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Source: Wildlife Biology, 20(5):285-290. 2014.
Published By: Nordic Board for Wildlife Research
DOI: http://dx.doi.org/10.2981/wlb.00048
URL: http://www.bioone.org/doi/full/10.2981/wlb.00048

Wildlife Biology 20: 285–290, 2014
doi: 10.2981/wlb.00048

Subject Editor: Camilla Sandström. Accepted 25 June 2014

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Hunters' preferences for different harvest principles and harvest regulations such as season length and harvest quotas provide important knowledge for wildlife management. We report results from a survey of 2788 willow ptarmigan hunters regarding commonly used harvest-principles and -regulations. A harvest quota strategy was the most preferred principle. Hunters were in general more positive to an annual bag, than daily quotas. Age was a particularly strong predictor of the 'no winter hunt' (after 23 December) regulation, and also a fairly strong predictor for the per annum and per day quota strategies respectively. This study has shown that ptarmigan hunters prefer annual quotas, rather than shortened hunting season or reduced number of hunters. We also emphasize the importance of social–ecological systems thinking when adaptive management strategies are developed and that management strategy evaluation models should be used to evaluate these strategies.

Several small game species in the northern hemisphere show large annual fluctuations driven by interactions between predation, climate and food availability (Cornulier et al. 2013). Harvest theory predicts that a threshold strategy is most optimal in stochastically fluctuating populations (Lande et al. 1995). A threshold could either be determined as a lower level where no harvest would be allowed below this level, but a threshold could also be set so that a maximum bag would be allowed before the harvest would be closed. The effects of harvest on small game species has been difficult to evaluate empirically, and there are to our knowledge no models that can predict breeding numbers after a prescribed harvest the previous autumn (Andersen and Thorstad 2013). Ptarmigans *Lagopus* spp. are by far the most popular small-game species in Norway. The hunting season runs from 10 September to 28 February, except in the northernmost part where the hunting season closes 15 March. Harvest of willow ptarmigan *Lagopus lagopus* and rock ptarmigan *Lagopus mutus*, both species hereafter referred to as ptarmigan, have declined since the late 1990s from 550 000 ptarmigan in the 1999/2000 hunting season, to 170 000 birds shot during the 2011/2012 season. The influence of harvest on population levels is unclear, but negative effects have been documented for harvest rates from 15% or more (Sandercock et al. 2011). A recent study in Fennoscandia (Lehikoinen et al. 2014) has shown that many ground nesting birds, including ptarmigans but also not hunted species, have declined in numbers during the same period, indicating that other factors than harvest alone affects the ecosystem.

A key management question is when to reduce harvest levels in order to reduce the impact on the future breeding population. Source–sink management models (Willebrand and Hornell 2001) has been proposed, and limits for the upper threshold of total hunter effort in management areas has been implemented on Swedish state land, as well as recently in Norway on the Finnmark estate and in Nordland and Troms Counties (Kastdalen 1992, Hörnell-Willebrand 2005). Timing of harvest can be important and late season harvest should have potentially larger effects than harvest early in the season (Kokko and Lindström 1998, Kokko 2001, Broseth et al. 2012). Harvest rates are more sensitive to variation in hunter effort than variation in density (Willebrand et al. 2011), which implies that hunters can sustain high harvest rates, despite low population density by increased effort.

Several management units have realised the need for an adaptive strategy for ptarmigan harvest management in Norway. There is no established system that is able to synthesise the large-scale outcome of actions in relation to management objectives such as population size, growth rate and harvest rates.

Regulations that are accepted by hunters are a prerequisite for management strategies aimed at optimizing ecological, social and economic outcomes of harvests. There are basically two ways to adjust harvest rates: 1) to limit the total number of ptarmigan harvested (total bag size), or 2) reduce the total effort by 2.1) reducing the length of hunting season, and/or 2.2) reducing the number of hunters (Wam

et al. 2013). Combinations of these three harvest principles are also possible. The only state level regulation in Norway is the length of the hunting season. Harvest regulations on ptarmigan were introduced by the wildlife managers roughly around year 2000 and are now a common tool for regulating harvest rates, despite the lack of systems to synthesise the outcome of management actions. The two most common regulations in Norway, set by the managers, is a daily bag limit (normally 1–4 ptarmigans) or a reduction in number of days for the hunting season as a whole. It is also common to split up the first part of the hunting season into periods of 5–7 days with a limitation in number of hunters allowed to hunt per period.

A recent study from Norway showed that 85% of the ptarmigan hunters were labelled as "semi-tolerant mainstream", typically hunters with few hunting days per annum and intermediate crowding tolerance (CT). CT was decreasing with increasing encounter rate with other hunters. Only 4% were labelled "the passionate crowd-avoiding", describing hunters with highest number of hunting days and very low crowding tolerance (Wam et al. 2013). Asmyhr (2012) found no effect of return rates to the same hunting area next year among ptarmigan hunters in Sweden, suggesting that the recreational carrying capacity is not reached (Asmyhr 2012).

Only a small fraction of Norwegian ptarmigan hunters actually achieve (with limit of four ptarmigan day^{-1}) the maximum daily bag (Andersen 2002), and hunters in areas with bag-limits are less satisfied compared to hunters that hunt in areas without any restrictions (Faye-Schjøll 2006, Faye-Schjøll et al. 2007). Aas and Vinsand (1996) showed that hunters had higher acceptance for postponing the opening of the hunting season from 10 September until 20 September, than to introduce a daily bag limit of three birds per hunter or a maximum of 15 birds per season (Aas and Vinsand 1996). To sum up, there is still a lack of knowledge about hunters' preferences for different management strategies in order to optimize the ecological, social and economic outcomes of harvest. In this paper, we synthesize the preferences for different harvest-principles and - regulations among hunters as a means to predict how different regulations will contribute to successfully achieve adaptive management strategies. The aims of the study are: 1) to test how different socio-demographic variables are associated with commonly used harvest-principles and -regulations affecting bag size and/or effort, and 2) to discuss how to combine harvest regulations in ptarmigan hunting with sustainable harvesting.

Methods

Survey design

A postal questionnaire was developed from a combination of experiences with previous studies on attitudes toward recreational fishing, wildlife, ptarmigan hunting (Aas and Vinsand 1996, Willebrand and Paulrud 2004) and harvesting in general (Bjerke et al. 2005). The questionnaire covered several aspects of hunting and logistics. For this study we used data on: 1) hunters' background information (gender, age, education level, degree of urban association and hunting experience), and 2) their responses regarding seven potential harvest regulations scored on a scale from 1 (strongly disagree) to 5 (strongly agree). These harvest regulations comprise the main response variables (Table 1). The three basic harvest principles (total bag size, season length and number of hunters) were computed from six regulations limiting the bag size, season length or number of hunters. Improved access is a kind of 'positive' regulation, by increasing the access to hunting grounds and was included to assess the hunters' recreational carrying capacity regarding the current hunting pressure. In addition, we asked the hunters, as an open question, what they considered a reasonable annual quota. A draft questionnaire was tested on a small sample (n = 10) before final modifications were made for the main study.

Sampling

Sample 1

Hunters were selected from municipalities in the following counties in central parts of Norway: Buskerud, Hordaland, Oppland, Hedmark and Sør-Trøndelag. The selected hunting areas consisted of both private and public land (hereafter labeled as management units). Management of game species is regulated by law. Public land must be managed in accordance to the 'Act of local public commons in mountain areas', which gives hunters living in the same municipality as they hunt (hereafter labelled as local hunters) extended rights. For example they are not required to seek permission to use a gundog in small game hunting, while

Table 1. Harvest regulations, means and standard deviations (SD) and standardized regression weights (β; 3–7 columns) for a path model with seven harvest regulations as dependent variables and five background variables as independent variables (n = 2113). Significant betas in bold ($p \leq 0.05$).Gender: female = 0, male = 1; Edu = Education level; HE = Hunting experience. HR response format: 1 = strongly disagree, 5 = agree very much.

Harvest regulation	Mean (SD)	Gender	Age	Edu	Urban	HE
Bag-limit (two per day)	3.32 (1.47)	**–0.08**	**0.11**	**–0.05**	–0.02	**–0.06**
Annual bag 15 birds	3.79 (1.40)	–0.01	**0.19**	0.02	0.01	**–0.06**
Shorter hunting season	2.46 (1.46)	0.00	**0.06**	–0.01	0.02	0.00
No hunting in winter	3.23 (1.65)	–0.02	**0.26**	**–0.06**	0.02	0.02
Reduce number of hunters	2.88 (1.35)	–0.03	–0.04	0.00	**–0.05**	**0.05**
Improved access	2.60 (1.21)	0.01	0.04	**–0.06**	**0.07**	**–0.06**
Split up season	3.19 (1.37)	–0.03	**0.09**	0.02	0.02	–0.03

non-local hunters must. The fees for hunting and fishing for locals are also lower, set at maximum 50% of the fee for a non-local hunter. On private land, the landowner must manage game only by the National Game Act, and there is no distinction in this law of local or non-local hunters. The selected areas covered typical willow ptarmigan habitats in the sub- and low-alpine zone, elevations ranging from elevations 600 m a.s.l. up to 1300 m a.s.l. These areas were considered representative for the major share of hunting areas for willow ptarmigan in the central parts of Norway.

We accessed 2717 complete addresses on hunters from management units within the participating municipalities. Hunters received the questionnaire in the beginning of March, immediately after the closing end of the willow ptarmigan hunting season. A short reminder was sent out 14 days later, and a second reminder with a similar questionnaire was sent out to 1263 respondents who had not responded to the questionnaire. The data collection resulted in 1876 answers (69% response). After excluding 233 respondents that reported they had not hunted and 38 responses without any information, 1605 complete responses were left, an effective response rate of 59% from the postal survey.

Sample 2

An identical survey (as used in sample 1) 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 sample 1 and 2) was therefore 2788. The sample size 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: see results) between the postal respondents (sample 1) and Internet participants (sample 2). Consequently the two samples were pooled.

Statistical analysis

Demographic variables consisted of: gender (0 = female, 1 = male), age (range: 14–87 years), education level in years (range: 7–21years), local, mixed (hunts both locally and outside their municipality) and non-local hunter (local = 1, mixed = 2, non-local = 3) and urban association (1 = site with less than 100 inhabitants, 2 = site with 100–3000 inhabitants, 3 = site with 3000–10 000 inhabitants, 4 = city with 10 000–40 000 inhabitants and 5 = city with more than 40 000 inhabitants). Hunting experience in years was grouped into four classes: (1 = 0–4 years, 2 = 5–9 years, 3 = 10–19 years and 4 = 20 years or more) to obtain a useful distribution in the three first classes. To assess the preference for the main principles of harvest regulations, 1) adjusting bag size, 2.1) adjusting the length of hunting season or 2.2) reducing number of hunters, we calculated an index value ranging from 1: totally disagree to 5: agree very much, by the average sum score of the two variables (daily limit and annual bag) comprising bag size ((variable A + variable B) / 2). The same procedure was used for calculating the index for length of hunting season (shorter season and no hunting after 23 December) and number of hunters in the hunting field (reduce number of hunters in general and split up season in shorter periods, with a limited number of hunters in each period). The statement "improved access for hunters", was included to see whether hunter crowding was approaching the hunters' perceptions of a recreational carrying capacity. We used an independent samples t-test to compare differences between the two sample sources. To compare preferences for harvest principles between local hunters, mixed and non-local hunters, we used analysis of variance (ANOVA). We conducted the analyses of harvest regulations (response variables) and demographic variables (predictors) as a path analysis, i.e. with all variables (including the seven response variables) entered into the equation simultaneously. Differences were considered statistically significant at $p < 0.05$. All analyses were run on either IBM SPSS (ver. 20.) software, or the Mplus software.

Results

Hunter characteristics

The sample consisted of 6% females (n = 164) and 94% males (n = 2520), while 104 respondents did not report on gender. A willow ptarmigan hunter was on average 45 years old (SE ± 0.3) and well educated. The average hunter had completed 14 years of school (SE ± 0.1). Education level was higher (14.5 years) in the internet-sample, compared to the postal questionnaire (13.8 years), and the age difference between the two samples was significant ($t_{1,2579} = 5.45$, $p = 0.001$). Hunters did on average consider 17 willow ptarmigan (SE ± 0.2) as a reasonable annual quota.

Harvest principles

A quota strategy was the most preferred harvest principle (average index score of 3.55), where non-local hunters had an index score of 3.66, local hunters had an index score of 3.43, while hunters who hunted both locally and outside their municipality, had an index score of 3.21. Differences between groups were significant ($F_{2,2387} = 28.13$, $p = 0.001$) Secondly, hunters preferred a reduction in number of hunters (average index score: 3.03), where non-local hunters, local hunters and mixed hunters had index scores of respectively 3.07, 2.97 and 2.94. Differences between groups were significant ($F_{2,2403} = 3.70$, $p = 0.043$). Shortening the length of hunting season, or splitting the season into short periods had an index score of 2.86, where non-local hunters, local hunters and mixed hunters had index scores of respectively 3.01, 2.70 and 2.33. Differences between groups were significant ($F_{2,2362} = 58.91$, $p = 0.001$). Non local hunters had consistently highest index score for all harvest principles.

Harvest regulations

Hunters preferred a seasonal quota of 15 birds (Table 1), secondly a daily limit of two 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. To strongly reduce the number of hunters and a shorter hunting season was the

least preferred regulations. The low score of the improved access-statement indicates that hunter crowding may be approaching the recreational carrying capacity in some areas in Norway (Table 1).

Hunters' demography and harvest regulations

Age was significantly associated with five of the seven harvest regulations (Table 1). Age was a particularly strong predictor of the "no winter hunt" regulation, indicated by the high standardized beta weight. It was also a fairly strong predictor of the per annum and the per day quota strategies respectively. This means that the acceptance level for these harvest regulations was positively associated with increasing age. Gender was significantly related to only one of these regulations, with female hunters being more supportive of the two birds per day quota than male hunters. Education level showed a weak, negative association with improved access, no hunting in winter and a daily bag limit. Urban association showed a weak, positive association with improved access, but a weak negative association with a reduction in number of hunters. Hunting experience showed a weak, positive association with a reduction in number of hunters, but only a weak, negative link with improved access and quotas on a per annum or per day basis (Table 1).

Discussion

Ptarmigan hunters in Norway are not supportive of all types of harvest regulations. Unrestricted harvesting within the seasonal limits has historically been regarded as an activity that only takes out a surplus of the populations (Pedersen et al. 2004), despite the fact that scientists provided new knowledge about the effects of hunting as early as in the 1990s (Kastdalen 1992, Smith and Willebrand 1999, Willebrand and Hornell 2001). The studies show quite clearly that harvesting may add to the natural mortality in willow ptarmigan in contrast to the old view of harvesting from a surplus (Sandercock et al. 2011). This view is still present among hunters and landowners, but even among these groups there is increasing recognition that hunting of willow ptarmigan has the potential to be unsustainable. Attitudes and understanding are likely to change as circumstances change (Majic et al. 2011), and in this case, changes is partly due to the ubiquitous reductions in harvest rates. Despite stable number of hunters, the annual bag has never been as low as in the 2011/2012 season. Further, demographic transitions of hunters and their environmental orientation can also be of importance. Hansen et al. (2012) have shown that for Danish hunters, the average age of recruitment for hunters increased from 21 to 34 between 1984 and 2006, and the percentage of new hunters younger than 20 declined from 63% to 19% during the same period. Similar trends have also been observed in Norway (Andersen et al. 2010, Statistics Norway 2014). Demographic changes are likely to affect hunters' view on harvest regulations in the future (Aprahamian et al. 2010, Johnston et al. 2011). For example, by shaping those who are recruited into small game hunting, in the sense that recruits starts their hunting carrier in a management regime with harvest regulations, and the fact that increasing age is positively associated with acceptance for regulations. It has also been shown that increasing environmental concern is positively correlated with higher acceptance of regulatory management actions aimed at preserving the resource (Kaltenborn et al. 2012).

Increased knowledge and acceptance of the negative effects of overexploitation on small game populations have led to development of harvest restrictions, such as bag-limits, narrower hunting periods (locally initiated) and controlling hunting effort (Angulo and Villafuerte 2003, Willebrand et al. 2011), which is practiced in Europe (e.g. Norway, Sweden and Spain) and North America (Wynveen et al. 2005). For willow ptarmigan, harvest regulations have been practiced for decades in Sweden and now also in the three northernmost counties in Norway; Nordland, Troms and Finnmark. Harvest regulations were not implemented in small game management in Norway before around year 2000. However, harvest regulations have been common in recreational fisheries for anadromous species since the 1990s in many Norwegian rivers (Anonymous 1999), so there is reason to believe that some hunters (many of them are also fishermen) are familiar with harvest regulations through recreational fishing. Di Minin et al. (2013) have shown that more experienced people (exemplified by tourists on safari in the KwaZulu–Natal province, South Africa) generally value biodiversity attributes more positively, which is in accordance to what Norton (2008) describes as the developmental stages in a hunters life. Our results support this; older, more experienced hunters are more supportive of harvest regulations as they may be more concerned with the sustainability of hunting.

In general, hunters gave the highest score to an annual bag of 15 ptarmigan per year, suggesting that hunters prefer to shoot as much as they want during a day or a limited time period, within the limitations of the annual bag limit. One explanation supporting this is that only 15% of the hunters in the sample shot more than 15 willow ptarmigan, and they hunted on average 7–8 days. Another explanation for the preference to hunt as much as they want is the observed increase in number of hunters with pointing dogs (Andersen et al. 2009), which can be seen as a kind of specialisation (Bryan 1977). We found that 54% of the hunters in this study always hunted with dogs and an additional 14% used dogs occasionally. Hunters with dogs may be more interested in having the opportunity to use the dog as much as possible, rather than shorten the season or limit the daily number of game they can shoot. Aas and Vinsand's findings are partly contradictory to our results. They found that hunters preferred no winter hunting, before a postponed start of hunting season (10 days), then a daily limit of three birds per day and a seasonal quota of 15 birds. The least preferred regulations was shorter hunting season (only hunting the two first weeks of the season), then five years with no hunting, and thirdly reduced number of hunters (Aas and Vinsand 1996). One explanation of this change in preference among hunters is that hunters now are more accustomed to harvest regulations than in the early 1990s where no harvest regulations was the general rule. Hunters may also be more supportive of regulations, as they see it as a tool for maintaining sustainable hunting and stewardship of nature (Kaltenborn et al. 2013). One of the most important drivers

of the tolerance towards an attribute is the novelty of the attribute itself. For example, people who have lived alongside wild animals tend to be less fearful of them (Kaltenborn et al. 2006, Roskaft et al. 2003). As new knowledge about effects of hunting on willow ptarmigan populations has been gained, management practice and hunters' preferences are likely to change by time.This may explain why hunters who are used to harvest regulations tend to accept them more easily.

Our data clearly demonstrates the need for increased knowledge about hunters' preferences for harvest regulations as a contribution to successful adaptive management strategies. 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 et al. 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 et al. 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 et al. 2011). This requires the integration of ecology with social sciences into social–ecological systems (SES) thinking, 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.

Management implications

A major objective of small 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, but also take into consideration the requirements of different groups of hunters, based on their specialisation and motivations for hunting willow ptarmigan. A 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. We also emphasize the importance of SES thinking when adaptive management strategies are developed and that management strategy evaluation (MSE) models should be used to evaluate these strategies.

Acknowledgements – this research was supported by the Norwegian Research Council, program Nature-based industry (grant 176321), Hedmark University College, Faculty of Applied Ecology and Agriculture, and Norwegian institute for nature research (NINA).

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