

1 **Behavioural responses of GPS-collared female red deer**

2 ***Cervus elaphus* to driven hunts**

3

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22 **(Abstract)**

23 Precise knowledge of how game species react to different hunting practises is a  
24 prerequisite for sound management of intensively hunted populations. We compared  
25 behavioural and spatial behaviour of five GPS-collared female red deer in Denmark  
26 before, during and after exposure to 21 driven hunts (2-5 times each). In 53 % of all  
27 hunts, deer left their normal home ranges within 24 hours, moving on average 4 km and  
28 remaining away for an average of 6 days. Compared to pre-hunt values, deer moved  
29 longer distances per unit time on the day of the hunt and the following two nights.  
30 Diurnal activity (based on motion sensors) did not increase significantly on the hunting  
31 day, but was lower than normal the day after the hunt. Nocturnal activity was equal  
32 before and after hunt. Deer spent 96 % of their time in (safer) forest habitats by day and  
33 43 % by night before and after hunts. No induced responses were conditional on  
34 distance to the hunters (0-1.5 km), hunt duration (1.3-6.4 hours) or the time elapsed  
35 since previous hunts (4 to >30 days). The inclination of deer to flee from areas  
36 following hunts might complicate attempts to optimise harvesting policies in landscapes  
37 with many landowners within a typical flight-range.

38

39 *Key words: activity, Cervus elaphus, disturbance, habitat use, home range, movements,*  
40 *spatial behaviour*

41

42 **Introduction**

43 Human activities in general, and hunting actions in particular, often have significant  
44 impacts on behaviour and spatial distribution of wildlife through the anti-predator

45 behaviours they evoke (Frid & Dill 2002). This applies particularly to large-bodied,  
46 long-lived species with a long evolutionary history of human persecution such as the red  
47 deer (*Cervus elaphus*, e.g. Jeppesen 1987a, Cole et al. 1997, Burcham et al. 1999,  
48 Conner et al. 2001, Vieira et al. 2003). Managers of intensively hunted deer populations  
49 should therefore not only address the impacts of harvest pressure, but also disturbance  
50 mediated impacts on individuals and populations (e.g. Phillips & Alldredge 2000,  
51 Jayakody et al. 2008).

52 Spatial reactions of red deer to recreational activities and hunting have mainly been  
53 studied in North American landscapes with continuous forests (e.g. Cole et al. 1997,  
54 Burcham et al. 1999, Conner et al. 2001, Vieira et al. 2003). Less information exists  
55 from the fragmented forest landscapes of Western Europe (Jeppesen 1987a, Jayakody et  
56 al. 2008) where escape possibilities are constrained by agricultural areas. Studies show  
57 that red deer react to hunters by leaving disturbed areas (Jeppesen 1987a, Cole et al.  
58 1997, Burcham et al. 1999, Conner et al. 2001, Vieira et al. 2003), but little is known  
59 about short- and long-term impacts on movements, activity and habitat use.

60 In this paper, we quantify and test changes in spatial behaviour, habitat use and activity  
61 levels of female red deer tagged with GPS- and activity loggers exposed to driven hunts  
62 within their home ranges. Danish red deer should be a good subject for studies of  
63 human disturbance effects on heavily exploited deer populations, as man has been the  
64 sole population regulating agent for >200 years. The hunting season extends over  
65 November to January for hinds and calves and September to January for stags. Owners  
66 of properties over 1 ha and renters of properties over 5 ha are free to shoot as many deer  
67 they like from sunrise to sunset. The Danish landscapes with forests and plantations  
68 which provide cover (Mysterud & Østbye 1999) during daylight surrounded by

69 agricultural landscapes (used for foraging at night), also provide an excellent  
70 opportunity to study disturbance responses of deer whose spatial escape possibilities are  
71 constrained by fragmentation of protective vegetation cover.

72

### 73 **Materials and Methods**

74 Red deer were captured, and all driven hunts took place in the privately owned  
75 plantation “St. Hjøllund Plantage” (14.0 km<sup>2</sup>, 98% conifers consisting mainly of  
76 Norway spruce *Picea abies*) in central Jutland, Denmark (N 56° 05', E 9° 25'), a  
77 lowland (0 – 170 m) region with coastal-influenced climate (average for Mid/Western  
78 Jutland 1960-90: 781 mm annual precipitation divided on 131 days, monthly mean  
79 temperatures ranging from -0.2 [Jan] to 15.4°C [Jul]) and sandy soils. Red deer numbers  
80 within the plantation varied seasonally from ca 100 (March) to ca 200 (September-  
81 October), i.e. 7-14 km<sup>-2</sup>) of which 20-24 are shot annually within the plantation. Herds  
82 appear to be diffusely organised into groups of 3-8 (usual), occasionally 80-90. The  
83 plantation is surrounded by agricultural land, with farms, villages and other conifer  
84 plantations (0.1 – 30 km<sup>2</sup>). During the 2-year-study, driven hunts in St. Hjøllund were  
85 practised in the same way and intensity as in all other years (5-6 per season, Table 2). In  
86 addition to driven deer hunts, 1-2 small game hunts annually were the only other  
87 disturbance activities in the plantations during the hunting season. Although the plantation  
88 is open to the public on foot, visitors were rarely encountered. No information was  
89 available on hunting pressure in neighbouring properties, but deer were intensively  
90 hunted everywhere in the neighbourhood throughout the hunting season.

91 Five female red deer were captured during March-April (Table 1), maintaining home  
92 ranges within St. Hjøllund estate during the following hunting season (November-  
93 January). We caught deer in 300m<sup>2</sup> large traps established in the plantation, baited with  
94 sugar beet during late winter. After being immobilised (Drug mixture of Etorfine and  
95 Rompun. Diprenofine and Antisedan used as antidotes) all deer were equipped with  
96 Lotek Wildcell GPS-GSM 4400M collars with a storage capacity of 7000 positions,  
97 registered at minimum intervals of 1 h and automatically transferred to the base station  
98 via SMS. This enabled us to register hourly positions for most deer throughout the  
99 following hunting season. The mean fix success rate of the GPS collars was 94%  
100 (range: 92-96 %) . Activity information from motion sensors (arbitrary value ranging 0  
101 [immobile] - 100 [maximum activity], logged every 5<sup>th</sup> minute) were retrieved from  
102 four deer after collar recovery (Table 1).

103

#### 104 *Quantification of deer behaviour and habitat use*

105 Hourly behavioural and spatial parameters were averaged for the diurnal (sun angle >  
106 0°) and nocturnal (sun angle < 0°) phases of each day for individual deer. Response  
107 variables were quantified as (1) mean hourly displacement distances, (2) mean motion  
108 score (activity sensor values), and (3) whether all fixes were located outside the deer's  
109 pre-hunting (September-October) home range and (if being outside for an entire day or  
110 night) (4) its maximum distance to the nearest home range border. The pre-hunting  
111 home range was defined as a 95% fixed kernel isopleth calculated with the Animal  
112 Movement extension for ArcView 3.2 (Hooge & Eichenlaub 1997) using the ad hoc  
113 option to select smoothing parameter (H). Each home range was based on ca 24 × 60 =

114 1440 locations sampled with 1 hour interval in September-October. Finally, we  
115 measured (5) habitat use defined as the proportion of time spent in forest vegetation (in  
116 this area almost entirely spruce) vs. other habitats as measured from the digital image  
117 TOP10DK.

118

### 119 *Quantification of hunting disturbances*

120 We considered a deer being potentially exposed to a hunting event if located within 1.5  
121 km of a hunted area. All hunting took place within the plantation where deer stood  
122 during daytime. Organized hunting sessions (Table 2) were registered as the mapped  
123 zones along which hunters were posted and in which beaters and dogs systematically  
124 searched the area to drive out deer towards a line of hunters. As a rule, 2-4 areas  
125 covering 50-300 hectares each were searched from dawn (09:00-10:00 h) to 1 h before  
126 dusk (15:00 h). Movements of beaters and dogs were registered with GPS-loggers.  
127 Positions of the surveyed deer in relation to the hunting activities were obtained from  
128 hourly GPS-positions.

129 The type and strength of the stress stimulus on individuals during a given hunting  
130 session (Table 2) was quantified as (1) the duration of the total hunting period, (2) the  
131 minimum recorded distance of an individual deer to a hunting zone, (3) the type of  
132 hunting practice (traditional driven hunts with large, free-ranging dogs vs. a presumably  
133 more gentle practice using smaller dogs called “motion hunts”) and (4) the (log-  
134 transformed) number of days passed since the previous hunting disturbance (Table 2).

135

### 136 *Statistical analyses*

137 Because deer in diurnally hunted populations behave differently in daylight and  
138 darkness (being more inactive in daylight), we analysed day and night values separately.

139 We used general linear mixed models (PROC MIXED in SAS 9.1) and generalised  
140 linear mixed models (PROC GLIMMIX in SAS 9.1) to contrast deer's reactions  
141 (spatial, behavioural and habitat choice) to hunting with the pre-hunt baseline values  
142 (last three days before hunts) across each individual hunting experience ('deer-specific  
143 hunting events' hereafter, Table 1). Time stage (categorised as 'before hunts' and day 0,  
144 1, 2, .. post-hunt) was entered as a fixed class variable. As experimental blocking units,  
145 we entered deer identity, the deer-by-time stage interaction and deer-specific hunting  
146 events nested within deer as random effects. Variance heteroscedasticity between time  
147 stages was included in all models. We used least-square means tests to test for  
148 differences between pre-hunt situation and the later stages.

149 Binary response variables (presence/absence in home range during an entire diurnal or  
150 nocturnal phase or whether a location was situated inside or outside forest) were  
151 modelled with a logit link function in GLIMMIX, estimating variance components and  
152 denominator degrees of freedom with Saittertwaitte's approximation (Littell et al.  
153 2006), adjusting for over-dispersion ("Random \_residual\_;" statement).

154 Normally distributed response variables (log-transformed if necessary: distance from  
155 home range of migrating deer, mean hourly movement distance, mean activity score)  
156 were modelled in MIXED, estimating variance components and denominator degrees of  
157 freedom with Kenward-Roger's approximation (Littell et al. 2006).

158 Durations of extra-home range excursions (Table 2) were modelled with Kaplan-Meier  
159 analysis (PROC LIFETEST in SAS, setting "survival time" = duration of excursion to 0

160 for non-migrating deer) as this approach enabled proper handling of censored cases  
161 (excursions lasting beyond the date of the next hunt or termination of the survey period:  
162 Tables 1, 2).

163

## 164 **Results**

### 165 *Spatial reactions to hunting*

166 After 53% of all hunts, female deer left their home range during the subsequent night,  
167 being significantly more likely to be away from their home range compared to the pre-  
168 hunt baseline for up to a week (Fig. 1A). Those deer that left their home range stayed  
169 away for an average of 4.7 (SE=1.04) days (maximum: 9.5 days, Table 2). Despite  
170 individual variation (log-rank test of equality over strata:  $\chi^2_4 = 9.83$ ,  $P = 0.043$ ),  
171 responses were not conditional on year, type or duration of hunt, the initial distance to  
172 the hunting zone nor the time elapsed since the previous hunt (log-rank tests, all  $P >$   
173 0.5). Deer leaving their normal home range after a hunting event, averagely migrated 4  
174 km (maximum: 17 km), significantly higher than the mean excursion distances before  
175 hunts (Fig. 1B).

176

### 177 *Behavioural reactions to hunting*

178 Motion sensor information showed that deer were considerably more active at night  
179 than by day (Fig. 2A). Diurnal activity was not significantly different on the day of the  
180 hunt compared to pre-hunt levels, but there was a significant drop on the day after the  
181 hunt (Fig. 2A). Nightly activity levels were identical before and after hunts (Fig. 2A).

182 Before hunts, deer moved 2.2 times longer distances per hour during night than during  
183 day (Fig. 2B). Compared to the pre-hunt daylight baseline, deer increased their mean  
184 hourly displacement distances on the day of the hunt, returning to normal values the day  
185 after the hunt. Relative to the nocturnal pre-hunt baseline, deer increased their mean  
186 hourly displacement distances significantly on the first and second nights after hunts  
187 (Fig. 2B).

188 Further statistical modelling revealed that the increased movement rates the first night  
189 after hunts were caused by those individuals moving out of the home range ( $F_{1, 116} =$   
190  $31.62, P < 0.0001$ ), whereas those deer that remained in their home ranges did not move  
191 significantly more the first night after than in the preceding nights (least square mean  
192 comparison:  $t_{55.6} = 0.49, P = 0.62$ ).

193 Activity responses on the day of the hunt and the following day were independent of the  
194 type of hunt, duration of hunting activities, the deer's shortest distance to the hunted  
195 area, and the elapsed time since the preceding hunt (48 tests: all  $P > 0.09$ ).

196

#### 197 *Time spent in forest cover before and after hunts*

198 Prior to hunts, deer spent 96 (95%CI: 83-99) % of the time in forest by day, compared  
199 to 43 (27-61) % at night. Deer spent equal amounts of time in forest before hunts, the  
200 first and second day during and after hunting (day:  $F_{2, 8.67} = 0.33, P = 0.73$ ; night:  $F_{2, 7.40}$   
201  $= 0.13, P = 0.88$ ).

202

## 203 **Discussion**

204 In about half of all cases traditional driven hunts and the less intensive motion hunts  
205 caused female red deer located within 1.5 km from hunted areas to leave their home  
206 ranges the following night, staying away for six days on average. Our study clearly  
207 shows that deer postponed their emigration response until after dark, i.e. after hunters,  
208 dogs and beaters had left the plantation. Thus, the deer did not shift as an immediate  
209 flight response, but because they assessed the disturbed area as being unsafe for the  
210 subsequent days. Even though hunting-induced migration responses varied across  
211 individuals, all marked deer left their range at least once, suggesting that migration was  
212 general response type to hunting disturbance in female red deer. This reaction pattern  
213 agrees well with anti-hunter responses of red deer previously reported from elsewhere in  
214 Europe (Jeppesen 1987a) and North America (Cole et al. 1997, Burcham et al. 1999,  
215 Conner et al. 2001, Vieira et al. 2003) and is basically similar to responses against  
216 natural predators that are also avoided on a scale above the home range level (e.g.  
217 Anderson et al. 2005). Temporary avoidance of areas following human disturbance is  
218 also known from other group-living cervids such as reindeer (*Rangifer tarandus*) (e.g.  
219 Reimers et al. 2003, Seip et al. 2007, Vistnes & Nellemann 2008) adapted to escape  
220 natural predators through migration (Fryxell & Sinclair 1988). By contrast, other  
221 European, forest-dwelling but less social cervids such as moose (*Alces alces*) (Neumann  
222 et al. 2009) or roe deer (*Capreolus capreolus*) (Jeppesen 1987b) do not appear to leave  
223 their home ranges as a delayed response to hunting activities.

224 Increased hourly displacement distances on the day of hunts and lowered diurnal motion  
225 indices on the day after hunts were the only detectable behavioural response to hunting  
226 apart from derived emigration responses (significantly increased hourly displacement  
227 distances the first two nights after hunts). As increased hourly displacement distances of

228 migrating individuals might be a mere result of straighter path lines rather than  
229 increased movement speeds, energy expenditure and foraging efficiency may therefore  
230 not necessarily have been severely affected after hunts, although no definite conclusions  
231 can be drawn from activity and spatial data alone as presented here.

232 Lack of change in usage of forest and non-forest vegetation after hunts also suggests  
233 that hunting activities did not severely distort basic foraging routines. This is probably  
234 because deer prior to hunts already showed anti-hunter avoidance responses, expressed  
235 by their habitat use at daylight, when they almost exclusively used forested habitats that  
236 deer perceive as safer (Mysterud & Østbye 1999), as opposed to the night when they  
237 spent less than half of their time in forests. Lack of response to hunting in daytime  
238 habitat use was therefore a trivial result of the fact that this anti-predator response could  
239 not be heightened. Unaltered use of non-forest habitats after dark across hunts might  
240 reflect an adaptive response to the actual hazard situation, as no shot must be fired at  
241 deer between sundown and sunrise.

242 In highly cultivated landscapes with no natural predators and multiple landowners  
243 within the radius of a hunting induced migration distance, the observed delayed  
244 migratory reaction to hunting may not be adaptive if deer thereby expose themselves to  
245 new hunters. In the present study this was exemplified by two of five hinds being shot  
246 during hunting-induced migrations to neighbouring estates. In Denmark at least,  
247 unsustainably high hunting pressures in areas with high landowner density is the likely  
248 reason for red deer populations being much more aggregated than habitat composition  
249 should predict (Sunde et al. 2008). With the caveat that disturbance-induced migration  
250 responses might vary across habitats (Jayakody et al. 2008) and countries with different  
251 hunting practise (see Milner et al. 2006), our results seem to suggest that even in areas

252 where hinds are seasonally stationary, hunting should be coordinated within units of  
253 spatial resolution of at least 10 x 10 km to avoid local overexploitation of hinds. As  
254 hunting activities also appeared to elicit emigration responses of deer staying adjacent to  
255 the hunted areas, organizers of deer driven hunts should furthermore be aware that  
256 hunting activities might affect deer even when not directly encountered by beaters, dogs  
257 or hunters.

258

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323

324 Table 1. Data on the five female deer exposed to hunting events. P: positioning data  
 325 (hourly GPS positions), A: activity data (movement sensor information logged every 5  
 326 min).

Deer	Age (yrs) at hunting	With calf at hunting?	Survey period	Reason for termination	95%kernel, ha (Sep-Oct)	Data	Hunting events
A1	1½	No	6-Mar-07 – 14-Dec-07	Shot wounded 15-Dec-07	415	P, A	2
A2	2½	No	15-Mar-06 – 26-Mar-07	Data storage filled	711	P, A	5
A3	≥3½	Yes	15-Mar-06 – 23-Jan-07	Shot 24-Jan-07	287	P, A	5
A5	2½	Yes	12-Apr-06 – 21-Mar-07	Data storage filled	330	P, A	5
A7	1½	No	6-Mar-07 – 20-Jan-08	Data storage filled	360	P	4

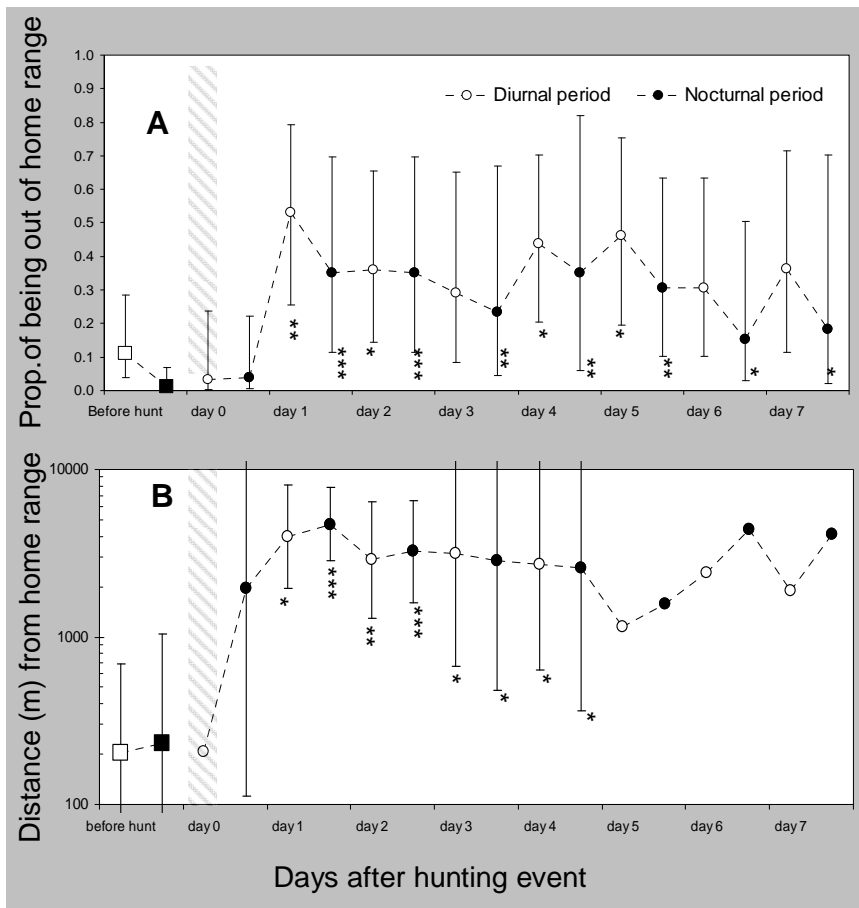
327

328 Table 2. The 10 hunts (D: traditional driven hunts, M: motion hunts) and 21 deer-specific  
 329 hunting events with information on the deer's shortest distance (m) to the hunting zone (DIST),  
 330 days elapsed since the deer experienced the previous hunt (DSPH), and duration of the survey  
 331 period of the actual hunt (lasting until the next hunt was initiated or termination of data  
 332 collection). Spatial reactions to hunts are categorized as "S": stayed (located in home range the  
 333 day after the hunt), "L-R": left home range within one day, returning during the survey period,  
 334 "L-C" left range within one day without returning within the survey period ("censored"). "S\*"  
 335 indicates a case of a deer staying within its home range until the second day after the hunt, being  
 336 shot the day after. MaxDIST indicates the maximum distance of a deer from its home range  
 337 during the pre-hunt period and the day after the hunt.

Hunting events				Deer-specific hunting events					Spatial reaction			
Hunt	Date	Type	hours	Deer	DIST	DSPH	Days		response	days away	MaxDIST (km)	
							before	after			before	after
A	11/3/2006	M	5.7	A2	132	>30	3	5	S	0	0.9	0.0
-	-	-	-	A3	124	>30	3	5	S	0	0.0	0.0
-	-	-	-	A5	215	>30	3	5	L-C	4	6.3	6.3
B	1/6/2007	M	4.6	A2	134	>30	3	6	L-R	4	0.0	6.1
-	-	-	-	A3	655	>30	3	7	S	0	0.0	0.0
-	-	-	-	A5	547	>30	3	7	S	0	0.4	0.7
C	1/13/2007	M	5.5	A2	295	7	3	4	L-R	4	1.1	17.3
-	-	-	-	A3	266	7	3	4	S	0	0.0	0.0
-	-	-	-	A5	285	7	3	4	S	0	0.3	0.7
D	1/17/2007	D	6.2	A2	228	4	1	9	S	0	8.8	0.0
-	-	-	-	A3	1182	4	1	4	S	0	0.0	0.0
-	-	-	-	A5	0	4	1	9	L-R	5.5	0.7	7.0
E	1/21/2007	D	5.7	A3	41	4	1	3	S*	0 (1)	0.9	0.3
F	1/27/2007	D	5.7	A2	653	10	3	7	L-R	1.5	1.6	3.4
-	-	-	-	A5	481	10	3	8	L-C	7	0.3	6.1
G	11/2/2007	D	6.4	A1	1491	>30	3	8	L-R	1.5	0.0	4.5
-	-	-	-	A7	293	>30	3	8	L-R	1	0.0	2.8
H	11/10/2007	D	1.3	A1	424	8	3	11	L-R	9.5	0.0	4.4
-	-	-	-	A7	298	8	3	11	L-R	1	0.2	4.2
I	12/15/2007	D	6.3	A7	721	>30	3	21	L-R	6.5	0.6	3.0
J	1/5/2008	D	1.9	A7	499	21	3	5	S	0	0.1	0.1

338

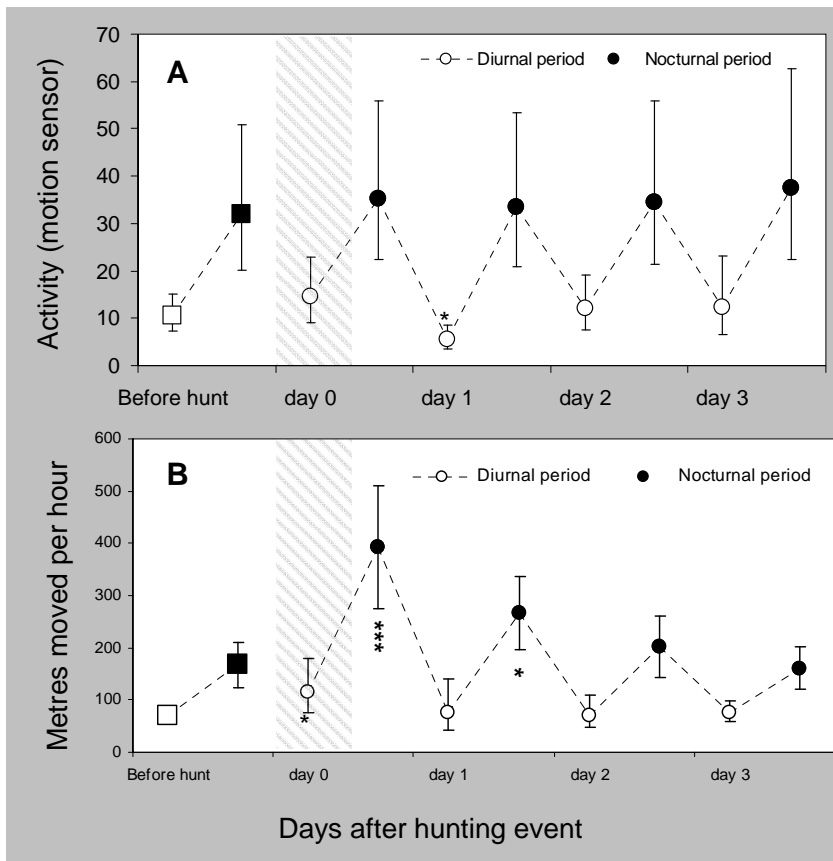
339 Figure 1. Spatial reactions of GPS-collared red deer to hunting events (occurring during  
 340 diurnal period of day 0) measured as (A) the probability of deer migrating out their  
 341 home range and – for those that migrate - (B) the harmonic mean migration distance  
 342 from the nearest home range border. Least square mean estimates (95% CI) for each day  
 343 (separate analyses for diurnal and nocturnal periods) are based on generalized linear  
 344 mixed models, accounting for variation across individuals and hunting events,  
 345 incorporating variance heteroscedasticity between time intervals. Significant deviations  
 346 from pre-hunt estimates are shown as \*:  $P < 0.05$ , \*\*:  $P < 0.01$  and \*\*\*:  $P < 0.001$ .



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349 Figure 2. Least square means (95% CI) of (A) activity (motion sensors, daily means of  
 350 17 hunting events from 4 deer; log-transformed in analysis) and (B) hourly  
 351 displacement distances (daily means from 21 hunting events from 5 deer, diurnal values  
 352 log-transformed in analysis) of GPS-collared red deer before, during (diurnal period of  
 353 day 0) and after hunting events. Separate analyses were run for diurnal and nocturnal  
 354 situations. Estimates are based on mixed models (see text). Significant differences in  
 355 least square means from the before-hunt situation (last 3 days before a hunt) are marked  
 356 as \*:  $P < 0.05$  and \*\*\*:  $P < 0.001$ .



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