Høgskolen i Hedmark

Faculty of Applied Ecology and Agricultural Sciences

Oddgeir Andersen

PhD Thesis

Hunter characteristics and preferences for harvest control rules

PhD in Applied Ecology
2015

Hedmark University College

Printed in Norway: Flisa Trykkeri
Place of Publication: Elverum, Norway

PhD Dissertations in Applied Ecology
Ph.d.-avhandlinger i anvendt økologi

ISBN: 978-82-7671-962-8
ISSN: 1894-6127

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Samtykker til utlån hos høgskolebiblioteket	JA ☒	NEI ☐
Samtykker til tilgjengeliggjøring i digitalt arkiv Brage	JA ☒	NEI ☐

Preface

When I started my studies in wildlife management at Hedmark University College, back in 1994, I was introduced to an extraordinary teacher in ecology, Dr. Torstein Storaas. His lessons were really inspiring , but he also acknowledged that there was quite a lot we really did not know much about in nature, for example the effects of human interaction with nature. Everything fluctuates, he said. That was the start of my curiosity for ecology. I already had the passion for being in - and harvesting from nature. That came from my father during my early childhood. When Hedmark University College started the education program in applied ecology in 2006, I joined the MSc program and that gave me the inspiration to continue my studies.

I am thankful to many people who have inspired me during this process. First, to the teachers on the Applied Ecology program at Hedmark University College, and to my colleagues. No one mentioned and no one forgotten. Thanks to my previous research director, Dr. Jostein Skurdal, and my employer, Norwegian institute for nature research (NINA), for giving me the possibility to start on my PhD education besides other working duties, which can be really stressful. A lot of thanks to my dear friend, colleague and co-supervisor Dr. Bjørn Petter Kaltenborn, for inspiring discussions and hunting trips together, to my supervisor Professor Tomas Willebrand for constructive and sometimes challenging discussions when I was frustrated with progress or struggled with analyses, and to co-supervisor Professor Joar Vittersø at the University of Tromsø for helping me with statistical questions and analyses.

However, I am most grateful to my nearest family; my wife, my children and friends who has tolerated a lot of mental absence from me although I physically was present, when thinking and focusing on my PhD-work during my spare time in the afternoons during the last year.

I dedicate this thesis to two of the most important persons in my life and a dog that was special to me. First, to my dearly beloved, patient and supportive wife Anne Lene, for always being there and encouraging me. Then, to my deceased Dad who taught me to love nature, and to gordon setter “Kikki” for all the good moments you gave me in the mountains when we hunted willow ptarmigan. I miss you both.

Lillehammer, 20. February 2015

Oddgeir Andersen

Content

Sammendrag

Målet med avhandlingen er å øke kunnskapen om jegere, og vise eksempler på hvordan denne kunnskapen kan tilpasses i jaktforvaltningen. Jeg har studert rypejegere og hjortejegere, fordi disse jegerne jakter på to arter som har ulike bestandsutvikling, antall skutte ryper har avtatt årlig, mens antall felte hjort har økt kraftig. Jeg har brukt spørreundersøkelser til jegerne for å samle inn data på deres jaktsuksess, preferanser for ulike former for beskatningsreguleringer og sett på hvordan ulike miljøholdninger spiller inn i synet på beskatningsreguleringer.

Fangst per innsats er et vanlig brukt mål for å indirekte si noe om tettheten av individer i en bestand. Jeg fant ingen signifikant sammenheng mellom antall ryper før jakt og fangst per innsats under jakta. Resultatene tyder på at fangst per innsats ikke er en god indikator for å si noe om bestandssituasjonen hos rype, fordi jaktsuksessen var sammensatt av flere faktorer. Eksempelvis var antall fuglekontakter per dag mer bestemmende for jaktsuksess enn estimert tetthet av rype før jakt.

Jegerne foretrakk en kvotestrategi, deretter foretrakk de en reduksjon i antall jegere eller å dele jaktsesongen inn i kortere perioder med færre jegere i terrenget samtidig. Det minst foretrukne reguleringsprinsippet, var å korte ned jaktsesongen. Et råd til forvaltere er derfor å utvikle reguleringer som baserer seg på kvoter over ett lengre tidsrom enn en dag.

Miljøholdninger var positivt korrelert med økende aksept for beskatningsreguleringer, mens andre demografiske variable hadde liten effekt på forholdet mellom miljøholdninger og synet på beskatningsreguleringer.

Videre identifiserte jeg flere jegertypologier som kan nyttes i forvaltningssammenheng. Noen egenskaper var knyttet til hvor konsumptivt orientert (viktigheten av fangst/viltkjøtt, såkalt fangstorientering) jegerne var, mens også når det gjaldt innsats kunne jegerne grupperes inn i tydelige grupper. Hvor ivrige jegerne var relatert til hvor fangstorientert de var og kan brukes i situasjoner hvor bestandsreduskjon eller – kontroll er et mål (eksempelvis for hjort). I situasjoner hvor overbeskatning er et mål (eksempelvis rype), jegere med sterkt fangstorientering og som legger ned stor innsats bør tilbys områder med færre jegere, og mulighet til å felle flere ryper mot en høyere pris. For «opplevelsessøkeren» holder det med en lav kvote fremfor å redusere antall jegere, fordi denne jegertypologien er mindre fokusert på fangst, men mer på opplevelser. Denne jegertypologien kan derfor tilbys jakt i områder

med flere jegere, strengere beskatningsreguleringer til en lavere pris. Dette differensieringen kan være relevant for både rypejegere som er fornøyd med å felle noen få ryper og hjortejegere som ønsker å jakte senere i sesongen eller skyter kalver, eller gevirløse dyr.

Jeg har i avhandlingen forsøkt å vise nytten av å skaffe mer kunnskap om jegernes preferanser når det gjelder regulering av beskatningen og satt disse i en sosi-økologisk system (SØS) sammenheng. Forvaltere bør inkludere kunnskap om jegernes preferanser bår beskatningsreguleringer skal utvikles. Morgendagens rypeforvaltning burde ligge et sted mellom adaptiv forvaltning og scenario planlegging og effekten av de innførte reguleringene burde evalueres i større skala, eksempelvis gjennom å utvikle «Forvaltningsstrategi evaluerings modeller» (Management Strategy Evaluation; MSE). For at modeller som inkludere menneskelig adferd skal ha god prediksjonsevne, må mennesket inkluderes i modellene. Dette krever at man integrerer økologi og samfunnsfag inn i en SØS sammenheng for å bedre prediksjonsevnen til MSE modeller. Utvikling og bruk av denne type modeller er et åpenbart tema for videre forskning.

Abstract

My thesis is concerned with improving harvest management of ptarmigans and red deer by increased understanding of hunters' preferences and by developing hunter typologies. These species where chosen to illustrate two contrasting management situations, since the number of harvested willow ptarmigan has been steadily declining, while the red deer harvest is rapidly increasing. Data is collected by using questionnaires to ptarmigan and red deer hunters. I have measured factors related to hunting success, preferences for different kinds of harvest regulations and the effect of environmental attitudes on harvest regulations by using the NEP scale.

CPUE is commonly used as a descriptor of game abundance. I found no significant relationship between CPUE and estimated ptarmigan density prior to hunting season. My results illustrates that using game abundance measured as bird density per km^2 alone, not necessarily are an adequate measure to adjusting harvest rates for ptarmigan. I found hunting success to be complicated by several intrinsic and extrinsic factors. For example, the number of ptarmigan observed per day was a better predictor than estimated ptarmigan density on hunting success.

A quota strategy was the most preferred harvest principle among ptarmigan hunters. Secondly, hunters preferred a reduction in number of hunters or dividing the season into short periods. Shortening the length of hunting season was the least preferred principle. Translated into ptarmigan management, mangers should develop regulations based on annual quotas or quotas over a longer time span than a daily limit.

Environmental orientation correlated positively with higher acceptance of regulatory management actions, while socio-demographic variables had limited effect on the relationship between environmental concern and attitudes toward management actions.

I identified several typologies useful for management purposes. Some characteristics related to the consumptive orientation, i.e. the importance of meat and the bag size. Also regarding hunting effort, the hunters grouped into distinct typologies. This eagerness related mostly to the respondents' catch-orientation and should be considered in situations where population reduction/control is an important task. On the other hand, in situations where avoiding overexploitation is the focus, hunters with strong catch orientation and high effort should be

channeled to areas where they pay more for exclusive access and the possibility to bag more game, in order to facilitate for these hunters. For example, in an area facilitated for "experience seekers", it may be wiser to keep a low bag limit, than to reduce number of hunters since they were least motivated by the importance of bag size. Conversely, the more appreciative- and less catch-orientated hunters, should be channeled to more crowded areas and stronger harvest regulations, and to a cheaper price. The latter may be relevant both for ptarmigan hunters (where the hunters may be satisfied with only a few birds) and deer hunters (for example hunting access later in the season, or only aiming for antlerless individuals, calves or yearlings).

I have in my thesis tried to demonstrate the need for increased knowledge about hunters' preferences for harvest regulations as a contribution to social-ecological systems when management strategies are developed. Managers should therefore include the hunters' preferences when implementing different types of harvest regulations. Management of ptarmigans should be placed somewhere between adaptive management and scenario planning. The effects of the implemented regulations should also be evaluated at a larger scale, for example by building management strategy evaluation models. In order to be truly predictive in any human-altered environment, the system under consideration must include human users. Therefore, the behavior of individual harvesters and their compliance with management rules must be included. This requires the integration of ecology with social sciences into social-ecological systems, in order to improve the predictive power of system dynamics models. Development of such models is clearly a topic for further research and advances in this field.

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Opponents:

Dr. Peter Sunde. Department of Bioscience, Aarhus University, Denmark

Dr. Jani Pellika. Natural Resources Institute, Finland

List of publications

This thesis is based on the following original publications, indicated in the text by their roman numerals, I-V below.

I. **Oddgeir Andersen** & Bjørn Petter Kaltenborn. 2013. Does a hunter's Catch-per-unit-effort reflect willow ptarmigan abundance? Utmark (www.utmark.org), No. 2b/2013 (special issue in Applied Ecology)

II. **Oddgeir Andersen**, Bjørn Petter Kaltenborn, Joar Vittersø & Tomas Willebrand. 2014. Preferred harvest principles and - regulations amongst willow ptarmigan hunters in Norway. Wildlife Biology 20 (5): 285-290.

III. Bjørn Petter Kaltenborn, **Oddgeir Andersen**, Joar Vittersø & Tore Bjerke. 2012. Attitudes of Norwegian ptarmigan hunters towards hunting goals and harvest regulations - the effects of environmental attitudes. Biodiversity and conservation (21): 3369-3384.

IV. **Oddgeir Andersen**, Hilde Karine Wam, Atle Mysterud & Bjørn Petter Kaltenborn. 2014. Applying typology analyses to management Issues: Deer harvest and declining hunter numbers. Journal of wildlife management 78 (7): 1282-1292; 2014; DOI: 10.1002/jwmg.770.

V. Hilde Karine Wam, **Oddgeir Andersen** & Hans Christian Pedersen. 2013. Grouse hunting regulations and hunter typologies in Norway. Human dimensions of wildlife 18 (1): 45-57.

1. Introduction

The aim of applied ecology is to link ecological theory and methodology to specific management-related issues (Memmott *et al.* 2010). Management of species subject to harvest basically consists of three elements; the game, the habitat or landscape used by game and the harvesters. The human part of this tripartite (the harvesters) has often been neglected (Heberlein 2012). In harvest management, managers use regulations that either adjusts the number of animals that can be harvested (total bag size) or regulates effort, which in turn may affects the total bag size. The idea of adjusting effort to affect bag size is based on the model of proportionality between catch-per-unit-effort (CPUE) as an index of abundance (for further details, see paper 1), although it has long been recognized that CPUE may not accurately reflect changes in abundance (Beverton & Holt 1957). Nonlinear deviations between CPUE and abundance is known as "hyperstability" if CPUE declines slower than abundance, or "hyperdepletion" if CPUE declines faster than abundance. Both cases can lead to erroneous conclusions regarding population size and thus, unsustainable harvest rates (Harley, Myers & Dunn 2001).

Human dimensions studies have shown that hunters are motivated by both consumptive (food, trophy hunting) or non-consumptive (recreation, cultural, human instinct) motives (Fischer *et al.* 2013). Utilization of the resource (meat, trophy, fur etc.) and recreation (various stages of the hunt, socialization, being in nature etc.) is two of the most fundamental motives for hunting (Fischer *et al.* 2013; Ljung 2014), where the latter has become more important by time, especially in the post-industrialized society. Implicitly, hunters that are motivated by either consumptive or non-consumptive motives can consider harvest regulations differently. For example, a reduction in number of hunters that are allowed to hunt or shortened length of hunting season can be seen as negative by some, but not by others. From the body of research using environmental orientation measures to describe outdoor recreationists, hunters have often been seen to belong more to the consumptive than the appreciative category of recreationists (Bjerke, Thrane & Kleiven 2005). However, the literature is not conclusive on the patterns of hunters' environmental orientations and its association with hunter typologies, opportunity preferences and attitudes toward wildlife management and conservation. Therefore, more data on environmental orientation among different hunter segments and – typologies are needed.

In Norway, cervids are managed according to the principle of adjusting the total bag size within management regions, where a quota per management area is calculated and licenses distributed in relation to age-classes (calves, yearlings, prime aged, see paper III). For small game, the most common harvest regulation is to set a daily bag-limit or reducing effort by reducing the number of hunters or shortening the hunting season. One criticism of daily bag-limits, is the lack of precision when it comes to adjusting harvest rates. During the first weeks of the hunting season, especially on public land, it is common to sell permits with a 5-7 days duration. If a daily bag limit is connected to this permit, the maximum number of birds that can be bagged is given as: the number of hunting days times daily bag limit (i.e. 7 hunting days x 2 birds per day= 14 birds in total). However, if the daily bag not is reached, birds not harvested are lost, because hunters are not allowed to compensate for days with lower catch. For example, some studies have reported that only a small proportion of the hunters actually fill their daily bag limit (Andersen 2002), and the large-scale outcome of the bag-limit regulation is still somewhat unclear (Asmyhr 2012).

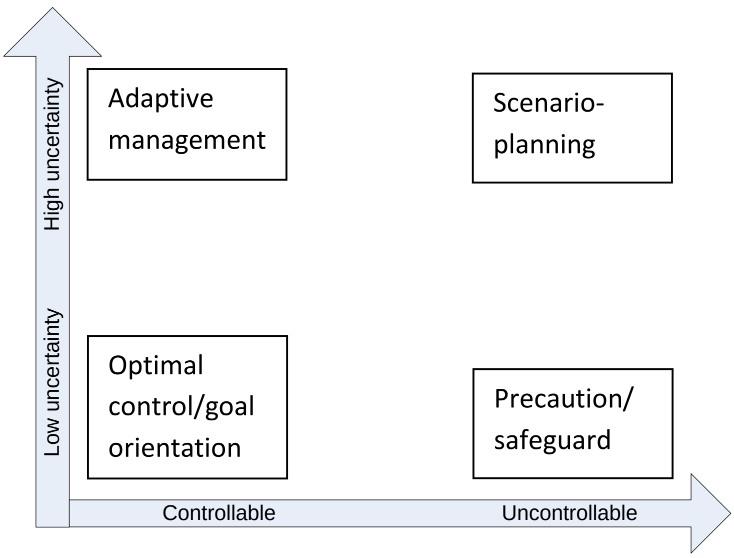


Figure 1. Some possible management strategies as a function of uncertainty about size and structure and managers' ability to control the natural resource through management actions/regulations (Adapted from Peterson et al. 2003).

Management of fish and game for recreational purposes is largely about handling uncertainty and managing people. Harvest models are of limited use, unless they are linked to clear and operationalized management goals. If we are not able to evaluate the outcome, uncertainty comes into play and must be considered in management decisions. Without adequate knowledge about the managed species, there can be a need for quick responses to sudden changes in the population size or structure. Peterson, Cumming and Carpenter (2003) recommends different management strategies depending on the degree of uncertainty and controllability of the natural resource (figure 1):

Adaptive management models have been proposed to meet these challenges given that: (1) the management goal is clearly defined, (2) the outcome can be evaluated (although there can be a high degree of uncertainty) and (3) proper actions can be taken if needed (controllable). One example that can fit in here is the current management strategy for Atlantic salmon (Forseth *et al.* 2013). Adaptive management has several definitions, but common for all is the description of a process where management of natural resources improves by learning from the current management regime, a "learning while doing" approach (Aldridge, Boyce & Baydack 2004; Meretsky & Fischman 2014).

In situations with less uncertainty about the resource under management, a *goal-orientated* management regime could be more suitable (Figure 1). The situation is considered to be under optimal control (Peterson, Cumming & Carpenter 2003). The current Norwegian management system of ungulates such as moose, red deer and wild reindeer may fit in here.

Scenario planning is a strategic planning method to make flexible long-term plans. This is recommended in situations where the resource is considered as uncontrollable and there is a high degree of uncertainty (Peterson, Cumming & Carpenter 2003). Scenario planning may involve aspects of system thinking, specifically the recognition that many factors may combine in complex ways to create sometime surprising futures. This way of thinking can be relevant in situations where biological invasions of non-native species or diseases are at risk. A system thinking used in conjunction with scenario planning leads to plausible scenario story lines because the causal relationship between factors can be demonstrated. The method also allows the inclusion of factors that are difficult to formalize, such as novel insights about the future, deep shifts in norm and values, or unprecedented regulations or inventions.

The *precautionary principle* or precautionary approach states that if an action or policy has a suspected risk of causing harm to the public or to the environment, in the absence of scientific consensus that the action or policy is harmful, the burden of proof that it is not harmful falls on those taking the action (Flavia *et al.* 2015). This principle allows policy makers and mangers to make discretionary decisions in situations where there is low uncertainty, but a possibility of harm from taking a particular course (because the resource is considered as uncontrollable) or making a certain decision when extensive scientific knowledge on the matter is lacking (Figure 1). To some extent, the current management of ptarmigans in Norway may fit in here.

One recent advancement to deal with uncertainty in harvest management is to build harvest models/-scenarios that integrate the harvest process in a feedback-loop from a management decision (Bunnefeld, Hoshino & Milner-Gulland 2011). Figure 2 is an example of a feedback loop, where managers implement a harvest regulation for some reason. The way harvesters respond to the given regulation will in some way affect the harvested population. Next, population monitoring may detect changes in population state, which is the mangers measure of the harvested population's response to the regulation they implemented (including environmental stochasticity). Managers are then able to evaluate alternative outcomes and communicate results in a transparent way. Several ways to achieve this has been developed for example by structured decision models, system dynamics, Bayesian networks, coupled component models, agent-based models and knowledge based models, which are sometimes referred to as expert systems (Kelly *et al.* 2013). Recent advances in fishery science regarding management of harvested fish stocks can also be transformed into terrestrial conservation (Bunnefeld, Hoshino & Milner-Gulland 2011; Andersen & Thorstad 2013). For example, evaluation of fishery management scenarios is done (in a virtual world) by including the behavior of individual harvesters (for further details on behavior, see chapter 1.1.1, theory of planned behavior) in relation to management rules, and by assessing the management procedures' robustness to uncertainty. This particular framework is called "Management Strategy Evaluation" (MSE) and represents coupled component models since it is able to predict outcomes and increase system understanding. MSE models has hitherto not been widely used in terrestrial conservation, but have gained considerable ground within fisheries science (Bunnefeld, Hoshino & Milner-Gulland 2011).

1.1 Conceptual model

Management strategy evaluation models (Figure 2) were initially developed with the aim of systematically evaluating the current management regime and provide feedback to the mangers on how to improve their practice (Smith, Sainsbury & Stevens 1999). One may argue that MSE is taking the concept of adaptive harvest management (a “learning while doing” process) a step further by incorporating the social processes underlying harvest behavior, while others might argue that these methods are basically the same. In simple systems, and when harvesters abide harvest control rules, as recreational hunters usually do, this may not be problematic. However, in complex systems with multiple stakeholders and severe uncertainties it is generally difficult to provide a single best harvest policy (Nicholson & Possingham 2007; Kelly *et al.* 2013). For example this may include situations with large-carnivore - livestock conflicts (Vitterso, Kaltenborn & Bjerke 1998; Kaltenborn, Nyahongo & Tingstad 2005; Kaltenborn *et al.* 2006), extensive poaching (Bitanyi *et al.* 2012; Gangaas, Kaltenborn & Andreassen 2013), massive damage to agriculture and forestry (Côte *et al.* 2004; Apollonio, Andersen & Putman 2010; Akashi, Unno & Terazawa 2011) or to society (i.e. game-vehicle collisions) caused by game (Côte *et al.* 2004; Danks & Porter 2010), or in situations where the harvested population show large annual fluctuations (Lande, Engen & Sæther 1995; Lande, Saether & Engen 1997). The MSE approach, or other quantitative management models are not yet common in the Norwegian small game management traditions since there are rarely any defined management goals (regarding population status, abundance or numbers), as there is for several ungulates and carnivore species. The only premise for hunting is that harvest shall be sustainable (The Norwegian Biodiversity Act 2009).

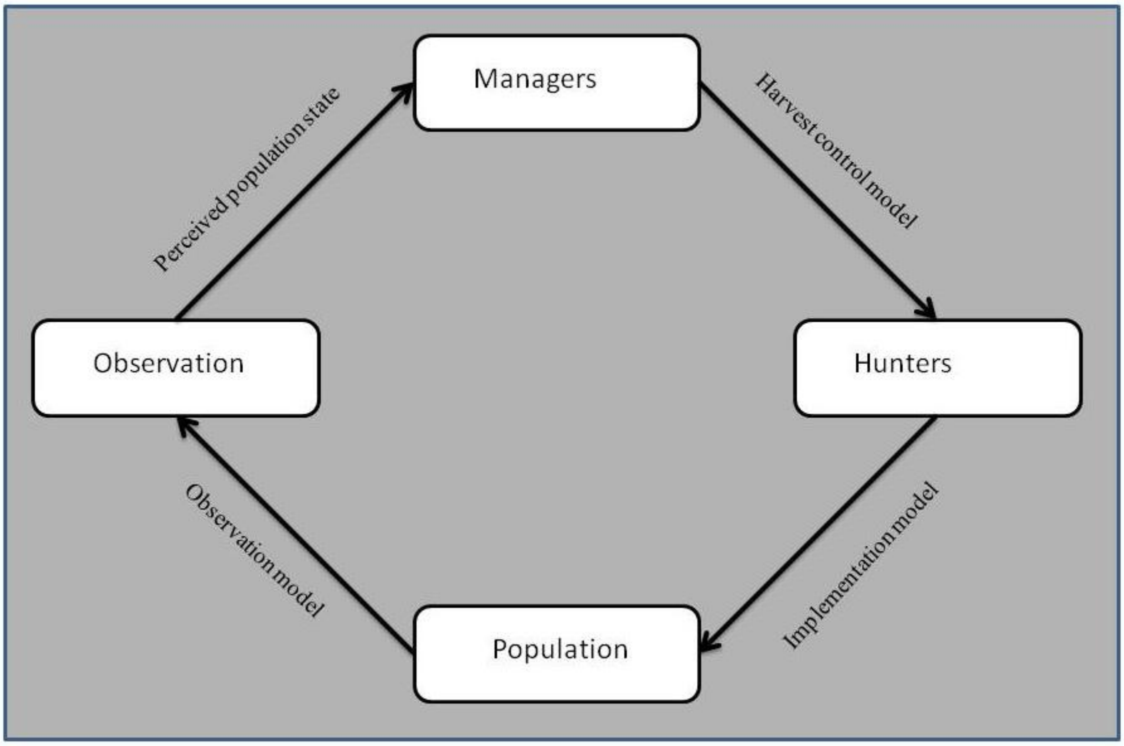


Figure 2. Conceptual model of a management strategy evaluation process. The population state is monitored in an observation model, the managers implement harvest control models (rules) based on perceived population state, and harvesters (hunters) implement the harvest control rules (HCR) on the hunted population. (Modified from Bunnefeldt et al. 2012).

A MSE model consists of four elements; (1) the management, (2) the harvesters, (3) the population subject to harvest and (4) monitoring (an observation-model) of the responses from the harvested population (Figure 1). This loop gives feedback to managers about the effect of harvest and/or the population status prior to the next hunting season. Each component in the MSE concept can be subject to modeling separately or integrated. For red deer (and other ungulates) a national reporting and monitoring system is established (www.hjorteviltregisteret.no), which can be broken down to the municipality level. In the current management system for willow ptarmigan in Norway there is a voluntary, extensive monitoring of populations status prior to hunting season. More than 200 hunting units have participated in recent years, and results are now stored in a national database (http://honsefugl.nina.no). For some willow ptarmigan areas, monitoring data exists back to 1995. This means that many management areas in Norway have time series of both harvest- and population monitoring data sufficient to build models/scenarios to predict possible outcomes from different harvest regulations and evaluate these in relation to management goals (if defined). This way of thinking may improve the knowledge basis for small game managers prior to making decisions about harvest levels.

The first component in finding successful management strategies (given a defined goal) is to have adequate understanding of the population dynamics when a population is not harvested (Aanes *et al.* 2002), but knowledge about the population's response to harvest is also essential (Figure 2). Despite increased knowledge about harvesting and its effects, poor natural resource management (e.g overexploitation related to both commercial- and recreational harvest) is still causing fish stocks and game populations to being heavily reduced (Post *et al.* 2002; Milner-Gulland *et al.* 2003; Dudgeon *et al.* 2006; Lewin, Arlinghaus & Mehner 2006; Storch 2007) or functionally extinct (IUCN 2015). Hundreds of species of mammals, birds and fish are listed as endangered because of human persecution (Vié, Hilton-Taylor & Stuart 2009). More effective harvesting techniques, i.e. weapons (and the improvement of hunting related gadgets such as rifle scopes) and fishing gear, has led to an increase in harvest efficiency and thus is an important factor in the exploitation of populations and the introduction of harvest regulations. Extinction or decimation of predators species has in many cases caused high abundances of prey species (Sinclair, Fryxell & Caughley 2006). Hence, harvesting is a tool to regulate or control wildlife populations, especially large ungulates (Solberg *et al.* 1999; Andersen, Fagerheim & Solheim 2009; Strand *et al.* 2012). Whether the management goal is to avoid overexploitation or limit numbers, wildlife and fish management has applied several different harvest models and regulations through history. The purpose of these models is primarily to suggest (or calculate) sustainable quotas and obtain stable population dynamics (with variable degree of success). For species with large population fluctuations (e.g. ptarmigans) it can be harder to isolate the effect from harvest on population dynamics. Harvest theory predicts that a threshold strategy is most optimal in stochastically fluctuating populations (Lande, Engen & Sæther 1995). Further, management goals and strategies should be clearly defined. This can be done by deciding an upper or lowest desired density (due to ecological and/or societal carrying capacity), age- or sex structure (for ungulates) or other measures describing the desired state of the harvested population. No such measures are defined for small game species in Norway.

Regarding societal and economic effects of hunting, increased knowledge about hunters' preferences for different harvest principles and – regulations are needed. This knowledge can be used to predict how different regulations may improve harvest management strategies and contribute to advancements in this field. This is relevant for both study cases (see chap. 1.2). One is where ptarmigans have been facing declining harvest rates, stable hunter numbers and the aim is to avoid overexploitation (ecological aspect) while simultaneously keeping the possibility to hunt (social and economic aspects). The other is red deer harvest management, which is facing a rapidly increasing population (which now seems to stabilise). In this case access to hunting may still be limited, yet harvest quotas and the management system is struggling to slow the population growth.

The second component is to develop a harvest control model by implementing harvest regulations, sometime referred to as "harvest control rules" (Milner-Gulland 2012). History has shown that the compliance of harvesters with regulations has been a major challenge in conservation worldwide (Bunnefeld, Hoshino & Milner-Gulland 2011), and it is still a topic in fish and game management (Milner-Gulland 2011; Gangaas, Kaltenborn & Andreassen 2013). Even if the harvesters follow these rules, they do not necessarily agree with them, for example if number of hunters that are allowed into the hunting ground is reduced without restricting their harvest by quotas. Compliance with regulations is a prerequisite for management strategies aimed at optimizing ecological, social and economic outcomes of harvests. There are basically two ways to adjust harvest rates: either limit the total number of game that can be harvested (total bag size), or reduce the total effort by reducing the length of hunting season, and/or reducing the number of hunters (Wam, Andersen & Pedersen 2013). Combinations of these harvest control rules are also possible. Other possibilities to reduce the impact of harvest is to establish non-hunted areas. The only state level regulation in Norway is the length of the hunting season. Harvest regulations on ptarmigans were gradually introduced by wildlife managers and was a common practice roughly around year 2000. Harvest regulations is still a common tool for regulating small game harvest despite the lack of systems to synthesise the outcome of management actions (Paper II). The two most common regulations in Norway set by the managers is a daily bag limit (normally 1-3 ptarmigans) or a reduction in number of days for the hunting season as a whole. For ptarmigan management to be adaptive it would need a management system that was able to evaluate the outcome of the different management measures in relation to the objectives. The red deer management system is more suited for evaluating different harvest regulations due to the the well established Norwegian monitoring program for cervids (Solberg *et al.* 1999; Mysterud *et al.* 2007).

The third component is to directly or indirectly monitor the effect of harvest on the population (an observation model). This can be done for example by collecting bag statistics (which is commonly used, but see Asmyhr 2012 and paper I) or in addition, monitor population measures describing abundance and recruitment into the population prior to hunting season. Finally, managers can use this information to evaluate the effect from harvest on next year's population performance, and according to this adjust the harvest control rules if needed (the 4th MSE component). Fryxell *et al.* (2010) show that asynchronous dynamics of harvested resources, hunting effort and quotas often occur. This pattern is due to delayed human responses to changing conditions. They also found that the predicted risk of population collapse increased with increasing levels of sensitivity to stochastic variation in population growth rates.

One criticism of adaptive harvest management practices is lack of experiments in the context of learning by doing (Aldridge, Boyce & Baydack 2004). Adjusting harvest rates is the cornerstone in management of different game species worldwide. Therefore it can be argued that adjusting harvest rates can be seen as an "experiment" itself. Experiments are basically a manipulation of a predictor variable (i.e. harvest rates) which measures the effect on a response variable (i.e. population status). Such large scale experiments are rare, but a natural experiment was the response in harvest rates of several small game species under the scaroptic mange in red fox (*Vulpes Vulpes*) during mid 1980's in Scandinavia. Smedshaug *et al.* (1999) used hunting records to examine whether red fox limits small game populations and presented correlative evidence that small game was limited by the red fox. Experiments controlled by scientist are often carried out on a smaller scale. Aldridge, Boyce and Baydack (2004) criticized the lack of experiments implemented in the adaptive management of sharp-tailed prairie grouse (*Tympanuchus phasianellus*) and greater sage-grouse (*Centrocerus urophasianus*) in Alberta. They point to the fact that lack of experiments is limiting the mangers ability to learn from the harvested population and thereby enhance conservation efforts for declining prairie grouse populations. Translated into management of ptarmigan species in Norway, there exists no evidence that hunting alone has eradicated populations/sub-populations. One solution to learning by doing is to manage populations to the extreme, for example by attempting a strong decimation (> 50% harvest rate) of a ptarmigan population in a large area and then monitor the population response.

Despite these uncertainties, several management units in Norway have recently realised the need for a more adaptive approach in their ptarmigan harvest management (Pedersen & Storaas 2013). For example, this can be done by defining management goals. One example to draw lessons learned from is the current management of Atlantic salmon (*Salmo salar*) in Norway. The majority of rivers containing Atlantic salmon in Norway are managed according to spawning targets, which are based on ecological and morphological criteria. (Forseth *et al.* 2013). If the mid-season evaluation indicates that the spawning target may not be reached, managers can take actions and immediate enforce harvest regulations. This system, translated into harvest management of ptarmigans can, as an example, lead to a hunting ban after a few weeks if game abundance is considered too low to be sustainably harvested. As mentioned, there is no established system that is able to evaluate the large-scale outcome of management actions in relation to management objectives such as desired breeding population size, population growth or abundance and adjusting harvest rates. Following Aldrigde and collegues's critique, large-scale management experiments (or evaluations) are still lacking. The MSE-concept can be a useful approach to bridge that gap and develop systems that enable us to increase our knowledge of the large-scale outcome of management actions.

1.1.1 The theory of planned behavior

I start this chapter with providing one example demonstrating the (lack of) correlation between attitudes, behavioral intentions and actual hunter behavior. I will describe the theory of later in this chapter. Some years ago, the Swedish hunting authorities decided to increase the daily fee for non-local ptarmigan hunting licenses on state owned ground. The fee increased from 200 Swedish kroner (SEK) per day to 300 SEK/day for non-local hunters. This increase was heavily debated in media and non-local hunters stated that they would quit hunting on these grounds. The next year, the number of non-local hunting licenses sold, was approximately the same as the year before (Willebrand 2015).

A motive is simply a want or a need that causes us to act (Sternberg 1995). Personal motivation is believed to have a direct effect on behavior, and thereby predictive power to explain why people behave the way they do. Several theories on behavior exist, e.g the "theory of reasoned action"(Fishbein & Ajzen 1975; Ajzen & Fishbein 1980), which was further developed into the "theory of planned behavior; TPB" (Ajzen 1991). TPB suggests that a person's behavior is influenced by its normative beliefs and subjective norms, perceived behavioral control, and attitudes toward the behavior (Figure 3), which in turn affects the persons behavioral intentions. Behavioral intentions are considered to be the immediate antecedents of behavior, and therefore an indication of a person's readiness to perform a given behavior (Ajzen 2005). Behavior is the observable response in a given situation and a function of compatible intentions and perceptions of behavioral control. During the last decades numerous studies have been published that have used different measures of motivation as the core segmentation criteria (Manfredo, Driver & Tarrant 1996; Swanson & Horridge 2006; Jonsson & Devonish 2008; Lee & Law 2012) and the TPB - concept have been used in well over 1000 independent studies (Ajzen 2011). The Theory of Planned behavior can be a useful approach for translating attitudes, norms and preferences into predictions of behavior. There is strong empirical support in the field of social psychology that the predictive power of an attitude to behavior increases with the strength of the attitude (Ajzen & Fishbein 1980). However, it depends on how it is measured (Heberlein 2012). In other words, the more specific an attitude is linked to a particular behavior, the better it predicts the behavior. This is termed as “The specificity principle”, which states that “*attitude measures more specific to the attitude object and the act itself show higher correlations with observed behaviors*” (Heberlein 2012). More general attitudes should therefore influence a greater variety of relevant behaviors, but at weaker levels, and attitudes measured at very general levels should not be expected to be associated with a specific behavior (Heberlein 2012). A weakness in several studies using TPB, is the lack of control or follow-up studies of the respondents’ actual behavior. In other words what they actually do, compared to what they intend to do (Figure 3).

Going back to the example of the increased hunting fee it became clear that the negative attitude to increased fees affected the hunters’ behavioral intentions, but there was a low correlation between attitude, behavioral intention and actual behavior (measured as the number of non-local hunters the next year). This may be explained by the strength of other factors, for instance their general interest in hunting, which overruled the intention to stop hunting in these areas, or lack of areas alternative opportunities.

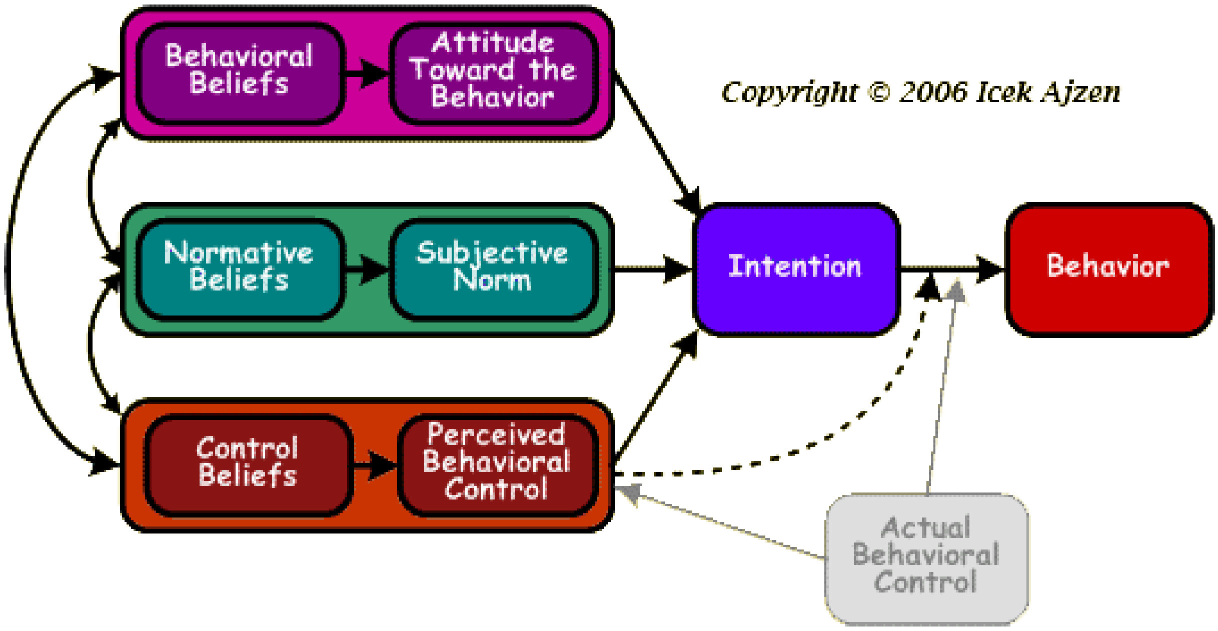


Figure 3. The theory of planned behavior. Figure reproduced with permission from Icek Ajzen's homepage: (http://people.umass.edu/aizen/tpb.diag.html).

1.2 The study

I have chosen to use ptarmigan- (*Lagopus spp.)* and red deer (*Cervus elaphus*) hunters to contrast the potential use of hunter typologies in a MSE setting. The reason I compare willow ptarmigan harvest management and red deer harvest management is simply to illustrate two contrasting situations, and to demonstrate the importance of gaining knowledge about hunters related to management issues. Currently, the number of harvested willow ptarmigan has been steadily declining (Figure 4), while the red deer harvesting is rapidly increasing (Figure 5).

Ptarmigan has a circumpolar range zone and is by far the most popular small-game species in Norway. Approximately 55-60 000 hunters hunt ptarmigans annually (Statistics Norway 2014). The hunting season runs from September 10th to February 28th, except in the northernmost part of the country (north of Tysfjorden/Hellemofjorden in Nordland County) where the hunting season closes March 15th. The popularity of ptarmigan hunting exist despite the fact that the population is characterized by large annual fluctuations which also differs between areas (Myrberget & Pedersen 1993; Lande, Engen & Sæther 1995; Aanes *et al.* 2002; Kvasnes *et al.* 2010; Kvasnes *et al.* 2014). Bag statistics from the last decades have shown a steadily decreasing numbers of bagged ptarmigans (Figure 4) and raised concerns about the sustainability of the current hunting practice, since there have been indices of overexploitation in some areas (Pedersen & Storaas 2013). Two decades ago, the common perception was that harvest mortality was completely compensatory and that harvesting did not affect population dynamics since dynamics where driven by microtine density (reduction in predation rates of ptarmigans, the alternative prey hypothesis) and weather conditions during hatching period (Steen *et al.* 1988). A study on effects of hunting advised that one could harvest around 30% of the population size (Pedersen *et al.* 2004), depending on the chick production (Kastdalen 1992). However, a recent study has shown that harvest levels below 15% have no additive effect on natural mortality, while harvest levels above 15 % leads to super-additive mortality (Sandercock *et al.* 2011). Yet, in years with high density and higher chick production there could be a larger harvest share than a fixed proportion (i.e. 15 %). We currently do not know the effects of harvest levels above 30%. The influence of harvest on population levels is still somewhat unclear (Hörnell- Willebrand, Willebrand & Smith 2014), but negative effects have been documented (Sandercock *et al.* 2011) as well as weak compensation of harvest in spite of strong density-dependent population growth (Pedersen *et al.* 2004). Determination of the effects of harvest is also complicated by dispersal patterns, the size of the management area and immigration and emigration as described by Hörnell- Willebrand, Willebrand and Smith (2014).

Compared to the extensive body of knowledge on ptarmigan ecology in Fennoscandia (and elsewhere), the knowledge about ptarmigan hunters in Scandinavia is still limited. However, there have been some advances in the field the recent years. Asmyhr (2012) studied hunter's behavioral response to changes in bag size and willow grouse density. Kaltenborn and Andersen (2009) studied habitat preferences for ptarmigan hunters regarding hunting techniques and published a study (this thesis, paper III) on effects of hunters' environmental orientation on harvest regulations and hunting goals (Kaltenborn *et al.* 2012). Wam, Pedersen and Hjeljord (2012) looked into the economics regarding harvest regulations and hunter satisfaction. In addition, some other work on hunter characteristics and behavior has been published in recent years (Willebrand & Paulrud 2004; Andersen 2008; Faye-Schjøll 2008; Andersen *et al.* 2009b; Andersen *et al.* 2013b; Andersen *et al.* 2013a).

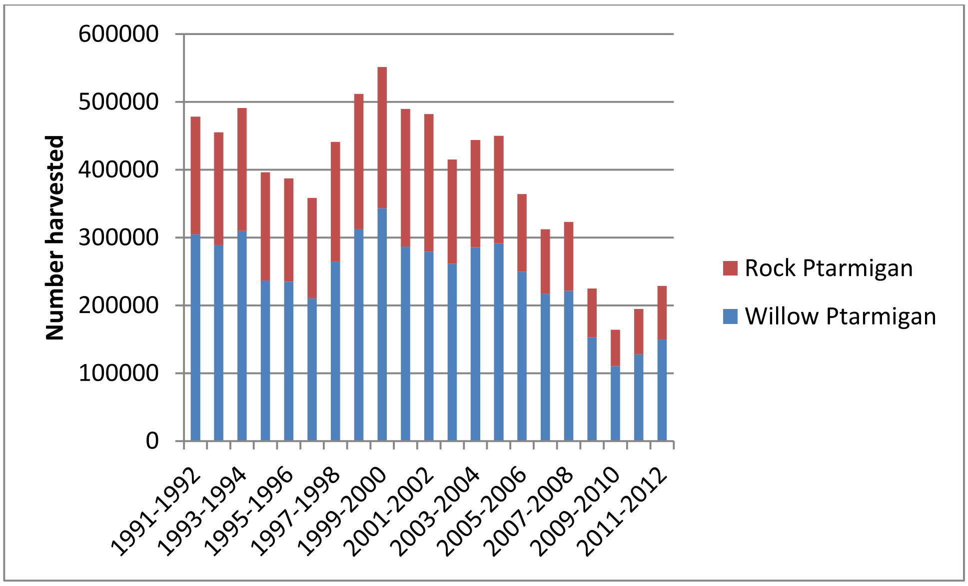


Figure 4. Number of bagged willow ptarmigan and rock ptarmigan from hunting season 1991/- 92 to 2011/-12.

Red deer populations have increased in abundance during the last decades (Figure 5), particularly in the western parts of Norway. During the three last hunting seasons, more red deer than moose (*Alces alces*) have been shot in Norway, and during the last hunting season (2013/14), 36141 red deer and 34 939 moose where bagged (Statistics Norway 2014). There is considerable focus on the ecological and economic consequences of overabundant red deer populations (Mysterud 2006) as well as discussions regarding the way hunting is organized. In the 2012 hunting season 43 710 hunters hunted red deer. It equals a 26 % increase in number of hunters compared to the 2007 season (the first year Statistics Norway reported the number of red deer hunters). Red deer hunting has long traditions in the western parts of Norway, but there are still challenges related to future development of the hunting opportunities since the major share of the landowners still hunt with family and friends (Olaussen & Mysterud 2012). In eastern parts of Norway red deer population densities have increased rapidly during the last decades. This population increase brings new income opportunities to the landowners, but also higher costs (e.g. damage to crops, forestry and agriculture). In addition, game-vehicle accidents can be a serious problem in areas with overabundant deer populations (Groot Bruinderink & Hazebroek 1996; Danks & Porter 2010; Meisingset *et al.* 2013; Meisingset *et al.* 2014).

A common way to distribute red deer licenses in the eastern parts of Norway is to connect them to the hunting party which holds the moose hunting licenses, although the hunting season for red deer starts earlier in the autumn. So far, there has been a lack of hunting traditions on red deer in eastern Norway (Mysterud *et al.* 2011). The way managers administrate their red deer quota (which is based on multi-annual harvest schedules) and offers/includes services such as accommodation, guides and other forms of facilitating is a key factor in increased commercialization of red deer hunting (Olaussen & Mysterud 2012). Paper III shows a useful approach to profile hunters. We use the typologies to tailor harvest management of red deer and discuss how to increase the economic and social benefits, and how to aid control undesired population growth.

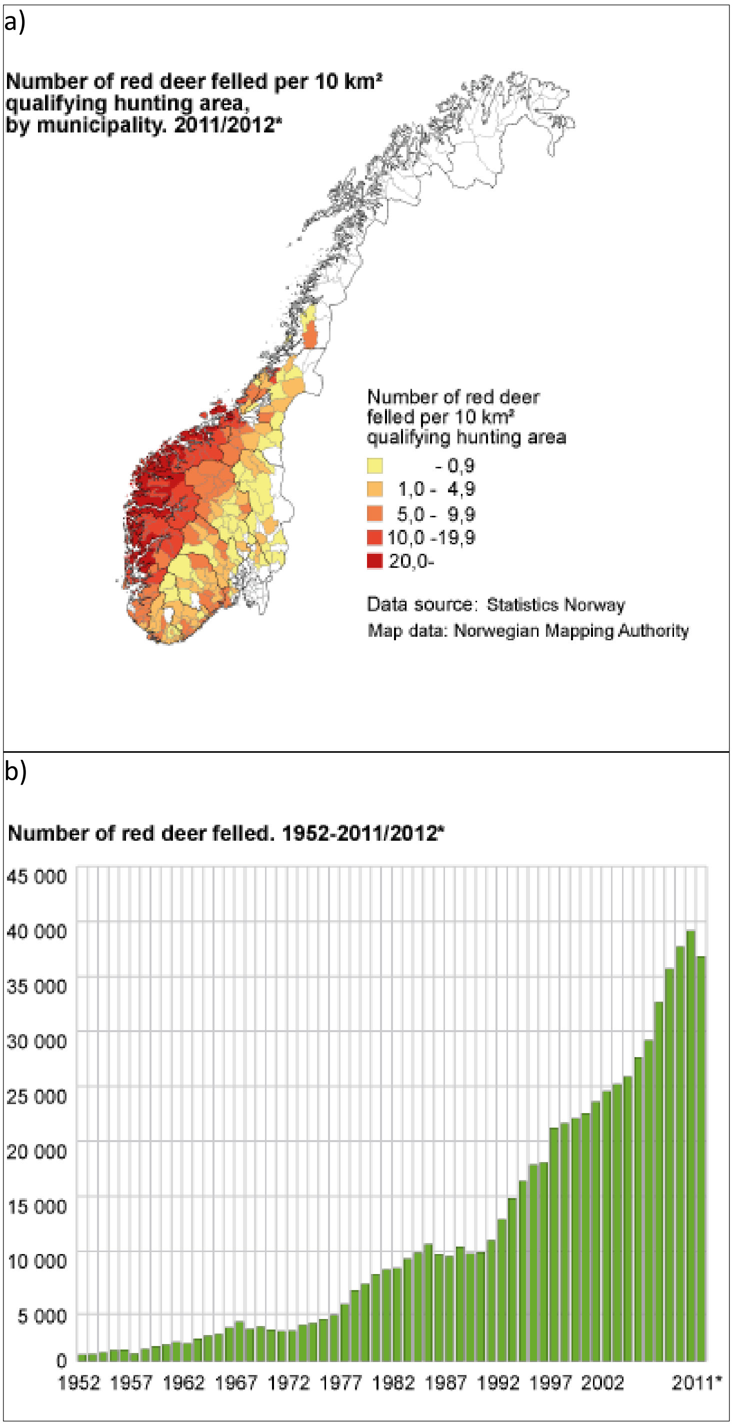


Figure 5 A-B. (**A**) Number of felled red deer per 10 km^2 qualifying area in 2011/2012 hunting season, and (**B**) Number of felled red deer in Norway from 1952-2012. Source: Statistics Norway.

1.3 Hunting and economy

Recreational hunting provides economic income for landowners and society (Wam, Pedersen & Hjeljord 2012; Andersen *et al.* 2013a; Wam, Andersen & Kaltenborn 2013). It is estimated that American hunters in 2011 spent 38.3 billion US$, created 680 300 jobs, and generated 11.8 billion US$ in taxes (Southwick Associates 2012). In Sweden, the yearly value of hunting is about 3.1 billion Swedish kroner (SEK), and 15 million kg of game meat is derived by 300 000 hunters (Boman & Mattsson 2012). This equals 1,7 kg meat per Swede (Ljung 2014).

Ptarmigan hunting in Norway generates somewhere between 500 000 – 1 000 000 hunting days per year, and most of the hunting occurs in other areas than their location of residence (Pedersen & Storaas 2013). Thus, the majority of the ptarmigan hunters are per definition hunting tourists and thereby significant contributors to the nature based tourism industry and rural communities. Ptarmigan hunters used on average 3000 NOK on ptarmigan hunting in 2006 (Andersen *et al.* 2009a), which generates approximately 165 million NOK if 55 000 hunters hunt ptarmigan.

During the 2013 hunting season, 43 700 Norwegian red deer hunters culled a total of 36141 red deer. Estimating 60 NOK per kilo meat and an average slaughter weight of 50 kg per red deer, this alone equals a meat value of approximately 108, 4 million NOK. In addition, red deer hunters had an average expenditure of 7750 NOK during the 2010 hunting season (Andersen *et al.* 2011), which gives a total expenditure of 338,7 million NOK.

1.4 Socio-ecological systems and sustainable harvest

The term “Socio-ecological systems” is simply the human use of natural resources and includes the resource (i. e. game species subject to harvest), a resource system (i.e. habitat or ecosystem), the resource user (i.e. hunters or non-consumptive users), the governance of the system (i.e. biodiversity or hunting legislation) and the interactions between them (Ostrom 1999; Milner-Gulland 2012), which requires integration of ecology and social science (Figure 6).

Harvest regulations are tools to be used in management strategies aimed at optimizing ecological, social and economic outcomes of the recreational harvest. For example, if the Norwegian principle of public access to small game hunting (without using dog) on public land should be sustainable (one definition of a sustainable yield is "a yield that can be taken year after year, without jeopardizing future yields" (Sinclair, Fryxell & Caughley 2006), it demands harvest principles and –regulations that are widely accepted among hunters so violations (for example of the daily bag limit) are reduced. Further, overabundant red deer populations can cause severe damage to society and successful strategies to keep deer populations in check must include knowledge about hunters' preferences, for instance by adjusting the number of red deer licenses per hunter and varying prices per license during the season to facilitate for optimal harvest (paper III). The term "Controllability" is used as a measure of the uncertainty in management (Figure 1). However, strategies to maintain sustainable harvest according to management goals may conflict with the optimization of social or economic outcomes (Wam, Pedersen & Hjeljord 2012). For example, if population abundance currently is approaching a level where harvesting is not considered sustainable (Lande, Engen & Sæther 1995), or if population parameters, such as body mass, indicate overabundant populations (Ims *et al.* 2007). To further adjust the conceptual framework as shown in figure 2, one should include policy and legislations for management. Figure 6 shows the interactions between ecological processes, social processes and management/policy decision systems.

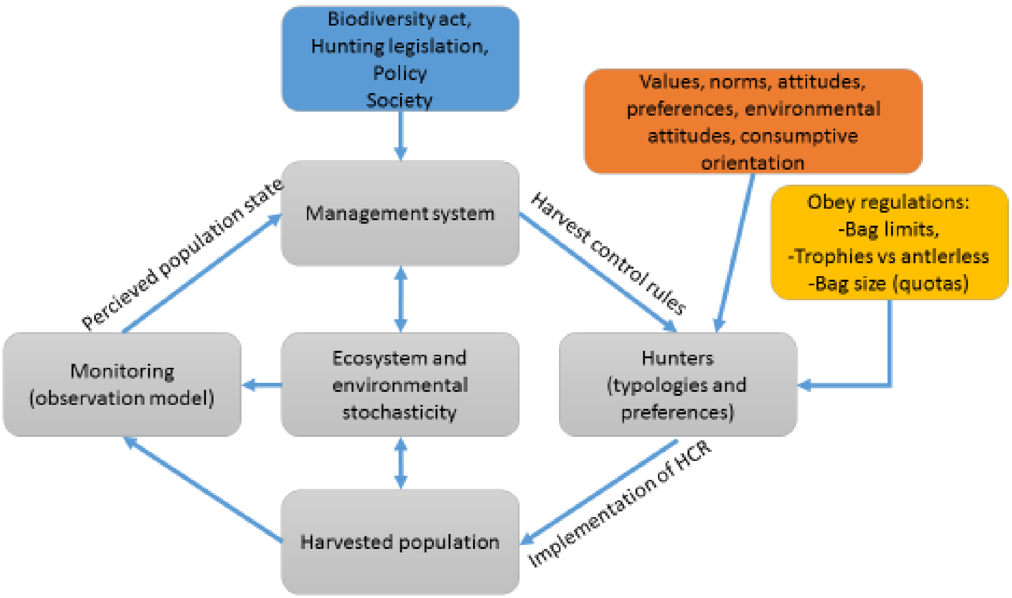


Figure 6. The extended MSE concept. It includes both legislative and policy decisions from society (blue box), the management systems' interaction with the ecosystem, ecological processes and populations subject to harvest (grey boxes), and factors related to the behavior of the harvesters (orange and yellow boxes).

1.5 Research questions

The main focus of my thesis is concerned with improving harvest management of ptarmigans and red deer by increased understanding of hunter preferences. I ask the following research questions:

1. To what extent is hunting success explained by game abundance (paper I), or are other factors necessary to explain hunting success (paper I, IV)?

2. What are the hunters' preferences for different harvest strategies and regulations (paper II), and how are they influenced by their overall environmental orientation (paper III)?

3. How can knowledge of hunter typologies be used to improve harvest management (paper IV, V)?

2. Material and methods

2.1 Sampling procedures

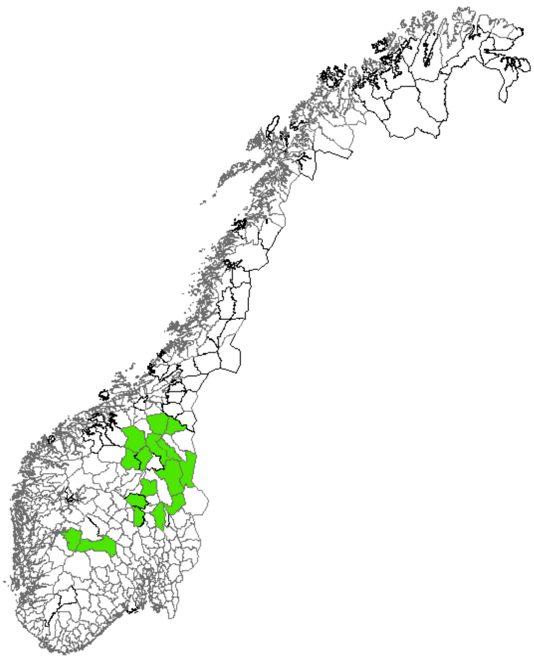


Figure 7. The municipalities where the postal survey (paperI, II and III) was conducted is indicated with green colour.

We used questionnaires to collect data, but the procedures for sampling differed. We followed the tailored design method as described by Dillman (2007) for the postal data collection among ptarmigan hunters used in paper I - III. First, we received 2717 complete addresses to ptarmigan hunters from management units within the participating municipalities in the following counties in central parts of Norway: Buskerud, Hordaland, Oppland, Hedmark and Sør-Trøndelag (Figure 7). We considered these areas as representative for the major parts of the hunting areas for willow ptarmigan in the central parts of Norway. We sampled by using a postal questionnaire (sample 1) and a web- survey (sample 2).

Sample 1: Hunters received a postal questionnaire immediately after the closing end of the willow ptarmigan hunting season (medio march). We sent a short reminder 14 days later, and a second reminder with a similar questionnaire was mailed to 1263 respondents who had not responded to the questionnaire. The data collection resulted in 1876 answers (69% response). After excluding 233 respondents who reported they had not hunted and 38 responses without any information, 1605 complete responses were left (an effective response rate of 59%) We had information about the estimated density of willow ptarmigan prior to hunting season in each of the hunting areas we received the hunters addresses from, and linked this information (density and hunting terrain) to each of the responding hunters. We used this sample in Paper I.

Sample 2: an identical survey to ptarmigan hunters as described above was posted on the Internet, open for everyone to answer. An e-mail filter was used to facilitate the participation of only new and unique respondents. At the closing date, the web-survey elicited 1183 answers.

The total number of responses from ptarmigan hunters in the postal and web survey (n=2788) comprises approximately 5% of the total population of ptarmigan hunters in Norway during hunting season 2006/07 (Statistics Norway 2007). Descriptive analyses of the response data did not reveal any major deviations (except education level, where average education level was 0.7 years higher in the internet (14.5 years) sample, compared to the postal sample (13.8 years), and the difference was significant, $t_{1,2579}$=5.45,p=0.001) between the postal respondents (sample 1) and Internet participants (sample 2). Consequently, the two samples were pooled (paper II and III).

The survey to red deer hunters (paper IV) was sent to individuals registered in the National Hunting Registry (NHR) who had hunted red deer at least once during the last decade (2002-2009) and who had purchased a national hunting license for the 2010-2011 hunting season. The latter ensured that the respondent recently had intended to hunt. We randomly selected 1500 recipients that had 1-4 years' experience with red deer hunting within the last decade and 1500 recipients with 5-9 years of experience to survey hunters with 2 levels of hunting experience (1-4 years experience, vs 5-9 years experience) and eagerness. Recipients were selected corresponding to the distribution of deer hunters at the county level. Data on the recipient's age, sex, education level and place of living (rural – urban) were extracted from the National Population Registry. Statistics Norway administrated the data collection according to their established standards. Out of 3000 questionnaires sent out, we received 1820 responses (response rate 61%). Because registry data were linked to the respondents, we were able to compare distributions of demographic variables between non-respondents and respondents (paper III, Table 1). The questionnaire to red deer hunters consisted of 45 questions, arranged in 5 sections; (1) backgrond information about the hunter such as the households gross annual income, number of years as a hunter, annual average hunting effort, environmental orientation and the importance of game meat, (2) recent hunter activity (red deer), travelling distance, use of dog, hunting technique, hunting in team or not and season of interest, (3) perception of the current situation (management practice and hunting access), regarding prices for licenses, hunting regulations, crowding, (4) preferences for red deer hunting in the future such as region of interest, preferred hunting technique, importance of bagging deer and preferences for possible additional facilitation (guide, standard of accommodation etc.) and (5) willingness-to-pay for hunting licenses, per kilo game meat, age-groups of deer and hunting seasons. We constructed categorical questions that used a balanced 5-point bipolar scale. No questions were mandatory. When relevant, the respondent had the option of choosing “I do not know” or “Not relevant”. To ensure that respondents had interpreted the more complex questions correctly, we used reverse keying, i.e. repeating the same question with a different phrasing.

Invitations to take part in the survey for paper V, were sent by personalized e-mail letters to those who had applied electronically for grouse hunting permits through the two large public agencies “Norwegian State-Owned Land and Forest Enterprise” (Statskog SF) and “The Finnmark Estate” (Finnmarkseiendommen), which manage approxiamtely 50 per cent of all outfields in Norway. We sent 8,129 invitations, of which 256 were neglected because of failed delivery, leaving 7,873 potential respondents. Prior to the analyses, we omitted 20 foreign, blank, or irrational questionnaires (e.g., age stated to be 110 years). In addition to the direct e-mails, the project team chose to sample with an open invitation, as I did in the sample for paper II and III. Invitations to participate in the open survey were posted on various Norwegian hunting-related websites. An e-mail filter was used to facilitate the participation of only new and unique respondents. Descriptive analyses of the response data did not reveal any deviations between the Internet participants and those invited by e-mail (almost the same result as for paper II and III), and therefore the two samples were pooled.

The questionnaire for paper V consisted of a total of 26 main questions, arranged in three sections. The first and last section contained questions about demography and hunting habits. A middle section contained questions addressing attitudes and willingness-to-pay, largely through the use of what-if scenarios (not used in my thesis, but published by Wam, Pedersen and Hjeljord (2012)). The answering format for numerical and complex attitudinal questions was left open (i.e., fill-in boxes) to avoid scale bias (Mitchell & Carson 1989), while for more simple categorical questions it was specified (tick boxes or balanced point scales). Topics that we considered particularly difficult were addressed twice in two differently phrased questions (reverse-keying). No questions were mandatory and, when relevant, the respondent had the option of choosing “unknown” or “other, please specify.” The majority of the respondents in our survey completed most of the questionnaire: 59% answered all of the 26 questions, 22%left out 1–2 questions and 8% left out 3–4 questions.

2.2 Data collection and possible sources of bias

In surveys, four types of errors can occur (Vaske 2008): (1) coverage error occurs if there is discrepancy between the target population and the subset of individuals who are included in the sampling frame, (2) measurement error is the difference between a respondents' answer and the "correct" answer. It occurs if respondents' answers are imprecise, inaccurate or cannot be compared to answers provided by other respondents, or poor questionnaire wording/construction. (3) Nonresponse error occurs when a significant number of people in the survey sample do not respond to the questionnaire and are different from those who do in a way that is important to the study. (4) Sampling error is the extent to which a sample is limited in its ability to perfectly describe a population because only some and not all individuals in the population are sampled.

A rule of thumb to reduce sampling error is to increase the sample size. Formulas have been developed to estimate the optimal random sample size of a population and to ensure the sample is within desirable error rates (Vaske 2008). Online resources are also available, i.e. (http://www.custominsight.com/articles/random-sample-calculator.asp). If you want to draw a random sample out of 55 000 ptarmigan hunters in Norway, you must obtain a minimum of 1047 respondents to sample with 95% confidence level, given a ± 3% sampling error. The sampling error and confidence level work together. For example, if you have 95% confidence level with an error of 3%, and conduct the same survey 100 times, the results would be within ± 3% of the first time you ran the survey in 95 times out of 100. If you want 99% confidence level, keeping the same sampling error, the sample size must be increased to 1783 randomly drawn respondents. The number of respondents of the postal survey to willow ptarmigan hunters was 1605, out of a sample population of 2717 hunters.

Coverage error could be an issue regarding paper I, II and III, since the sampling of the postal survey was based on ptarmigan hunters in the central part of Norway (Figure 4), although it covers large regions of the ptarmigan habitat in this part of the country. However, I believe the sample size is outweighing the possibility for major coverage errors. The open web survey can contribute to reduced coverage error. In paper II, we checked for demographic deviances in relation to the postal survey and found only differences in education level between the respondents in the two samples. I do not believe that persons who are not interested in hunting took the effort to answer the web surveys. Coverage error is not likely to be an issue for red deer hunters (paper III), since I sampled from all municipalities open for red deer hunting. To ensure that question formulation was clear, we pre-tested the surveys and used mostly 5 or 7-point bipolar scales, categories (i.e. 1-4 times, 5-9 times etc.) or continuous response formats and avoided open-ended questions. Regarding nonresponse error, we have not controlled in detail the representativeness for the respondent's age, sex and location of residence (urban-rural). Consequently, the results for ptarmigan hunters are not necessarily representative for all ptarmigan hunters in the country. However, in the survey of red deer hunters (Paper III), we had the possibility to control the representativeness (based on sociodemographic variables) of respondents in relation to non-respondents, because the survey was linked to registry data from the Norwegian population registry. We found only minor, non-significant deviances between the respondents and non-respondents in the sample. Further, we have tried to reduce the sampling error by increasing the sample size. For example, we sampled approximately 5% of the Norwegian ptarmigan hunters in 2006/2007, and draw 3000 red deer hunters, which equals 7.2 % of the 41 628 red deer hunters in the national hunting registry after the 2010/2011 hunting season, where 1820 responded.

2.3 Measurement instruments

Environmental orientation was measured using the New Environmental Paradigm (NEP) scale (Dunlap & Van Liere 1978; Dunlap *et al.* 2002). The NEP scale measures a persons' environmental orientation along an axis from an ecocentric to an antrophocentric view (Bjerke & Kaltenborn 1999; Dunlap *et al.* 2002) and can be related to the TPB as a descriptor of attitudes towards harvest regulations. Originally, the NEP scale comprised two sub scales: (1) the "new ecological world view" which basically says that humans are part of nature and must realize this in the use of resources (an ecocentric view), and (2) the "human exemptionalism paradigm", where humans are viewed as exempt from the laws of nature and rule over the physical world (an anthropocentric view). In paper III, we used a modified version of the NEP scale with 7 items (Table 2). The NEP scores range from 1-5 and a low NEP score is associated with an anthropocentric view (i.e. consumptive activities), while a high NEP score is associated with appreciative activities.

Table 2. Questions used to calculate the NEP-scores. Response format: 1= Strongly disagree, 5= agree completely.

1	The balance in nature is delicate and easily upset*
2	Humans are severely abusing the environment
3	The so-called 'ecological crisis' facing human kind has been greatly exaggerated
4	Plants and animals have the same rights to life on Earth as humans
5	The balance of nature is sufficiently stable to withstand the impacts from a modern industrial society*
6	If things continue on their present course we will soon experience a major ecological catastrophe*
7	Human ingenuity will ensure future life and living conditions on Earth

*these questions (human exemptionalism) were reverse keyed before calculating the NEP-Score.

To measure bag orientation, we used a 6 item scale adapted and modified from earlier catch orientation studies in recreational fishery (Kyle et al. 2007; Aas and Kaltenborn 1995; Fedler and Ditton 1986) since there are few studies on catch orientation among hunters. I simply replaced the word "fish" with "ptarmigan" and used the original questions (Table 3). This makes it possible to compare catch orientation among ptarmigan hunters with other studies of recreational harvesters such as anglers. As already shown, motives for recreational hunting varies among hunters, and catch orientation is often used to measure the importance of getting catch during performing an activity.

Table 3. Hunting goals and bag orientation. Response format: 1= Strongly disagree, 5= Strongly agree .

1	I am not satisfied with a hunting trip unless I shoot at least one ptarmigan
2	Much of the pleasure of hunting is reduced if I have to stop hunting when the bag limit is filled
3	The more ptarmigans I get the more satisfied I become
4	If I can strengthen a ptarmigan population by shooting fewer birds; I'll be willing to do it
5	I can be satisfied with a hunting trip even if I do not shoot any birds
6	I am just as satisfied with the hunting trip if I need to let some birds go due having reached the bag limit

The hunters' self-reported accept for ptarmigan refuges were measured with 10 % increments from 10 % to 50 % of the hunting area serving as a refuge where no hunting was allowed. For the same reason (the project objective) we measured the hunters' willingness to refrain from shooting single birds (which occur more often in years of low chick production), and we measured the willingness to refrain from shooting single birds for three alternative densities (10, 20 and 30 birds per km^2). The increments of percentage of protected area and alternative population densities were hypothetical measures based on former practical experience and judged by the project team of researchers to be plausible alternatives in future management strategies (paper III). We used hunters' acceptance for the proportion of the hunting terrain as game refuges and the willingness to refrain from shooting single birds at given densities in a few simplex models (Guttman 1954), which is useful for path analysis. More details about the use of simplex models are provided in Chapter 2.4

Different alternatives of harvest principles and regulations were listed as 5-point bipolar scale questions (paper II), where respondents scored their preference for each rule (see Table 4). Some of the harvest regulations were not commonly practiced at the time the survey was carried out, for example an annual quota of 15 birds, but similar practices were quite common as a harvest regulation in management of recreational fishing for Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) in Norway. We know from other studies that many hunters also engage in recreational fishing, so there is reason to believe that some of the hunters were familiar with annual quotas through their fishing. I also believe that game management can learn something from management of recreational fishery, since the challenges are similar for both.

2.4 Data analyses

To identify the most influential factors related to a hunters hunting success (paper I) I used an information-theoretic approach (Burnham & Anderson 1998). The principle of parsimony is simply the best compromise between explaining as much of the variation with as few parameters as possible. Data were analyzed with the program SAS ver. 9.1. We used a generalized liner model with the identity link function, and Bayesian information criterion (BIC) as the selection criterion. This procedure creates different combinations of the initial 14 predictor variables. We analyzed the data without specifying any interaction effects, and each combination (often labeled as competing models) is assigned with a BIC value. As a rule of thumb, competing models with ΔBIC < 2 can be considered as equally good. Three competing models had ΔBIC values < 2 (competing models were not discussed in paper I). Competing models included one the following additional parameters: (1) number of days training the gundog or, (2) the respondents age, or (3) number of days with physical training (Andersen *et al.* 2009a).

I used an independent samples t-test to compare differences between the two sample sources (the questionnaire and web sample) in paper II and III. To compare preferences for harvest principles between local hunters (group 1), mixed (group 2) and non-local hunters (group 3), I used One-way analysis of variance (ANOVA).

We conducted the analyses of harvest regulations (response variables) and demographic variables (predictors) as a path analysis (paper II). A path analysis is a multivariate approach that allows us to visually understand the relationship between variables (Vaske 2008). A high standardized beta weight indicates a high level of association between variables. A structural equation modeling (SEM) approach was used to analyze the interactions between environmental orientation, hunting goals and attitudes towards management interventions (paper III). Confirmatory factor analysis (CFA) and path models with latent variables were performed. Aside from analyzing ordinary CFA, we also present nested factor models (Gustafsson and Åberg-Bengtsson 2010). In a nested factor model, subfactors (nested factors) are modelled in addition to a general factor, in order to better explain the covariance among a sample of items representing a measurement scale. A general factor influencing all items is typically fitted first, and then more narrow factors are fitted to the subsample of items unexplained by the general factor. Figure 1 in paper III illustrates this principle.

We further analyzed two simplex models (Guttman 1954) where the variables are ordered in terms of complexity (a simple order of complexity, hence the name, here it means linearity), so that items reflecting simple or early stages in a concept are predictive of items of greater complexity within the same domain. For example, area protection acceptance 10% (APA 10) predicts APA 20%, which predicts APA 30%, which predicts APA 40%, which finally predicts APA 50%. We used the same simplex model procedure for willingness to abstain from shooting single birds at given densities (10, 20 and 30 birds/km^2), but data did not fit well into a simplex model (not a linear relationship). From the point of view of correlations, good fit is provided if variables close in the developmental trajectory correlate higher with each other than with variables further apart on the developmental path. A graphical illustration of a simplex model in a path analytic diagram is provided in figure 3, paper IV.

Latent Class Analysis (LCA) was used to identify hunter typologies in paper IV and V. LCA groups survey participants into unique clusters with shared identity, based on characterizing variables (also labeled as manifest variables in some papers) such as attitudes, motivations and habits (Lazarsfeld & Henry 1968). Compared to the more traditional clustering approaches (i.e applying distance measures), LCA clustering is based on distributional probabilities (maximum likelihood) from the characterizing variables (Magidson & Vermunt 2002). Continuous variables were transformed into <10 categories (a necessity for classification), while retaining the original distribution of data. This allows multiple statistical approaches for choosing the optimal clustering variables (step 1) and the number of segments (step 2). For a general introduction to LCA, see (Hagenaars & McCutcheon 2002).

LCA are normally conducted top-down, beginning with full models and refining these by removing variables that are not useful (Vermunt & Magidson, 2004). Bayesian Information Criterion (BICLL) was used to rank model parsimony and to select the optimal number of latent classes. Because our purpose was mainly identification and not prediction, we chose BIC over Akaike's Information Criterion (AIC) because of BIC's stronger penalty for additional parameters (Quinn & Keough 2003).

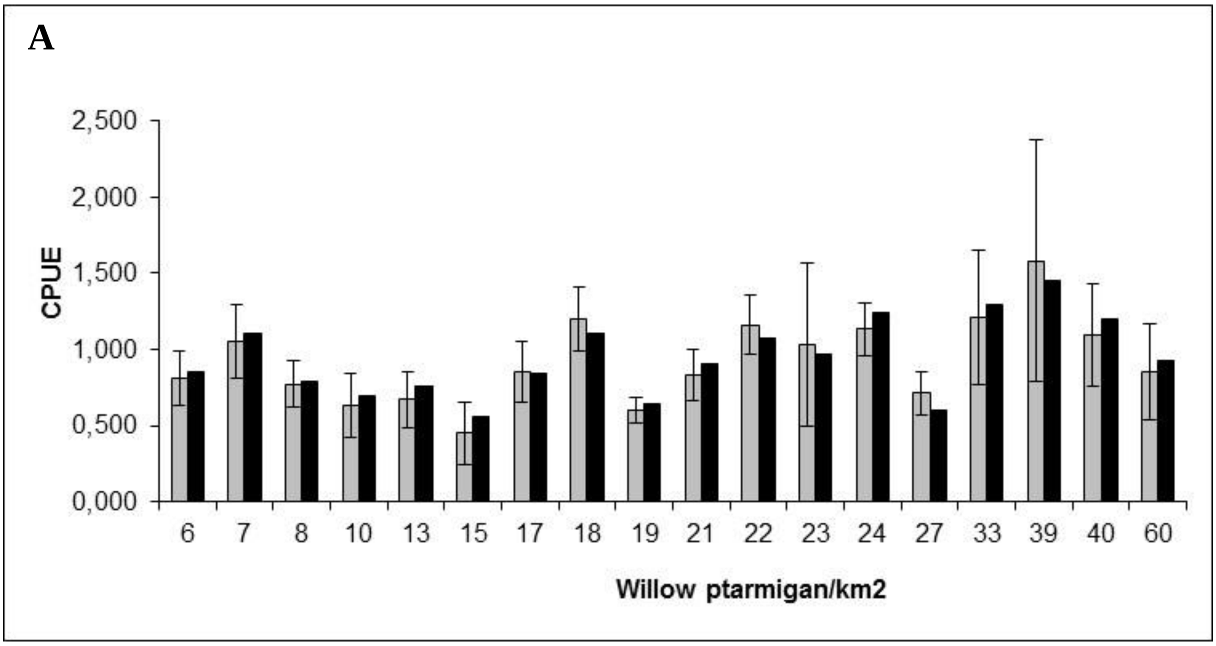
Differences were considered statistically significant at $p < 0.05$.

3. Results and discussions

3.1 Factors related to hunting success

Paper I identified several influential factors on a hunter's success. There was four competing models with differences in BIC values < 2 units (see methods). The most parsimonious model of individual hunting success (BIC:-280.284) included the following parameters: There was a weak, positive relationship between CPUE and distance from road (β=0.015, p=0.001), number of willow ptarmigans observed per day (β= 0.010, p=0.001) and number of years of experience (β=0.005, p=0.020). There was a weak, negative relationship between number of days spent on planning (β=-0,030, p=0.001), effort, in terms of number of hunting days (β=-0.023, p=0.001), and also how easily hunted the terrain was (β=-0.174, p=0.004) and hunting technique (β=-0.162, p=0.003), where hunters without dog where more successful during the hunting season, than hunters with dogs (Table 1 in paper I). Terrain properties or characteristics, such as ruggedness, can explain the negative relationship to hunting success. The number of willow ptarmigan observed per day can remain high, and also the hunting success (catchability), although the abundance is low. This phenomenon (hyperstability) can occur in situations where birds clusters, for example after brood break-up or in the moulting-phase when the first snow covers the mountains.

Another important finding was the lack of significant relationship between catch and estimated ptarmigan density prior to hunting season in the way it was measured here (Figure 7A). One solution to avoid unsustainable harvest rates is to estimate seasonal quotas per hunter, as suggested in paper II. I also found a positive relationship between distances from roadways to the hunting terrain and CPUE, which is in accordance with the research literature. For example, Brøseth and Pedersen (2000) fitted GPS transmitters to hunters, and found that willow ptarmigan hunters walked on average 16.2 km daily at a speed of 2.8 km/h, and they hunted for 9 hours each day, of which almost 6 hours was active hunting time. Hunting effort was strongly dependent on the starting point, and areas closer than 2.5 km to the base cabin were subject to 82% of the hunting activity. Areas furthest away, were subject to lower hunting activity.



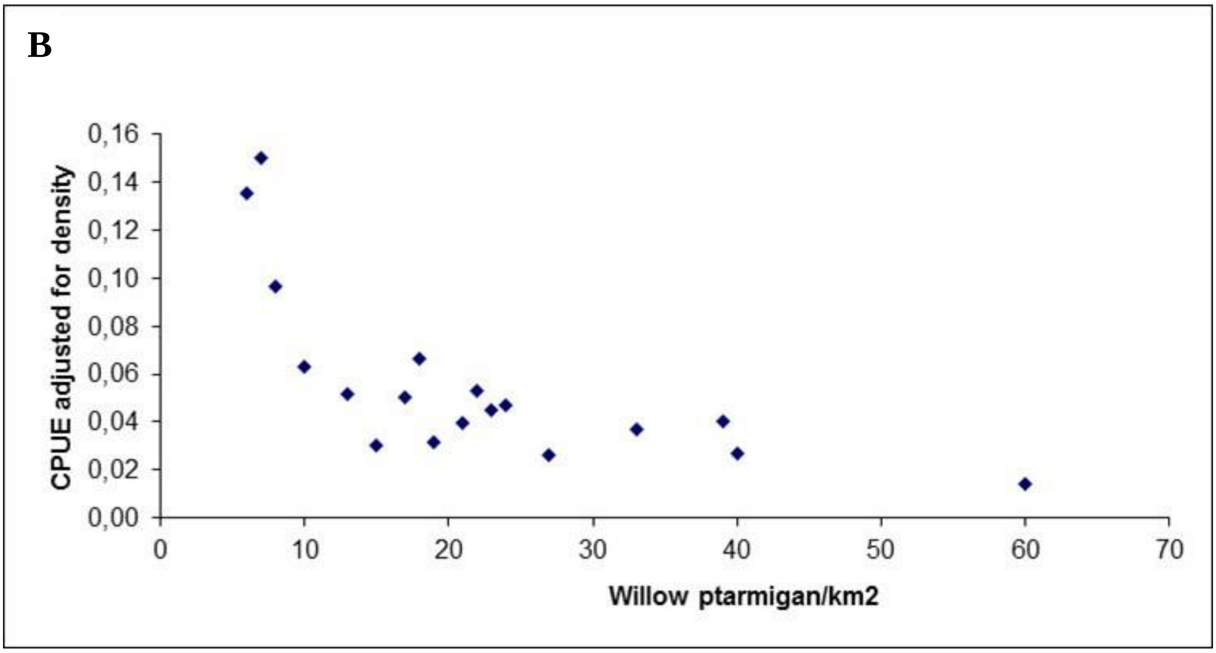


Figure 7 A- B. (**A**) Average individual hunting success (± 2 S.E, grey bars) and number of willow ptarmigan shot in the area/the total number of hunting days in the area (black bars) in relation to estimated density of willow ptarmigan prior to hunting season 2006/07.(**B**) CPUE adjusted for density (CPUE/willow ptarmigan per km^2).

Rugged terrain can explain the negative relationship between how easily-hunted the terrain was, and hunting success, because this type of terrain offers more hiding places for birds. It is also likely that some hunters avoid hunting in rugged terrain within their overall hunting areas. Hunting success also varied with hunting technique so that hunters without a pointing dog were more successful than hunters with a pointing dog throughout the season. This may be because of seasonal effects such as bird behaviour and clustering, which in turn can affect harvest rates. The effect of preparation, such as choosing hunting destinations, are more difficult to explain, because most of the hunting licences for the first weeks of the season are acquired by the non-local hunters during summer, before willow ptarmigan abundance is monitored.

Hunting success is complicated by several intrinsic and extrinsic factors. For example, deer harvest is not solely limited by quotas but also by hunter effort (paper III). The number of ptarmigan observed per day was a better descriptor than estimated density prior to hunting season (paper I). These two species represents fundamentally different management situations, as the red deer population has been rapidly increasing, while ptarmigan harvest has been steadily declining during recent years. In a situation where the management aim is to control undesired population growth (as for red deer), the decision to do so is in the hands of the hunters. In many cases, the deer hunting is carried out by the landowner with friends, and if they decide to not harvest the entire quota, the management goal will not be reached. On the other hand, attempts to increase effort, for example by improved accessibility for other (new) hunters, may improve deer harvest rates. For ptarmigans there was no effect of game abundance on hunting success. The number of game encounters was a better explanation for hunting success, which may be explained by the behaviour of ptarmigan during hunting season. In addition, hunting experience and features related to hunting terrain and distance from road also affected hunting success. Both Rimpi (2005) and (Asmyhr 2012) found a positive effect of experience on hunting success in Sweden. Experienced hunters can be more efficient in terms of not wasting time hunting in less attractive areas. In our study, hunting experience was positively associated with hunting success.

3.2 CPUE and game abundance

There was no clear support for the assumption that CPUE was linearly proportional to the estimated density prior to the hunting season. This was consistent with the findings of Asmyhr (2012) who reported that daily bag size was at best weakly density dependent. However, Cattadori et al. (2003) found such a relationship for red grouse when data were log-transformed. The most common form of non-proportionality between CPUE and abundance involves CPUE remaining high while abundance declines (Harley, Myers & Dunn 2001). We found a similar pattern when calculating CPUE corrected for ptarmigan density (Figure 7B), where CPUE was higher at low densities, indicating that hunters were more efficient at low densities (< 15 birds/km^2), compared to higher densities.

The increase in CPUE at low densities may be related to changes in catchability. The catchability coefficient can be influenced by several factors. First, game abundance is assumed to be associated with the number of bird encounters, but as birds can be temporarily clustered, a high CPUE may occur despite low densities (hyperstability). Secondly, the hunter's hit rate and the fact that only two shots can be fired at the same time from a shotgun, independently of whether one or 10 birds are flushed) may influence the harvest rate. Thirdly, the bird's behaviour and weather conditions (shyness) will also affect catchability. In addition, it may be speculated that in areas with high hunting pressure, the CPUE per hunter will be affected, as the number of hunting days per km^2 increases and the number of birds remaining decreases. Our study dealt with low densities (range 6-60 birds/km^2) compared with those ranging from 150 to 700 birds/km^2 reported by Cattadori *et al.* (2003). Ranta *et al.* (2008) found a linear relationship between CPUE and density for three grouse species; capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*) and hazel grouse (*Bonasa bonasia*) in Finland, when analysing data in the same way as Cattadori *et al.* (2003). Ranta and colleagues (2008) also reported that the pattern of population dynamics derived from bag data was different from that shown by census data. Asmyhr (2012) and Willebrand et al. (2011) urged caution in relying on bag size as an index of willow ptarmigan abundance because harvest rates were primarily determined by hunter effort and game encounters, and to a far lesser extent by bird density. These results illustrates the need for caution in interpreting wildlife bag data as reliable parameters in population dynamics (Ranta *et al.* 2008; Willebrand, Hornell-Willebrand & Asmyhr 2011; Asmyhr 2012).

Translated into harvest models and a MSE concept, these results illustrates that using game abundance (measured as bird density per km^2) alone, not necessarily is an adequate measure to adjusting harvest rates. Hunting effort should also be taken into consideration, since hunters may only have a limited time (i.e. number of available holidays or weekends) to spend on hunting. Attempts to increase effort (for example in red deer management), must therefore include the possibility of involving new, or more hunters. This has to be done by refining and adjusting the harvest control model (Figure 6), which not only means adjusting the harvest regulations, but also the way hunting is administrated (hence, the term " harvest control model"). One recommendation can be to design management solutions that are able to rapidly adjust hunters' effort if needed, or the possibility to adjust quotas during the hunting season.

3.3 Harvest strategies and harvest regulations

Paper II clearly demonstrates that a quota strategy was the most preferred harvest principle among ptarmigan hunters (average index core: 3.55). Secondly, hunters preferred a reduction in number of hunters or dividing the season into short periods (average index score 3.03). Shortening the length of hunting season or no hunting after 23 december, was the third most preferred principle (average index score 2.86). On public land in Norway, which covers approximately 50% of the areas with ptarmigan hunting in Norway, hunting opportunities can be legally differentiated between local and non-local hunters, and several municipalities also distinguish between hunters with and without dogs. Non-local hunters consistently had the highest index score and mixed hunters (people who hunt both locally and in areas outside their place of residence) scored consistently lowest for all harvest principles. I interpret this difference as a strong wish amongst non-local hunters to maintain access to ptarmigan hunting, since the major share (80%) of ptarmigan hunters hunts outside their local municipality (Pedersen & Storaas 2013).

Breaking these harvest strategies down to specific harvest regulations; hunters preferred a seasonal quota of 15 birds, secondly a daily limit of 2 birds per day, and no hunting in winter. Splitting up the hunting season in short periods, typically of 5-7 days length, during the first 2-4 weeks of the season was slightly less preferred, while shorter hunting season was least preferred (Table 4).

Table 4. Hunters' preference for harvest regulations (HR), means scores and standard deviations (SD). Response format: 1=Strongly disagree, 5=Agree very much. Standardized regression weights (β; 3-7 columns) for a path model With 7 Harvest regulations as dependent variables and 5 background variables as independent variables (N = 2113).

Harvest regulation	Mean (SD)	Gender	Age	Edu	Urban	HE
Daily bag-limit (2 per day)	3.32 (1.47)	**-.08**	**.11**	**-.05**	-.02	**-.06**
Annual quota 15 birds	3.79 (1.40)	-.01	**.19**	.02	.01	**-.06**
Shorter hunting season	2.46 (1.46)	.00	**.06**	-.01	.02	.00
No hunting in winter	3.23 (1.65)	-.02	**.26**	**-.06**	.02	.02
Reduce number of hunters	2.88 (1.35)	-.03	-.04	.00	**-.05**	**.05**
Improved access	2.60 (1.21)	.01	.04	**-.06**	**.07**	**-.06**
Split up season	3.19 (1.37)	-.03	**.09**	.02	.02	-.03

Note. Significant betas in bold ($p \leq .05$).Gender: female = 0, male = 1; Edu = Education level; HE =Hunting experience.

Quotas was the most preferred harvest strategy, which in this case included a daily bag limit (of 2 birds) or an annual quota (of 15 birds). A annual quota, or a quota for a longer time span, for example a week, was the most preferred regulation method, which also allows hunters to bag more birds per day if possible. In terms of harvest management, a total quota seems to be a better solution, since both the precision of the offtake and hunter satisfaction may increase, compared to baily bag limits. Secondly, a reduction in number of hunters was preferred. As mentioned, to split up the first weeks of the season in periods of 5-7 days is common, and was more preferred than shortening of hunting season in general. In an interesting study Sunde and Asferg (2014) examined the effect of manipulating length of hunting season for 28 species in Denmark. According to the authors, there has never been either bag limits or quotas implemented in the Danish hunting regulations. They identified 63 cases where the hunting season was adjusted. The motivation behind adjusting hunting season was either for population considerations, ethical reasons (i.e. avoid seasons where breeding activities takes place) or other reasons (mainly harmonization of hunting seasons across species to simplify hunting rules). The authors found no significant effect of season length change on bag size change (for species with hunting season more than a month duration). However, there was a difference between sedentary and non-sedentary species, and interaction with the motivation behind changing season length. For sedentary species, changes in season length had no effect on bag size. They also modelled that a reduction in season length less than 50%, is inefficient as a means to predictably changing harvest rates. Their explanation for this, is that hunters invest a fixed effort aimed at a specific yield within a season.

Translated into ptarmigan management, mangers should develop regulations that are based on annual quotas, or quotas over a longer time span than a daily limit. This may increase the precision of the offtake and in addition give hunters the opportunity to bag more birds over a shorter time, than they can do under a daily bag limit regime. Thus, hunter satisfaction is expected to increase. As shown in paper I, the number of ptarmigan observed per day was a better predictor than estimated ptarmigan density on hunting success. During the hunting season, both weather and bird behaviour (shyness, moulting, snow etc.) can affect the catchability and hunters may adjust their effort in relation to game abundance. In addition, more than half of the hunters use a dog. Hunters with dogs are probably more interested in having the opportunity to use the dog throughout the season, and therefore more negative to shortening the hunting season.

The red deer hunters also reported different preferences for harvest regulations, regarding the number of animals they were allowed to shoot (the size of the quota), interest in trophy hunting and the importance of game meat. For example, team hunters versus solitaire hunters and their preference for the size of the quota (Figure 2 in paper IV) and the need for meat as illustrated by the differences between the "deer enthusiast" and the "solitary locals". In the Norwegian management of red deer, adjusting effort is clearly an issue, if aiming to reach large-scale management goals. The hunting season for red deer has also been expanded recently, from 10. September to-15. November (66 days) up to the 2011/12 season, to 1. September to 23. December (114 days) from the 2012/13 season, which is a 73 % increase in length of season.

What can we learn from this? To manipulate the length of the hunting season (in a system with no quotas or bag limits), may have no effect on bag size at all, unless the length of hunting season is increased dramatically (>50 %). This may occur because hunters initially more or less have a fixed effort (number of available weekends or holidays to use), where effort may increase in years where populations peaks. Adjusting length of season was the least preferred principle in my study and seems to have negligible effects at a large scale (Sunde & Asferg 2014). This also leads back to refining the harvest control model in Figure 6. Based on these results, one advice would be to keep the open hunting season length and implement other regulations, such as long-term quotas (for the season, a week or a given number of days).

3.4 The effect of environmental orientation

In general, the participants in this sample were quite supportive of modest regulatory actions towards protecting a certain percentage of land from hunting. As expected, the mean scores decrease linearly from the 10 % item to the 50 % item. We found that 92.20 % of the sample would accept protection of 10 % of the land from hunting, whereas 62.70 % would accept protection of 50 % of the land (Table 3 in paper III). Given the nature of the five alternatives of area protection, we speculated that they may form a simplex structure—as illustrated in Figure 3, paper III. The simplex model fitted the data fairly well and the model was included in the subsequent SEM analysis of the current data.

Figure 8 presents the standardized regression weights as estimated in our structural equation model, but only significant paths are shown. All background variables were included as predictors for environmental concern (NEP), hunting goals (HG), acceptance of protected areas (APA10% - 50%) and willingness to abstain from shooting single birds at given densities

(WASB10 – 30). Education and income predicts willingness to abstain from shooting birds, but there were no associations between these variables and the NEP scores and the HG scales, or with the variables measuring acceptance of protected areas. However, age ($b = -0.07$, $p = 0.001$) and urbanization ($b = 0.05$, $p = 0.019$) did predict protection acceptance. This means that younger ptarmigan hunters, and those living in towns and cities, are more willing to protect some parts of the hunting areas. Neither age nor urbanization did predict NEP scores HG or willingness to abstain from shooting single birds.

We found no significant relationship between socio-demographic variables (age, education, income, urban association) and environmental concern (NEP). However, we found that male hunters have lower NEP scores than female hunters, and that the degree of environmental orientation was related to acceptance of protected areas, in addition to willingness to abstain from shooting single birds at density 10 birds/km^2 (WASB10). We did not find any unique effect from the NEP on the WASB30 variable, after the effect from WASB10 was controlled for. As shown in Figure 8, participants with high NEP scores tended to be satisfied with hunting trips even if they did not obtain much game ($b = -0.21$, $p=0.001$ for the path from NEP to HG)

The figure also illustrate how the APA variables conforms to a simplex model, due to the high betas between neighboring variables, and ignorable betas for the other APA variables (not shown in Figure 8). This pattern indicates homogeneity in the sense that APA50 expresses harvest regulations more strongly than APA40, which in turn expresses harvest regulation more strongly than APA 30, and so on. We next regressed the five APA variables on the NEP and HG factors, finding some small, but significant effects of NEP on higher levels of protection acceptance, even when the effect of the lower levels variables had been factored out. For the APA 20, APA30 and APA 40 variables, the effect sizes were $b = 0.05$ ($p = 0.013$), $b = 0.06$ ($p = 0.009$), and $b = 0.04$ ($p = 0.021$) respectively. We did, however, find an effect from the HG on both the WASB10 ($b = -0.23$, $p<0.001$) and the WASB30 variables ($b = -0.13$, $p<0.001$).

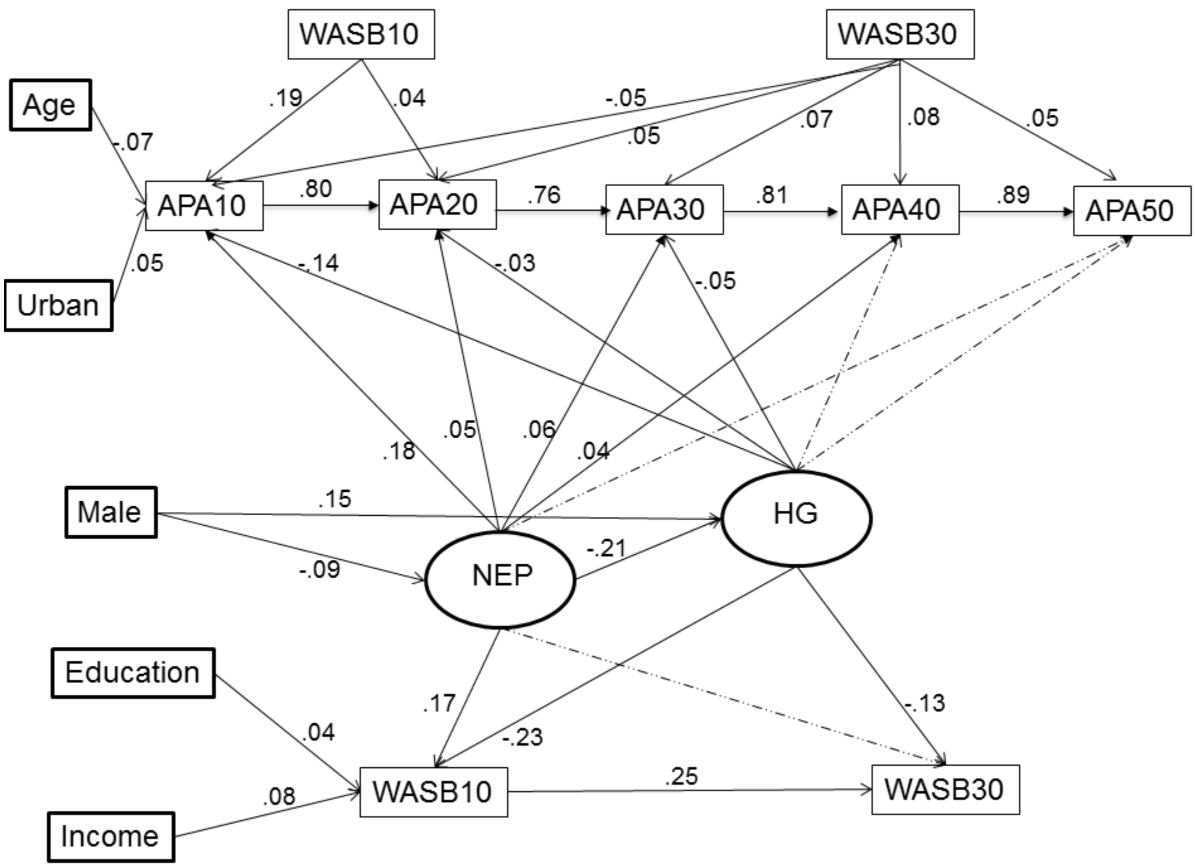


Figure 8. The full structural equation model with standardized regression coefficients. Non-significant coefficients (p>0.05) are shown as dotted lines. APA: acceptance of protected areas in per cent. WASB: abstaining from shooting single birds at given densities. NEP: environmental orientation and HG: hunting goals. In order to reduce crossing paths in the model, the two WASB variables appear twice in the figure.

These results (paper III) indicates that environmental concern was related to willingness to limit harvest, and that the more environmentally oriented the hunters are, the greater is the likelihood of enjoying other aspects of the trip, than just coming home with birds in the bag (the hunting goals). Environmental concern tends to decrease with age, but we found no effect of age in this study. Our results indicated that older people perceived the suggested harvest regulations as more inappropriate than younger, since ptarmigan hunting traditionally has been free from high levels of management interventions and control. This negativity may also be linked to the older hunters' attitudes. For example, the "old" belief that ptarmigan hunting only harvested from a surplus and no regulations are needed because harvest mortality was assumed to be compensatory to some degree. New knowledge on harvest mortality has changed this view (Pedersen *et al.* 2004; Sandercock *et al.* 2011). As known from the literature, attitudes needs time to change, while preferences may change faster (Heberlein

2012). Younger hunters may therefore be more familiar with regulations and therefore less negative.

We found that increasing environmental orientation correlated positively with higher acceptance of regulatory management actions, while socio-demographic variables had limited effect on the relationship between environmental concern and attitudes toward management actions (paper III). As shown is the human dimension literature (and also in this thesis), hunters' motivation can be classified along a consumptive – appreciative experience dimension (hunting goals, catch orientation) and that object specific attitudes tend to be affected by a person's set of environmental beliefs or environmental orientation (Klineberg, McKeever & Rothenbach 1998; De Groot & Steg 2007; De Groot & Steg 2008). The negative association between environmental concern and hunting goals (Figure 4 in paper III) indicates that persons with higher environmental concern tended to be more satisfied with hunting trips, even if they did not obtain much game. They simply are more on the appreciative side, than the consumptive side regarding hunting motivation and - goals. Additionally, higher acceptance levels for both area protection measures and their willingness to abstain from shooting single birds indicates higher willingness to accept harvest regulations aimed at reducing off-take and the chance of overexploitation.

3.5 Hunter typologies

3.5.1 Red deer hunters

The typologies of active deer hunters motivation and hunting approach (Figure 9A) were distinguished mainly by their interest in team hunting, their motivation to hunt trophies, and their place of residence. The 2-class and the 3-class models had equally good fit, but we believe the 3-class model had more applied value, because it identified a distinct group of local hunters. We therefore labeled 3 typologies regarding motivation and hunting approach: "Mixed visitors" (77%), "Deer enthusiasts" (13%) and "Solitary locals" (10%).

Both the more yield-oriented typologies ("Deer enthusiasts" and "Solitary locals") were more likely to live in rural areas, and were clearly distinguished by their interest in trophy and team hunting. In contrast to the "Deer enthusiasts", the "Solitary locals" preferred to hunt alone, and were not interested in trophies, only meat. The solitary hunter also spent fewer days hunting deer, and considered it less of a moral duty to keep deer numbers down than did the enthusiast.

Practically all urban hunters belonged to the large group of “Mixed visitors” to whom obtaining meat was less important. The typology was mixed regarding the importance of having large quotas. These hunters were willing to both travel and pay in order to hunt, probably because they had few or no close landowner relations.

A major distinction between hunter typologies in logistical preferences (Figure 9B) was their interest in long-term leasing of land for hunting. Naturally, the interest in leasing was in part linked to landowner relations and willingness-to-pay. The largest subgroup not interested in long-term lease agreements were hunters who had close landowner relations, and who were less willing to pay for hunting. We labeled 3 typologies: “Landowner acquaintances” (47%), “Less involved locals” (40%) and “Long-term visitors” (13%). We opted for the 3-scheme typologies because of its low classification error (9%), and because a fourth class mainly distinguished the actual landowners (who otherwise behaved largely similar to landowner acquaintances). It may nevertheless be useful to recognize this division, because landowners indicated they hunted less days than their acquaintances.

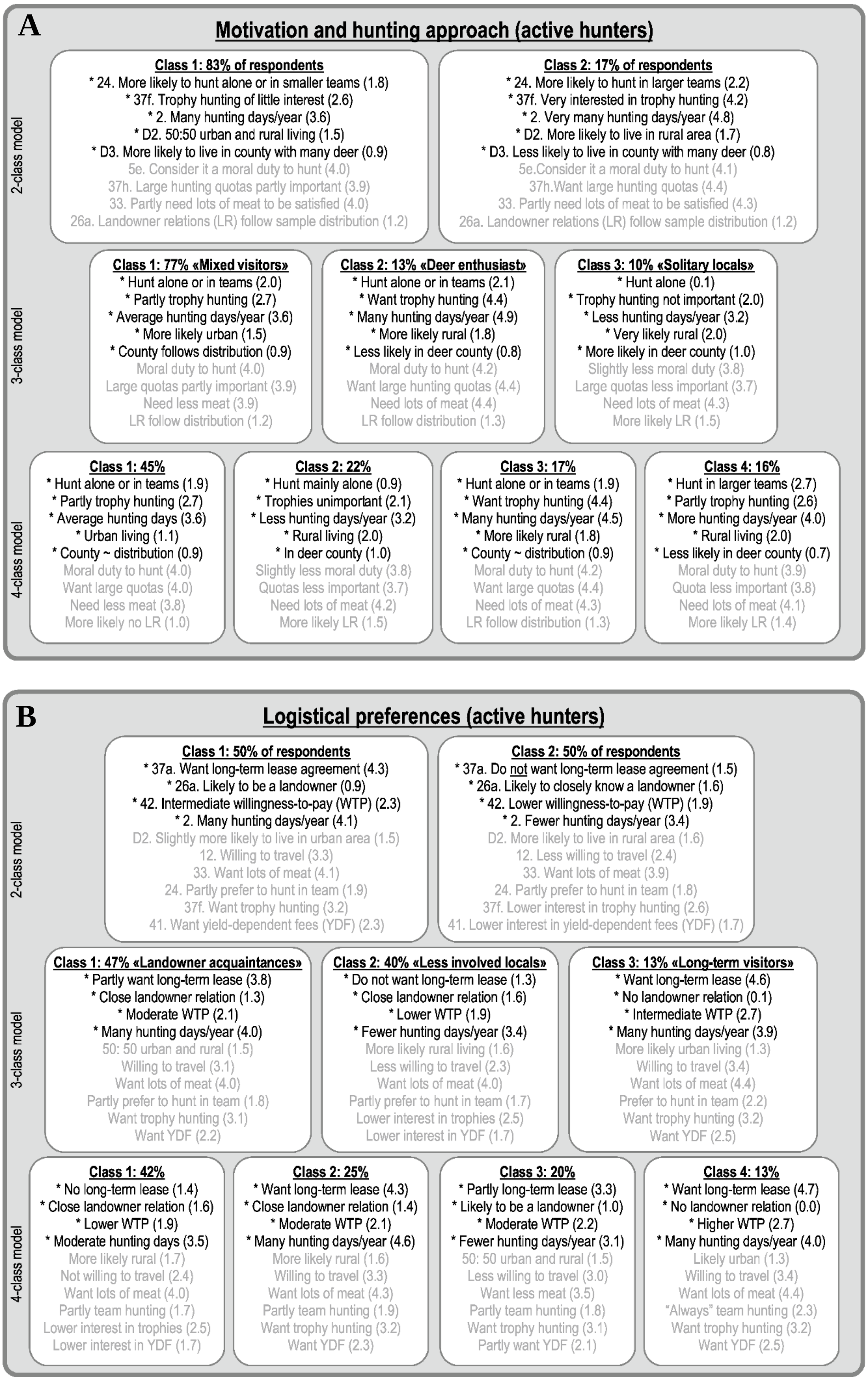


Figure 9 A-B. Variables segmenting active deer hunters in Norway by (**A**) motivation and hunting approach), and (**B**) logistical preferences. Explanatory variables (i.e. part of model estimation) listed in normal font, and inactive covariates listed in light font. Numbers in brackets are group means (see Table 2 in paper IV for scales of variables).

The best models for non-active hunters (N=620) consisted of a partial set of the same 5 variables as for active hunters (table 3, paper IV). Lack of time was a frequent reason for not hunting, which was reported by 70% of the respondents. Apart from lack of time, the non-active hunters showed no consistent pattern regarding factors facilitating future participation or whether they intended to start hunting again (consequently, these variables were not part of the best models).

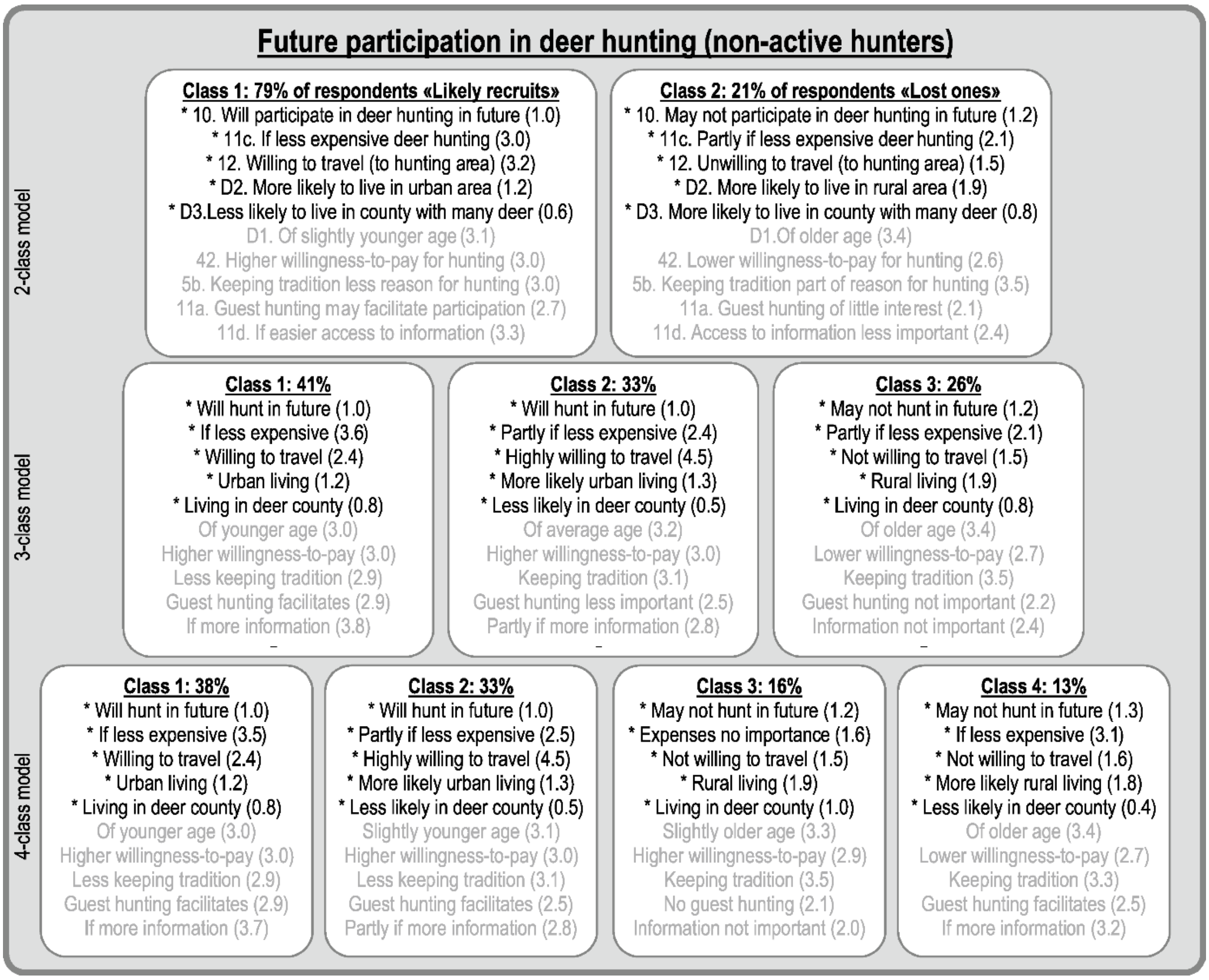


Figure 10. Variables segmenting non-active hunters. Explanatory variables (i.e. part of model estimation) listed in normal font, and inactive covariates listed in light font. Numbers in brackets are group means (see Table 2 in paper IV for scales of variables).

Hunters who were the least likely to start hunting again generally lived in rural areas and had a low willingness to travel (Fig. 10). Among these individuals, some also lived in counties with high deer densities (which means a short travel distance). The covariates suggests a fading interest due to age of the hunter, which may particularly apply to these individuals. The other group consisted of individuals who lived outside the core deer areas, who largely felt that deer hunting was too expensive, and partly that they lacked sufficient information about hunting opportunities.

Non-active hunters who intended to start hunting again were largely from urban areas, moderately to highly motivated to travel, feeling that deer hunting was too expensive, and wanting more information about hunting opportunities. Because much of the applied value (i.e. identifying which hunters should be targeted for recruitment) is covered by the 2-class scheme, we labeled only 2 typologies: "Likely recruits" (79%), and "Permanently gone" (21%). It is worth noting that likely recruits could be found both inside and outside the typical deer counties with high deer densities.

Overabundant populations of red deer has concerned several stakeholders, questioning the management systems's ability to keep growing populations of red deer in check. This skepticism is based on the fact that only around 60% of the red deer quota is harvested annually, and that studies of landowners with red deer quotas has shown that hunting to a large extent is based on the landowners and their friends (Olaussen & Mysterud 2012). However, this picture is now changing towards a more commercialized approach (Naevdal, Olaussen & Skonhoft 2012; Olaussen & Mysterud 2012).

What can we draw out of this study? First, there seems to be a mismatch between how landowners administers their quotas (hunting with family and friends) and what hunters prefer (i.e. team hunters and solitary locals). We therefore advice landowners to be more flexible in the way their quota is administered and accommodate for a diverse group of hunters, ranging from the solitary hunter to team hunters, the expressed importance of game meat and willingness to pay. Hunter typologies by using LCA can be very useful in future management with the aim of regulating undesirably dense deer populations. For example, this can be done by differentiating areas and time of season by the key factors determining hunter participation and by providing hunters incentives (for example reduced prices for licenses) to shoot antlerless deer or calves. The potential to re-activate currently lapsed hunters seems to be significant regarding red deer hunters, since 4 out of 5 non-active hunters comprised the group of likely recruits.

3.5.2 Ptarmigan hunters

Regarding the importance of bag size, we considered the 3-class models to be equally parsimonious and even better in terms of practical interpretation than 4- or 5-class models with slightly lower BIC-values (Figure 11 A). We labeled the three typologies as (1) "The bag oriented" (32 %), (2) "The northern traditionalist" (25 %) and (3) "The experience seeker" (43 %). The bag oriented was the most consumptive orientated and eager in terms of hunting days and willingness to pay for larger bags. The experience seeker was satisfied with lower bags and fewer hunting days and probably hunting for appreciative reasons, while the northern traditionalist resembled the bag oriented in terms of hunting days, but with much lower willingness to pay.

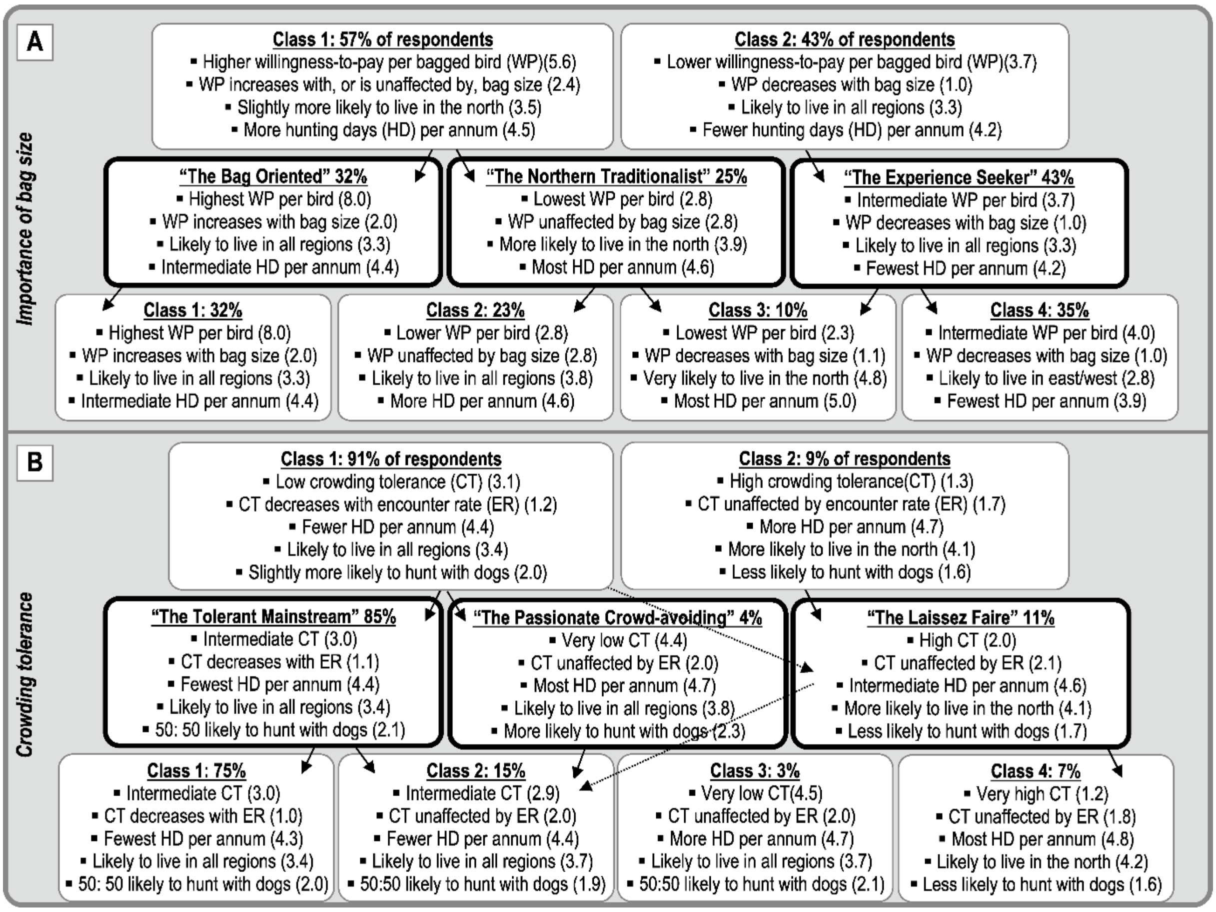


Figure 11 A-B. Ptarmigan hunter typologies regarding (**A**) Importance of bag size and (**B**) Crowding tolerance. Arrows indicates into which classes a lower-level typology model groups into if split further up (for example if the two-class model for importance of bag size are split into a 3-class model, class 1 (57 %) divides both into the "Bag oriented" and "The northern traditionalist" typologies, while class 2 (43 %) mainly goes into the "Experience seeker" typology).

The selection of number of typology classes of crowding tolerance was less clear, since BIC-values and classification errors differed only slightly between the 3- and 4-class models (Figure 11 B). We therefore opted to label three hunter typologies; (1) “The semi-tolerant mainstream” (85 %) had intermediate crowding tolerance, but a strong decrease in crowding tolerance with increasing encounter rate of other hunters and fewest hunting days among the typologies (2) “ The passionate crowd-avoiding” (4 %) had very low crowding tolerance, but this tolerance was unaffected by encounter rates from other hunters and had most hunting days per annum and finally, (3) “ The laizzes faire” (11 %), which was the most crowding tolerant type of hunter, and tolerance was also unaffected by encounter rate. It was also more likely for this kind of hunter to live in the northern parts of Norway.

In the above mentioned studies, I have described how hunter typologies can be used to facilitate more precise determination of the optimal implementation of harvest regulations. We identified several typologies useful for management purposes. Some characteristics related to the consumptive orientation, i.e. the importance of meat (deer hunters) and the bag size (both ptarmigan- and deer hunters). Also regarding hunting effort, the hunters grouped into distinct typologies. This eagerness related mostly to the respondents’ catch-orientation and should be considered in situations where population reduction/control is an important task (i.e red deer harvest in Norway). On the other hand, in situations where avoiding overexploitation is the focus, hunters with strong catch orientation and high effort should be directed to areas where they pay more for exclusive access and the possibility to bag more game. For example, in an area managed for “experience seekers”, it may be wiser to keep a low bag limit, than to reduce number of permits (hunters) since they are less motivated by bag size. Large management areas that can offer a wider range of hunting options, can for example channel different hunter segments to different areas, such as the “the bag oriented” to areas where there are the more shooting opportunities, and in addition higher willingness to pay for increased bag size. Conversely, the more appreciative- and less catch-orientated hunters (who are also more likely to obey harvest regulations), should be channeled to more crowded areas (higher density of hunters) and stronger harvest regulations, at a lower price. The latter may be relevant both for ptarmigan hunters (where the hunters may be satisfied with only a few birds) and deer hunters (for example hunting access later in the season, or only aiming for antlerless individuals, calves or yearlings).

4. Conclusions and further perspectives

To what extent is hunting success explained by game abundance, or are other factors necessary to explain hunting success?

In Norway, only two thirds of the quotas for red deer harvest are actually filled (currently 63%, Statistics Norway 2012). Clearly, deer harvest is not solely limited by quotas but also by hunter effort. Therefore, ways to increase effort might lead to increased offtake of deer, enabling better regulation of growing deer populations.

Bag limit is a commonly used harvest regulation for ptarmigans. The number of birds that can be taken per day is adjusted in relation to measures of abundance prior to hunting season. This adjustment is based on the model of proportionality between catch as an index of abundance, which only is valid if effort and catchability is constant. There was no significant relationship between CPUE and game abundance. Another important finding was the increased CPUE at low ptarmigan densities (indicating hyperstability) at densities below 15 birds/km^2. Lindberget (2009) reported that the willow ptarmigan harvest during the first four days or accumulated over the first eight days of the hunting season not did affect CPUE in the following four day period in Sweden (Lindberget 2009). Bunnefeld et al. (2008) analyzed harvest data from 43 drives on 8 moors in North-England. No effect of the number of grouse counted per square kilometer in July was found on subsequent harvest rate at the first shooting event, but they reported significant differences in intercept (lower for the second shooting event, compared to the first, and the third/fourth shooting event compared to the second), and the same slope in models of grouse shot per km^2 in relation to population density in July. These results indicate that effort strongly affects CPUE at high densities (Bunnefeld *et al.* 2008). By contrast, no such effect was found among willow ptarmigan hunters hunting on state land in Sweden, where ptarmigan density rarely exceeds 40-50 birds/km^2 (Lindberget 2009), and is similar to Norwegian conditions (see densities in Figure 7). These findings raise the question of whether the relationship between CPUE and abundance becomes density dependent at some threshold, since willow ptarmigan densities in Scandinavia are in general considerably lower than in Britain (Hudson 1992).

What are the hunters' preferences for different harvest strategies and –regulations, and how it is influenced by their overall environmental orientation?

For ptarmigan hunters, harvest quota strategy was the most preferred harvest principle. This solution may be more sustainable and reduce the risk for overexploitation, without excluding too many hunters in years when production or density is low. One solution can therefore be to implement conservation limits (CL), as is done for management of salmonids in Norway where spawning targets now plays a major role (Forseth *et al.* 2013). Despite the fact that the ecology for terrestrial species with large population fluctuations such as ptarmigans, compared to salmonids are different, these species have several common features (Andersen & Thorstad 2013). Both species have a negative density dependent response in population growth rates, indicating that limiting factors exists (Berryman 2004), and the environmental stochasticity can vary a lot from hatching to first breeding. To ensure a minimum breeding population in Salmon rivers, spawning targets are defined. If the principle of spawning targets are transferred into ptarmigan management, the management aim should be to ensure a minimum breeding population, defined as the threshold in figure 12. Further, if population abundance is above the pre-defined threshold, a proportional harvest rate should be implemented, which equals the share of the population that could be harvested (the allowed bag). How managers choose to distribute the allowed bag, may be determined by their management goals. Whether it is to maximize profit (i.e. private landowners) or provide public access to small game hunting (public land areas), the harvest should be sustainable (The Norwegian Biodiversity Act 2009). Interpreting my findings in a socio-ecological system framework, it is evident that a quota-system is a better solution than shortening of the length of hunting season. For example, landowners can sell licences with a fixed number of game allowed to bag. This solution will fit both the more appreciative oriented hunter and the consumptive oriented hunters, since the bag oriented simply can buy on more licences to bag more specimens if wanted. Then you pay for what you shoot, as you do in ungulate hunting.

Increasing environmental orientation was shown to be positively linked to acceptance for protecting increasing amounts of land as refuge for prey, as well as increasing flexibility in hunting goals, i.e., a higher likelihood of being satisfied with different aspects of the hunting experience, not just the catch. The degree of environmental orientation can be a useful predictor for likely responses by hunters to management interventions. Knowledge about hunters' environmental orientation or attitudes toward specific management questions is not easily available without performing interviews or surveys, but hunters will most likely respond in different ways to management interventions. Actions promoting flexibility, such as applying seasonal quotas rather than daily quotas, or permits that can be used within a longer timeframe will be preferred by many hunters. It is likely that hunters with a stronger environmental orientation will be more flexible in their attitudes toward strict regulations if the resource conditions dictate restraint in catch. The current context of providing inexpensive small game hunting for large groups only regulated through more or less ad-hoc limitations on numbers of hunters and length of season will change with time, necessitating management models based on scientific knowledge of ecological and social conditions (Thirgood and Redpath 2008). Hunters are more likely to respond favorably to restrictions due to resource scarcity if this is well documented, compared to the current practice based on incomplete knowledge of prey populations. Providers of small game hunting opportunities such as state agencies, landowners and tourism entrepreneurs can benefit from recognizing more explicitly how they can meet diverse demands for experiencing nature, skill development, social interaction with peers and harvesting food resources.

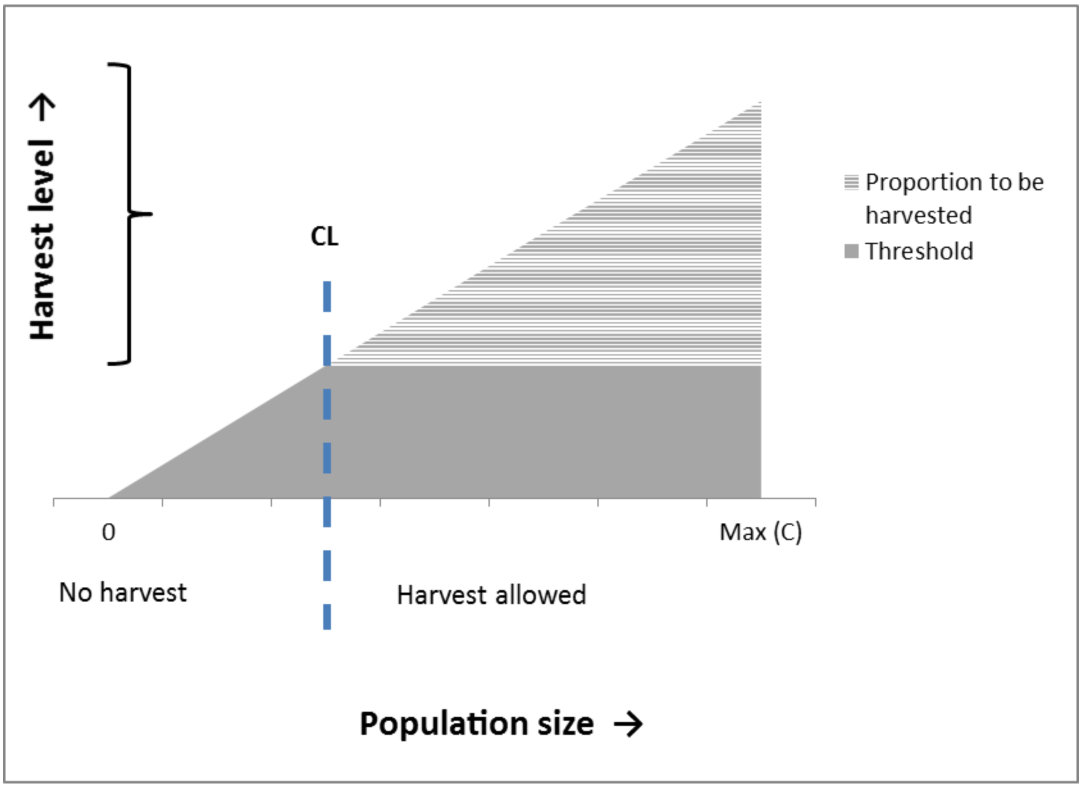


Figure 12. Management principle according to a conservation limit (CL). Quotas for ptarmigan that can be harvested (grey horisonal stripes) can be calculated. The CL must be defined to first meet criteria considered ecological sustainable (threshold), then economic (income) and societal criteria (i.e. hunting access) must be considered. Modified figure from Andersen and Thorstad 2013.

How should knowledge of hunter typologies be used to improve harvest management?
Generally, there is a need to be more flexible and accommodate a diverse group of hunters. An apparent strategy therefore is zone-based management, differentiating areas and time of season by the key factors determining hunter participation. For example, in a situation where the aim is to reduce population growth, harvest policies need to give hunters incentives (e.g., reduced prices for licenses) to shoot antlerless deer and calves voluntarily, or one needs to simply require them to do so by implementing harvest regulations (Brown et al. 2000). If the aim is to activate/recruit more hunters, the “Likely recruits” segment in paper IV comprised 4 out of 5 non-active red deer hunters, and thus, there is a large potential to re-activate hunters currently not participating in hunting activities. Understanding the reasons why hunters become passive is of crucial importance (Enck et al. 2000).

One general advice can be managing hunters, based on their attitudes and motivation for hunting by zoning. This can be done based on their acceptance for harvest regulations (more appreciative orientated and higher environmental concern) and willingness to pay for increased bag size (consumptive oriented and less environmental concern).

4.1 Conclusions

I have given some examples of the importance of SES thinking when adaptive management strategies are developed. Given the recommendations in Figure 1, management of ptarmigans should be placed somewhere between adaptive management and scenario planning. I believe a MSE approach should be a suitable tool to evaluate these strategies. Figure 12 illustrates this principle by first securing that ecological criteria is met, for example by securing a minimum breeding population size (defined as the conservation limit) for a specified region. For example, Hörnell- Willebrand, Willebrand and Smith (2014) estimated that a management unit should be around 400 km^2, if you should be able to manage 50% of the ptarmigan population. Clearly, estimates of conservation limits should be developed for large areas. When population density is above the conservation limit (a threshold or within limits), a gradually increasing proportion of the population can be harvested. How this harvestable proportion is distributed to hunters, has consequences both for the landowners’ income and the society regarding hunting access.

The hunter typologies (paper IV and V) shows that despite hunter diversity, consistent patterns emerge that may be useful for securing hunter recruitment and realizing the full potential of the hunter resources that are indeed available. Cultural traditions held by stakeholders may hamper such achievements, but with sufficient information of the potential benefits gained, these are likely receptive to change. In Norway, for example, red deer hunting has traditionally been conducted by the landowner with family and friends, and only a few landowners have allowed increased numbers of non-local hunters on their hunting grounds (Olaussen and Mysterud 2012). The LCA approach has also been used successfully on ptarmigan hunters (paper V) and demonstrates the applied value of this approach when profiling hunters into typologies for use in management purposes.

4.2 Further perspectives

A major objective of game harvest management is to provide hunting opportunities, while at the same time conserving the exploited species through sustainable harvest. Managers should consider developing harvest models or strategies that account for varying densities between years (especially for small game, see figure 12), but also take into consideration the requirements of different groups of hunters, based on their specialisation and motivations for hunting.

I have tried to demonstrate the need for increased knowledge about hunters' preferences for harvest regulations as a contribution to successful adaptive management strategies. That is mainly what is new on the table, compared to the current practices in game management. By involving stakeholder groups, such as hunters in decision processes can lead to a better understanding of the necessity of the regulation and reduce user conflicts (Austin, Urness & Shields 1992). Policy makers and managers should therefore include the hunters' preferences when implementing different types of regulations. The effects of the implemented regulations should also be evaluated at a larger scale, for example by building management strategy evaluation models (Bunnefeld, Hoshino & Milner-Gulland 2011; Milner-Gulland 2012) and by assessing the models' robustness to uncertainty. In order to be truly predictive in any human-altered environment, the system under consideration must include human users (Milner-Gulland 2012). Therefore, the behavior of individual harvesters and their compliance with management rules must be included, as this is a major challenge in conservation (Bunnefeld, Hoshino & Milner-Gulland 2011). This requires the integration of ecology with social sciences into social-ecological systems (SES) thinking (Schlüter *et al.* 2012), in order to improve the predictive power of system dynamics models. Development of such models is clearly a topic for further research and advances in this field.

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