How constraints affect the hunter's decision to shoot a deer

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Hunting is the predominant way of controlling many wildlife populations devoid of large carnivores. It subjects animals to mortality rates that far exceed natural rates and that differ markedly in which age, sex, or size classes are removed relative to those of natural predators. To explain the emerging selection pattern we develop behavioral microfoundations for a hunting model, emphasizing in particular the constraints given by the formal and informal norms, rules, and regulations that govern the hunter's choice. We show how a shorter remaining season, competition among hunters, lower sighting probabilities, and higher costs all lead to lower reservation values, i.e., an increased likelihood of shooting a particular animal. Using a unique dataset on seen and shot deer from Norway, we test and confirm the theoretical predictions in a recreational and meat-motivated hunting system. To achieve sustainability, future wildlife management should account for this predictable selection pressure.

hunting selection | optimal stopping | hunter behavior | social dilemma

Although natural large predators are now recolonizing many industrialized countries (1), their functional roles are still limited and most wildlife populations in Europe are mainly controlled by hunting (2). Hunting is the predominant cause of adult mortality for 80–90% of the individual animals in deer populations (3). Despite this high hunting pressure, populations have grown and expanded their range, often resulting in overabundance (4). Part of this increase is due to hunter selectivity having distorted the natural sex and age distribution (5). The reluctance to shoot females with offspring facilitates rapid population growth, but skewing sex ratio also affects evolutionary processes. In some ungulate populations with heavy trophy hunting, there is concern that selective removal of specific phenotypic traits leads to evolution even over short timespans of a few tens of generations (6). There is hence an urgent need to inform policies on how to manage wildlife in a way that does not endanger the health of the supporting ecosystem or the resilience of the hunted population. To better understand how overall hunting pressure maps to population dynamics and potential for evolution, we need to understand selectivity.

In Norway, the population size, distribution, and resulting hunting quota for red deer (*Cervus elaphus*) have increased dramatically. The west coast holds the majority of the population, with more than 75% of the red deer being harvested in the counties Møre and Romsdal, Sogn and Fjordane, and Hordaland (Fig. 1). Red deer is the second most valuable hunted species in terms of meat value (after moose, *Alces alces*), and there is an increasing interest for trophy hunting.

In the ecological literature, selectivity by hunters has been treated as a static property, focusing mostly on the extreme case of trophy hunting (7, 8). However, only a small proportion of hunting is for trophies; most hunting is for recreation, meat, or population regulation (9). Most hunters have quotas limiting their choices, and they may have limited time to fill their quota (5). There has been no study addressing how the decision to shoot a sighted animal depends on competition among team members or factors such as time and quota constraints. The economic literature has looked at hunting mainly from a valuation perspective (e.g., ref. 10), centered around land-use conflicts (11) or addressing the trade-off between meat and trophy hunting (12). So far, these studies have cast their analysis in the framework of harvesting models.

But hunting is not like harvesting; it is characterized by an individual and nonrecurring encounter between man and animal. Thus, we develop a model that focuses on the individual decision to shoot or not to shoot a given animal. By framing hunting as an optimal stopping problem we show how social constraints shape the emerging selection pressure: The way the hunt is organized, the length and timing of a dedicated hunting season, and the cost of shooting animals all affect the hunter's incentives and constrain his or her choice set.

We exploit a unique dataset on red deer hunting incidents to confront our theory with data. Our panel covers 256 locations in Norway between 1999 and 2010 (Fig. 1), where not only the number and type of hunted animal were recorded, but also which animals have been seen, but not shot. These data allow us to directly construct the conditional probability of shooting an animal. Matching these data with meteorological information on precipitation, temperature, and the moon phase, we can exploit 181,989 choice situations. We show that indeed the likelihood of shooting a given animal is higher the shorter the remaining harvest season is, the more hunters that participate in a given trip, and the lower the sighting probability is.

Significance

Wildlife populations in Europe and North America are regulated through hunting, as natural predators are still scarce. Therefore, wildlife is a social–ecological system with delicate feedbacks between the social and ecological subsystems. Both for population control and for evolution and because of cultural values, it is essential to understand how many and which animals are removed from the population. However, the question of how the social context influences the individual hunter's decision to shoot or not to shoot an animal has not been addressed. We apply insights from economic search theory to explain how hunter selection is shaped by social constraints. We provide convincing evidence, using a unique dataset from deer hunting, that selectivity declines with more hunters competing and a shorter remaining season.
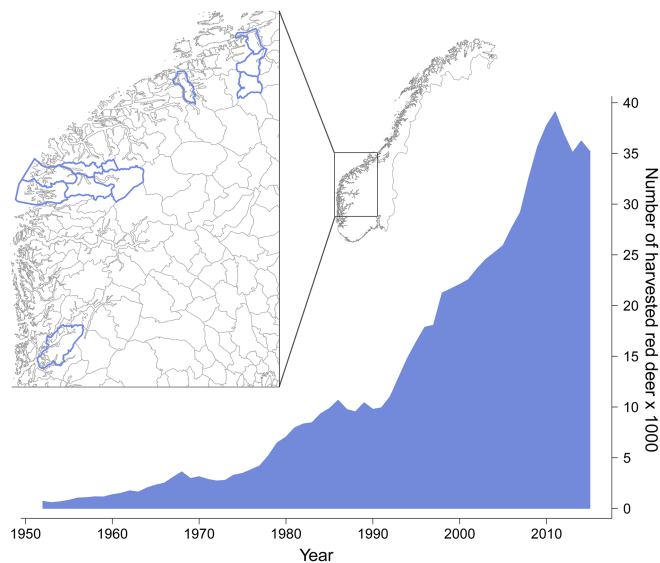
Fig. 1. Map of Western Norway to indicate our study area. The graph shows the numbers of shot animals in Norway.

Theoretical Results

We develop a behavioral model to predict how constraints on hunter decisions affect selectivity. The centerpieces of a model that describes the hunting decision are (*i*) that one shot can kill at most one animal, (*ii*) that the animal the hunter actually observes is essentially an independent and identically distributed draw from the population, and (*iii*) that the hunter is constrained on how many animals can be shot.

The first feature distinguishes hunting from harvesting, where many animals are removed from the population in one instant (there are, for example, thousands of fish in a trawl net). The second feature relates to the fact that animals move and that the hunter cannot be sure to see a given animal again when he or she lets it pass. The third feature stems from the fact that most hunting is actively managed by quotas. The constraint could also more generally result from specific investments that have to be made before hunting. Without loss of generality, we set this constraint so that the hunter is allowed to shoot exactly one animal.

These three features make it very natural to frame the hunting decision as an optimal stopping problem: At each sighting, the individual hunter has to choose whether to shoot the current animal and stop hunting or to continue and wait for the next opportunity.

Hunting as an Optimal Stopping Problem.
The animal population is heterogeneous with respect to a given trait (for example, antler size). Assume that a given hunter i has a monotone preference ordering over these trait values, where we define $x \in [0, \infty)$ as the value that this hunter assigns to a given animal. Let each animal have a unique value so that the hunter's valuation of the population can be described by a cumulative distribution function $F_i(x)$. Here, the population is defined with respect to the particular type of quota that the hunter holds. Assume that the distribution $F_i(x)$ is stationary and known to the hunter. This is unlikely to be literally true, but it is plausible that the hunter has a general idea about the distribution of trait values in the population and the opportunities to update his or her belief are so limited that they can be neglected. The assumption that the distribution is stationary is warranted when the relevant population is large with respect to the scale at which the decision is made. Note that a stationary distribution also implies that the vulnerability of animals does not change over time (but see *Discussion*).

The hunter incurs a fixed cost c_i per period (representing, e.g., his or her opportunity cost of labor, access fees to the hunting area, etc., measured in terms of utility), regardless of whether an animal is actually shot or not. Each period, the hunter observes one animal whose value is ex ante a random variable X. Clearly, the hunter goes hunting only if $\mathrm{E}[X] > c_i$.

The optimal policy in the basic setup is characterized by a "reservation value" that equals the expected benefit from following the optimal rule. Eq. **1** describes the "optimal shooting rule," where ξ_i is the reservation value:

$$\begin{aligned} \text{shoot animal if} \quad & x \geq \xi_i \\ \text{do not shoot animal if} \quad & x < \xi_i. \end{aligned} \quad [1]$$

The reservation value ξ_i thus defines the selection pressure exerted by this hunter i: All animals whose trait value is at or above the threshold are subject to being hunted, whereas all animals with a lower trait value are safe from being shot.

The expected net return from policy Eq. **1** is given by $\mathrm{E}[\max\{\xi_i, X\}] - c_i$ and the reservation value can be expressed as $\xi_i = \xi_i \int_0^{\xi_i} dF_i(x) + \int_{\xi_i}^{\infty} x \, dF_i(x) - c_i$, which implies

$$c_i = \int_{\xi_i}^{\infty} (x - \xi_i) \, dF_i(x). \quad [2]$$

Eq. **2** has an intuitive interpretation: The individual threshold value ξ_i is chosen so that the marginal cost incurred by not shooting in the current period and awaiting another period just equals the expected marginal return from one more observation. The right-hand side of Eq. **2** defines a function H_i that maps a given trait value x into the utility gain that hunter i can expect by waiting for the next observation. That is, $H_i(x) \equiv \int_x^{\infty} (y - x) \, dF_i(y)$.

The function H_i is convex and strictly decreasing, and it satisfies $\lim_{x \to \infty} H_i(x) = 0$ and $\lim_{x \to 0} H_i(x) = \mathrm{E}[X]$. This result implies that whether a hunter chooses to shoot an animal depends not only on characteristics of the animal (given by the trait value x), but also on characteristics of the hunter. Indeed, hunters may differ in terms of opportunity costs and also how they value a sighted animal. Fig. **2** illustrates how different costs and different valuations affect the reservation value ξ_i and, hence, the probability to shoot an animal.
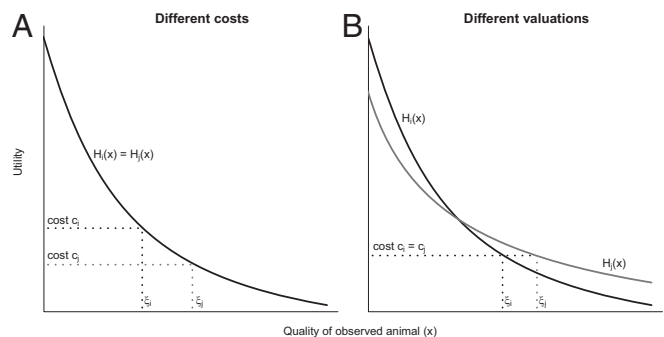

Fig. 2. The reservation value ξ_i is chosen so that the expected utility gain from not shooting the current animal (with value x) equals the cost of waiting for the next observation. When hunters differ in terms of cost but value animals in the same way (*A*), we can see that the hunter with the lower hunting cost c_j implies a higher reservation value ξ_j and a longer duration of search. Hunters may face the same costs, but differ in terms of valuation (*B*). For hunter i we use a standard log-normal distribution [$F_i = \ln \mathcal{N}(0, 1)$]. For hunter j, we use a distribution $F_j = \ln \mathcal{N}(-0.6, 2)$, which implies that the valuation function is skewed to the right. This may represent a trophy hunter who preferably shoots animals with large trait values, whereas many animals in the population are of low value to him. In this example, the trophy hunter has a higher reservation value and a longer duration of search.

Social Constraints. The model above does not account for the constraints that affect the hunter's decision. Here, we show how a finite length of the remaining hunting season, a higher number of hunters per quota, and a lower probability of sighting an animal all depress the reservation value and therefore imply less selective hunting pressure. We emphasize that we continue to model individual (and potentially heterogenous) hunters, but we now drop the subscript i for notational clarity.

First, we relax the assumption of an infinite time horizon. Let $k = 0, 1, ...K$ be the number of remaining shooting opportunities if the current opportunity is not used. If there is only a single opportunity ($k = 0$), the hunter will shoot any animal he or she sees. The reason is the following: Ex ante the hunter goes hunting only if $E[X] > c$, but ex post, after having paid c, the costs are sunk and there is no gain from not retrieving any positive value. We thus have $\xi_0 = 0$. In the next-to-last period, the hunter has, upon observing an animal, the choice to either shoot this animal or not shoot it, drawing a new animal with value X_0 in the last period. Knowing that the hunter will shoot any animal in the last period, the expected reward of going into the last period is given by $-c + \int_0^\infty x \, dF(x) = -c + H(0)$. This defines the reservation value ξ_1. Because $E[X] > c$, we know that $\xi_1 = -c + H(0) > \xi_0$. In general, we have

$$\xi_k = -c + H(\xi_{k-1}) + \xi_{k-1}. \qquad [3]$$

Because $H(\xi_k) > c$ for all k, it follows that $\xi_k > \xi_{k-1}$. Moreover, as $H' < 0$ and $H'' < 0$ we have $\xi_K \to \xi$ as $K \to \infty$.

Prediction 1. *The reservation value ξ_k is larger the larger k is: The longer the remaining hunting season is, the more selective the hunting pattern. Conversely, the likelihood of shooting a given animal is higher the shorter the remaining season is.*

We now consider the situation when several hunters share one quota. This is a common setup in Scandinavia, where several hunters form a team (jaktlag), but each hunter hunts for him- or herself or at least makes the decision to shoot independently.

We model the arising competition in the following way: When observing an animal, the hunter is allowed to shoot it, but before the next shooting opportunity, the hunter has to update his information on whether the quota has been filled by someone else in the meantime. If so, he or she has to stop hunting. Let there be N identical hunters and denote by p_k the probability that an animal has been shot by a given hunter $j \neq i$ in period k. In the purely competitive case, the probability that any hunter shoots is simply given by the probability that he or she sees an animal whose value is at least as high as his or her reservation value, making $p_k = \int_{\xi_k^c}^\infty dF(x) = 1 - F(\xi_k^c)$. The reservation value in this case ξ_k^c is then defined by

$$\xi_k^c = -c + (F(\xi_k^c))^{N-1} [H(\xi_{k-1}^c) + \xi_{k-1}^c]. \qquad [4]$$

Note that the logic of backward induction and the fact that $\xi_1^c = 0$ and $F(0) = 0$ imply that the reservation value will not be positive for any k when there is more than one hunter. In other words, unrestricted competition implies completely nonselective harvesting.

However, unrestricted competition may not be the best description of behavior within a hunting team. These are generally small and the participants know each other. It is thus very likely that there are norms that dampen incentives to act competitively. For example, hunters may agree to not shoot animals below the respective threshold values of a noncompetitive situation. This would amount to replacing $F(\xi_k^c)$ with $F(\xi_k)$ in Eq. **4**. The resulting reservation value would then represent the trait value at which a hunter should shoot an animal if he or she is more interested in shooting it him- or herself than honoring the social norm of the hunting team.

We denote the reservation value in such a situation by $\hat{\xi}_k^c$. It is defined by

$$\hat{\xi}_k^c = -c + (F(\xi_k))^{N-1} [H(\hat{\xi}_{k-1}^c) + \hat{\xi}_{k-1}^c]. \qquad [5]$$

Regardless of whether Eq. **4** or Eq. **5** better describes the situation, it is clear that competition implies less selective harvest. Insofar as there are concerns about a deterioration of the trophy values due to ecological and evolutionary effects, we thus have the paradoxical result that competition safeguards the qualitative properties of the animal population while it simultaneously depresses the expected reward for a hunter.

Prediction 2. *The larger the number of competing hunters is, the less selective the hunting pattern. Conversely, the likelihood of shooting a given animal is higher the more hunters participate in a given trip.*

When it is not certain that an animal is seen during a given hunting day, the reservation value will decline and hunting will become less selective. The reason is that, on average, the cost per sighted animal increases.

Let $q < 1$ be the probability to see an animal in a given period and denote by $\tilde{\xi}_k$ the corresponding reservation value. Concentrating on the effect of uncertain sighting, the optimal decision rule for the hunter can be deduced as follows: In the last period the hunter will shoot any animal he or she sees, so that $\tilde{\xi}_0 = 0$. If there is one period left, the hunter has to trade off the value of shooting the current value with the expected value of the next period (the expected value of an animal, weighted by the probability of seeing it, minus the certain cost c) so that $\tilde{\xi}_1 = q \int_0^\infty x \, dF(x) - c = -c + qH(0)$. Obviously, $\tilde{\xi}_1$ will be smaller the lower q is. More generally, we have

$$\tilde{\xi}_k = -c + qH(\tilde{\xi}_{k-1}) + \tilde{\xi}_{k-1}, \qquad [6]$$

where convergence of the difference equation for $\tilde{\xi}_k$ and the fact that $\tilde{\xi}_k > \tilde{\xi}_{k-1}$ again follows from the properties of the function H.

Prediction 3. *The reservation value $\tilde{\xi}_k$ is increasing in q. That is, the higher the probability is to see an animal in the next choice situation, the more selective the hunting pattern.*

In summary, abstracting from many real-life features and analyzing hunting as an optimal stopping problem yield three key predictions, namely that a given animal is more likely to be shot (*i*) the shorter the remaining harvest season, (*ii*) the more

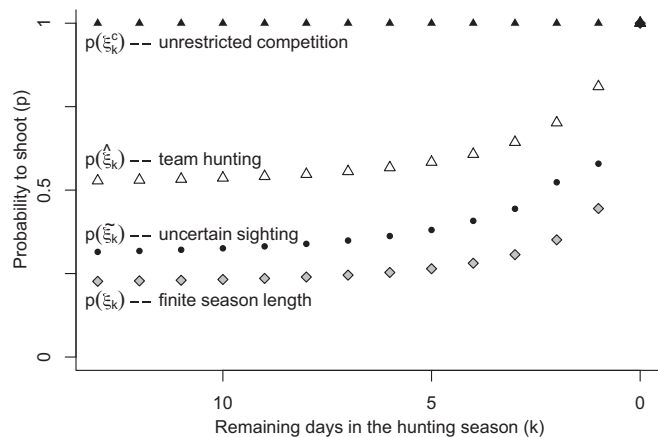**Fig. 3.** To illustrate how social constraints on the hunter's decision affect the probability to shoot, we plot the probability that the trait value X is below the reservation value for different values of $k = \{13, 12, ..., 0\}$, $q = \{1, 0.8\}$, and $N = \{1, 5\}$. We use log-normally distributed trait values (with the standard normal as the underlying function) and set the marginal hunting costs to $c = 1$.

hunters participate in a given trip, and (*iii*) the lower the sighting probability. Fig. 3 illustrates how these effects play out for a given hunter i with cost c_i and valuation F_i.

Empirical Evidence from Red Deer Hunting in Norway

In this section, we test our theory by analyzing a unique dataset on red deer hunting incidents in Norway. Red deer are a sexually dimorphic species, with large differences in body weight between males and females (14). Red deer prefer habitats that offer both forage and cover within close range. Mating takes place in October, with a distinct rutting period where males defend smaller harems of females or land occupied by females. Males mature around 1–3 y of age, but do not allocate much energy into the rut until they reach 3–4 y and females mature around 1.5 to 2.5 y (15). A single calf is born in June.

It is rare that red deer reach old age. Young individuals experience particularly high hunting pressure, and older males experience higher hunting pressure than older females (3). For males, the chance of survival from 1.5 y to 2.5 y is only 52%, and it is 55% from 2.5 y to 3.5 y. The corresponding survival rates for females are much higher (81% and 82%, respectively, based on capture–mark–recapture analyses in ref. 3).

In Norway, the hunting rights belong to the landowners. The land of one or more landowners constitutes the lowest level of the local management units (vald). Quotas are area specific to this level and set by the municipalities. Quotas are based on sex and age (calves, yearling males and females, adult males, and adult females). It is also allowed to shoot younger animals on adult quotas. Here, we concentrate on the older males as the main category of interest. Results for females, calves, and yearlings are shown in *SI Appendix*, Table S3.

Results

The reservation value in the mind of the hunter is unobservable. However, we can test the implications of the theoretical model. We estimate the probability of shooting a male deer conditional on seeing it with a probit binary outcome model that includes location-specific random effects and year-specific fixed effects; see *Materials and Methods* for details. The results, shown in Table 1, strongly support our theoretical predictions.

First, the coefficient on team size is positive and highly statistically significant, confirming our first theoretical prediction that more hunters in the team increase the probability to shoot an animal upon sighting. Second, the coefficient on the number of remaining days in the season is negative and highly statistically significant. This means that the more days that are left in the

Table 1. Probability to shoot an animal upon sighting: Results from a binary outcome model using probit regression with location-specific random effects and year-specific fixed effects

	Coefficient	SE
Team size	0.048***	0.006
Remaining days	−0.003***	0.001
Seen male	−0.079***	0.021
Seen yearling	−0.028**	0.011
Seen female	−0.016**	0.007
Seen calf	−0.030***	0.009
Weekend	−0.084***	0.023
Precipitation	0.000	0.001
Moon fraction	0.090***	0.033
Constant	−0.478***	0.137
Observations	22,705	
Log likelihood	−10,049.1	
Clusters	245	

SEs are clustered at the management unit (vald).
*$P<0.10$, **$P<0.05$, ***$P<0.01$.

season, the less likely it is to shoot a given seen male deer. In other words, the shorter the remaining time horizon is, the less selective the hunters are.

In contrast to team size and the number of remaining days in the season, there is no single covariate that captures our third theoretical prediction. However, if we consider the total number of observed animals in a given trip as a proxy for the probability of seeing an animal, we see that these coefficients are negative and statistically significant for all categories. This result suggests that the higher the probability to see an animal is, the less likely it is that a given male deer is shot, exactly as the theoretical model predicts.

Additionally, we control for weather, day of the week, and the moon phase. We find no effect of precipitation, but we find a lower probability of shooting a deer during weekends than during weekdays. Moreover, we find that a larger visible fraction of the moon is positively correlated with the probability of shooting. If a larger fraction of the moon implies better visibility, this may—at first sight—seem at odds with our third prediction. However, whereas better current visibility certainly increases the chances to take a clear targeted shot, it does not affect the hunter's general estimate of the probability of seeing an animal at future trips, which is the aspect that our third theoretical prediction relates to.

In addition to the three key predictions on season length, team size, and sighting probability, our model of hunters' shooting decisions implies that the probability of shooting a given animal increases nonlinearly as the season approaches its end. We test for nonlinearities by estimating the model with the variable remaining days in cubic form. The estimated relationships are plotted in Fig. 4, whereas the regression coefficients are shown in *SI Appendix*, Table S2, column 4. We find striking similarities with our theoretical predictions and our empirical results (compare Figs. 3 and 4). In particular, the probability to shoot increases nonlinearly as the season comes to an end. This effect is stronger the more hunters are in a team, also in line with theory. We do not find any evidence that hunters are guided purely by self-interest, which would imply that the presence of one fellow hunter would be sufficient to shoot every animal upon sighting. Our empirical results are, however, consistent with hunters being guided by social norms. Typically such norms are stronger in smaller groups, which is again supported by the empirical results.

We have extensively tested the robustness of our results and the restrictiveness of the implied linearity. First, we run several specifications of the estimation model (*SI Appendix*, section 2). Second, we discuss hunter heterogeneity (*SI Appendix*, section 3). Although there are no data on hunter preferences or hunter types (the data on hunting effort are anonymous), a first step is to distinguish trips taking place during the weekend from weekday trips. Despite the probability to shoot being lower during the weekend, we find that our theoretical predictions hold equally for weekend and weekday hunters. Third, animal behavior, not only hunter behavior, can also influence harvesting vulnerability [occurring through, e.g., differential use of open habitat (16) or behavioral responses to prevailing weather and moon phase (17)]. In addition, hunting early in the season will always change the size and composition of the population later in the season. If these effects are large and statistically significant, it will introduce bias. In *SI Appendix*, section 4, we show that a "population depletion" effect is not important. Finally, we address the possible concern of reverse causality that may arise if the number of hunters is not exogenous. We use an instrumental variable strategy to take such reverse causality into account. *SI Appendix*, Table S8 presents the results, confirming the robustness of our findings.

Discussion

Hunting has a crucial impact on many wildlife populations, and this is particularly the case for ungulates. For a large part of
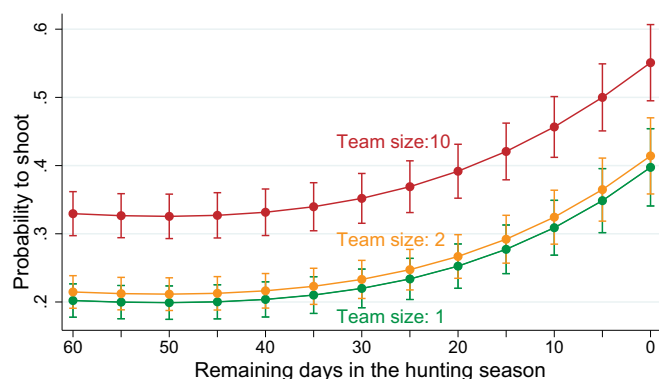
Fig. 4. The predictive probability on how season length and team size affect the decision to shoot with 95% confidence intervals. We find that the probability to shoot increases nonlinearly as the season comes to an end and also increases with the number of cohunters.

ungulate populations in industrialized countries, management centers around population control and recreational aspects (2, 4) or around conservation and balancing the exploitation for meat and trophies (12, 18). For both settings, there is a pressing need to understand how different selection patterns are formed and how they influence the development of wildlife populations. Age- and sex-selective harvest has implications both for short-term, population dynamical scales and for long-term, evolutionary scales. Our theoretical model and empirical results point to a main role of social context in which animals are harvested. We find that hunter selectivity declines the shorter the remaining season is, the more hunters share one quota, and the lower the probability to see a given animal. Our study links individual behavioral decisions of hunters to selectivity for age and sex classes, with potentially far-reaching implications for how to manage wildlife populations.

Population models are now well developed to quantify the direct effects on population growth for a given harvest (19). However, there is increasing concern that hunting, and in particular strongly selective hunting, may have unexpected ecological and evolutionary consequences (20, 21). Breeders have for thousands of years selected the most productive animals to reproduce and enhance the quality of future populations. In contrast, hunting may yield the opposite effect: As the value derived from the individual animal is inextricably linked to killing it, unregulated trophy hunting may mean that the finest and most productive animals are removed from the breeding population. If persisting over a few tens of generations, this may lead to undesirable human-induced evolution. Concerns regarding the sustainability of the growing trophy hunter industry are increasing (22), although some cultures already have practices to avoid such undesirable effects (23). Our study identifies two practical levers by which policy makers could address selectivity: the duration of the hunting season and the number of hunters that compete for a given quota.

Using the hunting season as a tool to achieve management aims is rarely assessed and only from the angle of how biological seasons of the animals affect the harvest (24). Our results show that more emphasis should be put on the hunter when assessing such changes. We would, for example, also expect to see that the identified end-of-the-season effect is present for a given hunter or within a given day (that is, more animals are shot at the end of a typical hunting trip than at the beginning). It remains to be determined whether the insight from human hunting has relevance for natural predators hunting year round without quotas. Large carnivores hunting migratory ungulates may face a similar challenge to having a distinct hunting season, and it would be

interesting to quantify whether their choice of prey changes as timing of migration approaches.

There is evidence that different hunter "types" can be distinguished among Norwegian red deer hunters (13), as well as among hunters more generally (25). Such socioeconomic differences among hunters will likely affect selectivity (26). Although our data do not allow us to identify individual hunters, our results show that the probability to shoot an animal is lower during the weekend, presumably due to differences in the composition of the hunter population. Linked to this, the way of hunting may differ predictably between groups. Sit-and-wait hunting at agricultural fields in morning and evening is common during weekdays for local hunters in between work, whereas drive hunting is more common during weekends when also non-residents are hunting. It is well known that differences in hunting methods also affect selectivity (27). This points to the potentially important aspects of culture and to fruitful future applications of our framework.

Another interesting aspect of our analysis is the indirect effect of climate that operates through hunter behavior in terms of selectivity. The climate effects literature is typically focused on explaining direct effects of severe winter weather (28) or how temperature and precipitation affect plant maturation and quality (29), whereas the wildlife management literature focuses on size and selectivity of quotas per se for population dynamics (30). Very little attention has been put on understanding how climate may affect the actual harvesting process operating indirectly on the hunters (17).

Our findings are highly policy relevant far beyond the trophy hunting case: Simply basing the new annual quota on past harvesting will lead to biased estimates of abundance and population structure with potentially unwanted consequences for wildlife and wider ecosystem management. To achieve sustainability, future wildlife management should account for the predictable manner by which social constraints and underlying institutions shape the emerging selection pattern.

Materials and Methods

Data. In Norway, it is mandatory by law to fill out a data form that contains daily number of hours hunted, the number of hunters, and the number of seen and shot deer of each sex and age class (calf, male or female yearling, older male or female). The hunters furthermore note the date and an ID number for the management unit (both vald and felt). Unsuccessful hunting trips yielding no harvested animals are also reported. These data are regarded as highly reliable. Data were available in time series of 2 y to 12 y from 11 different municipalities (Fig. 1) and included a total of 20,203 harvested and 214,628 seen red deer. We extracted daily data on temperature and precipitation (provided by the Norwegian Meteorological Institute; www.eklima.no). Data were available from one to five stations within each municipality, and we calculated the daily mean from these on the municipality scale. If a municipality lacked data on temperature, we calculated the daily mean from the closest stations in neighboring municipalities (one to four, depending on availability). Data on moon phase were downloaded from the US Naval Observatory (www.usno.navy.mil/USNO) as the fraction of the moon visible each day.

Moreover, we have calculated the remaining days in the season at each location, taking into account that whereas hunting traditionally starts on September 10, the end day varies from year to year and municipality to municipality. If quotas are filled toward the end of the season, this will prohibit shooting any more animals of a certain category. Ignoring those quota constraints would lead to biased estimates, because one would falsely conclude that a hunter chose not to shoot a certain animal, although this was in effect not due to hunter behavior, but due to regulation. There is no information on the total size of the quota and at what time quotas are filled. We overcome this obstacle by exploiting the fact that we do know that the quota is not filled as long as animals are being shot. Therefore, we identify the last day in the year where an animal of a certain category has been shot for that specific category and remove all remaining observations in that year (32,639 observations in total). Our remaining sample consists of 181,989 distinct choice situations. *SI Appendix*, Table S1 presents summary statistics of our data at the trip level.

Estimation Strategy. Knowing the number of both seen and shot animals of each category allows us to construct the conditional probability of shooting an animal. That is, we split each hunting incidence into several observations and assign our dependent variable a value of 1 when an animal of category i has been seen and shot and a value of 0 if it has been seen but not shot. We estimate the binary choice per category and provide all results category-specific (*SI Appendix*, section 2). The main specification then takes the (general) form

$$Pr(Y = 1) = \beta_0 + \beta_1 R_{j,k,t} + \beta_2 N_{j,k,t} + X'_{i,j,k,t}\beta_3 + c_j + y_t + u_{i,j,k,t},$$

where we estimate the probability to shoot animal Y of category i (conditional on seeing it) at hunting site j during trip k, in year t. Our key variables of interest are R, the number of remaining days (we expect β_1 to be negative; theoretical *Prediction 1*), and N, the number of hunters in the team (we expect β_2 to be positive; theoretical *Prediction 2*). Furthermore, $X'_{i,j,k,t}$ includes selected control variables that attempt to capture the sighting probability (*Prediction 3*). Furthermore, we include a location-specific random effect c_j and a year-specific fixed effect y_t. $u_{i,j,k,t}$ is the idiosyncratic error [with $u_{i,j,k,t} \sim \mathcal{N}(0, \sigma_u^2)$]. All regression results have been estimated in Stata, using the command "xtprobit." Fig. 4 has been produced with the command "margins," assuming that the random effect is zero.

1. Chapron G, et al. (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346 (6216):1517–1519.
2. Apollonio M, Andersen R, Putman R (2010) *European Ungulates and Their Management in the 21st Century* (Cambridge Univ Press, Cambridge, UK).
3. Langvatn R, Loison A (1999) Consequences of harvesting on age structure, sex ratio and population dynamics of red deer Cervus elaphus in Central Norway. *Wildl Biol* 5(4):213–223.
4. McShea W, Underwood H, Rappole J (1997) *The Science of Overabundance: Deer Ecology and Population Management* (Smithsonian Institution, Washington, DC).
5. Mysterud A (2011) Selective harvesting of large mammals: How often does it result in directional selection? *J Appl Ecol* 48(4):827–834.
6. Allendorf FW, Hard JJ (2009) Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proc Natl Acad Sci USA* 106(Suppl 1):9987–9994.
7. Garel M, et al. (2007) Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. *Ecol Appl* 17(6):1607–1618.
8. Douhard M, Festa-Bianchet M, Pelletier F, Gaillard JM, Bonenfant C (2016) Changes in horn size of Stone's sheep over four decades correlate with trophy hunting pressure. *Ecol Appl* 26(1):309–321.
9. Milner JM, et al. (2006) Temporal and spatial development of red deer harvesting in Europe: Biological and cultural factors. *J Appl Ecol* 43(4):721–734.
10. Ericsson G, Boman M, Mattsson L (2000) Selective versus random moose harvesting: Does it pay to be a prudent predator? *J Bioecon* 2(2):117–132.
11. Bulte EH, Horan RD (2003) Habitat conservation, wildlife extraction and agricultural expansion. *J Environ Econ Manag* 45(1):109–127.
12. Nævdal E, Olaussen JO, Skonhoft A (2012) A bioeconomic model of trophy hunting. *Ecol Econ* 73:194–205.
13. Andersen O, Wam HK, Mysterud A, Kaltenborn BP (2014) Applying typology analyses to management issues: Deer harvest and declining hunter numbers. *J Wildl Manag* 78(7):1282–1292.
14. Mysterud A, Yoccoz NG, Stenseth NC, Langvatn R (2001) Effects of age, sex and density on body weight of Norwegian red deer: Evidence of density–dependent senescence. *Proc Biol Sci* 268(1470):911–919.
15. Mysterud A, et al. (2008) The timing of male reproductive effort relative to female ovulation in a capital breeder. *J Anim Ecol* 77(3):469–477.
16. Ciuti S, et al. (2012) Human selection of elk behavioural traits in a landscape of fear. *Proc Biol Sci* 279(1746):4407–4416.
17. Rivrud IM, Meisingset EL, Loe LE, Mysterud A (2014) Interaction effects between weather and space use on harvesting effort and patterns in red deer. *Ecol Evol* 4(24):4786–4797.
18. Gordon IJ, Hester AJ, Festa-Bianchet M (2004) The management of wild large herbivores to meet economic, conservation and environmental objectives. *J Appl Ecol* 41(6):1021–1031.
19. Milner-Gulland EJ, Coulson TN, Clutton-Brock TH (2000) On harvesting a structured ungulate population. *Oikos* 88(3):592–602.
20. Mysterud A, Coulson T, Stenseth NC (2002) The role of males in the dynamics of ungulate populations. *J Anim Ecol* 71(6):907–915.
21. Festa-Bianchet M (2003) Exploitative wildlife management as a selective pressure for life-history evolution of large mammals. *Animal Behavior and Wildlife Conservation*, eds Apollonio M , Festa-Bianchet M (Island Press, Washington, DC), pp 191–207.
22. Knox MW (2011) The antler religion. *Wildl Soc Bull* 35(1):45–48.
23. Rivrud I, et al. (2013) Hunter selection and long term trend (1881-2008) of red deer trophy sizes in Hungary. *J Appl Ecol* 50:168–180.
24. Apollonio M, Putman R, Grignolio S, Bartos L (2011) Hunting seasons in relation to biological breeding seasons and the implications for the control or regulation of ungulate populations. *Ungulate Management in Europe; Problems and Practises*, eds Apollonio M, Andersen R, Putman R (Cambridge Univ Press, Cambridge, UK), pp 80–105.
25. Ward KJ, Stedman RC, Luloff AE, Shortle JS, Finley JC (2008) Categorizing deer hunters by typologies useful to game managers: A latent-class model. *Soc Nat Resour* 21:215–229.
26. Mysterud A, Tryjanowski P, Panek M (2006) Selectivity of harvesting differs between local and foreign roe deer hunters: Trophy stalkers have the first shot at the right place. *Biol Lett* 2(4):632–635.
27. Martinez M, Rodriguez V, Jones OR, Coulson T, San Miguel A (2005) Different hunting strategies select for different weights in red deer. *Biol Lett* 1:353–356.
28. Jacobson AR, Provenzale A, von Hardenberg A, Bassano B, Festa-Bianchet M (2004) Climate forcing and density dependence in a mountain ungulate population. *Ecology* 85(6):1598–1610.
29. Mysterud A, Yoccoz NG, Langvatn R, Pettorelli N, Stenseth NC (2008) Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. *Philos Trans R Soc Lond B Biol Sci* 363:2359–2368.
30. Sæther BE, Engen S, Solberg EJ (2001) Optimal harvest of age-structured populations of moose Alces alces in a fluctuating environment. *Wildl Biol* 7(3):171–179.
31. Greene WH (2008) *Econometric Analysis* (Pearson Prentice Hall, Upper Saddle River, NJ), 6th Ed.
32. Aguirregabiria V, Mira P (2010) Dynamic discrete choice structural models: A survey. *J Econ* 156(1):38–67.
33. Amemiya T (1981) Qualitative response models: A survey. *J Econ Lit* 19(4):1483–1536.

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