predatory deterrent may help to explain broader patterns in the timing of antler casting across ungulate species in temperate climates (Fig. 4). It is well-appreciated that predation risk for large ungulates varies across species and is also seasonally dynamic[33,40,42,57]. Elk and moose, both residents in our study system, provide a striking illustration. Elk, often strongly preferred by wolves in multi-prey systems[44,45,58], retain their antlers for ~3 months longer than moose whose large body size acts itself as a predatory deterrent[40,59]. This extreme difference in taking on the costs of carrying antlers occurs despite elk and moose both breeding at the same time (Fig. 4).

Similar to moose, male caribou also cast their antlers well before elk (Fig. 4). Many adult male caribou, in fact, begin casting their antlers shortly after the end of their rut[60]. The primary ways in which caribou avoid being killed by wolves include using their speed and spatially separating themselves from wolves during winter[59,61]. Lastly, both white-tailed and mule deer (*Odocoileus virginianus* and *Odocoileus hemionus*, respectively) retain their antlers throughout much of winter, which may be at least partially related to their later breeding seasons (Fig. 4). But these deer species still each cast their antlers 1–2 months before elk, resulting in a much shorter period of post-rut retention than elk. For deer, using their speed to flee is the primary way that they avoid wolf predation[59]. Conversely, male elk often stand their ground when encountered by wolves and are therefore more likely to benefit from a weapon[59].

That wolf predation was an important source of natural selection for a secondary weapon function (that is, predatory deterrence) is possible because wolves were once the most widespread of any land mammal, ubiquitously spread across much of the northern hemisphere[52]. Our across-species comparison suggests that the evolution of antler retention times may have been affected by how vulnerable various species were to wolf predation, an idea similar in many respects to previous work proposing that large carnivore predation was a driving force on the evolution of horns in female African antelopes[34]. There, females of most medium-to-large species have straight, sharp horns that provide an effective weapon for predator defence. For males with antlers, sexual selection determined the general characteristics of their antlers (for example, shape, number of tines)[62], as is also the case for bovids[34,62]. But the prolonged retention of antlers after the breeding season in elk, and possibly other medium-to-large species such as red deer that are also often preferred by predators[53,54], appears to have instead been influenced by selection for a predatory deterrent. Through keeping their antlers longer, males of these species may have reduced their risk of predation during the season of the year (for example, winter) when their vulnerability to wolf predation was highest.
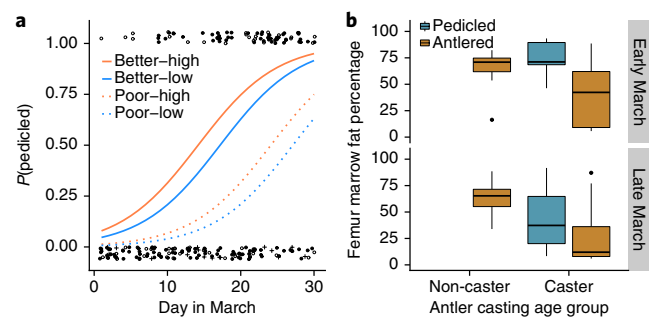

Fig. 3 | Characteristics of wolf-killed male elk and antler condition. a, Predicted probabilities, from our top model (Supplementary Table 3; Supplementary Fig. 8), of a wolf-killed adult male elk (≥5 years old) being a pedicled individual during March. Predicted probabilities are displayed for the first and third quartile of femur marrow fat percentage ('Poor', 12%; 'Better', 63%) and elk abundance ('Low', 7,601; 'High', 10,192). Only the filled circles were used in the analysis (*n* = 139). The plus signs indicate that the male was 2–4 years old (*n* = 18) and the open circles indicate that we did not have data describing both the male's age and nutritional condition (*n* = 59). **b**, Femur marrow fat percentage for wolf-killed male elk in relation to the March period and 'antler-casting age group'. For the antler-casting age group, 'Non-caster' indicates that the individual was 2–4 years old (plus signs in **a** and 'Caster' indicates the individual was ≥5 years old (filled circles in **a**). The box plot displays the median, as well as the first and third quartiles. The whiskers extend from the interquartile range to the largest value that is no further than 1.5× interquartile range, in each direction. The filled circles represent the outliers.

Conclusions

Our study highlights an evolutionary tension between the benefits and costs of an extreme, sexually selected weapon. Casting antlers early rids male elk of heavy, awkward structures and permits them to begin regrowth ahead of rival males, increasing the relative size of the next year's antlers. But early casting comes at a cost because the first males to drop their antlers are preferentially killed by wolves and thus experience greater risk of predation. For younger males not likely to breed in the upcoming rut anyway, this risk is too high; these males are among the last to cast their antlers. Old males in better nutritional condition, on the other hand, stand to benefit the most from increased antler size; it is these males who take the risk and cast their antlers first. Through identifying this trade-off, our study reveals the largely unexplored importance of secondary functions of sexually selected structures. We also suggest that the trade-off associated with delayed casting of antlers differs across cervid species, helping to explain species differences in weapon retention time.

Cervids are unusual in regularly shedding and regrowing their weapons; this means that the specific trait that we describe, antler
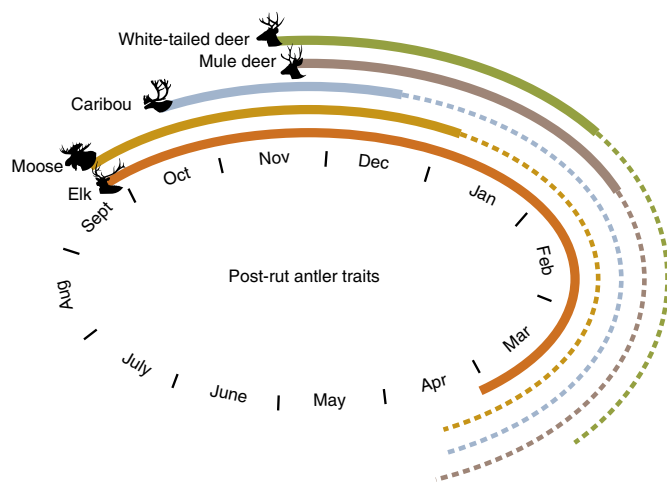
Fig. 4 | Antler traits of adult male North American ungulate species. For each species, the species symbol represents the peak of the rut, the solid portion of the line represents the period of antler retention following the peak of the rut and the dashed portion represents the pedicled period when each species is without antlers until new growth commences. Independent of other traits (for example, body size, speed), elk retain their antlers for longer post-rut than any other species because of their effectiveness as a predatory deterrent. Credit: illustration by E. Harrington, Missoula, MT, USA.

retention time, will be specific to these animals. Nevertheless, our study provides a new example of the many ways that secondary functions of sexually selected weapons can influence the evolution of these structures.

Methods

Data collection and preparation. *Wolf hunting behaviour on adult male elk.* We recorded 713 hunting encounters between wolves and their ungulate prey during March (2004–2016) through ground-based observations associated with our long-term monitoring of wolf predation dynamics[42,44,63] (further details follow). Of these, 446 encounters were of wolves hunting elk (Supplementary Fig. 9). For each encounter, we characterized the elk encountered by wolves as 'Mixed age class' (consisting of adult females, yearlings, calves and adult males; $n = 174$), 'Adult male' (only adult males; $n = 255$) or 'Unknown' ($n = 17$). From the 255 encounters with only adult males, we used a subset of 55 interactions, which mostly occurred from 2005 to 2008 (Supplementary Fig. 9) and came from one wolf pack (that is, 41 of the 55 observations were of the Leopold pack), where we recorded the antler condition of the adult male elk encountered by wolves. We observed the beginning of the encounter in 43 of 55 cases but included all 55 encounters, of which 37 involved wolves encountering a group of ≥ 2 elk and 18 an individual, adult male elk. We recorded whether an encounter included an attack (that is, wolves pursued or harassed prey)[63], as well as the maximum number of wolves and elk participating during the prey encounter[63].

Composition of wolf-killed adult male elk. We used data collected in northern Yellowstone as part of our long-term monitoring effort of wolf predation dynamics[42,44], but began our analysis with data from 2004 because antler condition of wolf-killed adult (≥ 2 years old) male elk was not routinely recorded before 2004 (Supplementary Table 2). The general methods of our monitoring included daily aerial radio-tracking of all wolf packs in northern Yellowstone, weather permitting, for 30 days during the 1–30 March period each year. Additionally, we also used ground radio-tracking to monitor, and then observe for as much of daylight hours as possible, three wolf packs. For both aerial and ground-based radio-tracking, the primary goal of our monitoring was to detect any kills the wolves had made. During the 1–30 March periods from 2004 to 2016 included here, we conducted, on average, aerial telemetry flights on 14.2 ± 1.6 s.e.m. days and visually observed wolf packs on 23.5 ± 0.6 s.e.m. days. In addition to aerial and/or ground-based monitoring, we also detected wolf-killed ungulates through searching clusters of wolf global positioning system locations[64] for 1–3 wolf packs during each March monitoring period since 2010. Wolves were captured and handled following guidelines of the American Society of Mammalogists[65] and approved under the University of Montana Institutional Animal Care and Use Committee protocol 043-15MHWB-121515.

We detected 223 adult male elk (of 596 total elk) killed by wolves during March in northern Yellowstone from 2004 to 2016 but restricted our data set to 216 wolf-

killed adult male elk for which we recorded antler condition (Supplementary Fig. 6). Rarely ($n = 3$), a wolf-killed adult male elk had one antler; in these cases, we classified the individual as pedicled (Supplementary Table 2).

For these 216 individuals, we determined age (through cementum annuli analysis; Matson's Laboratory, Milltown, MT, USA) for 180 individuals and femur marrow fat percentage[47] (an indicator of nutritional condition; see further on) for 166 individuals. For our analysis where we evaluated the influence of individual characteristics on the probability of a wolf-killed adult male elk having cast its antlers (see further on), we restricted our data set to individuals where we recorded both age and femur marrow fat percentage. Initially, our data set included 157 individuals. However, we limited our analysis to include only individuals ≥ 5 years old ($n = 139$) because we did not detect any wolf-killed individuals who were < 5 years old that had cast their antlers (Supplementary Fig. 7). We likely did not detect any pedicled individuals that were between 2 and 4 years old because we sampled for wolf-killed elk only in March during the antler-casting season[44], and the youngest adult males in the population typically cast their antlers after March[21].

Note that femur marrow fat percentage is an indicator of ungulate nutritional condition, but it is most useful for individuals that are in poorer nutritional condition. Specific to elk, femur marrow fat percentage is a reliable indicator of nutritional condition when femur marrow fat is $\leq 90\%$, which corresponds to body fat being $\leq 6\%$[48]. The ability of bone marrow fat to provide a reliable indication of nutritional condition was not limiting for our study because most individual ungulates are in fairly poor nutritional condition during late winter[66,67]. Specific to our data, 163 of the 166 femur marrow fat samples that we collected from wolf-killed male elk had femur marrow fat percentage values $\leq 90\%$.

Composition of the adult male elk population. We classified the availability of adult male elk with and without antlers (that is, 'antlered' and 'pedicled') during March 2005–2008. During each year, we conducted approximately weekly ground-based observational classification surveys on a 6.7 km² area in northern Yellowstone National Park (latitude, 44.9383; longitude -110.5576; Supplementary Fig. 6). Although we conducted surveys only in this one area of northern Yellowstone, proportional availability of pedicled and antlered adult male elk is relatively homogenous during March across the portion of northern Yellowstone National Park where we monitored wolf predation (Northern Yellowstone Cooperative Wildlife Working Group, unpublished data; see Supplementary Fig. 6). In total, we classified 460 individuals during 19 surveys ($n_{2005} = 4$, $n_{2006} = 6$, $n_{2007} = 6$, $n_{2008} = 3$). On average, 24.2 ± 4.5 (mean $\pm$ s.e.m.; median $= 22$; range: 1–69) adult male elk were classified during each survey (Supplementary Fig. 5).

Data analysis. *Wolf hunting behaviour on adult male elk.* We used generalized linear models (binomial) to evaluate the influence of the number of wolves (defined as the maximum number participating in any foraging state within the prey encounter[63]; log-transformed to account for the previously demonstrated non-linear influence of the number of wolves involved in prey encounters[68], the number of adult male elk and adult male elk group type (pedicled, mixed, antlered) on the probability of an encounter escalating to an attack. We did so in two ways. First, we included all encounters and next, only the encounters with adult male elk groups that included ≥ 2 elk. We evaluated encounters with groups separately because our data suggested that when wolves encountered a single adult male elk, the hunt was likely to include an attack, regardless of whether the antler condition of the individual was pedicled or antlered. We combined pedicled and mixed groups, since both of these groups included individuals without antlers. We did not evaluate models including interactions or use mixed-effect models to include a random effect for pack because of our relatively small sample size. We screened for collinearity and association among covariates; no covariates were highly correlated ($r \leq 0.26$) or showed evidence of being associated. All continuous covariates, here and in the following analysis, were standardized to facilitate comparison and estimation through subtracting the mean and dividing by the standard deviation. We also present beta coefficients from models where we did not standardize covariates and use the non-standardized beta coefficients from the top model to calculate the OR for the presence of pedicled individual(s) for all encounters and only encounters with ≥ 2 elk. For all analyses, we used small-sample-size corrected version of Akaike information criterion (AIC_c) to evaluate relative support among models. We conducted all analyses in R version 3.3.1 (R Core Team 2016). We used the package 'AICcmodavg'[69] for AIC model evaluation and selection and the package 'oddsratio'[70] to estimate ORs and their 85% CIs[71].

We did not evaluate what factors affected the probability of an encounter escalating to the attack of a specific individual because our relatively small sample size ($n = 27$ encounters that included an attack) was particularly limiting during this portion of wolf–elk encounters. This was because wolves sometimes attacked multiple individuals within the same wolf–prey encounter. Accordingly, the raw data that we present (Fig. 1b) include 32 predation attempts but only 27 encounters.

Wolf preference for pedicled and antlered adult male elk. We calculated a preference ratio[72] for pedicled and antlered adult male elk as:

$$\text{LN}\left(\frac{\text{proportion}_{\text{kills}}}{\text{proportion}_{\text{available}}}\right) \quad (1)$$

For the preference ratios calculated through equation (1), we used bootstrapping to estimate standard errors for the proportion of elk killed, available and preferred. To do so, we sampled with replacement the kill and classification count data for early and late March 10,000 times. For each iteration, we calculated the proportion of pedicled and antlered adult male elk killed and available, as well as the preference ratio.

Characteristics of wolf-killed adult male elk. We used generalized linear mixed-effect models (binomial; pedicled individuals = 1, antlered = 0; random effect for pack, see further on), to evaluate the effect of age, femur marrow fat percentage, day in March, winter severity and elk abundance on predicting whether a wolf-killed adult male elk (≥5 years old; n = 139) had antlers, since each of these covariates may affect the precise timing of when an individual casts its antlers[21,46,49]. To characterize winter severity, we used spatially explicit weekly predictions of snow water equivalent (SWE)[73]. More specifically, we used the mean SWE value for a 3 km buffered area around each kill (Supplementary Fig. 6) for the week within which the observation occurred. Elk abundance was estimated via an annual winter count conducted by the Northern Yellowstone Cooperative Wildlife Working Group; years without a count were interpolated using a state–space model and each count was adjusted for imperfect detection[43].

In our full model set, we included all combinations of additive models and models that also considered two-way interactions for (1) femur marrow fat percentage and age, winter severity or elk abundance and (2) age and winter severity or elk abundance. We considered these two-way interactions because we hypothesized (a priori) that each could be important. We also included a random effect for pack (or lone wolf if the wolf was not a member of a pack; see further on). We identified the pack or lone wolf (n = 23) that made the kill for 137 of the 139 kills included in our analysis. Many packs existed during multiple monitoring periods and, on average, we detected adult male elk (≥5 years old) killed by a particular pack (or lone wolf) during 2.5 ± 0.3 s.e.m. study periods (range: 1–5). Because we did not detect many kills for some packs or lone wolves (median = 3 kills, range: 1–26), we grouped together all packs as 'Other' for any packs for which we detected fewer than the median number of kills. Within 'Other', we also included the two kills detected where we did not know which pack made the kill. We did not, however, ultimately include pack in our final set of candidate models because the random effect for pack was non-existent or trivial in our top models. No covariates were highly correlated (r ≤ 0.22). As stated earlier, we present both non-standardized and standardized beta coefficient estimates and use the non-standardized beta coefficients to estimate ORs.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Data used for analyses is available at https://datadryad.org/resource/doi:10.5061/dryad.j72tt79.

References

1. Emlen, S. T. & Oring, L. W. Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223 (1977).
2. Clutton-Brock, T. H. *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (Univ. Chicago Press, Chicago, IL, 1988).
3. Darwin, C. *The Descent of Man, and Selection in Relation to Sex* (John Murray, London, 1871).
4. Andersson, M. *Sexual Selection* (Princeton Univ. Press, Princeton, NJ, 1994).
5. Godin, J.-G. J. & McDonough, H. E. Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait. *Behav. Ecol.* **14**, 194–200 (2003).
6. Johnson, S. & Candolin, U. Predation cost of a sexual signal in the threespine stickleback. *Behav. Ecol.* **28**, 1160–1165 (2017).
7. Stuart-Fox, D. M., Moussalli, A., Marshall, N. J. & Owens, I. P. F. Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. *Anim. Behav.* **66**, 541–550 (2003).
8. Goyens, J., Dirckx, J. & Aerts, P. Costly sexual dimorphism in *Cyclommatus metallifer* stag beetles. *Funct. Ecol.* **29**, 35–43 (2015).
9. Bildstein, K. L., McDowell, S. G. & Brisbin, I. L. Consequences of sexual dimorphism in sand fiddler crabs, *Uca pugilator*: differential vulnerability to avian predation. *Anim. Behav.* **37**, 133–139 (1989).
10. McLain, D. K., Pratt, A. E. & Berry, A. S. Predation by red-jointed fiddler crabs on congeners: interaction between body size and positive allometry of the sexually selected claw. *Behav. Ecol.* **14**, 741–747 (2003).
11. Bro-Jørgensen, J. The intensity of sexual selection predicts weapon size in male bovids. *Evolution* **61**, 1316–1326 (2007).
12. Clutton-Brock, T. H., Albon, S. D. & Harvey, P. H. Antlers, body size and breeding group size in the Cervidae. *Nature* **285**, 565–567 (1980).
13. Coltman, D. W., Festa-Bianchet, M., Jorgenson, J. T. & Strobeck, C. Age-dependent sexual selection in bighorn rams. *Proc. R. Soc. Lond. B* **269**, 165–172 (2002).
14. Kruuk, E. B. et al. Antler size in red deer: heritability and selection but no evolution. *Evolution* **56**, 1683–1695 (2002).
15. Goss, R. J. *Deer Antlers: Regeneration, Function and Evolution* (Academic, New York, NY, 1983).
16. Lincoln, G. A. Biology of antlers. *J. Zool.* **226**, 517–528 (1992).
17. Price, J. & Allen, S. Exploring the mechanisms regulating regeneration of deer antlers. *Phil. Trans. R. Soc. Lond. B* **359**, 809–822 (2004).
18. Clutton-Brock, T. H., Albon, S. D., Gibson, R. M. & Guinness, F. E. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus L.*). *Anim. Behav.* **27**, 211–225 (1979).
19. Malo, A. F., Roldan, E. R. S., Garde, J., Soler, A. J. & Gomendio, M. Antlers honestly advertise sperm production and quality. *Proc. R. Soc. Lond. B* **272**, 149–157 (2005).
20. Vanpé, C. et al. Antler size provides an honest signal of male phenotypic quality in roe deer. *Am. Nat.* **169**, 481–493 (2007).
21. Clements, M. N., Clutton-Brock, T. H., Albon, S. D., Pemberton, J. M. & Kruuk, L. E. B. Getting the timing right: antler growth phenology and sexual selection in a wild red deer population. *Oecologia* **164**, 357–368 (2010).
22. Bartoš, L. The date of antler casting, age and social hierarchy relationships in the red deer stag. *Behav. Processes* **5**, 293–301 (1980).
23. Bowyer, R. T. Antler characteristics as related to social status of male southern mule deer. *Southwest. Nat.* **31**, 289–298 (1986).
24. Van Ballenberghe, V. in *Antler Development in Cervidae* (ed. Brown, R.D.) 37–48 (Caesar Kleberg Wildlife Research Institute, Kingsville, TX, 1983).
25. Chapman, D. I. Antlers–bones of contention. *Mamm. Rev.* **5**, 121–172 (1975).
26. Polziehn, R. O. & Strobeck, C. A phylogenetic comparison of red deer and wapiti using mitochondrial DNA. *Mol. Phylogenet. Evol.* **22**, 342–356 (2002).
27. Meiri, M. et al. Subspecies dynamics in space and time: a study of the red deer complex using ancient and modern DNA and morphology. *J. Biogeogr.* **45**, 367–380 (2018).
28. Allen, B. J. & Levinton, J. S. Costs of bearing a sexually selected ornamental weapon in a fiddler crab. *Funct. Ecol.* **21**, 154–161 (2007).
29. Clutton-Brock, T. H. The functions of antlers. *Behaviour* **79**, 108–125 (1982).
30. Bobek, B., Perzanowski, K. & Weiner, J. Energy expenditure for reproduction in male red deer. *J. Mammal.* **71**, 230–232 (1990).
31. Rughetti, M. & Festa-Bianchet, M. Seasonal changes in sexual size dimorphism in northern chamois. *J. Zool.* **284**, 257–264 (2011).
32. Geist, V. New evidence of high frequency of antler wounding in cervids. *Can. J. Zool.* **64**, 380–384 (1986).
33. Owen-Smith, N. Changing vulnerability to predation related to season and sex in an African ungulate assemblage. *Oikos* **117**, 602–610 (2008).
34. Packer, C. Sexual dimorphism: the horns of African antelopes. *Science* **221**, 1191–1193 (1983).
35. Clements, H. S., Tambling, C. J. & Kerley, G. I. H. Prey morphology and predator sociality drive predator prey preferences. *J. Mammal.* **97**, 919–927 (2016).
36. Peterson, R. O. *Wolf Ecology and Prey Relationships on Isle Royale* (US Government Publishing Office, Washington, DC, 1977).
37. Fitzgibbon, C. D. & Fanshawe, J. H. The condition and age of Thomson's gazelles killed by cheetahs and wild dogs. *J. Zool.* **218**, 99–107 (1989).
38. Sinclair, A. R. E. & Arcese, P. Population consequences of predation-sensitive foraging: the Serengeti wildebeest. *Ecology* **76**, 882–891 (1995).
39. Husseman, J. S. et al. Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos* **101**, 591–601 (2003).
40. Sinclair, A. R.., Mduma, S. & Brashares, J. S. Patterns of predation in a diverse predator–prey system. *Nature* **425**, 288–290 (2003).
41. Wright, G. J., Peterson, R. O., Smith, D. W. & Lemke, T. O. Selection of northern Yellowstone elk by gray wolves and hunters. *J. Wildl. Manage.* **70**, 1070–1078 (2006).
42. Metz, M. C., Smith, D. W., Vucetich, J. A., Stahler, D. R. & Peterson, R. O. Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *J. Anim. Ecol.* **81**, 553–563 (2012).
43. Tallian, A. et al. Predator foraging response to a resurgent dangerous prey. *Funct. Ecol.* **31**, 1418–1429 (2017).
44. Smith, D. W., Drummer, T. D., Murphy, K. M., Guernsey, D. S. & Evans, S. B. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *J. Wildl. Manage.* **68**, 153–166 (2004).
45. Huggard, D. J. Prey selectivity of wolves in Banff National Park. II. Age, sex, and condition of elk. *Can. J. Zool.* **71**, 140–147 (1993).
46. Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. *Red Deer: Behavior and Ecology of Two Sexes* (Univ. Chicago Press, Chicago, IL, 1982).
47. Neiland, K. A. Weight of dried marrow as indicator of fat in caribou femurs. *J. Wildl. Manage.* **34**, 904–907 (1970).
48. Cook, R. C. et al. Development of predictive models of nutritional condition for Rocky Mountain elk. *J. Wildl. Manage.* **65**, 973–987 (2001).

49. Watson, A. Climate and the antler-shedding and performance of red deer in north-east Scotland. *J. Appl. Ecol.* **8**, 53–67 (1971).

50. Yoccoz, N. G., Mysterud, A., Langvatn, R. & Stenseth, N. C. Age- and density-dependent reproductive effort in male red deer. *Proc. R. Soc. Lond. B* **269**, 1523–1528 (2002).

51. Nussey, D. H., Pemberton, J., Donald, A. & Kruuk, L. E. B. Genetic consequences of human management in an introduced island population of red deer (*Cervus elaphus*). *Heredity* **97**, 56–65 (2006).

52. Boitani, L. in *Wolves: Behavior, Ecology, and Conservation* (eds Mech, L. D. & Boitaini, L.) 317–340 (Univ. Chicago Press, Chicago, IL, 2003).

53. Jędrzejewski, W. et al. Prey selection and predation by wolves in Białowieża Primeval Forest, Poland. *J. Mammal.* **81**, 197–212 (2000).

54. Gazzola, A. et al. Predation by wolves (*Canis lupus*) on wild and domestic ungulates of the western Alps, Italy. *J. Zool.* **266**, 205–213 (2005).

55. Pole, A., Gordon, I. J. & Gorman, M. L. African wild dogs test the 'survival of the fittest' paradigm. *Proc. R. Soc. Lond. B* **270**, S57 (2003).

56. Atwood, T. C., Gese, E. M. & Kunkel, K. E. Comparative patterns of predation by cougars and recolonizing wolves in Montana's Madison Range. *J. Wildl. Manage.* **71**, 1098–1106 (2007).

57. Jędrzejewski, W. et al. Kill rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland). *Ecology* **83**, 1341–1356 (2002).

58. Carbyn, L. N. Wolf predation on elk in Riding Mountain National Park, Manitoba. *J. Wildl. Manage.* **47**, 963–976 (1983).

59. Mech, L. D., Smith, D. W., MacNulty, D. R. & Landis, R. K. *Wolves on the Hunt: the Behavior of Wolves Hunting Wild Prey* (Univ. Chicago Press, Chicago, IL, 2015).

60. Bergerud, A. The annual antler cycle in Newfoundland caribou. *Can. Field Nat.* **90**, 449–463 (1976).

61. Seip, D. R. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Can. J. Zool.* **70**, 1494–1503 (1992).

62. Caro, T. M., Graham, C. M., Stoner, C. J. & Flores, M. M. Correlates of horn and antler shape in bovids and cervids. *Behav. Ecol. Sociobiol.* **55**, 32–41 (2003).

63. MacNulty, D. R., Mech, L. D. & Smith, D. W. A proposed ethogram of large-carnivore predatory behavior, exemplified by the wolf. *J. Mammal.* **88**, 595–605 (2007).

64. Metz, M. C., Vucetich, J. A., Smith, D. W., Stahler, D. R. & Peterson, R. O. Effect of sociality and season on gray wolf (*Canis lupus*) foraging behavior: implications for estimating summer kill rate. *PLoS ONE* **6**, e17332 (2011).

65. Sikes, R. S., Gannon, W. L & Animal Care and Use Committee of the American Society of Mammalogists. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J. Mammal.* **92**, 235–253 (2011).

66. Mautz, W. W. Sledding on a bushy hillside: the fat cycle in deer. *Wildl. Soc. Bull.* **6**, 88–90 (1978).

67. Parker, K. L., Barboza, P. S. & Gillingham, M. P. Nutrition integrates environmental responses of ungulates. *Funct. Ecol.* **23**, 57–69 (2009).

68. MacNulty, D. R., Smith, D. W., Mech, L. D., Vucetich, J. A. & Packer, C. Nonlinear effects of group size on the success of wolves hunting elk. *Behav. Ecol.* **23**, 75–82 (2012).

69. Mazerolle, M. J. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package v.2.1.1 (2017); https://cran.r-project.org/web/packages/AICcmodavg/index.html.

70. Schratz, P. oddsratio: Odds Ratio Calculation for GAM(M)s & GLM(M)s. R package v.1.0.2 (2017); https://cran.r-project.org/web/packages/oddsratio/index.html.

71. Arnold, T. W. Uninformative parameters and model selection using Akaike's Information Criterion. *J. Wildl. Manage.* **74**, 1175–1178 (2010).

72. Manly, B. F., McDonald, L., Thomas, D., McDonald, T. L. & Erickson, W. P. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies* 2nd edn (Springer Science & Business Media, Berlin, 2002).

73. Wockner, G., Singer, F., Coughenour, M., & Farnes, P. Yellowstone Snow Model. Colorado State Univ., Fort Collins, CO (2006).

Author contributions

M.C.M. conceived of the study. M.C.M., D.R.S., D.R.M. and D.W.S. collected the data and coordinated the study. M.C.M. and M.H. developed the methods and M.C.M. analysed the data. M.C.M., D.J.E. and M.H. wrote the paper with input from the other authors.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-018-0657-5.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to M.C.M.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

nature research

Corresponding author(s):   Matthew Metz

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see Authors & Referees and the Editorial Policy Checklist.

Statistical parameters

When statistical analyses are reported, confirm that the following items are present in the relevant location (e.g. figure legend, table legend, main text, or Methods section).

n/a	Confirmed	
☐	☒	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	An indication of whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistics including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☒	☐	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated
☐	☒	Clearly defined error bars *State explicitly what error bars represent (e.g. SD, SE, CI)*

Our web collection on statistics for biologists may be useful.

Software and code

Policy information about availability of computer code

Data collection	No software was used.
Data analysis	All software used for analyses is cited.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

Data used for analyses is available at https://datadryad.org/resource/doi:10.5061/dryad.j72tt79.

Field-specific reporting

Please select the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences   ☐ Behavioural & social sciences   ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/authors/policies/ReportingSummary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Our study evaluated wolf preference for antlerless male elk in northern Yellowstone National Park during the initial period (i.e., March) of antler casting.
Research sample	Our research sample consisted of a) 55 observations of wolf-adult male elk encounters (over an 11-year period) and b) detection of 216 wolf-killed adult male elk (over a 13-year period) during March in northern Yellowstone National Park.
Sampling strategy	Sample sizes were determined by a) the number of observations of hunting encounters of wolves on adult male elk individuals/groups for which we also recorded the antler condition of the male elk over an 11-year period and b) the number of wolf-killed adult male elk that we detected over a 13-year period.
Data collection	Described in the Methods.
Timing and spatial scale	Described in the Methods.
Data exclusions	No data were excluded from the analyses.
Reproducibility	Our findings in this paper are from observations of wild wolves and elk over a 13-year period in Yellowstone National Park and are not able to be replicated.
Randomization	Randomization was not relevant to our study because we attempted to detect each wolf-adult male elk hunting encounter and wolf-killed adult male elk in our study area. Individual male elk were assigned to classes dependent on their characteristics.
Blinding	Blinding was not relevant to our study of wild wolves and elk.

Did the study involve field work?   ☒ Yes   ☐ No

Field work, collection and transport

Field conditions	Our study occurred during March (2004 - 2016) in northern Yellowstone National Park. During March in northern Yellowstone National Park, temperatures generally range from -10 to 15 C, and snowfall is common.
Location	The location of our study is described in the Methods.
Access and import/export	Access and use of our field site was in accordance with Yellowstone National Park research permit (Milestones Research Project 2016-105; investigators include Smith, Stahler, and Metz).
Disturbance	Samples were collected in accordance with Yellowstone National Park research permit (Milestones Research Project 2016-105; investigators include Smith, Stahler, and Metz). Only samples allowed under this permit were collected.

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study
☒	Unique biological materials
☒	Antibodies
☒	Eukaryotic cell lines
☒	Palaeontology
☐	☒ Animals and other organisms
☒	Human research participants

Methods

n/a	Involved in the study
☒	ChIP-seq
☒	Flow cytometry
☒	MRI-based neuroimaging

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals

For laboratory animals, report species, strain, sex and age OR state that the study did not involve laboratory animals.

Wild animals

Wolves were captured in Yellowstone National Park via helicopter darting. Wolves were captured and handled following guidelines of the American Society of Mammalogists and approved under University of Montana IACUC protocol 043-15MHWB-121515.

Field-collected samples

All bone marrow samples were stored in a freezer until the bone marrow samples were dried in an oven.