

Implementation uncertainty when using recreational hunting to manage carnivores

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Summary

1. Wildlife managers often rely on resource users, such as recreational or commercial hunters, to achieve management goals. The use of hunters to control wildlife populations is especially common for predators and ungulates, but managers cannot assume that hunters will always fill annual quotas set by the authorities. It has been advocated that resource management models should account for uncertainty in how harvest rules are realized, requiring that this implementation uncertainty be estimated.

2. We used a survival analysis framework and long-term harvest data from large carnivore management systems in three countries (Estonia, Latvia and Norway) involving four species (brown bear, grey wolf, Eurasian lynx and wolverine) to estimate the performance of hunters with respect to harvest goals set by managers.

3. Variation in hunter quota-filling performance was substantial, ranging from 40% for wolverine in Norway to nearly 100% for lynx in Latvia. Seasonal and regional variation was also high within country–species pairs. We detected a positive relationship between the instantaneous potential to fill a quota slot and the relative availability of the target species for both wolverine and lynx in Norway.

4. Survivor curves and hazards – with survival time measured as the time from the start of a season until a quota slot is filled – can indicate the extent to which managers can influence harvest through adjustments of season duration and quota limits.

5. *Synthesis and applications.* We investigated seven systems where authorities use recreational hunting to manage large carnivore populations. The variation and magnitude of deviation from harvest goals was substantial, underlining the need to incorporate implementation uncertainty into resource management models and decisions-making. We illustrate how survival analysis can be used by managers to estimate the performance of resource users with respect to achieving harvest goals set by managers. The findings in this study come at an opportune time given the growing popularity of management strategy evaluation (MSE) models in fisheries and a push towards incorporating MSE into terrestrial harvest management.

Key-words: Cox proportional hazards model, hunting season, management strategy evaluation, quota-filling performance, survivor curves, sustainable exploitation, time to event analysis

Introduction

One of the roles of wildlife management is to ensure that resource exploitation remains sustainable, balancing popula-

tion persistence and yields. As such, managers provide a service to resource users like hunters and fishers. However, the relationship between wildlife managers and users is not necessarily one-sided – frequently, users contribute to wildlife management by providing information (e.g. observation reports or harvest data; Kindberg, Ericsson & Swenson 2009) or by helping to achieve management goals, such as target popula-

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tion levels. The recreational or commercial pursuit of a variety of species is used by authorities as a cost-efficient means to control wild populations and thus mitigate direct economic losses. For example, deer managers in North America and Europe often rely on hunters to assist in curtailing overabundant deer populations (Brown *et al.* 2000; Milner *et al.* 2006; Morellet *et al.* 2007), and the management of red kangaroo *Macropus rufus* commercial harvest in Australia is partially motivated by a desire to reduce grazing pressure on range lands (Thomsen & Davies 2005).

An especially high emphasis on using hunters to achieve population goals is apparent in carnivore management. Although mammalian predators are often pursued as trophies or for their fur, the primary motivation for harvest management in many jurisdictions is population control (Batcheller *et al.* 2000; Conover 2001; Baker *et al.* 2008; Treves 2009). A striking example of the high amount of control sometimes desired over predator populations is Norway's large carnivore management strategy. Current national goals for brown bear *Ursus arctos*, lynx *Lynx lynx*, wolf *Canis lupus* and wolverine *Gulo gulo* are set, respectively, at 13, 65, 3 and 39 annual reproductions (number of females that reproduce; Miljøvern-departementet 2005; Stortinget 2011). These are interpreted and treated as absolute targets, not upper or lower thresholds. Many other countries also have more or less specific objectives to limit the sizes of their large carnivore populations and rely at least in part on hunters in their effort to reach these goals. Reliance on hunters is driven in part by the high costs of having to use government employees to do the job. Just as importantly, it is also used as a mechanism to increase local involvement in large carnivore management and to convey a sense of empowerment, thereby increasing the legitimacy of what is always a controversial management exercise (Treves 2009). This is despite the potential legal problems that are presented when such species are protected by international legislation (Linnell *et al.* 2010; Hiedanpää & Bromley 2011).

Resource managers, fisheries and terrestrial alike, often use harvest models to aid in decision-making. The qualitative and quantitative predictions yielded by such models are essential prerequisites for operating within an adaptive management framework (Walters 1986; Williams, Nichols & Conroy 2002). In harvest models, exploitation is typically represented as being fully under the control of the manager, that is, harvesting regimes are implemented as intended (e.g. Sæther, Engen & Solberg 2001; Sabo 2005; Sæther *et al.* 2005; Nilsen & Solberg 2006). Resource managers, however, are not omnipotent external manipulators. Management itself is an integral part of the system, and its dynamics can be as difficult to explain or predict as those of the other components. For example, hunting quotas may not always be met and hunting regulation not always obeyed. This discrepancy between management decisions and their realization has been referred to as *partial controllability* (Nichols, Johnson & Williams 1995) or *implementation uncertainty* (Christensen 1997) and is arguably the rule to resource management rather than the exception.

Management strategy evaluation models (MSE), developed and first applied in fisheries (Butterworth & Punt 1999;

Sainsbury, Punt & Smith 2000), are now being extended to terrestrial resource management problems (Bunnefeld *et al.* 2011; Milner-Gulland 2011; Milner-Gulland *et al.* 2011). MSE represents a framework for capturing key dynamics of the resource, as well as its observation and monitoring through a managing agency and the design and implementation of management controls. Perhaps, the greatest strength of MSE is that the approach provides a means to comprehensively account for different sources of uncertainty in resource management, including environmental and structural variation in the resource, inaccuracies and imprecision in assessment of the system state, and the discrepancy between actual and intended management controls, that is, implementation uncertainty (Bunnefeld *et al.* 2011; see also Williams, Nichols & Conroy 2002).

To produce quantitative predictions for managers, an MSE requires estimates of its essential parameters, including implementation uncertainty. Quantifying this type of uncertainty is the goal of the present study. Using tools developed for survival analysis (Cox 1972; Therneau & Lumley 2009), we quantified and compared the performance of hunters to fill management quotas for four different large carnivore species (brown bear *Ursus arctos*, Eurasian lynx *Lynx lynx*, grey wolf *Canis lupus* and wolverine *Gulo gulo*) in three northern European countries (Estonia, Latvia and Norway).

We show that there is substantial variation in the degree to which resource users contribute to meeting management goals and that harvest rules (such as quotas and seasons) do not always match what is achieved on the ground. Finally, the approach taken in this study may give wildlife managers and applied ecologists a new way of looking at the interplay between resource management and resource use.

Materials and methods

CARNIVORE HUNTING DATA

We used harvest data (individuals harvested, with dates, gender and management unit) and information on annual quotas and season dates from lynx and wolverine in Norway (Brøseth *et al.* 2010; Linnell *et al.* 2010); lynx, wolf and brown bear in Estonia (Valdmann, Saarma & Karis 2001; Valdmann *et al.* 2005); and lynx and wolf in Latvia (Valdmann *et al.* 2005; Kawata, Ozoliņš & Anderson-Lilley 2008). Harvest data had been collected by each country's respective management authorities directly from hunters, which were required by law to provide information about the kill. Information summarizing these data is provided in Table 1. Regulated harvest through recreational hunters continues to be motivated by a combination of factors. Chief among these appears to be the desire of policy makers and managers to maintain or reach population levels that minimize agricultural damage and, in some cases, competition for game species, while maintaining viable carnivore populations and the prerequisite public acceptance for large carnivores which is believed to be enhanced by allowing recreational harvest.

SURVIVAL ANALYSIS

We used survival analysis to quantify the performance of hunters with respect to management-set harvest goals. Survival analysis (alterna-

Table 1. Summary of harvest data and seasons from the carnivore hunting systems explored in the analysis of quota-filling performance

Country	Species	Common season	Years of data	Number of regions	Annual quota	Annual harvest
Estonia	Bear	August 1–October 31	2003–2010	9–11	43 (30–60)	30.9 (12–57)
	Lynx	December 1–February 28	2003–2010	13–15	132.2 (95–210)	116.6 (76–183)
	Wolf	November 1–February 28	2003–2010	1–13	82.4 (16–173)	67.1 (15–156)
Latvia	Lynx	December 1–March 31	2003–2008	1	77.8 (50–117)	76.7 (50–117)
	Wolf	July 15–March 31	2004–2009	1	156.7 (130–200)	147 (113–200)
Norway	Lynx	February 1–March 31	1994–2010	5–7	97.6 (47–155)	73.8 (35–134)
	Wolverine	September 10–February 15	1994–2011	2–7	53.9 (11–119)	22.3 (4–37)

The range of values is shown in parentheses behind average annual quota and harvest. Sex-specific quotas were occasionally used for wolverine and lynx in Norway (see main text).

tively referred to as time to event analysis, reliability analysis, event history analysis or failure time analysis) is an umbrella term for a collection of statistical tools (Venables & Ripley 2002; Kleinbaum & Klein 2005) concerned with the time it takes for an event to occur. An ‘event’ (alternatively referred to as ‘failure’ or ‘death’) can be anything that happens to an individual, such as an actual death, an equipment failure or a first conception. ‘Individual’ may in turn refer to any entity, concrete or abstract that may experience an event, including a patient, a mechanical system or an entire population or species. The ‘survival time’ (also referred to as time to event or failure time) can be expressed in any feasible unit (seconds, days, decades, etc.) and is the main quantity of interest in survival analysis. We note that the term survival analysis as used here is not synonymous with the estimation of the proportion of surviving animals during a certain time period (e.g. annual survival rate).

An important concept in survival analysis is ‘censoring’. Censoring occurs when monitoring of an individual ceases without the focal event occurring (Kleinbaum & Klein 2005). For example, an animal that is part of a survival study may drop its radio-collar and be lost to follow-up or it may survive beyond the end of the study. In both cases, we have some information about survival time (i.e. we know the animal did survive for the duration of monitoring), but we do not know the actual survival time, as the event did not occur during monitoring. Censoring in survival analysis enables the use of incomplete information by allowing the inclusion of individuals without an event, thereby considering the time during which they were available for an event to occur, even if it did not occur.

In our case, we consider as the event of interest the filling of a slot on the hunting quota which results from a carnivore being killed by a hunter. The individual for which the event occurs in the analysis is not the animal killed, but the quota slot itself. The total quota set by managers at the beginning of the season is the population of individuals – that is, all the available quota slots – for which we measure the survival time. The latter is the time from the beginning of the season until a quota slot is filled. Because we are interested in the performance of hunters with respect to reaching quotas, we censor quota slots filled as a result of kills attributable to causes other than hunting at the time each slot is filled. This ensures that only the time during which that quota slot was available for hunters is considered (but see Appendix S1, Supporting Information regarding competing risks). Unfilled quota slots are censored at the end of the hunting season. Norwegian lynx and wolverine harvest was sometimes additionally constrained by a combination of female-specific sub-quotas and total quotas: the hunting season ended when either one of these two quotas was filled. We accounted for this by censoring all remaining quota slots at the time when either quota limit was reached (i.e. when that season was closed).

Quota-filling performance

From survival data, we estimated Kaplan–Meier survivor functions $S(t) = P(T > t)$, which give the probability P of surviving (i.e. the focal event not occurring) past a given time t , or, in other words, that the survival time T exceeds t (Kaplan & Meier 1958; Kleinbaum & Klein 2005). Survivor curves are the graphical representation of survivor functions and show cumulative survival over time (Venables & Ripley 2002; Fig. 1). In the context of our analysis, $S(t)$ represents the cumulative probability of a quota slot remaining unfilled beyond time t . A detailed example of quota-filling data set-up and survivor curve construction is provided in Appendix S2 (Supporting information). Survivor curves give an overview of how quota-filling proceeds (Fig. 1), but managers and policy makers may also want a single metric for the extent to which hunters (in the aggregate) fill quotas. We define quota-filling performance (QFP) in the light of quotas set by managers as the probability that a quota slot will be filled by the end of a hunting season of duration d , that is, the complement of the cumulative probability that a quota slot remains unfilled $1-S(d)$. We estimated survivor functions using the function `survfit` in the R survival package (Therneau & Lumley 2009) in R version 2.11.1 (R Development Core Team 2010).

Effect of time of year

Another fundamental entity in survival analysis, a hazard $h(t)$, is the instantaneous potential for the event of interest to occur at a time t per unit time, given that the individual has survived up to that time (Kleinbaum & Klein 2005). Consequently, hazards are rates, not probabilities, and in our analysis represent the instantaneous potential that a quota slot is filled per unit time, at a given time. To visualize the influence of time of year on the hazard, we arranged quota survival data with a fixed calendar date (July 1) as the starting point for the time to event variable, rather than the beginning of each hunting season. We used counting-process style input to account for different hunting season start and end dates within a country–species pair (Heisey & Fuller 1985; Pollock *et al.* 1989; Appendix S2, Supporting information). We calculated hazards following Maindonald & Braun (2007) as the proportion of quota slots available at time t that are filled per unit time. We then fit smooth curves using local polynomial regression (R function `locpoly` in the `KernSmooth` package; Wand & Jones 1995).

Effect of relative availability

In survival analysis, we are often interested in comparing the survivor curves of different groups or in evaluating the effect of covariates. We

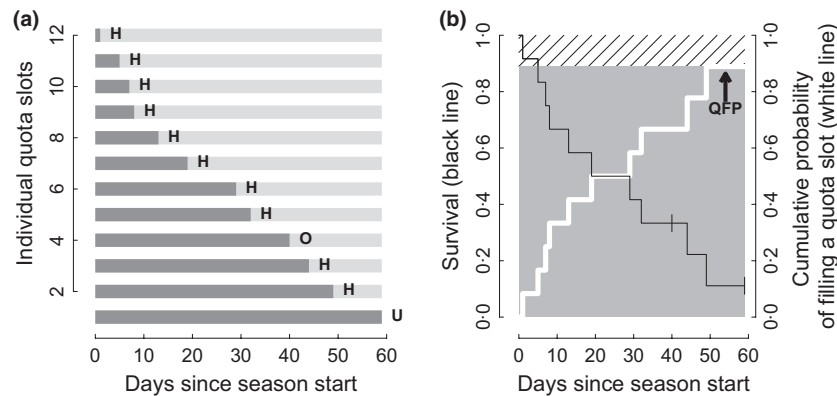


Fig. 1. (a) Illustration of survival data structure. Each line represents an individual quota slot, for a 59-day long lynx hunting season with a total quota set by managers to 12 lynx. The duration for which a quota slot is available is marked dark grey (survival time). Quota slots filled by hunters are marked with an 'H' next to the date of filling. Two quota slots were censored, because one was filled owing to a non-hunting mortality ('O') and the other remained unfilled ('U') until the end of the season. (b) Kaplan–Meier survivor curve based on the data in (a) shows the estimated cumulative probability that a quota remains unfilled (black line). Hash marks indicate censoring. The cumulative probability of filling a quota slot (white line) is calculated as the complement of the survivor curve. The performance of hunters in light of management-set quotas [quota-filling performance (QFP)] is the cumulative probability of filling a quota slot at the end of the hunting season.

used Cox proportional hazards models (CPH; Cox 1972) to test for a relationship between hazards (i.e. the instantaneous potential of filling a quota slot) and the relative availability of the target species, expressed as the estimated number of reproductions per quota item. Whereas for parametric survival regression models the shape of the baseline hazard has to be specified, this is not the case for the CPH model, making it the most popular regression approach in survival analysis (Fox 2002). In Norway, independent estimates of the annual number of reproductions (number of females producing offspring) are available on a regional scale for both wolverine and lynx (Linnell *et al.* 2010). Therefore any variation in hazards potentially explained by target species availability is fully absorbed by the division into regions and seasons, that is, each relative availability estimate was associated with a specific region in a given season. This meant we could stratify over region or season, but not both, and the results of the CPH have to be interpreted while considering confounding effects of time and/or space. The highest amount of variation was left for effect estimation when there was no stratification by either region or hunting season. We used penalized polynomial smoothing splines (R function *pspline* in the survival package; Therneau & Lumley 2009) to model nonlinear effects of relative availability on hazard ratios (continuous predictors: the ratio of hazards for one unit difference). We performed model diagnostics following Fox 2002; including tests for proportionality of hazards using the *cox.zph* function (Therneau & Lumley 2009) in R.

Results

QUOTA-FILLING PERFORMANCE

Quota-filling performance varied substantially between the harvest systems included in the study, ranging from very low (wolverine in Norway, 39.7%) to high (lynx in Latvia 98.3%, Table 2). This variation is also revealed by the trajectories of the cumulative probability to fill quotas (Fig. 2). For example, the slow ascent of cumulative probability of filling a wolverine quota slot in Norway is eventually arrested by the end of the hunting season, long before the target quota levels are reached.

Lynx hunters in Latvia, on the other hand, fill their hunting quotas rapidly, reaching prescribed harvest limits nearly 1 month before the end of the season. Seasonal and regional variation in QFP was also high within each system (Table 2).

EFFECT OF TIME OF YEAR

We found nonconstant hazards (i.e. hazards changing over time) for quota-filling in all of the species-country pairs explored. The instantaneous potential to fill a quota slot (i.e. the hazard) could decrease or increase during the year but was generally higher in mid-late winter than in summer/autumn (Fig. 3). This was particularly noticeable for lynx, where hazards increased with time in seasons that began in early November or December (Estonia and Latvia) and decreased with time in seasons that began later in the winter (February, Norway). Hunting seasons for Estonian brown bear began in late summer and ended in the fall; hazards showed an initial increase and then appeared to level off (Fig. 3). The common pattern evident in Fig. 3 of a widening confidence interval around the smoothed hazard may in part be attributed to the growing distance from the lower hazard boundary (0; except Norwegian lynx), but mostly to the increasing uncertainty in the estimate because fewer and fewer quota slots are available for filling as the season progresses.

EFFECT OF RELATIVE AVAILABILITY

Cox proportional hazards models revealed a positive relationship between the instantaneous potential of filling a quota slot (hazard) and the estimate of relative target species availability (number of annual reproductions observed divided by the number of quota slots) for both wolverine and lynx in Norway (Fig. 4). Tests of proportionality of hazards (Fox 2002; Therneau & Lumley 2009) suggested that this assumption was met for wolverine (smallest individual *P*-value = 0.37 for a

Table 2. Quota-filling performance of hunters during recreational hunting seasons for large carnivores

Country	Species	QFP (%)	SD (%)		
			Season × Region	Season	Region
Estonia	Bear	71.7 (68.1–75.4)	39.2	17.6	25
	Lynx	85.0 (83.3–86.7)	24.0	8.1	22.5
	Wolf	83.2 (81.0–85.8)	28.5	20.6	13.6
Latvia	Lynx	98.3 (97.4–99.3)	3.0	3.0	NA
	Wolf	94.7 (93.5–95.7)	8.5	8.5	NA
Norway	Lynx	78.6 (76.1–81.0)	22.8	10.3	10.6
	Wolverine	39.7 (37.1–42.2)	28.6	18.4	16.7

QFP is the quota-filling performance for a season of average length over the combined data for each country–species pair. Bootstrapped 95% CI limits around the QFP estimates are given in parentheses. Standard deviations (SD) for QFP are provided over all individual seasons and regions ('Season × Region'), over all regions pooled by season ('Season'), and seasons pooled by region ('Region'). NA, not available because no regional subdivision.

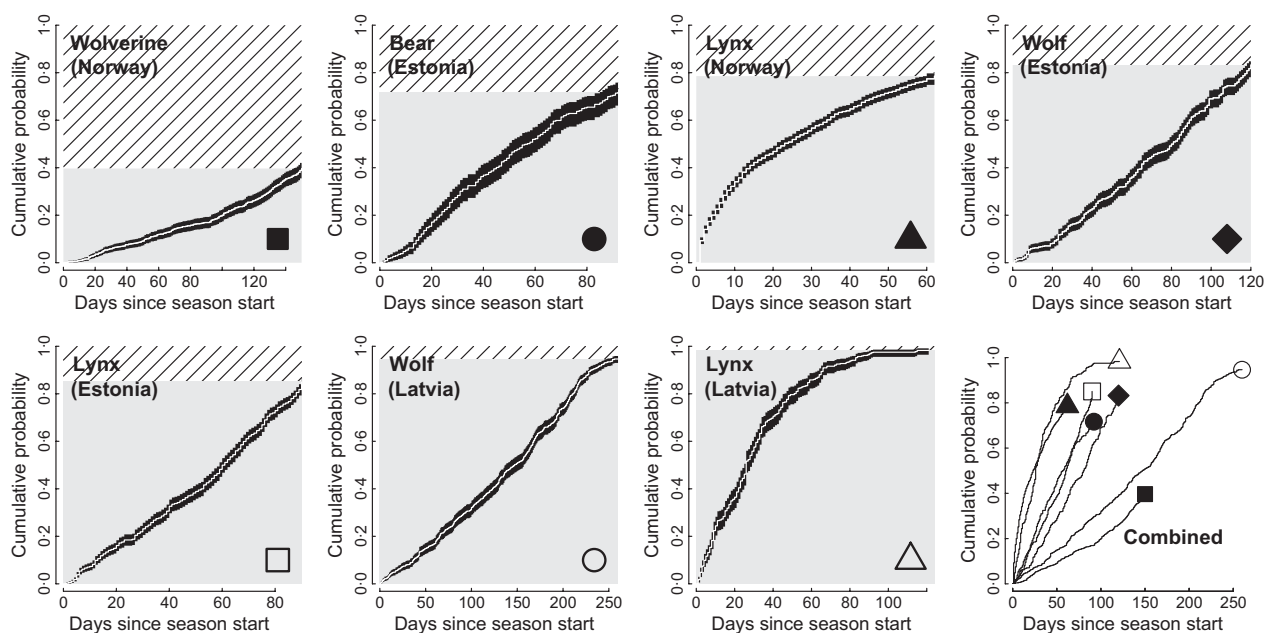


Fig. 2. Cumulative probability of filling hunting quota slots (white lines) for four different carnivore species in three different countries. The black bands around the estimates indicate their 95% confidence limits. Quota-filling performance (QFP) for a season of average length is indicated by the boundary between the grey and the hashed areas in each plot. The graph in the bottom right corner combines all cumulative probability curves (symbols correspond to species–country pairs) for comparison of temporal scale.

smoothing segment), whereas for lynx we had to stratify by region to meet the proportionality of hazards assumption (several P -values < 0.05 before stratification; smallest P -value = 0.56 after stratification).

Discussion

Resource users, such as hunters, are one of the benefactors of sustainable resource management, but can themselves be used as instruments to reach management objectives. This is the case when population control is attempted through the use of recreational hunting, and, as we have shown here, resource managers do not necessarily always get exactly what they want. The discrepancy between harvest intentions by managers and how harvest is realized can be substantial, even when harvest pro-

ceeds legally. In only two out of the seven species–country pairs was the overall QFP of hunters within 10% of the target. This phenomenon is not unique to the systems explored in our study; others have reported harvests that were deficient with respect to quota limits, both in systems with individual (hunter-specific) and overall quotas (African lion *Panthera leo*: Creel & Creel 1997; African lion and cougar *Felis concolor*: Packer et al. 2009; white-tailed deer *Odocoile virginianus* and mule deer *O. hemionus*: Boulanger et al. 2006; elk *Cervus elaphus* Cooper et al. 2002; brown bear *Ursus arctos*: Bischof et al. 2008).

Treating harvest and quota information within a survival analysis framework is an intuitive way of quantifying implementation uncertainty regarding management-set harvest quotas. The approach not only yielded an objective measure of the extent to which harvesters fill quotas (QFP),

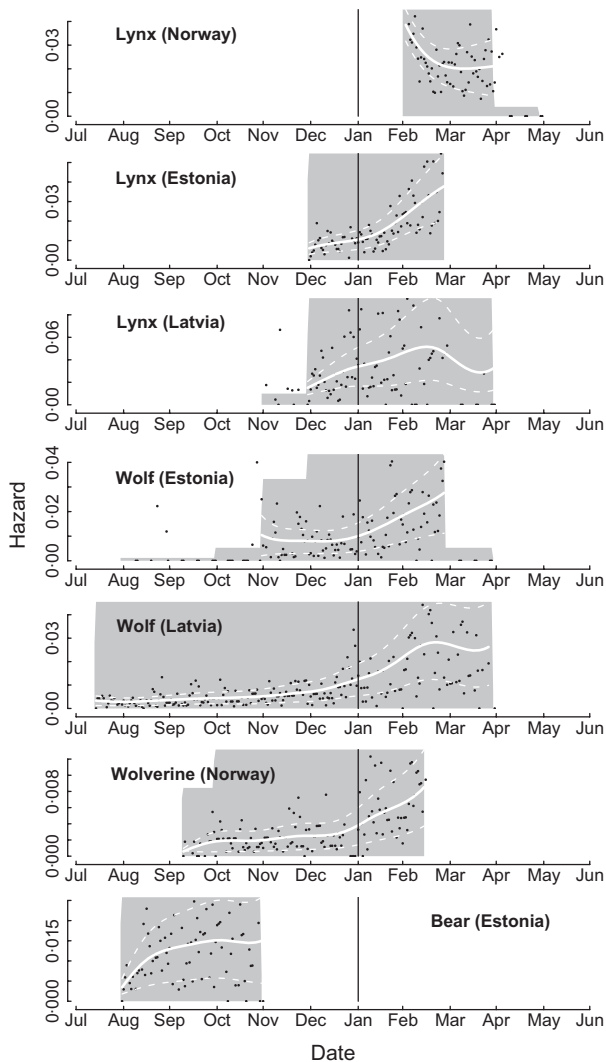


Fig. 3. Instantaneous potential that a quota slot is filled (hazard) during a calendar year. Smooth curves were fit to hazards (black dots) using local polynomial regression (thick white lines). White dashed lines show the fit to the point-wise 95% CI of hazards. Grey blocks provide a visualization of the relative amount of data available for estimating survival; they denote the sum of the number of quota slots (scaled to the range of the y -axis) available at the beginning of all seasons of a given length. To avoid a disproportional influence of rare seasons on the overall shape of the hazard curves, curves were only fit to hazards during common seasons.

but also an assessment of how quota-filling proceeds throughout the season. Much can be gleaned from the shape of the curves of the cumulative probability of filling quotas (Fig. 2), as well as the instantaneous potential to fill quota slots (hazard, Fig. 3). We found evidence of non-constant hazards in all seven systems that we explored. Managers should expect heterogeneity in quota-filling hazards as a result of changing environmental conditions during and between hunting seasons (Kwan, Marsh & Delean 2006). Spatio-temporal variation in hunter effort (Brøseth & Pedersen 2000; Van Vliet *et al.* 2010), and changes in target species availability (Fox & Madsen 1997; Brøseth & Pedersen 2010), are further reasons for expecting heterogeneity in hazards over time. For example, the majority

of lynx hunting in all three countries relies on detecting tracks in the snow, consequently, the probability of filling quotas is likely higher during the winter months with snow (Ozoliņš *et al.* 2007). An increase in hazards for Norwegian wolverine may be explained with the greater vulnerability of the species towards the end of the winter. The majority of wolverines in Norway are harvested using hunting over bait, which is likely to become more enticing as body condition declines and alternative food sources decrease in availability, as has also been suggested for red fox *Vulpes vulpes* (Galby & Hjeljord 2010). Similarly, an increase in the instantaneous potential of filling quotas during the Estonian bear hunting season (Fig. 3) could be due to an increase of susceptibility during the period of increased foraging activity to build up fat deposits which precedes hibernation.

The cumulative probability of filling quota slots and the hazards can provide indication of the effect that changes in hunting seasons and quotas may have. Season extension, without increasing quotas, will have little effect in situations where quotas are filled (or nearly filled) before the end of the current seasons (e.g. wolf in Estonia, lynx and wolf in Latvia). Yet, in such cases, managers are not without control, as they can both increase harvest take by setting higher quotas, perhaps in combination with season extension, or reduce take by reducing quotas and/or season duration. For systems where quotas fall short of management targets, the shape of the hazard curve can give indication about the potential effect of changing the timing of the season. Assuming that the higher hazard we detected during mid to late winter is indeed caused by better lynx hunting conditions, beginning the season earlier, rather than extending it to last longer, may be a more effective way for Norwegian lynx managers to get closer to their harvest goals. This is highly relevant, as it has been suggested that in Norway recreational hunting only serves to limit livestock depredation if it succeeds in reducing the lynx population (Herfindal *et al.* 2005). By contrast, if practically feasible, delaying the end of the hunting season for wolverine in Norway, and bear and lynx in Estonia may bring harvest numbers closer to quota objectives. This could be particularly relevant for wolverine management in Norway. Wolverine hunters are far from reaching the quotas set by the Norwegian management authorities (Fig. 2, Table 2), prompting controversial and costly management operations involving killing of lactating females and cubs in the den and/or helicopter darting/shooting (Tangeland, Skogen & Krangle 2010).

One of the advantages of the approach taken here is that it requires no or little data beyond what most agencies managing hunted species already collect: information about hunting quotas and the date when an individual was killed. However, when additional data are available, a multitude of survival analytical tools provide a robust platform for evaluating as well as predicting the outcome of changes in harvest rules or conditions. For example, CPH models allow for the estimation of effects of space- and time-dependent covariates associated with the hunter community (or even individual hunters, in the case of individual tags rather than overall quotas), management system, the environment, or the game population itself. For

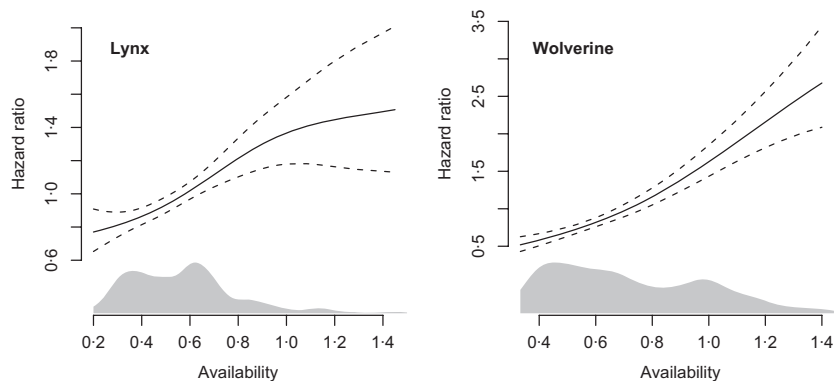


Fig. 4. Ratio of the instantaneous potential to fill a quota slot (hazard ratio) as a function of relative target species availability (number of annual reproductions per quota item) for lynx and wolverine hunting in Norway. Shown are predictions (solid lines) with 95% confidence limits (dashed lines) from Cox proportional hazard models, smoothed using polynomial penalized smoothing splines. The relative amount of data (between quantiles 0.025–0.975) to which models were fitted is shown in grey below each prediction.

illustration, CPH regression confirmed that Norwegian hunters were more likely to fill hunting quotas for lynx and wolverine when the relative availability of these species (per quota slot) was greater (Fig. 4).

Although patterns in the hazards (Fig. 3) and the cumulative probability to fill quota slots (Fig. 2) may help predict the response to changes in season start and end dates, other ethical, socio-economic, or biological constraints also have to be considered. For example, delaying the season end or shifting the entire bear hunting season in Estonia towards a later time in the year could lead to overlap with the period bears spend hibernating in their winter dens. Delaying the season end date for wolverine hunting in Norway would increase the probability of shooting females that have already given birth. Shooting of females that care for dependent young and are lactating is often a cultural taboo among hunters, typically reinforced by regulations (Nilsen & Solberg 2006; Laundre & Hernandez 2008). Furthermore, managers would have to be concerned about unintended demographic and potential economic effects as a result of social disruption (Treves 2009; Creel & Rotella 2010). Although not of major importance in our case studies, fur harvesting is often an important motivation for carnivore hunters and trappers elsewhere. Thus, the ability to influence QFP through adjustments in season lengths or quotas, can be further constrained by the period during which furs are in prime condition (Novak 1987), as well as changing fur prices and bounty levels (Siemer *et al.* 1994; Bartel & Brunson 2003).

Based on our experiences with common large carnivore management policies in the countries studied, our analysis was preoccupied with quotas being left unfilled as quotas were almost never overfilled. By contrast, in many harvest systems hunting rules, such as quotas and seasons, are prescribed with the main motivation to limit user access and thereby reducing the possibility of overharvesting. In such cases, managers will be more concerned about harvests exceeding the limits and may focus on a different set of deviations from goals, for example poaching. Owing to the stealthy nature of illegal resource use, the quantification of implementation uncertainty caused by poaching is more challenging, but nonetheless pressing (Gavin, Solomon & Blank 2010; Liberg *et al.* 2011).

Conclusions

Resource managers and modellers have been encouraged to consider not only the dynamics of a harvested resource, but also account for the rules and uncertainties underlying resource assessment, the process of decision-making behind management controls, and their implementation (Fryxell *et al.* 2010; Milner-Gulland 2011; Milner-Gulland *et al.* 2011). Our results emphasize the need to estimate and incorporate implementation uncertainty into decision-making, possibly aided by an MSE or other comprehensive framework. Illustrating how survival analysis can be used to assess implementation uncertainty in reaching harvest quotas, we have shown that (i) actual resource use may diverge substantially from management-set harvest goals and (ii) the degree to which goals are achieved is highly variable over space and time, both between and within management systems. Whether hunting is considered as an ecological service or not (e.g. Warren 2011), quantifying the discrepancy between what managers want and what hunters do should be considered an important step in adaptive wildlife management.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Accounting for competing risks.

Appendix S2. Example quota data set-up for survival analysis.

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