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**The optimal foraging theory, crowding and Swedish grouse hunters.**

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**Abstract**

Hunters that have options to hunt in different areas should evaluate their previous hunting success when they decide where to hunt. Following optimal foraging theory for non-human predators we investigated if hunting success and density of other hunters on the hunting area will affect the probability of return to the same area, and if such behavioural changes will result in a higher hunting success compared to hunters that change to a new area. For this purpose we used detailed information about willow grouse (*Lagopus lagopus*) hunters on state owned land in Sweden. We found support for the optimal foraging theory application on grouse hunters' behavioural changes according to hunting success. The return rate increased with increasing hunting success and hunters that returned to the same area also increased their success compared to hunters that changed to a new area. Only one third of the hunters returned to the same area the subsequent year. We also found a negative effect of density of hunters in an area on hunters return rates and their hunting success, suggesting crowding among Swedish grouse hunters.

**Key words:** catch per unit effort, hunters, hunting area, recreational carrying capacity, return rate, willow grouse.

## Introduction

The decision of hunters whether or not to return to the same area may be viewed in a framework of optimal foraging theory (Charnov 1976; Pyke et al. 1977); a predator should abandon a patch when the density of prey reaches below the average density of the available patches. A predator can probably not evaluate density but will likely compare the kill rate in a patch to previous experience of kill rates in other patches. Many prey species in the northern ecosystems show large multi annual fluctuations (Lindström et al. 1994; Small et al. 1993), and kill rate will vary both between years and seasons in a patch. A predator must be able to evaluate previous encounters and need a minimum time in a patch to change behaviour, but the understanding of the behavioural process and handling of uncertainty by predators in dynamic environments is limited (Mangel 1990). Predators are often restricted by social constraints as territoriality (Sutherland 1996, Höner et al. 2005), and knowledge of prey distribution from previous encounters is probably an important contribution to the cost of territoriality.

Optimal foraging theory has also been used to understand human hunter-gatherer societies (Hill et al. 1987). Kurland et al. (2009) suggested that optimal foraging theory could help explain the development of hominids from hominoids, since the benefits of sharing information on food patches would require a social system to frame the tension between reciprocity and manipulation. In an experiment, the time used before switching among ponds with varying fish abundance by fishermen was longer than expected from foraging theory (Hutchinson, et al. 2008), but could be a strategy to gain experience and improve future decisions on giving up densities (Curio 1987).

Sport hunters constitute a heterogeneous group with different motivations for hunting (Andersen 2008; Asmyhr et al. 2012a; Schroeder and Fulton 2006; Wam et al. 2012). The motivation and criteria for satisfaction vary among sport hunters, and is influenced by cultural traditions tied to different game species and countries (Andersen 2008; Frey et al. 2003; Hayslette and Armstrong 2001; Hazel et al. 1990; Kennedy 1974; Vaske et al. 1986). Different studies have reached varied conclusions regarding how strong the effect of success, number of game bagged, has on hunter satisfaction (Faye-Schjøll 2008; Frey et al. 2003; Hayslette and Armstrong 2001; Hazel et al. 1990; Kennedy 1974; Vaske et al. 1986). Willow grouse (*Lagopus lagopus*) (hereafter referred to as grouse) hunters satisfaction does not seem to depend on grouse density as hunters satisfaction hardly changed despite a 3.5 fold increase in grouse density (Faye-Schjøll, 2008). Encounter rate of game for a single hunter is probably too small and variable to evaluate even major differences to previously hunted areas. A high hunter density that results in many interactions with hunters will many times reduce the hunting experience due to crowding (Vaske and Shelby 2008). It is well known that behaviour is determined by multiple factors so success and crowding alone might not have a large influence on subsequent behaviour (Heberlein, 2012). Grouse hunters often report that good dog performance and nice weather are among the most important factors contributing to increase the satisfaction with hunting (Willebrand and Paulsrud 2004).

We have earlier shown that grouse hunters with extensive hunting experience do not benefit from previous experience of grouse distribution in the area (Asmyhr et al. 2012a). These experienced hunters would probably not benefit from returning to the same area in subsequent years, but should select parts of the mountain range where available information on grouse abundance suggests higher densities. However, for the major part of the less experienced grouse hunters (90% of the grouse hunters in Sweden) the decision to change area may be less beneficial. Instead, they would benefit from returning to an area even if they only have been moderately successful in shooting grouse. The return would make it possible to evaluate if previous experience increase encounters of grouse, which would contribute to overall hunter proficiency.

Grouse is one of the most popular small game species for sport hunting in Sweden and Norway. Asmyhr et al. (2012b) found that variation in grouse density had limited effect on the daily hunting success of grouse hunters. The authors suggested that hunters probably compensated for low number of grouse encounters by extending the day in the field and increase the time pursuing flushed grouse that had escaped. Weak density dependence was also found in total numbers of grouse harvest in a hunting area, where accumulated hunter effort had a ten times higher impact than grouse density on the total harvest (Willebrand et al. 2011). The hunting permits for grouse on the state owned land (60 000 $km^2$) in the mountain region of Sweden is divided into 440 smaller management units from which the individual hunters are free to choose where to hunt. Daily bag statistics of individual hunters are mandatory reported on these management unit levels which make it possible to trace bag and effort for each hunter from year to year. This setting gives an excellent opportunity to empirically evaluate grouse hunters from an optimal foraging perspective.

In this study we test the application of optimal foraging theory for predators on Swedish grouse hunters. Translating the optimal foraging theory to hunters, the theory predicts that; a hunter should abandon a hunting area when the hunting success reaches a lower threshold than the hunter’s expectation. Accordingly, we would predict that hunters with higher success rates would be more likely to return to the same area next year. We would further predict that those hunters who hunt in high hunter density areas will be less likely to return to these areas since interference from other hunters and crowding may be a detractor.

## Methods

In Jämtland county, Sweden, the state owned mountain region (10 600 $km^2$ in size) is divided in 94 smaller management areas ranging from 11 to 271 $km^2$ (mean = 75 $km^2$) in size (Figure 1). More than 80% of all hunting days activated on the state owned land in Jämtland are by a Swedish citizen, 18% of persons living in a Nordic country except Sweden and 2%

living outside the Nordic countries. It is not uncommon to use helicopter transport to reach areas far away from a road, and 14% of the Swedish hunters and 30% of hunters from other Nordic countries use helicopters for transportation. The hunter category that most frequent use helicopters (50%) to reach remote hunting areas are from outside Scandinavia and represents 1-2% of the hunters in Jämtland (Länsstyrelsen 2007). The current management practice for grouse in Sweden is based on a threshold for maximum harvest rate (Aanes et al. 2002), and a crude relationship between effort and harvest rates (Hörnell-Willebrand 2005). There is a daily bag limit of 8 grouse per hunter but the limit is only reached by < 2% of the hunters (Hörnell-Willebrand 2005, Lindberget 2009). When the hunting effort in an area exceed three accumulated hunter days per $km^2$ the area is considered to be closed for hunting the rest of the hunting season. Also the hunting effort in the neighbouring areas is implemented in the decision on whether the practice is put into action or not. However, none of the areas in Jämtland 2006-2008 reached three accumulated hunter days per $km^2$ during the data period in our study (Table 3). The hunting season for willow grouse in Sweden is from $25^{th}$ of August to the end of February, where the most intense hunting is performed in August and September. The hunting technique for grouse in Sweden is with shot guns over pointing dogs and less than 5% of Swedish grouse hunters are hunting without the use of a pointing dog (Länsstyrelsen 2007). The present web based system of reporting bag size and effort was implemented in 2004, which has made it possible to track the success of individual hunters on a daily basis through their social-security number. Hunters can buy daily permits for a period of maximum five days at a time and must report number of grouse shot each separate day before it is possible for them to buy a new day permits on state land. Hunters with seasonal permits can hunt in any of the management areas that are within their municipality, but they must activate their permit for a period of maximum five days before a hunting trip. They also have to complete a hunting report after the five days to be able to activate their permit for a new hunting period. This system has led to that more than 95% of the hunters report number of grouse shot.

We analysed Swedish hunters return rates to the same hunting areas subsequent year with data from 2006 to 2007 and 2007 to 2008. The hunting season for willow grouse extend until the end of February, and we restricted our analysis to the most intensive part of hunting from 25$^{th}$ of August until the end of September. More than 80% of the total bag size is harvested between the start at 25$^{th}$ of August and the end of September; 87%, 85%, 85%, respectively in 2006, 2007 and 2008. There were hunters who hunted two years in a row in 75 of the 94 management areas and the number of hunters was decreasing over the three years, 2450, 2173 and 2092, respectively for 2006, 2007 and 2008. There were 864 hunters who hunted within the county all three years. Grouse densities in the different part of the county, based on the yearly counts on state owned land in the four areas highlighted in figure 1 can be found in table 1.

## Data Analyses

Return rate (i.e. the probability for a hunter to return to the same area in 2007 or 2008 as used in the previous year 2006 or 2007) was treated as a binary response variable (returned=1, not returned =0) at the level of individual hunters with generalized linear model (GLM) with logit link and binomial errors. Explanatory variables included were, hunting success in the first year 2006 or 2007 (∑ bag size / ∑ hunting days, by area), total number of hunters km$^{-2}$ in the hunting area the first year 2006 or 2007 from 25$^{th}$ of August until the end of September. Both explanatory variables were centred by subtracting the sample mean to increase the interpretability of the effect sizes (Schielzeth 2010).

The change in hunting success for hunters returning to the same area or a new area the following year was compared with student's *t* tests.

## Results

Hunters increased their return rate to the same area significantly with increasing hunting success. At average hunter density (1.05 hunters $km^{-2}$), a one unit increase in average daily hunting success for hunters in an area increased the probability of hunters to return to that area the next year with 23 % (*estimate* = 0.23, *SE* = 0.02, *df* = 7424, $p$ = <0.001). Overall only 27 % of the hunters returned to the same area the next year. But, groupings of hunting success show that the return rate increased markedly with hunting success and hunter effort (Table 2).

Increasing density of hunters decreased the return rate of hunters to the same area the next year. At average hunting success (0.89 grouse shot per hunter/day), a one unit increase in average number of hunters $km^{-2}$ decreased the probability of hunters returning to that area the next year with 9 % (*estimate* = 0.09, *SE* = 0.05, *df* = 7424, $p$ = 0.049). Around a hunter density of 1.5 $km^{-2}$ there seem to be a drop in the return rate for hunters. Also the hunting success seems to decrease above 1.5 hunter's $km^{-2}$ (Table 3).

Hunters hunting in the same area two subsequent years increased their average hunting success significantly the second year (from 1.02 to 1.24 grouse per day ($t$ = 4.44, *df* = 3935 $p$ = <0.001)). The hunters returning to the same area also had a higher hunting success than hunters who changed hunting area the next year (respective average number of grouse/day was 1.02 and 0.73 ($t$ = 6.30, *df* = 3485, $p$ = <0.001)).

## Discussion

As predicted from optimal foraging theory for non-human predators, grouse hunters that were more successful tended to return the same area compared to hunters that had been less successful. Those who stay in a patch according to optimal foraging (Charnov 1976; Pyke et al. 1977) significantly increased their hunting success compared to hunters that went to a new area. Although the difference in hunting success was not large, an average difference of 0.3 grouse per day represents approximately one grouse less in four day for hunters who changed hunting area than hunters who returned to the same area. It seems probable that hunters that returned to an area also searched the patches where they had encountered grouse the previous year. We believe this behaviour increased their success, but that such local knowledge is not easily generalized and transferred to other areas.

A search image that can be adapted to different areas probably require repeated returns to many areas, and it may take many years to reach a similar experience of the experimental hunters involved in the study of Asmyhr et al. (2012a). The large annual variation in grouse abundance (Hörnell-Willebrand et al. 2006; Marcström and Höglund 1980; Steen et al. 1988; Willebrand et al. 2011) and lack of unique habitat (Lande 2011) adds uncertainty to building a search image. This is also implicated by similar encounter rate of grouse for hunters when walking along line transects covering a total management area compared to when actively searching during hunting (Asmyhr et al. 2012a). Even the most experienced hunter will search empty patches and not always detect grouse even if they are present. We suggest that hunters view the possibility to return to an area as important to increase their hunting skill, and that this contributes to why grouse hunters report that it is important to be able to hunt in the same area between years (Faye-Schjøll 2008).

Overall there were only around one third of the hunters that returned to the same area as the previous year. This rather low return rate probably reflects the difficulties in finding and shooting grouse for most hunters (Asmyhr et al. 2012a). We speculate that these hunters move to a new area in the subsequent year to increase their chance to encounter more grouse, which is important for their satisfaction with a hunt (Faye-Schjøll 2008) and/or to better gain experience of where to find grouse in an area (Bryan 1977).

Further we also found support for our second prediction, that hunters hunting in areas with high hunter density reduced their return to those areas. Also the hunting success seemed negatively affected by high hunter density and may consequently be a cause for the lower return rate. However it is not likely that competition between hunters to shot grouse reduce their hunting success. Hunters hunting success remained unchanged the first 16 days of the hunting season (Lindberget 2009) and grouse would stay in the area (Olsson et al. 1996), but tend to move into habitats with more vegetation cover after being flushed during hunting (Brøseth and Pedersen 2010). We believe high interference between hunters and crowding function as a detractor for hunters. Both for, hunters' daily effort, which could reduce their hunting success, and hunters will to return to the area the next year. Contradictory, Wam et al. (2013) suggested that most grouse hunters show a quite high crowding tolerance. The result may imply that the recreational carrying capacity was reached (Shelby and Heberlein 1986), and may be the reason for the harvest management with an upper limit of three accumulated hunter days per $km^2$ in all management areas was not put into action during our study period.

As shown by Wam et al. (2012) there is a large variation in the motivation among grouse hunters. A large proportion of the hunters seldom bag any grouse (Asmyhr et al. 2012a), and these hunters will exert a small impact on the grouse population. We doubt that this group of hunters is interested in developing their hunter skill and can be termed "*experience seekers*" according to Wam et al. (2012). On the other hand, Asmyhr et al. (2012a) showed that highly experienced hunters can take out a large part of the total bag in an area. Especially at low grouse densities they can remove a considerable proportion of the grouse as their hunting success appear insensitive to grouse abundance. However, such hunters probably contribute to only a small proportion of the hunter population (Asmyhr et al. 2012a; Wam et al. 2012).

This is the first time the behavior of individual hunters have been tracked over time, and our results show that optimal foraging theory can be used to understand return rates to the management units where they have previously hunted. However in a management perspective concerning sustainable harvest levels, the result of gained experience is small and has few implications. The variation in hunting effort within Jämtland county is small between years (Willebrand et al. 2011) and with the low return rate of hunters to the same area subsequent year, there seem to be a large redistribution of a quite similar number of hunters within the county each year. Few hunters can be expected to gain such experience that there should lead to any concern related to unsustainable harvest levels. Implying that, the more local management strategy through regulation of hunter effort in each area, seem to be a preferable strategy to sustain sustainable harvest levels. But the spatial dynamic of hunters also show indications for the harvest to be self-regulatory through hunter crowding, below harvest levels considered safe for grouse. We would like to stress the importance of studying the actual behavior of hunters with empirical data in other systems of hunters and game species. Furthermore, when managing game species where populations exhibit large annual fluctuations independent of harvest, restricting hunter effort to achieve a safe proportional harvest has been suggested as a safe harvest strategy (Aanes et al. 2002; Willebrand and Hörnell 2001; Willebrand et al. 2011), then the understanding how hunters respond to hunting success and changes in prey abundance will be important.

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Table 1.

Summary of density and breeding success of willow grouse in four monitoring areas (c.f. Figure 1) on state owned land in Jämtland county, 2006, 2007 and 2008. Data are presented as averages for the three years and values in parentheses are coefficient of variation.

| Area | Adult density (grouse $km^{-2}$) | Breeding success (chicks per two adults) |
|---|---|---|
| A | 3.85 (0.27) | 4.02 (0.06) |
| B | 9.14 (0.11) | 4.00 (0.27) |
| C | 5.42 (0.58) | 2.94 (0.67) |
| D | 3.82 (0.26) | 3.83 (0.45) |

Table 2.

Summary of number of hunters, return rate (percentage hunters returning to the same area next year) and average hunter effort (area vice number of days hunted by hunters), divided in groups according to hunters hunting success (number of grouse shot by hunters).

| Hunting success | Number of hunters | Average hunter effort | Return rate |
|---|---|---|---|
| 0 | 3783 | 1.64 | 0.19 |
| 1-2 | 1712 | 1.98 | 0.27 |
| 3-4 | 864 | 2.39 | 0.37 |
| 5-6 | 411 | 2.86 | 0.36 |
| 7-8 | 259 | 2.87 | 0.46 |
| 9-10 | 150 | 3.58 | 0.48 |
| 11-15 | 163 | 3.79 | 0.58 |
| 16-20 | 50 | 4.52 | 0.48 |
| 20< | 35 | 4.74 | 0.69 |

Table 3.

Summary of number of hunters, return rate (percentage hunters returning to the same area the next year), average hunter effort (area vice number of days hunted by hunters) and hunters hunting success (area vice number of grouse shot by hunters), according to area vice hunter density per $km^2$ divided in groups.

| Hunter density per $km^2$ | Number of hunters | Average hunting success | Average hunter effort | Return rate |
|---|---|---|---|---|
| 0 - <0.6 | 1959 | 2.21 | 2.01 | 0.26 |
| 0.6 - <1.0 | 1771 | 2.26 | 2.14 | 0.28 |
| 1.0 - <1.5 | 2135 | 1.66 | 1.97 | 0.29 |
| 1.5 - <2.0 | 1125 | 1.87 | 2.03 | 0.22 |
| 2.0 - 2.5 | 437 | 1.86 | 1.82 | 0.22 |

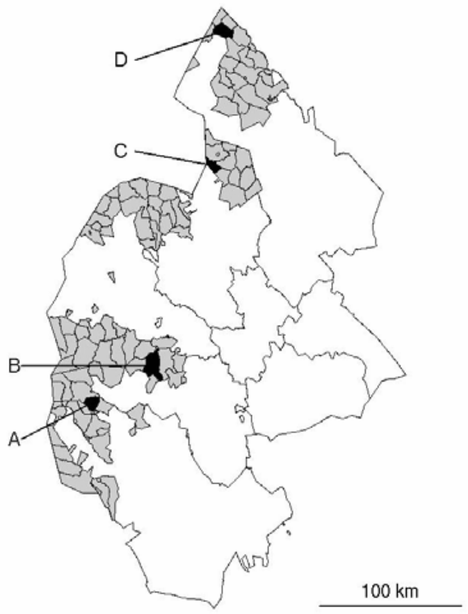


Figure 1. Map of Jämtland county, Sweden, where the grouse management areas are grey, the black areas A-D are areas with annually monitoring of the grouse populations (c.f. Table 1).