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Authors: Sunde, Peter, Olesen, Carsten R., Madsen, Torben L., and Haugaard, Lars

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Behavioural responses of GPS-collared female red deer *Cervus elaphus* to driven hunts

Peter Sunde, Carsten R. Olesen, Torben L. Madsen & Lars Haugaard

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

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

Peter Sunde, Carsten R. Olesen & Lars Haugaard, Aarhus University, National Environmental Research Institute, Department of Wildlife Ecology and Biodiversity, Grenaaevej 14, DK-8410 Ronde, Denmark - e-mail addresses: psu@dmu.dk (Peter Sunde); cro@dmu.dk (Carsten R. Olesen); laha@dmu.dk (Lars Haugaard)
Torben L. Madsen, St. Hjöllund Plantage, Faurholtvej 12, DK-7362 Hampen, Denmark - e-mail: tlmvrad@post.tele.dk

Corresponding author: Peter Sunde

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Human activities in general, and hunting actions in particular, often have significant impacts on behaviour and spatial distribution of wildlife through the anti-predator behaviours they evoke (Frid & Dill 2002). This applies particularly to large-bodied, long-lived species with a long evolutionary history of human persecution such as the red deer *Cervus elaphus* (e.g. Jeppesen 1987a, Cole et al. 1997, Burcham et al. 1999, Conner et al. 2001, Vieira et al. 2003). Managers of intensively hunted deer populations should therefore not only address the impacts of harvest pressure, but also disturbance-mediated impacts on individuals and populations (e.g. Phillips & Alldredge 2000, Jayakody et al. 2008).

Spatial reactions of red deer to recreational activities and hunting have mainly been studied in North

American landscapes with continuous forests (e.g. Cole et al. 1997, Burcham et al. 1999, Conner et al. 2001, Vieira et al. 2003). Less information exists from the fragmented forest landscapes of Western Europe (Jeppesen 1987a, Jayakody et al. 2008) where escape possibilities are constrained by agricultural areas. Studies show that red deer react to hunters by leaving disturbed areas (Jeppesen 1987a, Cole et al. 1997, Burcham et al. 1999, Conner et al. 2001, Vieira et al. 2003), but little is known about the short- and long-term impacts on movements, activity and habitat use.

In this paper, we quantify and test changes in spatial behaviour, habitat use and activity levels of female red deer tagged with GPS- and activity-loggers, and exposed to driven hunts within their home

Table 1. Data on the five female red deer exposed to hunting events. P indicates positioning data based on hourly GPS positions, and A indicates activity data based on movement sensor information logged every five minutes.

Deer	Age in years at hunting	With calf at hunting?	Survey period	Reason for termination	95% kernel in ha (Sep.-Oct.)	Data	No. of hunting events
A1	1½	No	6 Mar.07 - 14 Dec.07	Shot/wounded on 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 on 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

ranges. Danish red deer should be a good subject for studies of human disturbance effects on heavily exploited deer populations, as man has been the sole population regulating agent for >200 years. The hunting season extends from November to January for hinds and calves, and from September to January for stags. Owners of properties >1 ha and renters of properties >5 ha are free to shoot as many deer as they like from sunrise to sunset. Danish landscapes with forests and plantations (which provide cover during daylight; Myrsetrud & Østbye 1999) surrounded by agricultural landscapes (used for foraging at night), also provide an excellent opportunity to study disturbance responses of deer whose spatial escape possibilities are constrained by fragmentation of protective vegetation cover.

Material and methods

Red deer were captured, and all driven hunts took place in the privately-owned plantation of 'St. Hjøl-lund Plantage', which covers 14.0 km² (98% conifers, consisting mainly of Norway spruce *Picea abies*) in central Jutland, Denmark (56°05'N, 9°25'E). St. Hjøl-lund Plantage is situated in a lowland (0-170 m a.s.l.) region with a maritime climate (average annual precipitation for mid and western Jutland, 1960-90: 781 mm spread over 131 days; monthly mean temperatures ranging from -0.2 in January to 15.4°C in July) and sandy soils. The numbers of red deer within the plantation varied seasonally from ca 100 (in March) to ca 200 (in September-October; i.e. 7-14 km⁻²) of which 20-24 are shot annually. Herds appear to be diffusely organised into groups of usually 3-8 and occasionally 80-90 red deer. St. Hjøl-lund Plantage is surrounded by agricultural land, farms, villages and coniferous plantations (0.1-30 km²). During our two-year study, driven hunts in St. Hjøl-lund Plantage were carried out in the same way and intensity as in all other years (i.e. 5-6 hunts per season, see Table 2). In addition to driven

deer hunts, 1-2 small-game hunts per year were the only other disturbance activities which occurred in the plantation during the hunting season. Although the plantation is open to foot-access by the general public, visitors were rarely encountered. No information was available on hunting pressure on neighbouring properties, although deer were intensively hunted everywhere in the neighbourhood throughout the hunting season.

During March-April, we captured five female red deer (Table 1) which maintained home ranges within the St. Hjøl-lund estate during the following hunting season (November-January). We caught the deer in 300 m² traps established in the plantation which were baited with sugar beet *Beta vulgaris* during late winter. After being immobilised by a mixture of the drugs Etorfine and Rompun (Diprenofine and Antisedan were used as antidotes), all deer were equipped with a Lotek Wildcell GPS-GSM 4400M collar with a storage capacity of 7,000 positions, registered at minimum intervals of one hour and automatically transferred to the base station via SMS. This enabled us to register hourly positions for most of the deer throughout the following hunting season. The mean fix success rate of the GPS collars was 94% (range: 92-96%). We retrieved activity information from motion sensors (arbitrary value ranging from 0 (immobile) to 100 (maximum activity), logged every 5th minute) from four deer after collar recovery (see Table 1).

Quantification of deer behaviour and habitat use

Hourly behavioural and spatial parameters were averaged for the diurnal (sun angle >0°) and nocturnal (sun angle <0°) phases of each day for each individual deer. Response variables were quantified as 1) mean hourly displacement distances, 2) mean motion score (activity sensor values), and 3) whether all fixes were located outside an individual deer's pre-hunting (September-October) home range and (if being outside for an entire day or night) 4) its maximum distance to the nearest home-range border.

The pre-hunting home range was defined as a 95% fixed kernel isopleth calculated with the Animal Movement extension for ArcView 3.2 (Hooge & Eichenlaub 1997) using the *ad hoc* option to select smoothing parameter (H). Each home range was based on ca 24 × 60 = 1,440 locations, sampled with 1-hour intervals throughout September-October. Finally, we measured 5) habitat use, defined as the proportion of time spent in forest vegetation (in this area almost entirely spruce) vs other habitats as measured from the digital image TOP10DK.

Quantification of hunting disturbances

We considered a deer to be potentially exposed to a hunting event if it was located within a distance of 1.5 km of a hunted area. All hunting took place within the plantation where deer remained during daytime. Organised hunting sessions (Table 2) were registered as the mapped zones along which hunters were posted and in which beaters and dogs systematically searched the area to drive out deer towards a line of hunters. As a rule, 2-4 areas covering 50-300 ha each were searched from dawn (09:00-10:00)

to 1-hour before dusk (15:00). Movements of beaters and dogs were registered using GPS-loggers. Positions of the surveyed deer in relation to the hunting activities were obtained from hourly GPS-positions.

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

Statistical analyses

Because deer in diurnally hunted populations behave differently during daylight and darkness hours (being less active in daylight), we analysed day and night values separately. We used general linear mixed models (PROC MIXED in SAS 9.1) and generalised linear mixed models (PROC GLIMMIX in SAS 9.1)

Table 2. The 10 hunts (A-J; where type D indicates traditional driven hunts, and M motion hunts) and 21 deer-specific hunting events with information on the deer's shortest distance (in m) to the hunting zone (DIST), days elapsed since the deer experienced the previous hunt (DSPH), and duration of the survey period in days before and after the actual hunt (lasting until the next hunt was initiated or termination of data collection). Spatial reactions to hunts are categorised as 'S': stayed (located in the home range the day after the hunt), 'L-R': left home range within one day, returning during the survey period, 'L-C': left range within one day without returning within the survey period ('censored'). 'S*' indicates a case in which a deer stayed within its home range until the second day after the hunt, and was shot the day after. MaxDIST indicates the maximum distance (in km) of a deer from its home range 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	
							before	after			before	after
A	11/3/2006	M	5.7	A2	132	>30	3	5	S	0	0.9	0
-	-	-	-	A3	124	>30	3	5	S	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	6.1
-	-	-	-	A3	655	>30	3	7	S	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
-	-	-	-	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
-	-	-	-	A3	1182	4	1	4	S	0	0	0
-	-	-	-	A5	0	4	1	9	L-R	5.5	0.7	7
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	4.5
-	-	-	-	A7	293	>30	3	8	L-R	1	0	2.8
H	11/10/2007	D	1.3	A1	424	8	3	11	L-R	9.5	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
J	1/5/2008	D	1.9	A7	499	21	3	5	S	0	0.1	0.1

to contrast the deers' reactions (spatially, behaviourally and concerning habitat choice) to hunting with the pre-hunt baseline values (last three days before hunts) across each individual hunting experience (hereafter 'deer-specific hunting events'; see Table 1). Time stage (categorised as 'before hunts' and day 0, 1, 2, .. post-hunt) was entered as a fixed class variable. As experimental blocking units, we entered deer identity, the deer-by-time stage interaction and deer-specific hunting events nested within deer as random effects. Variance heteroscedasticity between time stages was included in all models. We used least-square means tests to test for differences between the pre-hunt situation and the later stages.

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

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

Durations of extra home-range excursions (see Table 2) were modelled using Kaplan-Meier analysis (PROC LIFETEST in SAS, setting 'survival time' = duration of excursion to 0 for non-migrating deer), as this approach enabled proper handling of censored cases (excursions lasting beyond the date of the next hunt or termination of the survey period: see Tables 1 and 2).

Results

Spatial reactions to hunting

After 53% of all hunts, female deer left their home range during the subsequent night, being significantly more likely to be away from their home range compared to the pre-hunt baseline for up to a week (Fig. 1A). Those deer that left their home range stayed away for an average of 4.7 days (SE = 1.04) and a maximum of 9.5 days (see Table 2). Despite individual variation (log-rank test of equality over strata: $\chi^2_4 = 9.83$, $P = 0.043$), responses were not con-

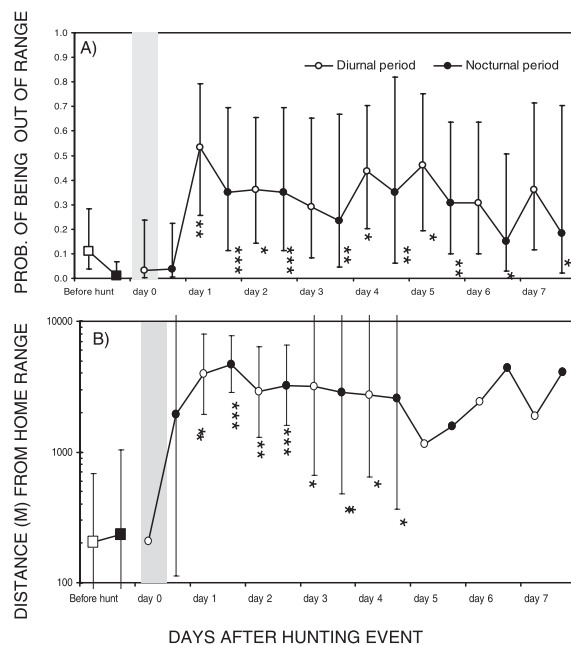


Figure 1. Spatial reactions of GPS-collared female red deer to hunting events carried out during the diurnal period of day 0 measured as the probability of deer migrating out their home range, for hinds which migrate (A), and the harmonic mean migration distance (in m) from the nearest home-range border (B). Least square mean estimates (95% CI) for each day (with separate analyses for diurnal and nocturnal periods) are based on generalised linear mixed models, accounting for variation across individuals and hunting events, incorporating variance heteroscedasticity between time intervals. Significant deviations from pre-hunt estimates are shown as *: $P < 0.05$, **: $P < 0.01$ and ***: $P < 0.001$.

ditional on year, type or duration of hunt, the initial distance to the hunting zone nor the time elapsed since the previous hunt (log-rank tests: all P s > 0.5). Deer leaving their normal home range after a hunting event migrated, on average, 4 km (maximum: 17 km), which is significantly higher than the mean excursion distances before hunts (Fig. 1B).

Behavioural reactions to hunting

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

Before hunts, deer moved 2.2 times longer distances per hour during the night than during daytime hours (Fig. 2B). Compared to the pre-hunt daylight baseline, deer increased their mean hourly displacement distances on the day of the hunt, returning to

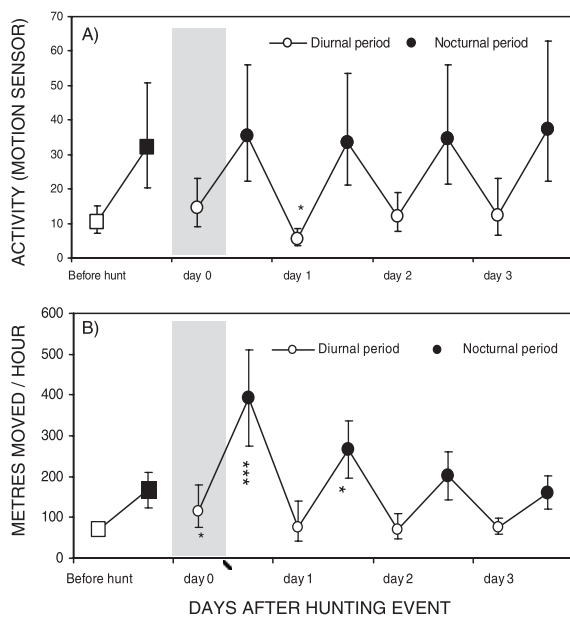


Figure 2. Least square means (95% CI) of activity (A; based on motion sensors with daily means of 17 hunting events from four deer; log-transformed in analysis) and hourly displacement distances (B; with daily means from 21 hunting events from five deer using diurnal values log-transformed in analysis) of GPS-collared female red deer before, during (diurnal period of day 0) and after the hunting events. Separate analyses were run for diurnal and nocturnal situations. Estimates are based on mixed models (see text), and significant differences in least square means from the before-hunt situation (last three days before a hunt) are marked as *: $P < 0.05$ and ***: $P < 0.001$.

normal values the day after the hunt. Relative to the nocturnal pre-hunt baseline, deer increased their mean hourly displacement distances significantly on the first and second nights after hunts (see Fig. 2B).

Further statistical modelling revealed that the increased movement rates recorded during the first night following hunts were caused by individuals which moved out of their home range ($F_{1,116} = 31.62$, $P < 0.0001$), whereas deer which remained in their home range did not move significantly more the first night after the hunt than in the preceding nights (least square mean comparison: $t_{55,6} = 0.49$, $P = 0.62$).

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

Time spent in forest cover before and after hunts

Prior to hunts, deer spent 96% (95% CI: 83-99) of their time in forest during the daytime, compared to

43% (27-61) at night. Deer spent equal amounts of time in forest before hunts, and the first and second day during and after hunting (day: $F_{2,8.67} = 0.33$, $P = 0.73$; night: $F_{2,7.40} = 0.13$, $P = 0.88$).

Discussion

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

Increased hourly displacement distances on the day of hunts and lowered diurnal motion indices on the day after hunts were the only detectable behavioural response to hunting apart from derived emigration responses (significantly increased hourly displacement distances the first two nights after hunts). As increased hourly displacement distances of migrating individuals might be a mere result of straighter path lines rather than increased movement speeds, energy expenditure and foraging efficiency may therefore not necessarily have been

severely affected after hunts, although no definite conclusions can be drawn from activity and spatial data alone, as presented here.

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

In highly cultivated landscapes with no natural predators and with multiple landowners within the radius of a hunting-induced migration distance, the observed delayed migratory reaction to hunting may not be adaptive if deer thereby expose themselves to new hunters. In our study this was exemplified by two of five hinds being shot during hunting-induced migrations to neighbouring estates. In Denmark at least, unsustainably high hunting pressure in areas with high landowner densities is the likely reason for red deer populations being much more aggregated than habitat composition would predict (Sunde et al. 2008). With the caveat that disturbance-induced migration responses might vary across habitats (Jayakody et al. 2008) and between countries with different hunting practices (see Milner et al. 2006), our results seem to suggest that even in areas where hinds are seasonally stationary, hunting should be coordinated within units with a spatial resolution of at least 10×10 km to avoid local overexploitation of hinds. As hunting activities also appeared to elicit emigration responses in deer located adjacent to the hunted areas, organisers of deer driven hunts should furthermore be aware that hunting activities might affect deer even when not directly encountered by beaters, dogs or hunters.

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