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1 Running head: IMPORTANCE OF LOCAL KNOWLEDGE FOR GROUSE HUNTERS

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3 General Experience Rather than of Local Knowledge is Important for Grouse Hunters Bag
4 Size

5

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Abstract

Wildlife harvest management require understanding of hunter behavioural interactions with the game. Hunter harvest is indicated to be more dependent on experience and attitudes than game abundance. We tested how the bag size of grouse hunter's was affected by having local knowledge of the hunting ground, grouse density and distribution or not. The local knowledge was acquired through, approximately a decade of conducting pre-hunt counts, and was tested against hunters without the local knowledge, but which had similar experience of counting grouse from other areas. Hunters with local knowledge were not more efficient in bagging grouse than hunters without local knowledge. Rather there seems to be the general variation in experience among hunters that regulated harvest rates, through number of grouse encounters hunters and gender of the hunters. The results add support to the concern of using bag statistics as an index for population changes of wildlife species.

Keywords: harvest, density dependence, human-wildlife interaction, hunting, willow grouse.

38

Introduction

39 Understanding the relationship between hunter success and knowledge of game
40 abundance is needed to interpret harvest data correctly and ensure sustainable harvest levels.
41 The behaviour of hunters can be compared to predators hunting for prey, and predator-prey
42 theory may be used to understand hunter response to changes in prey abundance (Choquetot,
43 Hone, & Saunders, 1999). The functional response (Holling, 1959) predicts a decrease in
44 proportion of prey removed as prey abundance increases since there is a limit to how many
45 prey a predator can handle per unit time (Sinclair, Fryxell, & Caughley, 2006). Additionally,
46 optimal foraging theory (Pyke, Pulliam, & Charnov, 1977) predicts that a predator (hunter)
47 should abandon a patch when the expected return reaches a lower threshold. Hutchinson,
48 Wilke, and Todd (2007) examined patch leaving decisions in humans exposed to a simulated
49 fishing in ponds with varying fish abundance, and found that subjects delayed the switch to
50 another pond longer than expected from theory. This apparent irrational behaviour, termed the
51 Concorde fallacy, is observed in both animals and humans, and may be an investment to gain
52 enough experience to make more correct decisions in the future (Curio, 1987). The hours
53 required to observe a deer by deer hunters in North America increased dramatically at low
54 densities (Van Deelen, & Etter, 2003), and it can be expected that hunters extend their hunting
55 day when encounters of game and catch per unit effort (CPUE) are less than expected from
56 earlier experience.

57 In Scandinavia and North-America, hunting rights are commonly either managed by
58 the state or large land-owners that often apply an open access policy to small game hunters
59 (Bergström, Huldt, & Nilsson, 1992; Butler, Teaschner, Ballard, & McGee, 2005). These
60 large areas can exhibit substantial spatial dynamics of hunters in relation to anticipated game
61 abundance and previous experience from other areas. The accumulated local ecological
62 knowledge (Brook, & McLachlan, 2008; Gilchrist, Mallory, & Merkel, 2005) over several

63 years should probably make hunters more efficient and show higher CPUE rates compared to
64 hunters with similar experience but from a different area.

65 Willebrand, Hörnell-Willebrand, and Asmyhr (2011) showed that variation in effort
66 had a stronger effect than variation in density when explaining annual changes in harvest
67 numbers of willow grouse (*Lagopus lagopus*) in Sweden. Hunters were relatively more
68 efficient at low compared to high grouse densities, and they suggested that using harvest
69 numbers from hunters that at least harvested one grouse could improve the relationship
70 between grouse density and CPUE. Wam, Andersen, and Pedersen (2012) identified different
71 willow grouse hunter typologies in Norway according to importance of bag size and crowding
72 tolerance, and the different typologies would be expected to respond differently to changes in
73 game abundance.

74 Few studies have investigated the dynamics of hunters to understand the effects of
75 harvest regulations on game abundance (Guthery et al., 2004; Hardin, Brennan, Hernandez,
76 Redeker, & Kuvlesky, 2005), and there is a lack of controlled experiments of hunter
77 behaviour in areas with known game abundance. Since 1996 we have been counting willow
78 grouse in the same management areas on state managed land in Sweden (Asmyhr,
79 Willebrand, & Willebrand-Hörnell, 2012; Hörnell-Willebrand, 2005) using hunters trained in
80 distance sampling (Buckland et al., 2004). Hunters in the counting crews tend also to hunt in
81 the area they count, and there has been a low turn-over of hunters in the counting crews. Here
82 we report an experiment where we tested if hunters that had participated in willow grouse
83 counting in the hunting area for several years were more successful than hunters that had
84 counted willow grouse elsewhere. We expected that the experimental contrast between
85 hunters with and without local knowledge of willow grouse (hereafter referred to as grouse)
86 density and distribution to be an important positive determinant for the daily bag size.

87 **Study Area**

88 The study was conducted in four areas (A-D) situated in the state owned mountain
89 region of Jämtland County, Sweden. The size of the areas varied from 54-174 km² and their
90 positions were on a south to north gradient in the county. Areas were selected to represent the
91 different parts of state managed land in the alpine mountain range of the county, and were
92 part of the nationwide monitoring program of grouse (for further details see Hörnell-
93 Willebrand, 2005). State owned land in Sweden was opened for the public (national and
94 international) to grouse hunting in 1993. All hunters with a valid license from the National
95 Fund for Game Management can obtain a hunting permit. The areas are open for small game
96 hunting from 25 August to the end of February with a daily bag limit of eight grouse per
97 hunter. Grouse hunting is mainly performed as walked-up shooting with pointing dogs to
98 locate and flush grouse (Bergström et al., 1992). The study areas are the same as in
99 (Willebrand et al., 2011) study, where detailed description on harvest levels, hunting effort
100 and grouse demography from 1996 to 2007 is given.

101 **Methods**

102 **Pre-Harvest Willow Grouse Population**

103 Pre-harvest density and breeding success of grouse has been estimated annually since
104 1996 in all four study areas. In early August, carefully recruited and trained dog handlers
105 count grouse along line transects, evenly spaced and over entire management areas. Distance
106 sampling was used to obtain the total and adult density each year (Buckland et al., 2004;
107 Hörnell-Willebrand, 2005). Breeding success was calculated as chicks per pair from the ratio
108 of chicks to adults observed during counts.

109 **The Experiment**

110 In 2007 and 2008, we monitored dedicated grouse hunters, which also were pointing
111 dog enthusiasts, which were allowed to hunt over two constitutive days immediately before

112 the start of the hunting season, 23 and 24 of August in 2007, and 22 and 23 of August in
113 2008. The hunters, both male ($n = 44$) and females ($n = 11$) were randomly drawn from those
114 who had participated the longest in the counts and were certified to count grouse. All of the
115 experimental hunters had counted grouse with their dogs in their counting area one to two
116 weeks prior to the experiment.

117 In each of the four management areas, six to eight hunters were allowed to enter and
118 hunt with their pointing dogs. Three or four had been counting grouse the year of the
119 experiment and at least 10 of the previous years. In that way they both knew where the grouse
120 usually were found in the hunting area and had detailed knowledge about grouse density and
121 distribution for the years of the experiment. Half of the hunters had also counted grouse in a
122 similar fashion but in another area and had no experience of grouse distribution in the hunting
123 area. We emphasise that all hunters had at least six years, most of them over 10 years of
124 experience with counting grouse. The hunters were hunting separately with their pointing
125 dogs within the boundaries of the different hunting areas. All hunters kept a detailed diary of
126 all events in a day, and recorded number of grouse encounters, number of grouse observed in
127 each encounter, if there were a possibility to shoot grouse or not in the encounter and if they
128 bagged grouse at the encounter. They were equipped with a GPS unit to record distance
129 walked.

130 **Analysis**

131 We used a generalized linear model (GLM) with Poisson error to compare daily bag
132 size of hunters with and without local knowledge. We started with a beyond optimal model
133 including three continuous and three factors as predictors: the two hunter categories (with (1)
134 and without (0) local knowledge), distance walked (km), chicks per pair, adult density km^{-2} ,
135 grouse encounters (possibility to bag grouse), failure by dog (dog flushed grouse before the
136 hunter came within shooting distance), first (0) or second (1) day of the hunt, and the gender

137 of the hunter; (male (1) and female (0)). All two-way interactions were initially included. All
138 continuous explanatory was centred by subtracting the sample mean (Schielzeth, 2010) and
139 standardized by dividing all centred input variable values by two standard deviations
140 (Gelman, 2008), to increase the interpretability of effect sizes and comparison of effect sizes
141 between both main effects and interactions. The final model was obtained by removing
142 predictors and interactions one by one if the coefficient was insignificant ($p > .05$), beginning
143 with the interaction terms. A predictor with an insignificant coefficient was not removed if
144 included in a significant interaction. Model validation was done by plotting residuals against
145 predicted values, response variable and explanatory variables (Zuur, Ieno, & Elphic, 2010;
146 Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The pseudo R^2 was calculated as a measures of
147 predictive power of the model (Zuur et al., 2009).

148 **Comparing Experimental Results with Ordinary Hunting**

149 The bag size of the experimental hunters was compared to the hunters entering the
150 same areas the first two days of the official hunting season, 25 and 26 of August (further
151 referred to as ordinary hunters). Data on the ordinary hunters were obtained from the county
152 management agency. The hunting licenses and harvest records are obtained and reported
153 through a web based system operated by the county management agency and their local
154 dealers. The return rate of harvest reports was close to 90%. It is believed that the practice of
155 banning non-respondents from hunting on state owned land within the county the following
156 year is an important factor contributing to the high report rate.

157 **Results**

158 **Pre-harvest Grouse Populations and Descriptive Characteristic of the Hunt**

159 Density and breeding success in the grouse populations varied between years and areas
160 (Table 1), and the adult density was not correlated with chicks per pair ($t = 0.30, p > .05$). The
161 total bag consisted of 344 grouse. In area C in 2007 there was only hunted one day since a

162 local landowner closed the road into the hunting area without any notice. The data from this
163 area were therefore excluded from the analysis in that year, and we were left with 94
164 hunter/days and 322 bagged grouse. An average hunting day lasted for 5h 31 min (min: 2h 02
165 min, max: 9h 20 min), covered a distance of 11.9 km (min: 4.3 km, max: 19.3 km) and
166 contained observation of 24 grouse (min: 0, max: 118) that were distributed on six encounters
167 (min: 0, max: 17). Only 13 of the hunter days reached the daily bag limit of eight grouse,
168 three hunters reached the bag limit both the first and second day of hunting. The average
169 number of grouse encounters was almost identical during the counts and the hunting
170 experiment (0.59 and 0.54 km⁻¹ respectively).

171 **Experimental Results**

172 The final model contained six explanatory variables, and five interactions (Table 2).
173 Grouse encounters was the most important variable explaining the variation in bag size, a unit
174 increase in average number of grouse encounters resulted in an increase of two grouse in the
175 bag. Number of encounters became even more important the second day of hunting, adding a
176 third grouse to the bag with a one unit increase in average number of grouse encounters
177 (Table 2). The number of grouse encounters was lower the second day of hunting, but the bag
178 size of males was less affected by the number of grouse encounters than females due to a
179 negative interaction between gender and encounters (Figure 2 & Table 2). Gender was one of
180 the most important factors that affected the bag size, and the bag size of males was higher
181 than females (Figure 1). Gender also significantly interacted with local knowledge and grouse
182 encounters. Contrary to what we expected, the bag size of hunters with local knowledge was
183 not higher than hunters without local knowledge. The experimental knowledge factor
184 interacted significantly with gender which resulted in a similar effect on males independent
185 on whether they had local knowledge or not (according to coefficients provided in Table 2:
186 $1.28-1.87+1.76=1.39$ and $1.28-0+0=1.28$, respectively). Local knowledge even appeared to be

187 negative for females, (-1.87 and 0, respectively). Average bag size for female hunters was 1.4
188 and 1.7 grouse per day, respectively with and without local knowledge, while average bag
189 size for male hunters was 3.6 and 4.1 grouse per day, respectively with and without local
190 knowledge. On average male hunters bagged 2.3 grouse more in a day than female hunters.

191 Number of grouse encounters was not correlated with neither adult density ($r = 0.11$, p
192 $> .05$) or to chicks per pair ($r = 0.11$, $p > .05$). The bag size was positively density dependent
193 to both pre-harvest adult density km^{-2} and chicks per pair. The positive effect of pre-harvest
194 adult density, was however not present the second day of hunting. Also, the effect of number
195 of grouse encounters was a so much stronger determinant for daily bag size that it outpaced
196 the positive effect of pre harvest adult density km^{-2} (Table 2). Neither the distance walked by
197 the hunter nor the frequency of the dog flushing the grouse before hunters could reach within
198 shooting distance turned out significant for the bag size. The final model explained 60%
199 (pseudo R^2) of the total variance in daily bag size.

200 The comparison of the experimental hunters with ordinary hunters showed that hunters
201 participating in the experiment had three times higher bag size on average, 3.4 and 1.1 grouse,
202 respectively. The difference between the experimental and ordinary hunters became even
203 more pronounced when the proportion of hunting days that resulted in zero bagged grouse is
204 considered; 20% in the experiment and 64% in the first two days of the open hunting season.

205 Discussion

206 Hunters that had gained local knowledge of grouse distribution and abundance during
207 more than a decade was contrary to our expectations not more effective in bagging grouse
208 than hunters with similar experience but from other areas. We believe that the close to
209 identical grouse encounter rates during the systematic line transect counts and during the
210 active search by hunters is an important cue. These management areas contain a widespread
211 availability of preferred habitat, and what appear as a random distribution of grouse (Lande,

212 2011). In this case, the harvest success will depend on the overall experience and skill of
213 hunters and their dogs to locate and shot grouse, and previous knowledge on where grouse
214 tend to be encountered provide little advantage (Kaltenborn, & Andersen, 2009; Lande,
215 Herfindal, Finne, & Kastdalen, 2009; Schmidt, 1998). We speculate that the difference
216 between genders can be attributed to attitudes that probably are formed early in life
217 (Manfredo, 2008), and it was obvious in our discussions with the experimental hunters that
218 the female hunters were more occupied with the performance of their dogs compared to the
219 males. The hunter's success was positively affected by increasing grouse density and breeding
220 success, but the estimates for these two parameters were the two lowest and a high number of
221 grouse encounters counteracted the effect of adult density. As previously shown (Willebrand
222 et al., 2011), hunter's success was at best weakly density dependent to grouse, and the range
223 in both density and breeding success of the grouse populations in this study was similar to
224 what is commonly reported from Scandinavia (Sandercock, Nilsen, Brøseth, & Pedersen,
225 2011; Willebrand et al., 2011).

226 The hunters in our experiment were more efficient than the ordinary hunters entering
227 the areas after the experiment. Intense hunting can cause a redistribution of game, including
228 grouse (Brøseth, & Pedersen, 2010), but we believe this to be an unlikely response in our
229 experiment where only 4-8 hunters entered areas of 54 - 174 km². It has been suggested by
230 grouse managers that grouse abandon hunting grounds with intense hunting, but radio marked
231 willow grouse both in Sweden and Norway have shown that this is not the case (Brøseth,
232 Tufto, Pedersen, Steen, & Kastdalen, 2005; Olsson, Willebrand, & Smith, 1996). The
233 reduction of the grouse populations after the experiment could also be an explanation, but the
234 overall CPUE of willow grouse hunters during a four day period was not found to be affected
235 by the hunting during the immediately preceding four days hunting (Lindberget, 2009). In our
236 experiment, hunters reduced the grouse population by 13% at the lowest density, but removed

237 only 1% of the population at the highest density. The different harvest rates of experimental
238 hunters did not seem to affect the success of ordinary hunters, and the harvest success of
239 hunters the first days of the hunting in the open season was not different from the years when
240 there had not been any experimental hunting. We suggest that the difference between
241 experimental and ordinary hunters are attributed to other factors than grouse density, most
242 likely that the experienced experimental hunters reach higher encounter and kill rates than
243 ordinary hunters. About 7% of the hunters in the official statistics bag 5-7 grouse per day,
244 and can probably be used as an estimate of the proportion of hunters that are as experienced
245 as our experimental hunters among all grouse hunters.

246 Willebrand et al. (2011) concluded that hunting effort could be used to reduce the risk
247 of reaching potentially unsustainable harvest levels, and suggested that bag statistics from
248 successful hunters could provide a better proxy for population change than from the average
249 hunter. Our results show that a high proportion of experienced male hunters and low game
250 density could result in high harvest rates and the hunting success of experienced hunters do
251 not track population change better than the bag statistics from ordinary hunters. A critical
252 question is if there are thresholds where hunters will refrain to hunt due to low encounter
253 rates. An absence of hunting thresholds at low densities and weak density dependence could
254 potentially lead to overexploitation and risk an inevitable collapse as suggested in sport
255 fisheries (Post et al., 2002; Post, Persson, Parkinson, & Kooten, 2008). We conclude that this
256 study add support to the concern of using bag size as a proxy for game abundance we have
257 raised earlier. Especially in areas where the hunting effort and average hunter experience may
258 change from year to year.

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- 352

353 Table 1.

354 Pre-Harvest Grouse Populations Breeding Success and Distance Sampling Density km⁻²

355 Estimates

Area	Year	Total	Adults	Chicks per Pair
A	2007	8.4 (27.6)	2.7	3.2
	2008	13.2 (24.1)	4.5	3.9
B	2007	35.7 (16.1)	10.3	5
	2008	21.1 (18)	8.8	2.8
C	2007	11.2 (32.7)	3.8	3.9
	2008	12 (31.5)	9	0.7
D	2007	19.4 (18.1)	5	5.8
	2008	7.2 (22)	3.2	2.5

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357 Note. Numbers in parentheses refers to the coefficient of variation in percent.

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363 Table 2.

364 The coefficients of the generalized Linear Model Explaining Daily Bag Size of Grouse for

365 Experiment Hunters

Parameter	Effect Size	Std. Error
Intercept	0.18*	0.37
Chicks per Pair ^a	0.39***	0.14
Adult Density km ^{-2a}	0.40**	0.19
Grouse Encounters ^a	1.97***	0.54
With (1) and Without (0) Local Knowledge	-1.87**	0.77
Male (1) and Female (0) Hunters	1.28***	0.14
First (1) and second (0) Day of Hunting	-0.17*	0.38
Adult density km ^{-2a} : Grouse Encounters ^{a b}	-0.90***	0.30
Adult Density km ^{-2a} : First (1) and second (0) Day of Hunting ^b	-0.54**	0.26

Grouse Encounters ^a : First (1) and second (0) Day of Hunting ^b	1.06***	0.30
Grouse Encounters ^a : Male (1) and Female (0) Hunters ^b	-1.34**	0.57
With (1) and Without (0) Local Knowledge : Male (1) and Female (0) Hunters ^b	1.76**	0.78

366

367 Note. The pseudo R^2 for the model is 0.60, residual deviance is 91.36 on 70 *df*.

368 ^aContinuous parameters that are centred and standardized. ^bTwo way interactions.

369 * $p > .05$. ** $p < .05$. *** $p < .01$

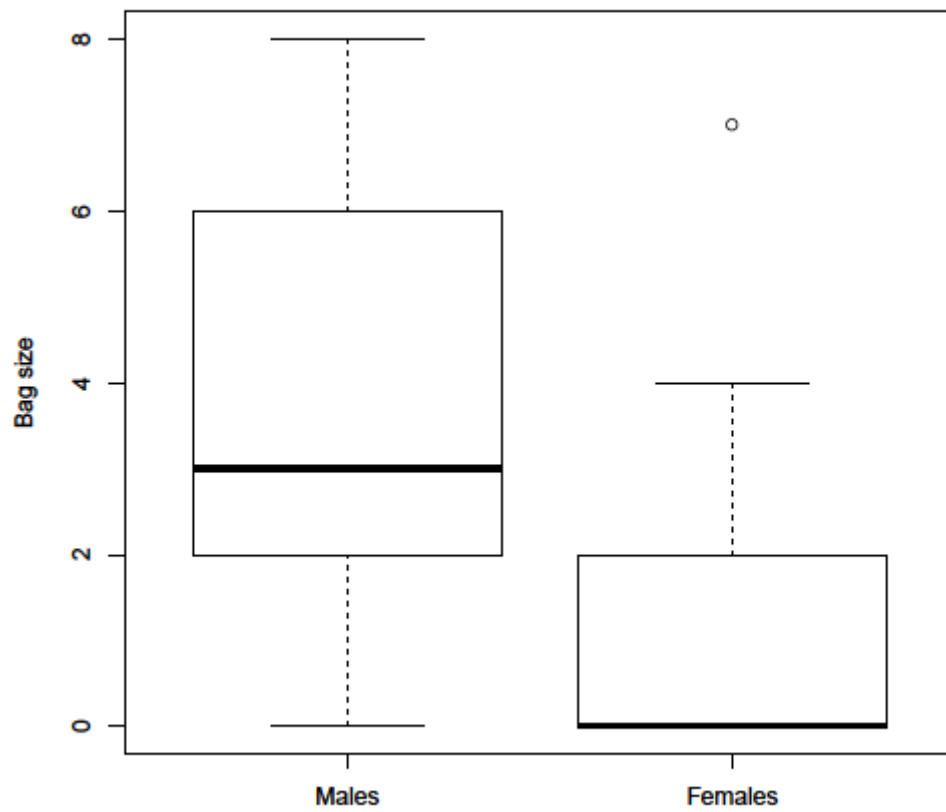
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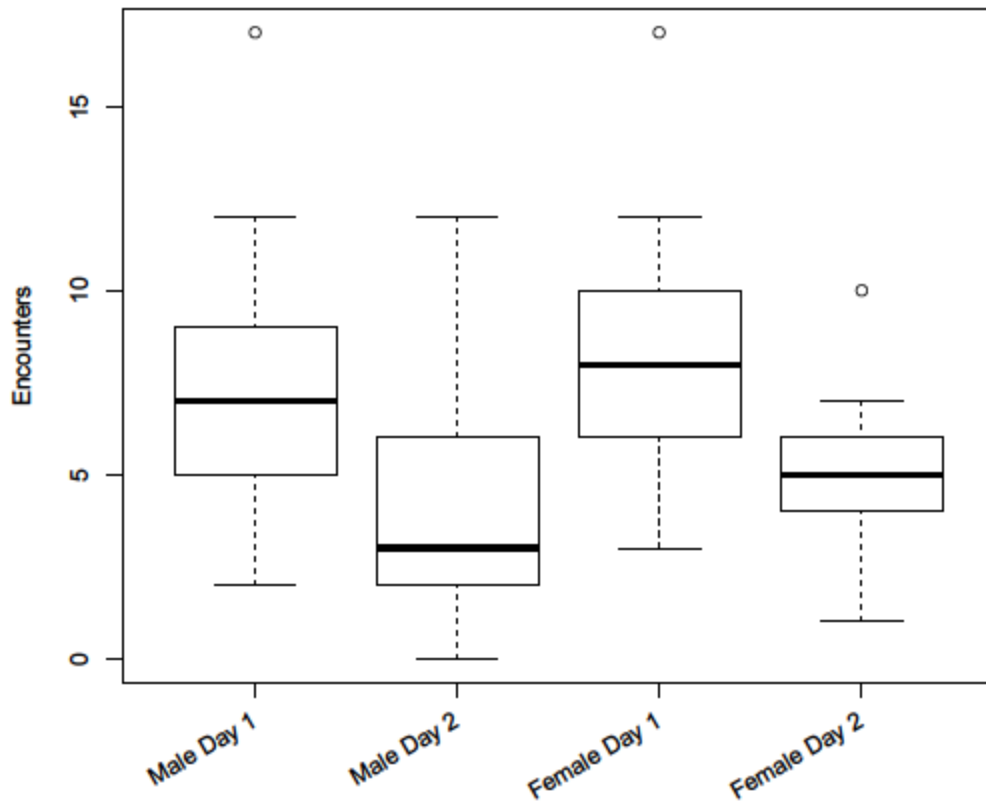
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376 Figure 1. Box plot depicting the difference between genders in daily bag size of willow

377 grouse. The daily bag limit for the hunters was eight grouse per hunter.



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379 Figure 2. Box plot depicting difference in number of grouse encounters achieved between
380 genders, day one and two of the hunt.

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