frontiers in Ecology and Evolution

PERSPECTIVE
published: 26 September 2017
doi: 10.3389/fevo.2017.00118

Harvest Regulations and Implementation Uncertainty in Small Game Harvest Management

Pål F. Moa[1], Lasse F. Eriksen[1,2] and Erlend B. Nilsen[2]*

[1] *Faculty of Biosciences and Aquaculture, Nord University, Steinkjer, Norway,* [2] *Department of Terrestrial Ecology, Norwegian Institute for Nature Research, Trondheim, Norway*

A main challenge in harvest management is to set policies that maximize the probability that management goals are met. While the management cycle includes multiple sources of uncertainty, only some of these has received considerable attention. Currently, there is a large gap in our knowledge about implemention of harvest regulations, and to which extent indirect control methods such as harvest regulations are actually able to regulate harvest in accordance with intended management objectives. In this perspective article, we first summarize and discuss hunting regulations currently used in management of grouse species (*Tetraonidae*) in Europe and North America. Management models suggested for grouse are most often based on proportional harvest or threshold harvest principles. These models are all built on theoretical principles for sustainable harvesting, and provide in the end an estimate on a total allowable catch. However, implementation uncertainty is rarely examined in empirical or theoretical harvest studies, and few general findings have been reported. Nevertheless, circumstantial evidence suggest that many of the most popular regulations are acting depensatory so that harvest bag sizes is more limited in years (or areas) where game density is high, contrary to general recommendations. A better understanding of the implementation uncertainty related to harvest regulations is crucial in order to establish sustainable management systems. We suggest that scenario tools like Management System Evaluation (MSE) should be more frequently used to examine robustness of currently applied harvest regulations to such implementation uncertainty until more empirical evidence is available.

Keywords: game management, sustainable harvest, grouse, implementation, MSE-framework

OPEN ACCESS

Edited by:
James Guy Castley, Griffith University, Australia

Reviewed by:
Viorel Dan Popescu, Ohio University, United States
Robert Justin Irvine, James Hutton Institute, United Kingdom

***Correspondence:**
Erlend B. Nilsen
erlend.nilsen@nina.no

Specialty section:
This article was submitted to Conservation, a section of the journal Frontiers in Ecology and Evolution

Received: *27 June 2017*
Accepted: *14 September 2017*
Published: *26 September 2017*

Citation:
Moa PF, Eriksen LF and Nilsen EB (2017) Harvest Regulations and Implementation Uncertainty in Small Game Harvest Management. Front. Ecol. Evol. 5:118. doi: 10.3389/fevo.2017.00118

INTRODUCTION

An important part of sustainable harvest management is that managers should be able to regulate harvest in agreement with general models, guided by first principles or harvest models developed for a specific system (Sutherland, 2001). Thus, the managers must have a toolbox that allows them to set policies that result in hunter behavior and realized harvest bags that are consistent with their objectives. As a very important background for forming harvest policy, a series of studies in the 1990s identified three main principles that after have been highly influential (Lande et al., 1997): Constant harvest (constant quota), where a fixed number of animals are removed each year; proportional harvest, where a constant proportion of the standing population is harvested each year; and threshold harvest, where only the proportion of the population higher than a predefined threshold is removed through annual harvest (Lande et al., 1995, 1997). From these and other studies, it is well-known that threshold harvesting outperform proportional harvest in terms of optimizing the offtake over a long time span, as well as reducing the risk of population extinction. In addition, constant quota harvest generally perform poor and are associated with an unacceptable high risk of population extinction (Lande et al., 1997).

Going from general principles to on-the-ground implementation in wildlife management is not trivial. A main challenge for managers is to establish systems and policies that align management objectives with realized harvest. Multiple uncertainties affecting the management process makes this particularly challenging (Milner-Gulland et al., 2009; Milner-Gulland and Shea, 2017). Following Williams et al. (2002), four main sources of uncertainty can be recognized in a management cycle: Uncertainty related to environmental variation; uncertainty related to different monitoring uncertainty; implementation uncertainty related to how management decisions are met by the practitioners; and finally, uncertainty related to how a certain system functions and responds to management actions (ecological or structural uncertainty). Compared to other types of uncertainties in the management cycle, implementation uncertainty is much understudied and is thus a poorly understood part of the harvest management cycle (Bicknell et al., 2010; Mustin et al., 2011; Caro et al., 2015). Despite the lack of terrestrial studies focusing on implementation of harvest regulations, we know from the fishery literature that such uncertainty might be even more influential than the other types (Deroba and Bence, 2008), it seems to a large extent to be glossed over in the wildlife harvest management (Bischof et al., 2012). In small game management implementation uncertainty may severely limit our ability to predict the outcome and sustainability of different harvest regulations (Andersen, 2015; Stevens et al., 2017).

To better understand the outcome of different management decisions despite the inherent implementation uncertainty, use of simulation tools may be helpful. One such model framework is known as management strategy evaluation (MSE) (Bunnefeld et al., 2011a). MSE enables comparison of alternative management strategies using numerical simulations, while incorporating uncertainty (Milner-Gulland and Shea, 2017). An MSE model consists of four elements or submodels; (1) a management or harvest decision model, (2) an harvest implementation or user model, (3) a model describing the population dynamics of the harvested species, and (4) and a model simulation the observation processes (i.e., monitoring) (**Figure 1**). This loop simulates feedback to managers about the effect of harvest and the population status prior to the next hunting season, and is thus suitable for testing the outcome of different management decisions. Each component in the MSE concept can be subject to modeling separately or integrated. The aim of this article is to illuminate the hunting regulations used in today's management of grouse (*Tetraonidae*) species in Europe and North-America, with a special focus on the implementation uncertainty that lies in operationalization links from the chosen harvest strategy to the practical solutions and how an MSE-model could be appropriate in such an approach. The bird family *Tetraonidae* includes 20 species distributed in temperate and subarctic regions of the Northern Hemisphere (Storch, 2015), today devoted considerable attention because of a an increasing level of red-listing on one side, and a relatively widespread harvest on the other side (Mustin et al., 2011; Storch, 2015). A better understanding of the precision of the harvest management in these species is therefore a pressing conservation issue.

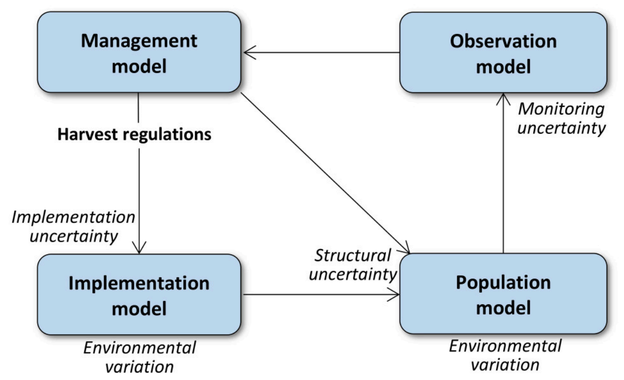

FIGURE 1 | Framework of an MSE model suited for testing scenarios in small game harvest management, through modeling feedback on management decisions. Population estimates obtained through monitoring are basis for harvest regulations set by the management, the regulations are implemented by hunters, and actual harvest rates are incorporated in a population model. The different sources of uncertainty must be taken into consideration in the loop.

FROM PRINCIPLES TO ON-THE-GROUND IMPLEMENTATION

Our synopsis of the literature on grouse harvest management in Europe and North-America suggest that proportional harvest schemes are often used or recommended used, with threshold harvest or proportional threshold harvest also being reported. Examples include those used or suggested for willow ptarmigan (*Lagopus lagopus*) in Sweden and Norway (Willebrand and Hörnell, 2001; Pedersen et al., 2004; Sandercock et al., 2011; Eriksen et al., 2017), forest grouse in Finland (Kurki and Putaala, 2010), red grouse (*Lagopus scotica*) in UK (Hudson and Newborn, 1995; Hudson and Dobson, 2001), as well as greater sage-grouse (*Centrocercus urophasianus*), and greater prairie-chicken (*Tympanuchus cupido*) in USA (Connelly et al., 2003; Gibson et al., 2011; Powell et al., 2011).

Even if estimates of population density (or abundance) is needed to make management decisions in most of the reported cases, management decisions are also sometimes based solely on knowledge about annual reproduction as derived from adult:juvenile ratios. One example is found in Norway, where it has been suggested that willow ptarmigan harvest should only take place in years when chicks per hen is >2.5 in autumn (Kastdalen, 1992; Steen and Erikstad, 1996). A caveat with such an approach is that high harvest rates in years with high recruitment even if population densities are low, is counter to general recommendations of more conservative harvest at low densities.

LIMITING TOTAL ALLOWABLE CATCH (TAC)

When managers try to regulate harvest offtake in accordance with general principles such as proportional harvest, they often do so by limiting total allowable catch (TAC). This can be done either by limiting the number of hunting permits and/or regulating the size of the quota allocated to each permit (i.e., bag limit). Although our synopsis does not allow any quantitative assessment of frequency of use, we notice that daily bag-limits are frequently reported (**Table 1**). Interestingly, bag limits are often criticized because they lack precision in the ability to control harvest rates, even if the bag limit changes in response to population size (Andersen, 2015). In addition, concerns have been raised because the catchability coefficient seem to be inversely density dependent (Andersen and Kaltenborn, 2013; Eriksen et al., 2017) creating a risk that harvest rates become higher at low population densities (se e.g., from the fishery literature; Harley et al., 2001; Ward et al., 2013; van Poorten et al., 2016). It has been indicated that managers can achieve more control of offtake by allocating seasonal quotas to individual hunters or hunting teams (see e.g., Gibson et al., 2011), where the hunters/teams are allocated a given proportion of total area quota (see e.g., Kurki and Putaala, 2010). While some support might be found in e.g., Eriksen et al. (2017), the generality of this statement remains unstudied. Reducing the number of hunting permits will also reduce TAC as long as bag limits are not increased as a response (Caro et al., 2015). Obviously, a cap on the total number of permits is common, and some land owners in addition restrict access to the hunting terrains based on residency, either differing between national vs. international hunters (Lindberget, 2009) or local vs. non-local residents (e.g., on state land in southern Norway; Andersen, 2015). However, because of its potential negative social and economic effects at a local scale, regulating the number of licenses as a direct response to the population size does not seem to be a common regulation tool (Andersen et al., 2010).

Beyond the more common quota-based regulations described above, use of selective harvest of certain age- and sex categories has also been suggested. Selective harvest of males has been reported in species with clear sexual dimorphism, such as e.g., the capercaillie (*Tetrao urogallus*) (Lindén, 1991; Helle et al., 1999). The suggestion relating to age categories is based on the fact that harvest of adults are more likely to be additive to other mortality sources (Pedersen et al., 2004; Péron, 2013), so the harvest is skewed toward the juveniles. Even if the demographic effects of age-selective harvest could be significant in e.g., ptarmigans (Bunnefeld et al., 2011b), this kind of regulation does not seem to be commonly used in the management of these species (**Table 1**).

LIMITING TOTAL HUNTING EFFORT OR EFFICIENCY

Limiting total hunting effort (e.g., measured as number of hunting days km^{-2}) is another way to indirectly control harvest, and has been reported used, for instance on state owned land in Sweden (**Table 1**). There, a constant effort model (allowing a total effort of three hunting days km^{-2}) is used to limit harvest rates where harvest is closed once are reached (Willebrand et al., 2011). For proportional harvest from to arise from constant effort policy, the underlying assumption is that the catchability coefficient is not density dependent (Fryxell et al., 2014). The sustainability of constant effort models might be compromised if there are large variations in the catchability between habitats, groups of hunters, and in particular if the catchability coefficient is density dependent (Mackinson et al., 1997; Willebrand et al., 2011; Eriksen et al., 2017). Based on current knowledge from field studies of grouse (Willebrand et al., 2011; Eriksen et al., 2017) and theoretical models (Mackinson et al., 1997), caution should be exercised when applying constant effort models to regulate harvest. Rather than a direct regulation of hunting effort, restricting the length of the hunting season is also used to limit (but not regulate) effort. When using season length to limit harvest, higher demographic value late in the hunting season comlplicates calculations of sustainable harvest rates (Kokko and Lindström, 1998; Kokko, 2001; Brøseth et al., 2012; Sunde and Asferg, 2014). Non-synchronized onset of the hunting season across regions could also result in increased harvest effort, if the most eager hunters tour to take part in the first week of the hunt as new areas are opened for hunting (Connelly et al., 2003; Pedersen and Karlsen, 2007; Blomberg, 2015).

Complicating the implementation of harvest strategies further, hunting pressure will most often be spatially heterogeneous also within management units (see e.g., FitzGibbon, 1998). For instance, hunting pressure has been reported to be higher closer to access points for the hunt, such as roads and cabins (Brøseth and Pedersen, 2000). To limit the size of the harvest bags, some managers therefore reduce access to the hunting areas by closing roads and/or cabins used by hunters as reported from willow ptarmigan management in Norway (Moa et al., 2013). Establishment of no-hunt areas (refuges) are also known from the management of ptarmigans in Sweden and Norway (Willebrand and Hörnell, 2001; Andersen, 2015). The main idea is to establish a source-sink dynamic (Pulliam, 1988) between harvested and non-harvested areas (see e.g., Novaro et al., 2005). So far, the effect of refuges on ptarmigan population dynamics remains unclear because of uncertainty related to the spatial distribution and settlement strategies (Kvasnes et al., 2015). Besides from addressing hunting effort, regulations aiming to reduce the hunting efficiency may also be implemented. These may include restrictions on hunting techniques or equipment, mainly related to gun types and/or banning hunting with dogs (**Table 1**).

IMPLEMENTATION UNCERTAINTY IN CURRENT GROUSE MANAGEMENT

Our discussion above on the main results from the available literature suggests that in most cases, managers do not know how to best achieve the target harvest rates or harvest bag,

TABLE 1 | Harvest regulations with related practical solutions described or reported applied in the management of grouse in Europe and North America.

Harvest regulations		Practical solutions	Described (D) or applied (A)	Species	Study area	References
Limit the total allowable catch (TAC)	Reduce the number of hunting permits and/or size of quota	Area quota	D	Forest grouse*	Finland	Kurki and Putaala, 2010
			A	Red grouse (*Lagopus lagopus scotica*)	UK	Hudson and Dobson, 2001 and references therein
			D	Red grouse (*Lagopus lagopus scotica*)	UK	Newey and Smith, 2010
			A	Willow ptarmigan (*Lagopus lagopus*)	Norway	Sandercock et al., 2011
			D	Willow ptarmigan (*Lagopus lagopus*)	Norway	Andersen et al., 2010
			D	Willow ptarmigan (*Lagopus lagopus*)	Norway	Andersen et al., 2014
		Seasonal/ periodical quota (bag limit) per hunter	A	Greater sage-grouse (*Centrocercus urophasianus*)	USA (Idaho)	Connelly et al., 2003
			A	Greater sage-grouse (*Centrocercus urophasianus*)	USA (California)	Gibson et al., 2011
			A	Greater prairie-chicken (*Tympanuchus cupido*)	USA (Nebraska)	Powell et al., 2011
			D	Willow ptarmigan (*Lagopus lagopus*)	Norway	Andersen et al., 2010
			D	Willow ptarmigan (*Lagopus lagopus*)	Norway	Andersen et al., 2014
			A	Willow ptarmigan (*Lagopus lagopus*)	Norway	Eriksen et al., 2017
		Daily quota (bag limit) per hunter	D	Forest grouse*	Finland	Kurki and Putaala, 2010
			A	Greater sage-grouse (*Centrocercus urophasianus*)	USA (Idaho)	Connelly et al., 2003
			A	Greater sage-grouse (*Centrocercus urophasianus*)	USA (California)	Gibson et al., 2011
			D	Willow ptarmigan (*Lagopus lagopus*)	Norway	Andersen et al., 2010
			D	Willow ptarmigan (*Lagopus lagopus*)	Norway	Andersen et al., 2014
			A	Willow ptarmigan (*Lagopus lagopus*)	Norway	Eriksen et al., 2017
	Selective hunting	Selective hunting related to sex	A	Capercaillie (*Tetrao urogallus*)	Finland	Helle et al., 1999
			A	Black grouse (*Tetrao tetrix*)	France	Caizergues and Ellison, 1997
			D	Forest grouse**	Finland	Lindén, 1991
		Selective hunting related to age	A	Willow ptarmigan (*Lagopus lagopus*)	Norway	Røstad, 2008
Limit the total hunting effort	Reduce the number of hunters	Reduce the number of sold hunting permits	D	Willow ptarmigan (*Lagopus lagopus*)	Norway	Andersen et al., 2010
			D	Willow ptarmigan (*Lagopus lagopus*)	Norway	Andersen et al., 2014
	Affect the length of the hunting season	Narrower hunting period	A	Blue grouse (*Dendragapus obscurus*)	USA (Colorado)	Hoffman, 1985
			A	Greater sage-grouse (*Centrocercus urophasianus*)	USA (Colorado)	Braun and Beck, 1985
			A	Greater sage-grouse (*Centrocercus urophasianus*)	USA (Colorado)	Blomberg, 2015
			D	Rock ptarmigan (*Lagopus muta*)	Iceland	Beck and Sigursteindóttir, 2010
			A	Willow ptarmigan (*Lagopus lagopus*)	Norway	Eriksen et al., 2017
		Equal starting point for the hunting season	D	Willow ptarmigan (*Lagopus lagopus*)	Norway	Pedersen and Karlsen, 2007
	Reduce the access to the hunting area	Close roads leading to hunting areas and/or cabins for overnight in hunting areas	D	Ruffed grouse (*Bonasa umbellus*)	USA (Wisconsin)	Small et al., 1991
			D	Willow ptarmigan (*Lagopus lagopus*)	Norway	Pedersen and Karlsen, 2007
		Use of non-hunting areas (refuges)	A	Willow ptarmigan (*Lagopus lagopus*)	Sweden	Willebrand and Hörnell, 2001
			D	Willow ptarmigan (*Lagopus lagopus*)	Sweden	Hörnell-Willebrand, 2010
			A	Willow ptarmigan (*Lagopus lagopus*)	Norway	Moa et al., 2013
Limit the total hunting efficiency	Techniques or equipment restrictions	Ban hunting with dogs	D	Willow ptarmigan (*Lagopus lagopus*)	Norway	Andersen et al., 2010
		Limitations on the number of shots that can be fired from a gun before recharging	D	Willow ptarmigan (*Lagopus lagopus*)	Norway	Andersen and Kaltenborn, 2013

** Capercaillie (Tetrao urogallus), black grouse (Tetrao tetrix), hazel grouse (Bonasa bonasia), and willow ptarmigan (Lagopus lagopus).*

*** Capercaillie (Tetrao urogallus), black grouse (Tetrao tetrix), and hazel grouse (Bonasa bonasia).*

and that harvest rates rarely can be controlled directly. Rather, managers are using indirect means to limit or regulate harvest off take. This means that even in cases where the managers have good knowledge about the ecological processes that drives the system dynamics, and access to accurate monitoring of population abundance, they still might not know which tools to grab for in their toolbox to ensure effective implementation of management decisions. Although not explicitly addressed in grouse management, it is to be expected that the uncertain implementation of harvest management regulations will vary depending on the degree of controllability (Andersen et al., 2014; Andersen, 2015). So too are the consequences; in the context of grouse management, failing to reach a given TAC is rarely considered an ecological sustainability problem (Andersen, 2015). Nevertheless, failing to properly include this in the management plans, the management might still sub-optimal from a socioeconomic perspective if quotas are too restrictive when population abundance is high (Wam et al., 2012, 2013). Violations of regulations could on result in unsustainable management also in cases when TAC is based on sound ecological principles, and management systems should therefore contain elements of control, i.e., monitoring of compliance with regulations, to examine whether there is accordance between the rules in question and the compliance (Wiedenmann et al., 2013).

When field studies or experiments are not feasible, setting up mathematical simulation models to assess how the system behaves under a range of conditions, and how sensitive management objectives are to certain parameters is often a useful way forward. In the management of natural resources, MSE models are particularly suitable because they allow complex relationships between the biological resource and the harvest management (Bunnefeld et al., 2011a; Punt et al., 2016). Eriksen et al. (2017) recently showed that increased implementation uncertainty can have a substantial effect on the risk of overharvest in the management of willow ptarmigan in Norway. By numerical simulations, they found that the risk of exceeding commonly used ptarmigan harvest thresholds was notably higher with increased implementation model uncertainty, especially at medium game densities. In addition to contributing to the understanding of uncertainty in the harvest of a small game species, the example shows the advantage of collecting high quality data for model development, as high model uncertainties will result in less precision in an integrated MSE model. Even if the MSE models only recently have been introduced to the management of terrestrial biodiversity (Milner-Gulland et al., 2010), we believe that applying this framework in modern grouse management may provide greater precision in predicting actual harvest given different management decisions.

CONCLUSION

Based on our synopsis of the literature, it seems clear that there is a dearth of detailed studies on how harvest policies and regulations actually limit harvest rates. Similar concerns were raised by Stevens et al. (2017) in a recent study using structured decision making models to establish wild turkey (*Meleagris gallopavo*) harvest reference points. Such uncertainty makes it hard to design harvest management plans based on first principles (e.g., proportional harvest strategies), because even if the managers change TAC in response to fluctuations in population density, a proportionate change in realized harvest rates do not necessarily follow. To date, the relative contribution of various sources of uncertainty to our ability to predict the ecological outcome of different harvest management strategies has not been quantified in grouse harvest. Based on our synopsis, we do not know if the contribution from implementation uncertainty to the overall uncertainty is higher or lower that the other sources of uncertainty in the management cycle, but we suspect it to resembles the situation reported by Deroba and Bence (2008) from the fisheries. The most serious consequence of this is probably the increased risk of excessive harvest rates as population densities declines (Eriksen et al., 2017), due to density dependent catchability coefficients (Mackinson et al., 1997). If science should continue to guide harvest management it is crucial that this we start filling this knowledge gap. From our perspective we need both empirical and simulation studies to start filling this gap. First, inspired by the fisheries literature (e.g., Harley et al., 2001) we need large-scale and cross species examinations of know how often, and under which conditions, density dependent catchability coefficients (i.e., hyperstability) are most likely to arise. In these cases, we suspect that strict regulations are particularly important at low population densities. For this to be achievable more complete and accurate data sampling from the management process is needed. Second, until we have a better empirical understanding of the relationship between harvest policy and regulations and realized harvest, use of simulations tools like MSE will be useful to better understand the sensitivity of the socio-ecological systems at stake to untested assumptions about how harvest regulations actually regulate harvest rates.

AUTHOR CONTRIBUTIONS

EN conceived the main idea. PM reviewed the literature. PM, LE, and EN wrote the manuscript. PM, LE, and EN approved the final version.

FUNDING

This research was funded by a grant from “Regionale forskningsfond Midt-Norge (RFF-MIDT)” (grant # 245818).

ACKNOWLEDGMENTS

The manuscript benefited from discussions with colleagues at NINA, local and regional grouse managers in Norway, and project-partners from Naturporten in Lierne, Norway.

REFERENCES

Andersen, O. (2015). *Hunter Characteristics and Preferences for Harvest Control Rules*. PhD thesis, Hedmark University College.

Andersen, O., and Kaltenborn, B. P. (2013). *Does a Hunter's Catch-Per-Unit-Effort Reflect Willow Ptarmigan Abundance?* Utmark. Available online at: www.utmark.org

Andersen, O., Kaltenborn, B. P., Pedersen, H. C., Storaas, T., Solvang, H., Moa, P. F., et al. (2010). *Survey among Willow Ptarmigan Hunters after Hunting Season 2006/07. Data and Key Findings from The Grouse Management Project 2006-2011*. NINA Report 379. English summary.

Andersen, O., Kaltenborn, B. P., Vittersø, J., and Willebrand, T. (2014). Preferred harvest principles and-regulations amongst willow ptarmigan hunters in Norway. *Wildl. Biol.* 20, 285–290. doi: 10.2981/wlb.00048

Beck, S. R., and Sigursteindóttir, H. (2010). "Ptarmigan Lagopus muta in Iceland," in *"Game Monitoring Systems Supporting the Development of Sustainable Hunting Tourism in Northern Europe: A Review of Current Practises,* eds S. Newey, F. Dahl. and S. Kurki (Helsinki: University of Helsinki; Ruralia Institute Reports), 66.

Bicknell, J., Smart, J., Hoccom, D., Amar, A., Evans, A., Walton, P., et al. (2010). *Impacts of Non-native Gamebird Release in the UK: A Review*. RSPB research report.

Bischof, R., Nilsen, E. B., Brøseth, H., Männil, P., Ozolinš, J., and Linnell, J. D. (2012). Implementation uncertainty when using recreational hunting to manage carnivores. *J. Appl. Ecol.* 49, 824–832. doi: 10.1111/j.1365-2664.2012.02167.x

Blomberg, E. J. (2015). The influence of harvest timing on greater sage-grouse survival: a cautionary perspective. *J. Wildl. Manage.* 79, 695–703. doi: 10.1002/jwmg.887

Braun, C., and Beck, T. (1985). "Effects of changes in hunting regulations on sage grouse harvest and populations," in *Game Harvest Management*, eds S. L. Beason and S. F. Robertson (Kingsville, TX: Caesar Kleberg Wildlife Research Institute), 327–334.

Brøseth, H., and Pedersen, H. C. (2000). Hunting effort and game vulnerability studies on a small scale: a new technique combining radio-telemetry, GPS and GIS. *J. Appl. Ecol.* 37, 182–190. doi: 10.1046/j.1365-2664.2000.00477.x

Brøseth, H., Nilsen, E. B., and Pedersen, H. C. (2012). Temporal quota corrections based on timing of harvest in a small game species. *Eur. J. Wildl. Res.* 58, 797–802. doi: 10.1007/s10344-012-0625-3

Bunnefeld, N., Hoshino, E., and Milner-Gulland, E. J. (2011a). Management strategy evaluation: a powerful tool for conservation? *Trends Ecol. Evol.* 26, 441–447. doi: 10.1016/j.tree.2011.05.003

Bunnefeld, N., Reuman, D. C., Baines, D., and Milner-Gulland, E. J. (2011b). Impact of unintentional selective harvesting on the population dynamics of red grouse. *J. Anim. Ecol* 80, 1258–1268. doi: 10.1111/j.1365-2656.2011.01862.x

Caizergues, A., and Ellison, L. N. (1997). Survival of black grouse *Tetrao tetrix* in the French Alps. *Wildl. Biol.* 3, 177–186.

Caro, J., Delibes-Mateos, M., Viñuela, J., López-Lucero, J. F., and Arroyo, B. (2015). Improving decision-making for sustainable hunting: regulatory mechanisms of hunting pressure in red-legged partridge. *Sustain. Sci.* 10, 479–489. doi: 10.1007/s11625-015-0302-z

Connelly, J. W., Reese, K. P., Garton, E. O., and Commons-Kemner, M. L. (2003). Response of greater sage-grouse *Centrocercus urophasianus* populations to different levels of exploitation in Idaho, USA. *Wildl. Biol.* 9, 335–340.

Deroba, J. J., and Bence, J. R. (2008). A review of harvest policies: understanding relative performance of control rules. *Fish. Res.* 94, 210–223. doi: 10.1016/j.fishres.2008.01.003

Eriksen, L. F., Moa, P. F., and Nilsen, E. B. (2017). Quantifying risk of overharvest when implementation is uncertain. *J. Appl. Ecol.* doi: 10.1111/1365-2664.12992. [Epub ahead of print].

FitzGibbon, C. (1998). *The Management of Subsistence Harvesting: Behavioral Ecology of Hunters and their Mammalian Prey: Behavioural Ecology and Conservation Biology*. Oxford, UK; New York, NY: Oxford University Press.

Fryxell, J. M., Sinclair, A. R., and Caughley, G. (2014). *Wildlife Ecology, Conservation, and Management, 3rd Edn.* Oxford, UK: John Wiley & Sons.

Gibson, R., Bleich, V., McCarthy, C., and Russi, T. (2011). Hunting lowers population size in greater sage-grouse. *Stud. Avian Biol.* 39, 307–316.

Harley, S. J., Myers, R. A., and Dunn, A. (2001). Is catch-per-unit-effort proportional to abundance? *Can. J. Fish. Aquat.* 58, 1760–1772. doi: 10.1139/f01-112

Helle, P., Kurki, S., and Linden, H. (1999). Change in the sex ratio of the Finnish capercaillie *Tetrao urogallus* population. *Wildl. Biol.* 5, 25–31.

Hoffman, R. (1985). "Effects of changes in hunting regulations on blue grouse populations," in *Game Harvest Management*, eds S. L. Beason and S. F. Robertson (Kingsville, TX: Caesar Kleberg Wildlife Research Institute), 327–334.

Hörnell-Willebrand, M. (2010). "Willow grouse in the Swedish mountains," in *Game Monitoring Systems Supporting the Development of Sustainable Hunting Tourism in Northern Europe: A Review of Current Practises,* eds S. Newey, F. Dahl, and S. Kurki (Helsinki: University of Helsinki; Ruralia Institute Reports), 66.

Hudson, P. J., and Dobson, A. P. (2001). Harvesting unstable populations: red grouse *Lagopus lagopus scoticus*(Lath.) in the United Kingdom. *Wild Biol.* 7, 189–195.

Hudson, P., and Newborn, D. (1995). *Red Grouse and Moorland Management*. Game Conservancy Trust, Fordingbridge.

Kastdalen, L. (1992). *Skogshøns og jakt.* Rapport. Norges jeger og fiskerforbund.

Kokko, H. (2001). Optimal and suboptimal use of compensatory responses to harvesting: timing of hunting as an example. *Wild Biol.* 7, 141–150.

Kokko, H., and Lindström, J. (1998). Seasonal density dependence, timing of mortality, and sustainable harvesting. *Ecol. Modell.* 110, 293–304. doi: 10.1016/S0304-3800(98)00089-1

Kurki, S., and Putaala, A. (2010). "Forest grouse species on state land in northern Finland," in *Game Monitoring Systems Supporting the Development of Sustainable Hunting Tourism in Northern Europe: A Review of Current Practises,* eds S. Newey, F. Dahl, and S. Kurki (Helsinki: University of Helsinki; Ruralia Institute Reports), 66.

Kvasnes, M. A., Pedersen, H. C., Solvang, H., Storaas, T., and Nilsen, E. B. (2015). Spatial distribution and settlement strategies in willow ptarmigan. *Popul. Ecol.* 57, 151–161. doi: 10.1007/s10144-014-0454-1

Lande, R., Engen, S., and Saether, B.-E. (1995). Optimal harvesting of fluctuating populations with a risk of extinction. *Am. Nat.* 145, 728–745. doi: 10.1086/285765

Lande, R., Sæther, B.-E., and Engen, S. (1997). Threshold harvesting for sustainability of fluctuating resources. *Ecology* 78, 1341–1350. doi: 10.1890/0012-9658(1997)078[1341:THFSOF]2.0.CO;2

Lindberget, M. (2009). *Användande av Avskjutningsstatsitik i Förvaltning. Påverkar Tidigare Jakt Cpue?* Master thesis, Sveriges lantbruksuniversitet.

Lindén, H. (1991). Patterns of grouse shooting in Finland. *Ornis Scand.* 22, 241–244.

Mackinson, S., Sumaila, U. R., and Pitcher, T. J. (1997). Bioeconomics and catchability: fish and fishers behaviour during stock collapse. *Fish. Res.* 31, 11–17. doi: 10.1016/s0165-7836(97)00020-9

Milner-Gulland, E., and Shea, K. (2017). Embracing uncertainty in applied ecology. *J. Appl. Ecol.* doi: 10.1111/1365-2664.12887. [Epub ahead of print].

Milner-Gulland, E., Arroyo, B., Bellard, C., Blanchard, J., Bunnefeld, N., Delibes-Mateos, M., et al. (2010). New directions in management strategy evaluation through cross-fertilization between fisheries science and terrestrial conservation. *Biol. Lett.* 6, 719–722. doi: 10.1098/rsbl.2010.0588

Milner-Gulland, E., Bunnefeld, N., and Proaktor, G. (2009). "The science of sustainable hunting," in *Recreational Hunting, Conservation and Rural Livelihoods,* eds B. Dickson, J. Hutton, and W. A. Adams (Oxford, UK: John Wiley & Sons), 75–93.

Moa, P. F., Nilsen, E. B., Hagen, B. R., and Sund, T. (2013). *Natural Ptarmigan Refuges; Do They Exist and Do They Result in Higher Ptarmigan Densities?* Utmark. Available online at:www.utmark.org.

Mustin, K., Newey, S., Irvine, J., Arroyo, B., and Redpath, S. (2011). *Biodiversity Impacts of Game Bird Hunting and Associated Management Practices in Europe and North America*. RSPB research report.

Newey, S., and Smith, A. (2010). "Red grouse *Lagopus lagopus scoticus* in Scotland," in *Game Monitoring Systems Supporting the Development of Sustainable Hunting Tourism in Northern Europe: A Review of Current Practises,* eds S. Newey, F. Dahl, and S. Kurki (University of Helsinki; Ruralia Institute Reports), 66.

Novaro, A. J., Funes, M. C., and Walker, R. S. (2005). An empirical test of source–sink dynamics induced by hunting. *J. Appl. Ecol.* 42, 910–920. doi: 10.1111/j.1365-2664.2005.01067.x

Pedersen, H. C., Steen, H., Kastdalen, L., Brøseth, H., Ims, R. A., Svendsen, W., et al. (2004). Weak compensation of harvest despite strong density–dependent growth in willow ptarmigan. *Proc. R. Soc. Lond. B Biol. Sci.* 271, 381–385. doi: 10.1098/rspb.2003.2599

Pedersen, H., and Karlsen, D. (2007). *Alt Om Rypa*. Oslo: Tun forlag.

Péron, G. (2013). Compensation and additivity of anthropogenic mortality: life-history effects and review of methods. *J. Anim. Ecol.* 82, 408–417. doi: 10.1111/1365-2656.12014

Powell, L. A., Taylor, J. S., Lusk, J., and Matthews, T. W. (2011). "Adaptive harvest management and harvest mortality of greater prairie-chickens," in *Ecology, Conservation, and Management of Grouse: Cooper Ornithological Society* (Berkeley; Los Angeles: University of California Press), 39.

Pulliam, H. R. (1988). Sources, sinks, and population regulation. *Am. Nat.* 132, 652–661. doi: 10.1086/284880

Punt, A. E., Butterworth, D. S., Moor, C. L., De Oliveira, J. A., and Haddon, M. (2016). Management strategy evaluation; best practices. *Fish* 17, 303–334. doi: 10.1111/faf.12104

Røstad, H. (2008). *Selective Hunting Mortality in Willow Ptarmigan (*Lagopus lagopus*) and Uncertainty in Harvest Data Based on Wing Samples*. Master thesis, Norwegian University of Life Sciences.

Sandercock, B. K., Nilsen, E. B., Brøseth, H., and Pedersen, H. C. (2011). Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. *J. Anim. Ecol.* 80, 244–258. doi: 10.1111/j.1365-2656.2010.01769.x

Small, R. J., Holzwart, J. C., and Rusch, D. H. (1991). Predation and hunting mortality of ruffed grouse in central Wisconsin. *J. Wildl. Manage.* 55, 512–520. doi: 10.2307/3808983

Steen, H., and Erikstad, K. E. (1996). Sensitivity of willow grouse Lagopus lagopus population dynamics to variations in demographic parameters Wildl. *Biology* 2, 27–35.

Stevens, B. S., Bence, J. R., Porter, W. F., and Jones, M. L. (2017). Identifying target reference points for harvesting assessment-limited wildlife populations: a case study. *Ecol. Appl.* 27, 1916–1931. doi: 10.1002/eap.1577

Storch, I. (2015). "Conservation status and threats to grouse worldwide: an update," in *13th International Grouse Symposium* (Reykjavik)

Sunde, P., and Asferg, T. (2014). How does harvest size vary with hunting season length? *Wildl. Biol.* 20, 176–184. doi: 10.2981/wlb.00021

Sutherland, W. J. (2001). Sustainable exploitation: a review of principles and methods. *Wildl. Biol.* 7, 131–140.

van Poorten, B. T., Walters, C. J., and Ward, H. G. M. (2016). Predicting changes in the catchability coefficient through effort sorting as less skilled fishers exit the fishery during stock declines. *Fish. Res.* 183, 379–384. doi: 10.1016/j.fishres.2016.06.023

Wam, H. K., Andersen, O., and Pedersen, H. (2013). Grouse hunting regulations and hunter typologies in Norway. *Hum. Dimens. Wildl.* 18, 45–57. doi: 10.1080/10871209.2012.686082

Wam, H. K., Pedersen, H. C., and Hjeljord, O. (2012). Balancing hunting regulations and hunter satisfaction: an integrated biosocioeconomic model to aid in sustainable management. *Ecol. Econ.* 79, 89–96. doi: 10.1016/j.ecolecon.2012.04.022

Ward, H. G. M., Askey, P. J., and Post, J. R. (2013). A mechanistic understanding of hyperstability in catch per unit effort and density-dependent catchability in a multistock recreational fishery. *Can. J. Fish. Aquat.* 70, 1542–1550. doi: 10.1139/cjfas-2016-0260

Wiedenmann, J., Wilberg, M. J., and Miller, T. J. (2013). An evaluation of harvest control rules for data-poor fisheries. *N. Am. J. Fish. Manage.* 33, 845–860. doi: 10.1080/02755947.2013.811128

Willebrand, T., and Hörnell, M. (2001). Understanding the effects of harvesting willow ptarmigan *Lagopus lagopus* in Sweden. *Wildl. Biol.* 7, 205–212.

Willebrand, T., Hörnell-Willebrand, M., and Asmyhr, L. (2011). Willow grouse bag size is more sensitive to variation in hunter effort than to variation in willow grouse density. *Oikos* 120, 1667–1673. doi: 10.1111/j.1600-0706.2011.19204.x

Williams, B. K., Nichols, J. D., and Conroy, M. J. (2002). *Analysis and Management of Animal Populations*. Cambridge: Academic Press.

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.