UNIVERSITY OF TROMSØ UIT

Faculty of Biosciences, Fisheries and Economics
Department of Arctic and Marine Biology

Hunter's behavioural responses to changes in bag size and willow grouse density – implications for management and interpretation of harvest data

Lasse Asmyhr

A dissertation for the degree of
Philosophiae Doctor

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List of papers

This thesis is based on the following original publications and submitted manuscripts which are indicated in the text by their roman numerals, I – IV below.

I. Willebrand, T., Hörnell-Willebrand, M. and Asmyhr, L. 2011. Willow grouse bag size is more sensitive to variation in hunter effort than to variation in willow grouse density. *Oikos* 120, 11: 1667-1673.

II. Asmyhr, L., Willebrand, T. and Hörnell-Willebrand, M. 2012. General experience rather than of local knowledge is important for grouse hunters bag size. Accepted for publication in *Human Dimension of Wildlife*: 1-20

III. Asmyhr, L., Willebrand, T. and Hörnell-Willebrand, M. 2012. Successful adult willow grouse are exposed to increased harvest risk. *Journal of Wildlife Management* 76, 5: 940-943.

IV. Asmyhr, L., Willebrand, T. and Hörnell-Willebrand, M. (2012) Previous catch per unit effort (CPUE) increases rate of subsequent return and CPUE of willow grouse hunters. *Manuscript*: 1-20.

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Abstract

An important aspect of ecological research is to provide guidelines and tools to wildlife managers. The ecological feature of density dependence which shapes population responses to harvest are important for wildlife management, but monitoring practices and exploiter dynamics to the changing resources and management regimes should also be included. Bag records are often collected by wildlife managers as part of their management regime, in which monitoring of the harvest is crucial. However, bag records are also commonly used as an index for population abundance and reproductive success. Bag records are valuable for their accessibility at a low cost and are used by researchers to parameterize harvest models and in studying population dynamics. However, seldom are bag records utilised as an index for abundance and reproduction, properly evaluated against abundance estimates based on count data. Moreover, which factors influence hunters' effort and success (and hence bag size), are not well explored for many game species.

In this thesis I present my aims, by means of long-term monitoring records and more short-term experimental data, are (1) to evaluate bag records of willow grouse (*Lagopus lagopus*) as indices for willow grouse abundance and breeding success and (2) to provide advancement in understanding of the underlying mechanisms determining the harvest rates; the hunters and their behavioural responses to willow grouse and (3) to derive implications for rational management of willow grouse populations.

I found the bag size and harvest rate to be more dependent on hunter effort than on willow grouse density and breeding success. The vulnerability of grouse to harvest was different for young and adult birds; young were most vulnerable. Among adults vulnerability depended on whether they had bred successfully or not; reproductively successful adults were most vulnerable. The sex ratio of the adult grouse in the harvest tended to be male-biased, in

accordance with what has been found earlier, and independent of willow grouse density and breeding success. Hunter's daily bag size was at best weakly density dependent. The number of grouse encounters, which was independent of willow grouse density, and gender of the hunter were the two strongest determinants for daily bag size. Hunters general experience in willow grouse hunting seems highly variable and of great importance for their success in bagging grouse. Still, hunters with several years of local knowledge from the hunting area were equally efficient in bagging grouse as hunters with equal experience, but from other hunting areas. Hunters considered less experienced in grouse hunting managed to increase their Catch Per Unit Effort (CPUE) in an area from one year to the next. Less than one third of the hunters return to the same area from one year to the next and the return rate was dependent of their previous CPUE, contrary to what hunters express is important for their satisfaction.

In conclusion, I urge caution in relying on bag size and harvest age ratios as indexes for willow grouse abundance and breeding success. The harvest rate was mostly determined by hunter effort and implies a potential for the regulation of hunter effort to maintain sustainable harvest rates. The finding that hunters appear to be selective towards key demographic components of willow grouse populations, such as adults with high reproductive success, suggests that this aspect of hunters' behaviour should be taken into account when deciding on sustainable harvest levels for willow grouse populations.

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1. Introduction

An important of task of applied ecology is to provide guidelines and tools for the sustainable harvesting of exploited species. Theoretical work has greatly improved the understanding of species resilience to different harvest regimes (Boyce et al. 1999; Jonzén et al. 2002; Kokko 2001; Kokko and Lindström 1998; Lande et al. 1997; Sæther et al. 1996), but to be applicable and helpful to the sustainable management of game populations, the assumptions for harvest models must be valid. If not, the consequence can be overexploitation, as exemplified by the collapse of marine fish stocks due to the exploiters ability to compensate for regulations and declining resources (Cook et al. 1996; Lauck et al. 1998; Roughgarden 1996). Of particular importance are the natural mechanisms of population regulation, i.e. density dependence in recruitment and survival, which shapes the demographical responses of populations to harvest through compensatory natality and mortality (Boyce et al. 1999; Hilborn et al. 1995; Sinclair et al. 2006). However, it is also necessary to understand the intention and behaviour of hunters to manage sustainable harvests. For highly fluctuating populations with a substantial natural mortality, restricted threshold harvest below an estimated maximum sustainable yield has been suggested to ascertain a safe level of harvest (Aanes et al. 2002). Due to poor compensation by harvesters to changing resources, it has been suggested that a threshold in hunting effort would be a better alternative than a threshold for harvest levels (Fryxell et al. 2010; Rist 2007; Willebrand and Hörnell 2001). A critical common premise for the understanding of mechanism of population regulation, parameterization of harvest models and understanding exploiter dynamics to changing resources, is reliable monitoring data. In this, the question whether to monitor the harvest or the population also becomes important (Freckleton et al. 2006; Sutherland 2001).

The annual change in harvested numbers and the age distribution of the harvest are commonly used as an index for abundance and breeding success. Such harvest data is not only important for harvest management to determine the harvest level and population status, but are also used as research data to explore the different mechanisms and interactions that determine annual fluctuations (Krebs 2002; Ranta et al. 2006; Royama 1992). The perhaps most famous long-term harvest data are those of the Canadian lynx (*Lynx canadensis*) (Ranta et al. 1997; Stenseth et al. 1999) and the red grouse (*Lagopus lagopus scoticus*) (Haydon et al. 2002; Shaw et al. 2004). Harvest records are commonly used because of the availability from management agencies that record harvest records as part of their management plans. Sampling or total collection of harvest records is also easy and cost efficient compared to field intensive techniques to obtain proper population density estimates, which are often limited by financial requirements and logistics for the most desired spatial and temporal scales. However, harvest records are often uncritically used and without knowledge of whether the indices actually track population changes or not. The red grouse harvest data has been validated according to count data and found to be reliable as an index for abundance (Cattadori et al. 2003). This has, however, not been performed for the Canadian lynx data. It is tempting to extrapolate the positive validation results from other species to those of interest to other studies. In case of grouse; beside Cattadori et al. (2003), the reliability of harvested number as an index for abundance has been evaluated for three other grouse species, the capercaillie (*Tetrao urogallus*), black grouse (*Lyrurus tetrix*) and hazel grouse (*Bonansa bonansia*). The relationship between harvested numbers and count data was found to be biased for these three species and the authors urged caution when in using harvested numbers as an index of population dynamics (Ranta et al. 2008). Also, the harvest age ratios (i.e. young : adults) seem to be biased for many game species. Among the *galliformes* there is commonly reported change in harvest age ratios during the hunting season (Bergerud 1970; Davis and Stoll 1973;

Durbian et al. 1999; Flanders-Wanner et al. 2004; Helminen 1963; Roseberry and Klimstra 1992). However, only for red grouse and bobwhite quail (*Colinus virginianus*) have the harvest age ratios been compared with pre-harvest estimates (Bunnefeld et al. 2009; Pollock et al. 1989; Shupe et al. 1990). For both species, the age and sex ratios in the harvest were biased, apparently due to game and hunter interactive behaviours. Also, the season and different hunting techniques apparently interact with game behaviour and are found to bias harvest age and sex ratios (Galby and Hjeljord 2010; Litvaitis 1994; Murton et al. 1974; Parker et al. 2002). This quite widespread lack of essential knowledge regarding the assumption for harvest records as an index for both abundance and age distribution means that the reliability of the index is seldom known. Despite that the indices should track population changes, it is not known how the indices capture the magnitude of changes, since it is not known whether there is a linear relationship or a saturating effect underlying the relationship.

The underlying mechanism determining the vulnerability to harvest of prey is probably the interaction between hunter and prey dynamic. This can be viewed as similar to predator and prey interactions, so that it is hunter skills and the anti-predator behaviour of the prey that should determine whether an encounter occurs and the outcome of the encounter. Furthermore such interactions may in combination with hunting effort and the game abundance impact upon the total harvest in an area. However, there is a large variation in skill and motivation among hunters which therefore results in a large variation in hunting success given the same game abundance (Andersen 2008; Faye-Schjøll 2008; Rist 2007; Wam et al. 2012). Hunters may also adjust their hunting effort in response to game abundance, previous experience from game encounters in a hunting area or to an anticipated hunting success (Schmidt et al. 2005; Van Deelen and Etter 2003). Regarding prey, there are also a large variation in anti-predator adaptations and vigilant behaviour which could determine if a hunter and prey encounter occurs and the outcome of the encounter (Brown et al. 1999; Caro 2005; Conover 2007; Lima 1986; Lima and Dill 1990).

1.1. Aims and objectives

The overall aim of this thesis is to evaluate bag records of willow grouse (*Lagopus lagopus*) (hereafter referred to as grouse) as indices for grouse abundance and breeding success, through understanding of hunters' behaviour and their responses to changes in bag size, grouse density and breeding success.

The specific objectives addressed in my papers (I - IV) were to:

I. Investigate to what extent the annual variation in bag size can be explained by variations in the grouse population and hunting effort; whether the catch per unit effort (CPUE) would be more sensitive to population change than bag size; and if it is possible to use a threshold of hunting effort to avoid high harvest rates. For this purpose long-term monitoring statistics on bag size and hunting efforts were analytically matched with pre-harvest population count data obtained from distance sampling.

II. To evaluate the influence of hunter experience on hunting success by specifically testing if hunters that had participated in willow grouse counting in a hunting area for several years were more successful in bagging grouse than hunters that had counted grouse elsewhere. Furthermore, which other factors may determine grouse hunters daily bag size; i.e. what are the effects of gender, grouse encounters, grouse density and/or breeding success? For this purpose a controlled hunting experiment was performed with hunters that participated in the pre-harvest population count and subsequently conducted the grouse harvesting.

III. To test the hypotheses that the composition of hunters' bag with respect to age, sex and reproductive success of grouse is unbiased compared to independent estimates of the hunted population. For this purpose further data from the controlled hunting experiment (cf. II) were analysed.

IV. To evaluate hunters' behaviour and success by assessing if the return rate of hunters to the same area from one year to the next is determined by their previous Catch Per Unit Effort (CPUE) and experienced level of hunter crowding. Furthermore, as potential determinants of current year CPUE hunters' site tenacity (i.e. if hunters returned to the same area or selected a new area) and previous year CPUE were tested. For this purpose large-scale monitoring data on individual hunters' behaviour and hunting success over three years were analysed.

1.2. The species willow grouse

Willow grouse is widespread and inhabits primary arctic tundra, openings in boreal forest, forest edge habitats, sub-alpine vegetation and is one of the most popular small game species for recreational hunting in Scandinavia. Willow grouse is a short-lived species where females breed their first year and have a high potential reproductive output (Hagen 1952; Hannon and Smith 1984; Myrberget 1974). The annual variation in nest loss and chick mortality is high (Munkebye et al. 2003; Myrberget 1988) and predation is the most notable cause (Marcström and Höglund 1980; Steen, et al. 1988a), but willow grouse have the ability to re-nest if their first attempt fail due to nest predation (Erikstad et al. 1985; Parker 1981).

Most willow grouse broods are accompanied by both parents that participate in parental care. During incubation, the males are found within short distances from the incubating females. Adults show distraction displays when encountered by a predator during incubation and chick rearing (Martin 1984; Martin and Horn 1993; Pedersen and Steen 1985), but different individuals may show a different intensity (Sonerud 1988). The effect of the maternal nutritional status of willow grouse females on breeding success has been investigated in several studies. Most studies have found weak support for breeding success or chick viability to be related to body condition (Erikstad et al. 1985; Robb et al. 1992; Steen et al. 1985; Steen et al. 1988a; Steen, et al. 1988b).

2. Study area and hunting regime

The study was conducted within the state owned mountain range in Jämtland county, Sweden (10 600 km^2) (paper I and IV). The state owned part is divided in 94 smaller management areas ranging from 11 km^2 to 271 km^2 in size (mean = 75 km^2). The state owned part of the mountain regions was opened to the public (national and international) for grouse hunting in 1993. All hunters with a valid license from the National Fund for Game Management can obtain a hunting permit. Two types of hunting permits are available, daily permit and a seasonal municipality permit for hunters resident in one of the municipalities in the county. Hunters is maximum allowed to buy daily permits or to activate a seasonal permit for five days at a time, before hunters are allowed to buy or activate permit for new days the hunters must report their hunting results for each day in a web based system. The hunter's social security number is their ID in the system and enables for hunters to be tracked through days, years and management areas. The areas are open for small game hunting from 25 August to the end of February with a daily bag limit of eight grouse per hunter. Grouse hunting is mainly performed as walked-up shooting with pointing dogs to locate and flush grouse (Bergström et al. 1992).

In Jämtland county there are four management areas selected to represent the different parts of state managed land in the alpine mountain range of the county, and are part of the nationwide monitoring program of willow grouse (for further details see Hörnell-Willebrand 2005) (Figure 1) (paper I, II and III). The size of these areas ranges from 54 km^2 to 174 km^2. The vegetation cover is dominated by alpine heath and shrub land above the tree line and mountainous birch (*Betula pubescens*) forest below the tree line (Lande 2011).

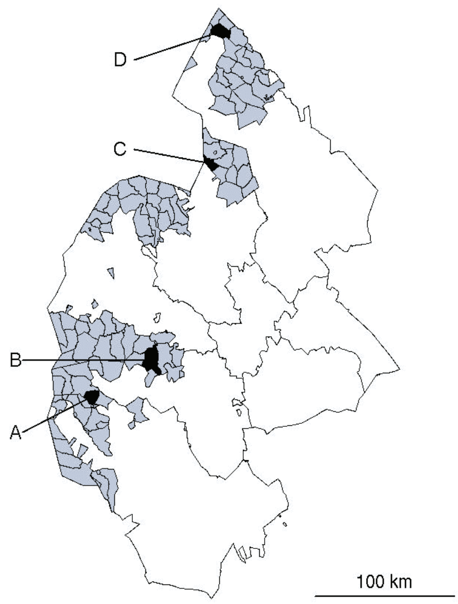

Figure 1. Map of Jämtland County where willow grouse management areas are grey and experimental areas are black.

3. Materials and Methods

3.1. Willow grouse count data (paper I, II and III)

Counts of willow grouse were done in early August (1996 – 2008) about two weeks prior to the opening of the hunting season. Density (total and adults per km^{-2}) was estimated using distance sampling methodology (Buckland et al. 2004). The counts were performed along transects about 400 m apart covering all of the area below 1100 m.a.s.l. within each management area. The counts were performed with pointing dogs by dog handlers carefully recruited and who received annual training and evaluation. The totals transect lengths varied between 78 and 151 km. The breeding success (chicks per pair) was calculated from the total and adult density estimates [∑(chicks) / (∑(adults)*0.5)].

3.2. Harvest data

3.2.1 Harvest data (paper I)

Bag records (days hunted and grouse shot) from 1996 - 2007 were received from 70 - 96% of all small game hunters in all areas, with the highest return rates in recent years. Most (about 75%) of the hunters obtained a licence valid for 1 - 3 days, and the hunters with a seasonal permit had to activate their hunting card for the days they planned to hunt. The number of hunting days exercised by hunters was thereby known in detail. Bag records were later automatically adjusted for missing reports, in the database at the county management agency, assuming that non-respondents and respondents did not differ. Hunting effort was defined as total number of hunting days per km^2, bag size was defined as total number of grouse shot per km^2 and the harvest rate as a proportion of the total grouse related to the estimated density that were shot.

3.2.1 Harvest data (paper IV)

Individually bag records of number of days and grouse shot, by management area, years (2006-2008) and hunting permit type (daily and seasonal for residential municipality) was extracted from the county management agency's database. The data were restricted to the most intense hunting period 25 August to the end of September, where over 80% of the total number of grouse for the season is shot. The total number of grouse shot km^{-2}, hunting day's km^{-2} and number of hunters km^{-2} were also extracted from the database for the respective study period.

3.3. Hunting experiment (paper II and III)

Forty-four males and 11 females were selected from the groups of dog handlers participating in the grouse counts of the study areas. They were allowed to hunt over two constitutive days immediately before the start of the hunting season, 23/24 of August in 2007 and 22/23 of August in 2008. The hunters entering an area belonged to two different groups to test the effect of local knowledge and previous knowledge of grouse encounters and locations in the area. One consisted of hunters that were part of the counting team for that area and had participated with their dogs in the count one to two weeks prior to the hunt and for at least the ten previous years. The other represented hunters which belonged to a counting team in a different area, where they also had participated in counting grouse one to two weeks prior to the hunt and for at least the six previous years. Three to four hunters with pointing dogs from each group (6 – 8 in total) were randomly assigned to a hunting area. The hunters were hunting separately as walked-up shooting with pointing dogs and hunted as they preferred within the boundaries of the different hunting areas. All hunters were equipped with a GPS unit to record their daily effort (distance walked and hours hunted during a hunting day), they recorded the number of grouse in all encounters and if they bagged grouse or not. Hunter's ID marked all grouse which were further aged and sexed. Age was determined based on moulting following Bergerud et al. (1963) and sex was determined by inspection of the gonads.

3.4. Analytical approaches

Different statistical analysis was used to analyse responses of the hunter's to grouse density and features related to the hunting practice. All models were linear but with different error structure, linear models (paper I), generalized linear models with poisson- (paper II) and binomial- error structure (paper III), linear mixed models (paper I and IV) and generalized linear mixed models with binomial error structure (paper IV). Continuous explanatory variables were centred and standardized to increase the interpretability of effect sizes and for a comparison with categorical variables. This was done by subtracting the sample mean from all input variable values (paper II and IV) and dividing by two standard deviations (paper II) (Gelman 2008; Schielzeth 2010). All statistical analysis was done using the statistical software R (R Development Core Team 2010).

4. Results and discussions

4.1. Grouse density, harvest, and biases: how and why.

Annual changes in bag size and the harvest rates of willow grouse were mainly determined by changes in accumulated hunter effort rather than grouse density (figure 3 and 4 c.f. figure 2). Bag size and harvest rate were density dependent, but the response was weak and accumulated hunter effort produced twice as high response (figure 2 and paper I). Daily effort (km walked) was not found to be an important determinant of the daily bag size of individual hunters, but the daily bag size was weak positive density dependent. Daily bag size was more determined by the gender of the hunter and the number of grouse encounters (Paper II). Male hunters were more efficient in bagging grouse than females (figure 5). Female hunters appeared to prioritize the performance of their dog's more than male hunters. Male hunters were also interested in their dogs, but also in the factors that affected their possibility to shot grouse at different encounters, e.g. if grouse were flushed within shooting distance and whether their shot missed or hit the grouse. The number of grouse encounters was not density dependent and the encounter rate (grouse encounters per km walked) during the hunt was almost the same for personnel walking straight-lined pre-defined transects through the terrain and hunters allowed to search freely through the terrain so as to optimize the number of grouse encounters (paper II). This may imply quite homogenous habitat distribution and/or that the distribution of grouse in the management areas at this time of the year was quite random (Lande 2011). It is interesting to note that the hunters had a lower probability to encounter single grouse than when they walked transects and counted grouse (paper III). This suggests different habitat use by single adult grouse and broods (Hannon and Martin 2006), and that hunters could identify brood habitat where they concentrated their effort. Hunters were also less likely to shoot grouse when encountering a single bird rather than a brood (paper III), hence grouse from broods was over-represented in the bag. The hunter's success seems to be more dependent on overall experience and skill of hunters and their dogs to locate and shoot grouse rather than the grouse density. However, it is interesting to note that the density dependence in bag size and harvest rate was opposite; for the bag size it was positive whilst for the harvest rate it was negative (i.e. harvest rate increased with decreasing grouse density) (paper I). The hunters must somehow compensate for a lower potential number of grouse encounters at low grouse densities and Schmidt et al. (2005) found that moose (*Alces alces*) hunters hunting effort was dependent on their success. I suggest a similar response among grouse hunters. I believe they adjust their hunting effort according to anticipated bag size, by extending their daily effort to compensate for low number of grouse encounters. Also to be considered is the behaviour that hunters are pursuing scattered brood members after an initial flush (paper III). This behaviour certainly would compensate for low encounter rate of grouse at low densities and hence increase the bag size.

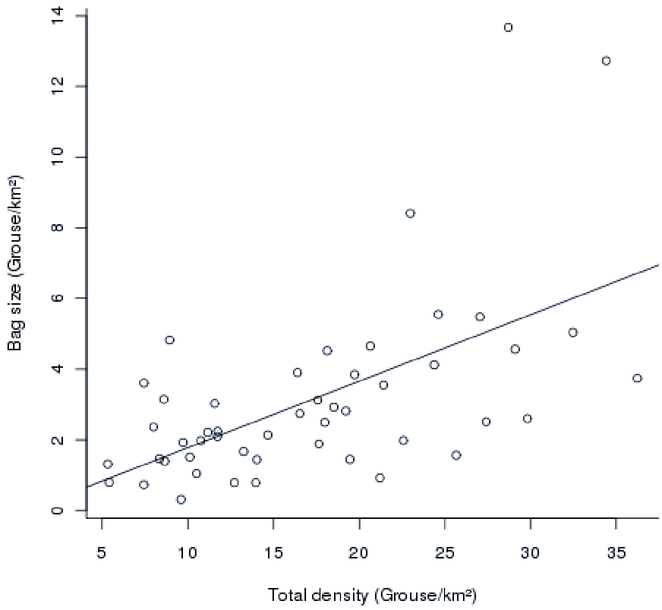

Figure 2. Bag size (grouse per km^2) as a function of total grouse density (grouse per km^2). The regression line showing the trend is included.

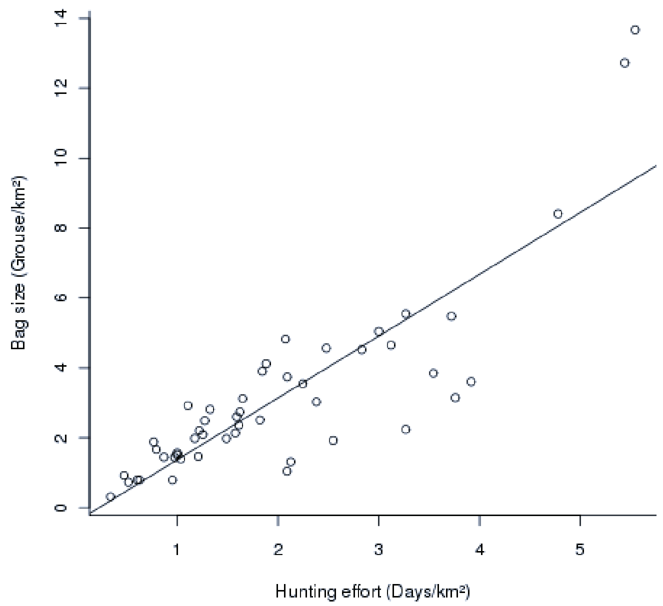

Figure 3. Bag size (grouse per km^2) as a function of hunting effort (days per km^2). The regression line showing the trend is included.

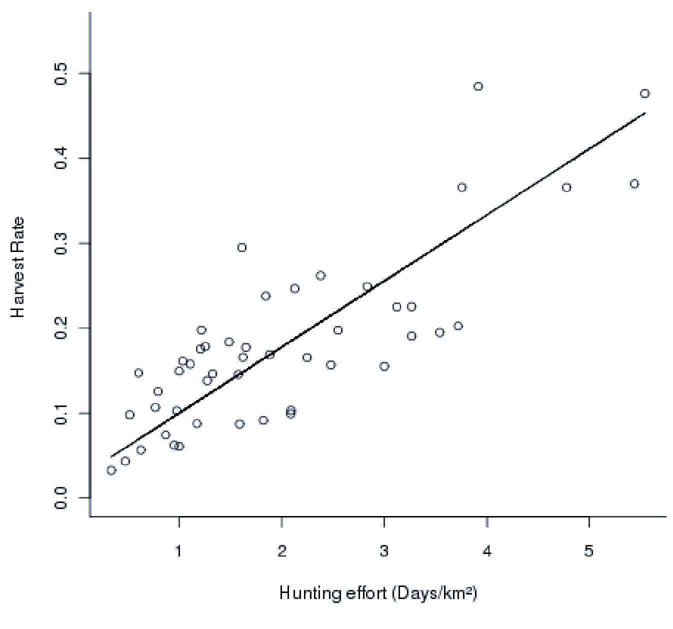

Figure 4. The relationship between harvest rate and hunting effort. The regression line refers to the relationship at average values of adult density (adult grouse per km^2) and breeding success (chicks per pair).

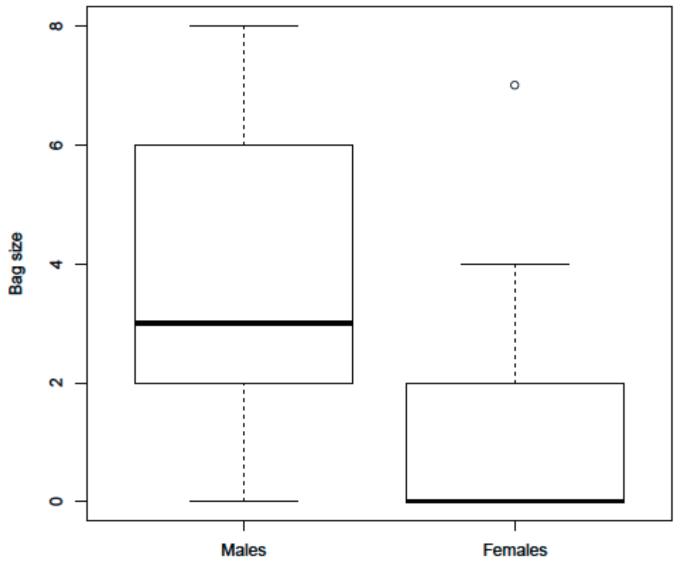

Figure 5. The difference between genders in daily bag size of willow grouse. The daily bag limit for the hunters was eight grouse per hunter.

4.2. Bag and population age- and sex - ratios and biases; how and why.

The proportion of adults in the bag increased with increasing adult density (figure 6), but increasing adult density was not equal to a proportional increase of adults in the population. Hence there was an inconsistent relationship between bag and population-age ratios. I have earlier shown (cf. 4.1 and paper II) that grouse from broods are overrepresented in the bag compared to single grouse, which is due to differences in the encounter and shooting probability of grouse as single birds and in broods. Furthermore there was a close to fifty-fifty chance that a shot grouse was an adult independent of whether hunters encountered either one or ten grouse (figure 7). The true difference in the encounter rate of single grouse and broods was probably larger than my estimate since about 40% of the grouse shot as single birds were chicks (figure 7). Only 10 % of grouse encountered as single birds during the counts were chicks (paper III), and I conclude that most chicks shot as singles were shot after an initial flush of the brood were the brood was scattered. It is well known that adults show distraction display to divert the attention of predators from their chicks (Martin 1984; Martin and Horn 1993; Pedersen and Steen 1985; Sonerud 1988). However, this behavior will increase the risk of being shot by the hunter when flushed and can explain why the proportion of adults in the bag was independent of brood size. It was unusual that hunters shot more than two grouse when encountering a brood, and initial brood encounters would result in an adult-biased bag. But single adults are underrepresented in the bag records (paper III) and counteracted the bias toward adults in the bag. Furthermore, the subsequent encounters of broods must have a lower probability of shooting an adult than the first encounters and more re-encounters will result in a higher proportion of chicks in the bag. Many re-encounters imply higher harvest rates and as shown (paper I), the harvest rates were highest at low grouse densities. This could explain why the proportion of adults in the bag increases with increasing adult density (figure 6).

The sex ratio of adult grouse in the harvest (being male-biased) was in accordance with what has been reported earlier for willow grouse populations (Hannon 1983) and was not related to either the adult density or breeding success in the pre-harvest population.

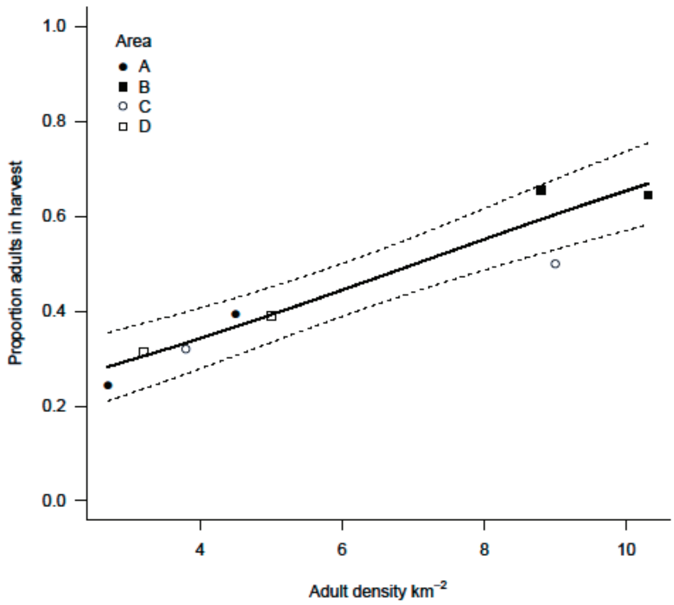

Figure 6. Change in proportion adults in harvest with pre-harvest adult density km^{-2}. The solid line is predicted from a generalized linear model and broken lines are 95% CI.

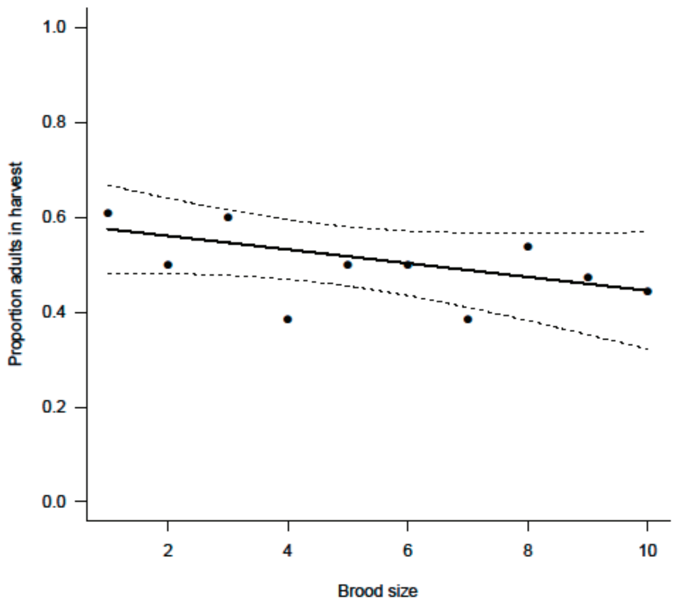

Figure 7. Proportion adults in harvests at brood size encounters. The solid line is predicted from a generalized linear model, broken lines are 95% CI.

4.3. Hunting experience, bag size and return rates

The general experience among grouse hunters seem highly variable and to be an important determinants of both an individual hunters daily bag size and for the total bag of an area. The highly experienced and committed hunters taking part in the hunting experiment (Paper II) were over three times as successful in bagging grouse than ordinary (average) hunters (paper II). However, still these experienced hunters seemed quite unaffected by having (or not) local knowledge of the hunting ground, grouse density and distribution. Ordinary hunter's success in bagging grouse was however positively affected by having at least one year of experience of an area (paper IV). I believe the variable efficiency in bagging grouse and effect of local knowledge is a matter of commitment to hunting, included skill of/with dogs and shooting, and the ability to gain knowledge from previous experiences. To develop a search image for grouse suitable for different areas, time of the year and weather situations probably require years of experience and commitment from hunting in different conditions and areas. These are skills likely to be posed by the hunters participating in the experiment (Paper II) and which most ordinary hunters lack.

The choice of returning to the same area a subsequent year is dependent on hunters CPUE (paper IV) (figure 8) as a likely determinant of their satisfaction, which increase with their bag (Faye-Schjøll 2008). Further hunters appear to manage to increase their CPUE at return to the same area, also compared to the hunters who chose a new area (paper IV). This is probably due to that they return to the spots within the area where they encountered grouse the preceding year. I could not detect any negative effect of crowding on return rates (paper IV), implying that hunter densities were below the carrying capacity for these hunting areas (Shelby and Heberlein 1986). Despite that hunters report that it is important for them to hunt in the same area year after year (Faye-Schjøll 2008), only one third of the hunters actually return to the same area a subsequent year (paper IV). The fact that the likelihood of returning to the same hunting area is dependent on hunters' CPUE the preceding year (paper IV) appears to be in conflict with hunters' expression that the bag size not are important for their satisfaction with hunting (Faye-Schjøll 2008). I believe the cause for the above contradictions is a mismatch between general attitude and specific behaviour (Heberlein and Black 1976; Schuman and Johnson 1976; Ajzen and Fishbein 1977). However, this may also be due to multiple other determinants of satisfaction with the hunt/harvest and the overall hunting trip experience (Hendee 1974; Hammitt and McDonald 1989).

Resident hunters with a seasonal hunting permit had a higher return rate to the same area the next year at average CPUE compared to hunters with a daily hunting permit. But hunters with daily permits increased their return rate faster with increasing average CPUE than resident hunters with seasonal permits (paper IV) (figure 8). This difference may be due to the fact that resident hunters with a seasonal permit have fewer areas to choose from (municipality level) compared to hunters with daily permits (county level).

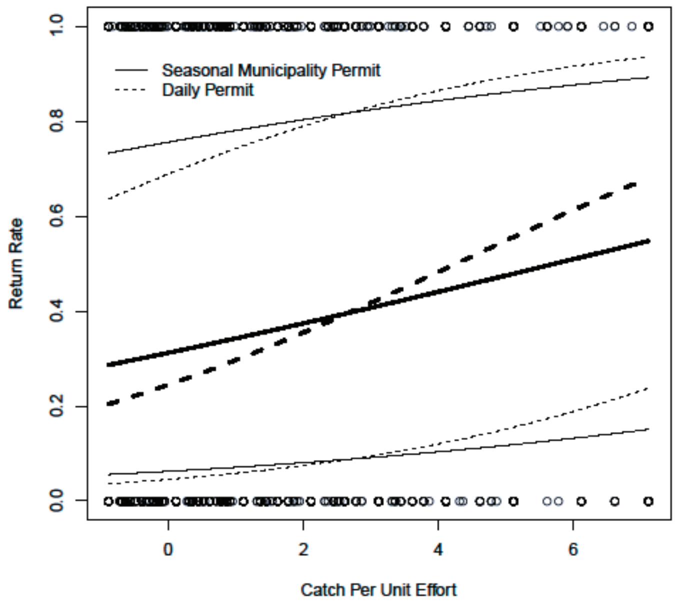

Figure 8. Predicted return rates of grouse hunters to the same area the subsequent year according to their CPUE in the area the previous year. The thick solid line refers to hunters with seasonal municipality permits, and the thick dashed line is the response of hunters with daily permits. The thin solid and dashed show the respective 95% confidence limits for predicted values.

4.4. Management implications

Harvest rate and hunter effort was tightly related and both of these statistics have a potential use for sustainable management (figure 4 and paper I). Aanes et al. (2002) suggested that a proportional harvesting below a predetermined bag limit for an area was a preferred sustainable harvest strategy. With the shown relationship between harvest rate, hunter effort and density estimates however (figure 4 and paper I), restricting the hunter effort according to a sustainable harvest rate is probably the most practical strategy for managing willow grouse populations (Willebrand and Hörnell 2001). Determining the threshold for a sustainable harvest for willow grouse is however complicated owing to unresolved issues regarding the strength of density dependent reproduction and/or survival in populations, and the ability for the population to compensate for harvest mortality. The degree of harvest mortality compensated for has been subject to some studies in Scandinavian willow grouse (Pedersen et al. 2004; Sandercock et al. 2011; Smith and Willebrand 1999) showing a great deal of additive effect of hunting. Still the impact of hunting is likely to vary between populations, depending on local conditions like predator community, density and alternative prey. Also, the selective harvest of successful adults (paper III) may affect the degree of harvest compensated for if there is different survival between age groups and if the ability to breed successfully is a heritable trait. Higher rates of winter survival for adult than juvenile willow grouse have been reported earlier (Hannon et al. 2003; Sandercock et al. 2011, but see Smith & Willebrand 1999), and a lower breeding success of female yearlings is reported for both willow grouse (Sandercock et al. 2005) and black grouse (Marjakangas & Törmälä 1997; Willebrand 1992). For willow grouse the difference is probably outpaced by stochastic nest and chick predation (Sandercock et al. 2005).

The unintentional selection of adults with broods (paper III) could affect the breeding populations more than anticipated if juvenile survival is reduced due to the loss of one or both parents. It is difficult to predict the subsequent survival of juveniles after loss of parents. The opening of the hunting season in Sweden is approximately one month prior to brood break up and juvenile dispersal (Hörnell-Willebrand 2005). Natural mortality could also result in both adults in a brood being killed, but no study has investigated the effects on behaviour and/or the survival of juveniles who have lost both parents. Whether the ability to breed successfully or not is a heritable trait has not yet been explicitly quantified by any study, but long term data on the breeding success of willow grouse show no indications of harvest having the potential to alter the genetic ability to breed successfully (Hörnell-Willebrand et al. 2006).

Whether or not adults are recorded as having bred successfully or not in August, is likely to be influenced more by stochastic predation rather than representing a heritable feature.

5. Conclusions and future perspectives

I urge caution in using changes in bag size as a reliable index for the population fluctuation of willow grouse. Though, there was a weak density dependent relationship between bag size and population density and I acknowledge that large changes in bag size of grouse and other small game occurring over large areas result in valuable information. Examples of useful insights based on bag data is the correlation between the vole cycle and small game in the Scandinavian boreal forest (Small et al. 1993) or perhaps the general increase in small game populations after the epizootic of sarcoptic mange (*Sarcoptes scabiei vulpes*), which killed a large part of the red fox (*Vulpes vulpes*) population in central Sweden (Lindström et al. 1994). However, I encourage landowners and managers to record hunter effort in addition to bag size for monitoring harvest levels and harvested populations.

I also urge caution in using harvest age ratios as a measure for breeding success within willow grouse populations. Differences in vulnerability to harvest can probably explain the bias towards adults in hunting bags and close to identical distributions of chicks per adult in long-term bag records from different areas of Norway and Sweden (Hörnell-Willebrand et al. 2006; Steen, et al. 1988a). This bias will vary in relation to adult density, the proportion of adults with a brood, the average brood size and harvest rate. Years with a large average brood size and low harvest rate will greatly underestimate the chicks per adult in the population, but it is difficult to see how this bias could be adjusted accordingly since the harvest age-ratios showed no relationship with pre-harvest population density. The effects of selective harvest of certain demographic categories for species with high turnover and where the natural mortality exceeds harvest mortality should be further investigated (Bunnefeld et al. 2011). Furthermore, the subsequent survival of young after the loss of both parents and the importance of the age structure in such populations should be studied.

Restricting hunter effort according to a sustainable harvest rate seems to be a safe management strategy to avoid too high harvest rates of willow grouse (Aanes et al. 2002). However, the level at which a harvest rate is sustainable requires further investigation (Pedersen et al. 2004; Sandercock et al. 2011; Smith and Willebrand 1999). A rate deemed as sustainable for one area is not likely to represent a sustainable rate for all willow grouse populations and the level of risk managers are willing to take regarding this would also be important. A focus on deriving sustainable harvest rates for species, according to their varying environmental conditions should be emphasized in future studies, together with their community structures and the predator - prey interactions.

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8. Paper I – IV

PAPER I

PAPER II

PAPER III

PAPER IV

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