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Impacts of human disturbance on flight response and habitat use of red deer

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Abstract

Many wild animals perceive humans as predators, and human disturbance, especially in the form of hunting, triggers antipredatory behavior among prey. Yet, knowledge of how game species react to different types of human disturbance and adapt to repeated disturbances is limited. We investigated how disturbance in the form of a solitary human approacher (stalker) impacted behavior (flight response and short-term habitat use) of 28 GPS-collared red deer (*Cervus elaphus*) in two populations with contrasting population densities in Norway. We studied how the behavioral response differed: (1) with season (pre-hunting vs. hunting); (2) by consecutive approaches within a day; (3) among replicated experiments within the same season; and (4) between two regions with contrasting densities of red deer. The average flight initiation distance (FID) increased by 15% during the hunting season, and consecutive approaches within the same day caused the red deer to move 49% longer distances. Flight initiation distance was longer in the high-density population, while escape distance was longer in the low-density population. Red deer moved out of their weekly home range after 52% approaches, and after the onset of hunting season, time spent outside the home range increased by 89%. Red deer preferred denser resting sites after the disturbance and animal sites had shorter sighting distance and higher canopy cover than control plots. Tree density and canopy cover at animal sites increased at the onset of hunting season, from first to second approach within day, and after replicated experiments within season. Our results suggest that red deer preferred dense resting sites, especially in the hunting season. However, these animal sites had the same amount of the favorable forage plant bilberry (*Vaccinium myrtillus*), indicating no clear food–cover trade-off in selection of habitat. Our study showed that onset of hunting initiates stronger fear responses in red deer, which may in turn affect red deer distribution and harvesting efficiency.

INTRODUCTION

All animals have an underlying fear of being killed by predators. This fear triggers antipredator responses, which are adaptations to increase survival (Boissy, 1995; Lima & Dill, 1990). Many wild animals may perceive humans as predators, and human disturbance might trigger natural antipredatory behavior among prey (Frid & Dill, 2002; Sibbald et al., 2011). When encountered by humans, most animals that use flight as a response will inevitably move away. However, the prey's perception of predation risk might not be equally distributed over time and space (Laundré et al., 2001; Lone et al., 2014; Norum et al., 2015). For animals there is a trade-off between perceived risk of being predated and the liability of increased energy expenditure and lost forage time (Cooper & Frederick, 2007; Ydenberg & Dill, 1986), and the flight response might therefore vary. Flight initiation distance (FID) is a measure of the distance from the predator to the prey when it starts to move (Blumstein, 2006; Holmern et al., 2016; Runyan & Blumstein, 2004; Stankowich & Blumstein, 2005; Ydenberg & Dill, 1986). FID, as well as escape distance (the distance they move away), might be different across predators and vary among species (Møller et al., 2013), and it might be context dependent. Population density might impact flight responses, as larger groups of individuals or denser populations have a higher detection rate of predators due to collective detection, often called "safety in numbers" (Bednekoff & Lima, 1998; Lima & Zollner, 1996; Pulliam, 1973). As the optimal escape distance is found at the intersection between cost of escape and predation risk, a longer FID (which should be less threatening) will result in a shorter escape distance (Ydenberg & Dill, 1986). Repeated low-risk exposure to a predator can diminish the perception of risk toward the specific predator and studies across species have shown that flight responses are reduced due to habituation (Engelhardt & Weladji, 2011; Mbise et al., 2019; McGowan et al., 2014; Rodriguez-Prieto et al., 2009). In general, it is advantageous to adjust antipredator behavior in accordance with the faced risk (Ydenberg & Dill, 1986).

As the actual risk from humans changes drastically at the onset of the hunting season, it is reasonable to predict that the antipredator behavior changes with it (Behrend & Lubeck, 1968; Ydenberg & Dill, 1986). Human hunting may alter and modify spatial behavior (Jeppesen, 1987; Rivrud et al., 2016), activity (Kamler et al., 2007),

and habitat selection (Benhaiem et al., 2008; Lone et al., 2015). Knowledge of shelter for security and forage resources carries fitness advantages (Webb et al., 2011). For this reason, deer species often have a strong seasonal site fidelity (Edge & Marcum, 1985; Kropil et al., 2015; Webb et al., 2011). However, human hunting might decrease site fidelity, and disturbance can make deer move out of their usual home range (HR; Burcham et al., 1999; Conner et al., 2001; Jeppesen, 1987; Sunde et al., 2009; Vieira et al., 2001). Thus, understanding antipredator behavior and how animals respond to human hunting is therefore vital to manage and conserve many wildlife populations. There is a growing body of research of deer behavior in relation to human disturbance in general (Stankowich, 2008) and connected to permanent infrastructure, such as traffic and hiking trails (Jayakody et al., 2008; St. Clair & Forrest, 2009). However, less is known about the short-term and repeated effect of direct human disturbance on deer flight response, forage decisions, and habitat use.

Red deer (*Cervus elaphus*) are widespread in Europe and targeted for human hunting over most of its range. Their distribution often stretches into semi-urban areas, and high population densities are often found in heterogeneous landscapes intersected with cultivated farmland (Godvik et al., 2009). Even though red deer often use habitats close to humans, human activity is shown to affect red deer behavior (Coppes et al., 2017; Jayakody et al., 2008; Jeppesen, 1987; Jiang et al., 2008). However, increased level of habituation is a common behavioral adaptation, especially for nonhunting activities (Thompson & Henderson, 1998). The main cause of mortality in most managed red deer populations is human hunting (Langvatn & Loison, 1999). Consequently, red deer are shown to increase flight response and be more sensitive to interaction with off-trail hikers, such as hunters, compared with the more traditional on-trail hikers (Westekemper et al., 2018).

Here, we examine flight responses and changes in short-time behavior of 28 GPS-collared red deer disturbed by a solitary stalking human, a common red deer hunting technique (Martinez et al., 2005). We carried out the experiment in two populations with contrasting population density. We tested the hypothesis that flight response will vary as a function of actual predation risk (Frid & Dill, 2002). Our main issue was to investigate changes in behavior from nonhunting season (August) to

the hunting season (September), and if behavior was related to population density. We expected that the flight responses (FID and escape distance) will be higher during the hunting season. Further, repeated encounters without predation (or a close-to-predation event) will cause a lowering of flight response (due to habituation). Therefore, we expected that red deer will reduce their FID and escape distance after repeated encounters within the same day and replicated experiments within same season. We further expect that FID will be higher in the high-density population due to collective detection (larger group size), but that escape distance will not be affected by population density. We also expected that males will have less flight responses (FID and escape distance) than females because females usually have a calf at heel. We expected that the disturbance will change red deer spatial behavior and habitat use, by causing them to move out of their weekly HR and that they will seek more concealing cover after the human disturbance. Lastly, we expected that such sites with more concealing cover contained less of the favorable forage plants, that is, bilberry (*Vaccinium myrtillus*) and grass.

MATERIALS AND METHODS

Study area

The study was conducted in two separate regions in Norway, a northern and a southern region (Figure 1). The northern region (61°98′–62°95′ N, 006°70′–010°62′ E) is one of the core areas for red deer in Norway (hereafter "the high-density population"), whereas in the southern region (59°40′–58°05′ N, 009°39′–006°47′ E) red deer has emerged during the last two decades and the population density is much lower (hereafter "the low-density population"). The number of shot deer in the low-density population was 0.06 individuals/km^2 during the two-year study period, whereas it was 1.02 individuals/km^2 in the high-density population. Even though the population density is quite different, red deer hunting is implemented and carried out more or less equally in both the regions. Hunters can access all parts of the red deer's habitat and a variety of hunting methods are used, with stand hunting and drive hunting together with stalking as the most common. Deer are harvested throughout the hunting season from 1 September to 23 December, but the hunting activity peaks when the season opens and 34% and 24% of all animals were shot until 25 September in the high-density and low-density population, respectively (www.hjorteviltregisteret.no). The northern region ranges from coastal to inland areas in heterogeneous landscapes and contains approximately 1649 km^2 of

suitable red deer habitat. The landscape is dominated by deep valleys with forested steep slopes stretching to the montane alpine areas, while the valley floors are often dominated by agricultural land. The southern region ranges from coastal to inland areas in heterogeneous landscapes and contains approximately 2767 km^2 of suitable deer habitat. This region has fewer steep slopes and lower mountains, but nonetheless a rugged topography. All the experiments were conducted within the altitudinal range of 20–1100 m above sea level. In both regions, temperature and precipitation generally decline from coast to inland, while snow depth and duration of snow cover increases (Langvatn et al., 1996). Both areas are mostly dominated by either deciduous forest, with European white birch (*Betula pubescens*) as the main species, or coniferous forest dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*).

Capture and radiotelemetry

Twenty-eight adult red deer (14 in each region, 9 were males and 19 were females) were darted and marked with numbered plastic ear tags (75 × 97 mm, Allflex, Denmark) and GPS collars with an integrated VHF transmitter (VECTRONIC Aerospace GmbH, Berlin, Germany; collar mass: ~850 g, 0.5%–1.0% of animal body mass) at feeding sites spread across the regions. We aimed for a balanced sex ratio, but due to a skewed sex ratio toward females in both populations, a limited number of collared males were available for marking. All collaring of study animals was conducted in accordance with standard procedures by approved field personnel (Sente et al., 2014), after permits were granted by the Norwegian Animal Research Authority. The GPS collars originally logged positions every hour throughout the year, but because we needed high-resolution data, the sampling frequency was changed during the experimental period. Using a web-based SMS scheduling service, the logging frequency was changed three days before the experiment began and logged every 12 min from midnight of the experiment day, every third minute one hour before the experiment, every minute throughout the three-hour long experiment, and then back to every 12 min until the following midnight.

Experimental design

The experiment was designed to simulate a hunting situation, with a solitary human approacher (stalker) provoking a flight response from the GPS-collared red deer (Figure 2). This was done by locating the deer using recent GPS positions received from the collar and
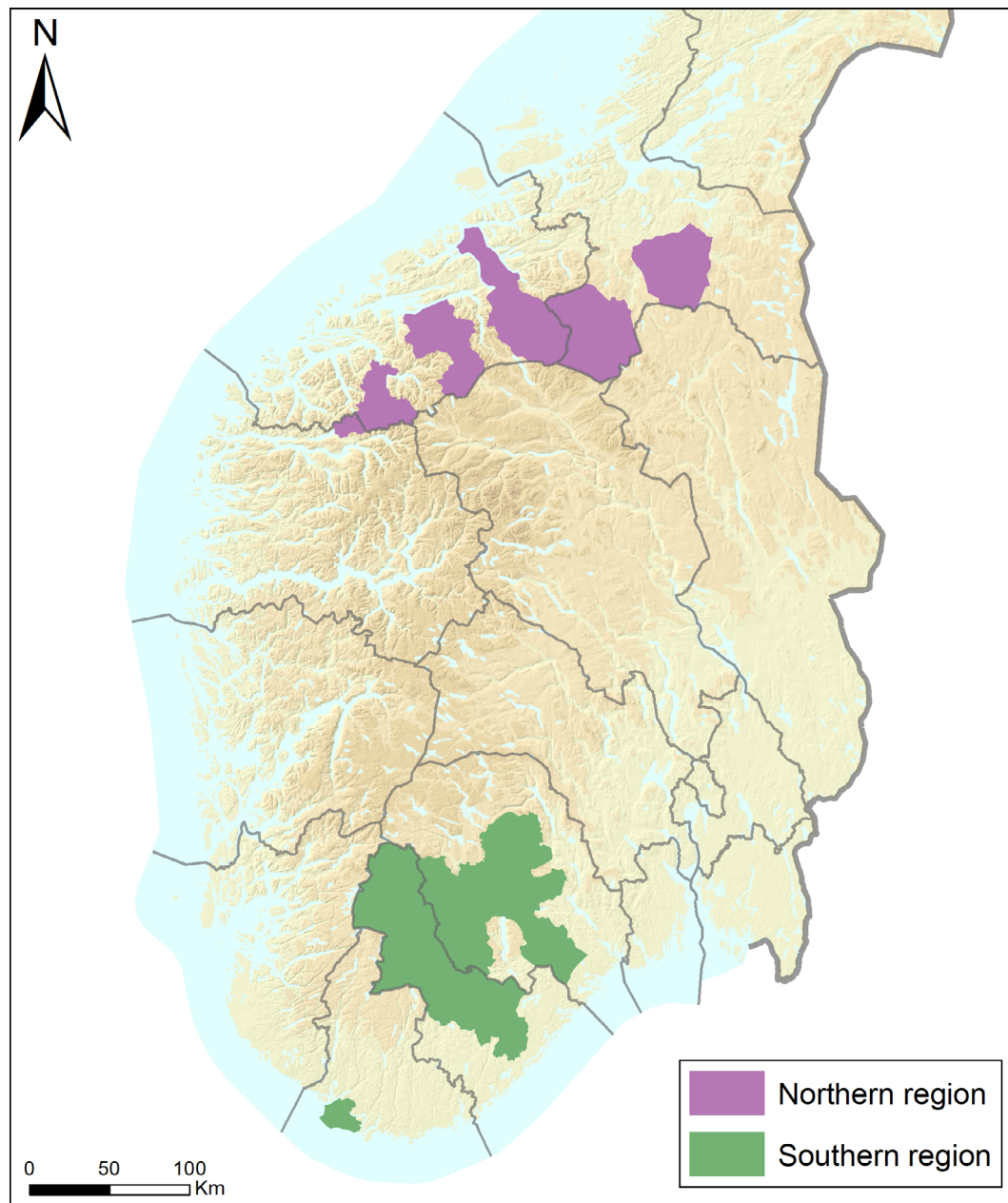
FIGURE 1 Map of the study area in South Norway. The northern region (violet) included the municipalities with high-density red deer populations (1.02 shot deer/km^2) and the southern region (green) included municipalities with low-density populations (0.06 shot deer/km^2).

thereafter manually track the deer using a handheld VHF receiver (RX-98H). We walked steadily toward the study animal with an approximate speed of 2–3 km/h until the deer moved from its original site (Moen et al., 2012). Because of the topography, we were not able to able to consider the wind direction systematically; however, we did not perform stalking in heavy rain and windy weather. The whole experiment was conducted within dense forested areas, and the experimental animals were hardly observed before they started to move away. High productive dense forest habitats are preferred by red deer during daylight hours and they are then often inactive (Godvik et al., 2009). When we visually observed the deer move, heard it flee off, or noticed a change in VHF signal's strength or rhythm, we logged both the position of the deer and the approacher with a handheld GPS (Garmin Montana 580 or Garmin GPSMAP 60CSx) together with exact time. If we were unable to notice the location and time of escape in the field, the actual escape position was found by analyzing the GPS locations, by manually checking the deer and the approacher's positions within the timeframe of the experiment.
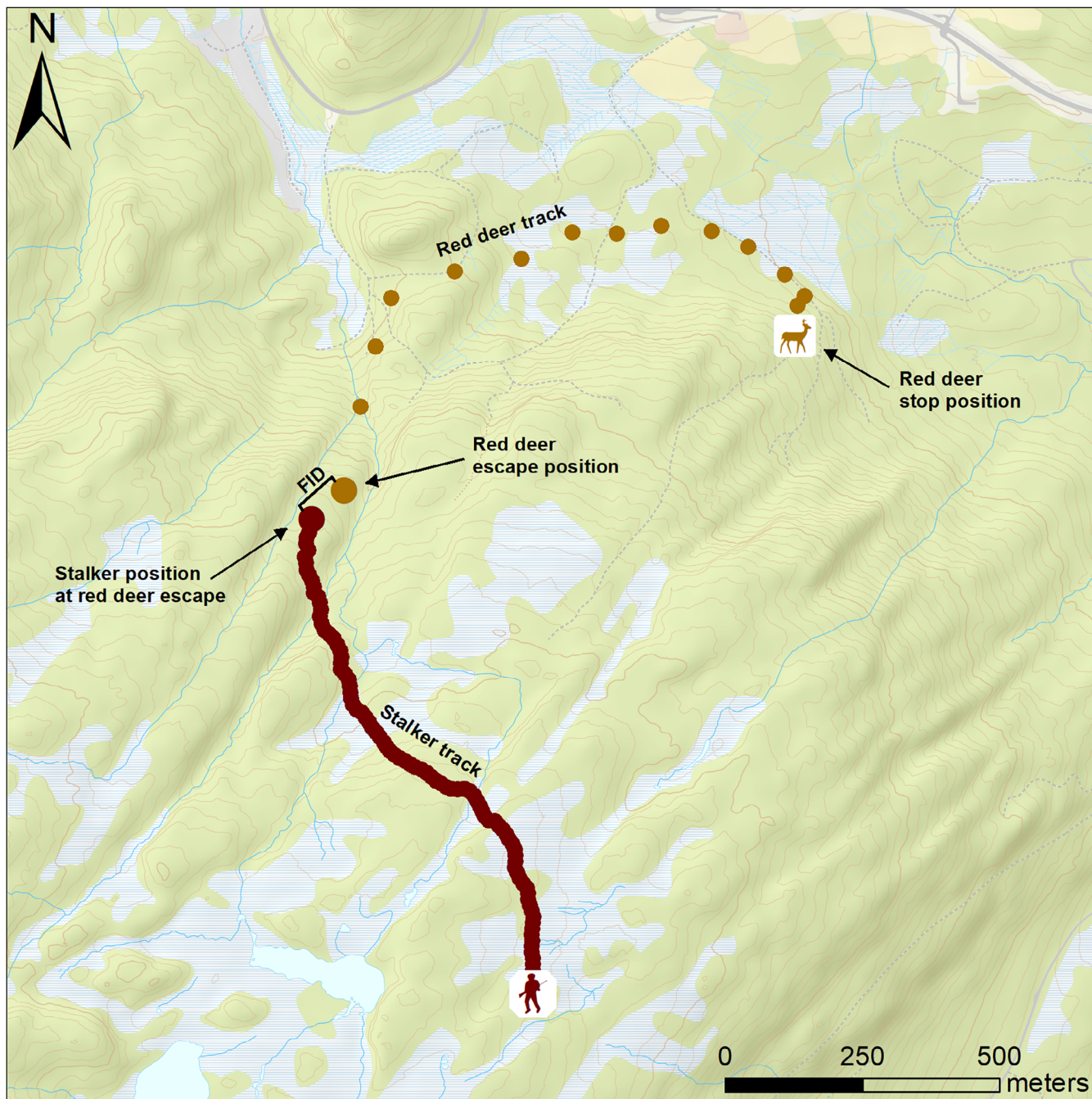
FIGURE 2 Example of an approaching experiment. Brown dots: Stalkers positions during the approach. Large brown dot: Stalker position at the time when the red deer escaped. Large light brown dot: Red deer position when it started to escape. Light brown dots: Red deer positions during the escape. Red deer positions were logged every minute during the escape. The deer symbol shows the red deer stop position. FID, flight initiation distance.

We tested this approach by plotting all verified field observations against the GPS analyzing method. These coordinates were then logged and used for further analyses. We usually provoked two flight responses per experimental day (called "approaches within day"), to measure the effect of consecutive disturbances, which may often be the case in hunting events. Therefore, after at least 1 h, the study animal was located again at its new site and the same procedure was repeated once more. After the experiment, the approacher's tracklog was downloaded via the Garmin Basecamp tool and further uploaded to QGIS 3.4. The period was divided into one pre-hunting season period (8–31 August) and one hunting season period (1–24 September). The experimental setup was set to conduct two replicated experiments per individual red deer within each period

(called "experiments within season"), with at least one week between. The approaches were carried out during daylight hours, between 8:00 AM and 10:35 PM. As most hunting and recreation activities require daylight, this is the time most likely to create human disturbances (Coppes et al., 2017). The study was conducted in 2015–2016 in the low-density population and in 2019 in the high-density population and stalking was done by only two different persons. To further minimize a "stalker effect," the stalker who conducted the field work in 2015–2016 trained the stalker who did the field work in 2019. Due to intensive moose hunting by 25 September and onwards, especially in the southern region, we ended the experimental period on 24 September to avoid conflicts with local hunters.

Flight response

Flight response is here used as a term including both FID and escape distance. FID was found by measuring the distance (in meters) in a straight line from the approacher's position to the starting position of the escaping deer using the Pythagoras equation: $\sqrt{[(\text{animal UTM 32-coordinate}) - (\text{approacher UTM 32-coordinate})]^2 + [(\text{animal UTM 32-coordinate}) - (\text{approacher UTM 32-coordinate})]^2}$. The escape distance was measured by adding the distance between each GPS position logged by the deer collar during the flight and was defined as the distance from the position where the deer started to escape to the stop position where the deer stayed for a minimum of 20 min (Figure 2). The same equation as above was used for estimating the distance between each position recorded along the route of the deer and the accumulated distance was found by adding the distance between them. Since the approacher's handheld GPS records the positions each 10th meter and the GPS collars record the positions each minute, a quite high accuracy was achieved.

Spatial behavior

Norwegian red deer are partially migratory, that is, some individuals in the population regularly migrate between winter and summer ranges, whereas other individuals stay sedentary all year (Mysterud et al., 2011). For migrating deer, the autumn seasonal migration was expected to start within the study period (8 August–24 September) (Mysterud et al., 2011). We created weekly HRs prior to an experiment, describing the area during the period before the disturbance to avoid movements due to seasonal migration (these migrations would greatly affect the size of the HRs). However, we excluded four

individuals' HR, due to migrations within the week prior to the experiment. We created 99% minimum convex polygons for HR estimation to include the whole range used the prior week using the adehabitatHR package (Calenge, 2019). Further, ArcMap GIS 10.7.1 (ESRI, USA) was used to manually check whether the deer moved out of the HR, and if so, how much time it took for them to return.

Habitat characteristics

We derived a measure of terrain ruggedness from GIS maps. Terrain ruggedness index was calculated as the sum change in elevation between a grid cell and its eight neighbor grid cells and is assumed to be an objective quantitative measure of topographic heterogeneity (Riley et al., 1999). The maps were prepared and rasterized using ArcGIS, with a resolution of 10×10 m and topographical variation around each deer site (radius = 500 m) was derived from a digital elevation model. Digital land resource maps were obtained from the Norwegian Institute of Bioeconomy Research.

At each of the escape positions (the animal's position when it started to move), a vegetation analysis was conducted and compared with the vegetation at a control site, which was chosen randomly 100 m away from the escape position. A total of 324 vegetation analyses were conducted while the experiments were ongoing and latest within 14 days, and we chose the first and second position of the day for the analyses. The vegetation analyses were conducted following Lone et al. (2015) and consist of the following measures:

1. Ground cover was registered within three 2×2 m quadrats, 10 m apart facing north–south from the GPS position. The accumulated sum of dead material, heath (*Ericaceae* spp.), ferns (*Polypodiopsida*), horsetails (*Equisetum* spp.), mosses (*Bryophyta*), lichens, grass (*Poaceae* spp.), and herbaceous plants in percentages was set to end in a total of 100%. Cover of grasses and bilberry (important forage resources in August and September) were used further in the analyses as measures of food availability (Albon & Langvatn, 1992).

2. Sighting distance (horizontal visual cover) in all four cardinal directions from the GPS position was found using a cover board (height: 120 cm, width: 30 cm). We used the mean distance of the values of the four directions when the whole coverboard was covered by either vegetation or topography. The coverboard's height was enlarged according to an earlier study (Lone et al., 2014) from 80 to 120 cm, to account for

the height difference between a roe deer (*Capreolus capreolus*) and a red deer.

3. A spherical concave densiometer was used to measure canopy cover in all four cardinal directions. By dividing each of the 24 squares into 4 smaller squares, we could count and record how many of these 96 squares were free of the canopy cover (Lemmon, 1956). The mean value of the four cardinal directions at each site for actual cover was used in the analysis.

4. At each vegetation plot a horizontal point sampling of trees was done using a relascope, giving the tree density. Each tree that fills the gap of the relascope represents a basal area of minimum 1 m²/ha (Bitterlich, 1984).

Data analyses and model selection

All statistical analyses were performed using the statistical software R 4.0.3. We tested whether the response variables (FID and escape distance; log-transformed) were related to several predicted explanatory variables by fitting a linear mixed-effects model (LMM) using the "lmer" function in the lme4 package (Bates et al., 2015). The log transformation secured normality and variance homogeneity and thus the LMM was chosen to account for the random effect of individual deer (ID) and thereby avoid biases caused by pseudo-replication. Season (pre-hunting period: 8–31 August; hunting period: 1–24 September), population (low density or high density), approaches within a day (first or second), experiments within season (first or second), and sex were fitted as fixed effects in both models. In the model for escape distance, we also included FID as an explanatory variable. In both models, we included an interaction between season and population, and season and sex, to test whether there were different patterns across seasons between sexes and populations. ID was included as a random intercept to account for nonindependence between data from the same animal (Zuur et al., 2009). We tested for variability between years (i.e., if year should be included as a random variable together with animal ID) by using a likelihood-ratio test for each response variable.

To investigate the probability for a deer moving out of their HR after an approach, a generalized linear mixed-effects model (GLMM) was fitted using the "glmmTMB" function from the glmmTMB package (Brooks et al., 2017). The GLMM was fitted using the binominal distribution (move out of HR = 1, staying within HR = 0) and to account for the random effect of each ID (Zuur et al., 2009). The following fixed effects were fitted in the model: season, population, approaches within day, experiments within season, sex, FID, escape

distance, HR size, and the interactions between season and population and season and sex. The numerical variables (FID, escape distance, and HR size) were log-transformed to secure normality and variance homogeneity prior to modeling. We excluded approaches where the deer had already run out of its HR, usually the second approach on the same day. For testing time spent outside the HR (log-transformed), we fitted an LMM with the same predictors as the model for probability to move out of HR, but we left out the interactions between season and population and season and sex due to few observations ($n = 60$).

To test if the animal escape position was different from a random control site and different from the stop sites after flight in relation to habitat characteristics, we fitted separate models for each of the following response variables: sighting distance (in meters), tree density (basal area; integer), canopy cover (0%–100%), and ground cover of bilberry and grasses (0%–100%). Sighting distance (log-transformed) was created using the mean sighting distance of all four cardinal directions at a site and was modeled with an LMM. Proportion canopy cover, bilberry, and grass cover were modeled by separate GLMMs with a Poisson distribution. For tree density, the Poisson distribution was used in the GLMM through the function glmmTMB. The following explanatory variables were fitted in all the separate models: season, population, approaches within day, experiments within season, and animal/control site. To actually test for the effect of human disturbance, that is, if the difference between animal site and the related control site changed, we included the interactions between animal/control site and season, approaches within day, experiments within season, respectively. Again, ID was included as a random intercept to account for nonindependence data from using the same animal, and we tested for the effect of variability between years by using a likelihood-ratio test for each response variable. Model selection for all analyses was based on Akaike information criterion (AIC) corrected for small sample size (AIC$_c$) (Burnham & Anderson, 2002). From the initial full models including all variables and interaction terms, we did backwards selection based on AIC$_c$ using likelihood-ratio tests using the drop1 function in the lme4 package. We compared the full model to all models where one variable or interaction term was removed to identify the parameter that would yield the lowest AIC$_c$ value if removed from the model. The model was refitted without the identified variable/interaction term, and the process was repeated until the most parsimonious model was identified (see tables in Appendix S1). The 95% confidence interval (CI) was then calculated for the retained predictors. We assessed the influence of a variable depending on whether the 95%

CI overlapped zero. We calculated conditional R^2 as a measure of model fit in the final models (Nakagawa & Schielzeth, 2013). Conditional R^2 is interpreted as variance explained by both fixed and random factors (i.e., the entire model).

RESULTS

Among the 28 GPS-collared adult red deer, a total of 179 approaches were conducted. Of these, 89% ($n = 159$) were successful and resulted in a flight response. In all the following models, we tested whether year should be included as a random variable together with animal ID. However, in all models, year was excluded based on likelihood-ratio tests ($p < 0.05$). Variance explained

(conditional R^2) varied between 0.15 and 0.89, showing an overall good fit of the final models (Tables 1–3).

Flight response

Overall, the red deer moved from their initial sites when the FID was on average 57 ± 48.0 m (range = 4–365 m) and escaped for a mean distance of 2036 ± 1876.5 m (range = 63–9453 m). They moved 43 min on average (median = 35 min, range = 2–270 min) before stopping. The selected mixed model for FID included season, population, and topographic variation (Appendix S1: Table S1), whereas the model for escape distance returned with season, approaches within day, and population in the selected model (Appendix S1: Table S2).

TABLE 1 The selected mixed models linking (1) flight initiation distance (FID; in meters) and (2) escape distance (in meters) of red deer to several predictors in the two regions in Norway, 2015–2019.

Variable	Estimate	SE	Lower 95% CL	Upper 95% CL
(1) FID				
Intercept	3.628	0.132	3.374	3.883
Season (pre-hunt vs. hunt)	**0.288**	**0.100**	**0.094**	**0.483**
Population (low density vs. high density)	**0.620**	**0.123**	**0.382**	**0.859**
Terrain ruggedness	**−0.164**	**0.057**	**−0.273**	**−0.054**
(2) Escape distance				
Intercept	7.031	0.152	6.729	7.334
Season (pre-hunt vs. hunt)	0.244	0.154	−0.059	0.547
Approaches within day	**0.500**	**0.153**	**0.196**	**0.803**
Population (low density vs. high density)	**−0.361**	**0.178**	**−0.725**	**−0.003**

Note: Model terms with estimates, standard error (SE), lower and upper 95% confidence limits (CLs) from the selected mixed-effect model are displayed. Random effect of individual red deer ($n = 28$): Model 1, variance = 0.02697, SD = 0.1642; Model 2, variance = 0.05604, SD = 0.2367. Parameters with 95% CIs not overlapping zero appear in boldface. Conditional R^2 was 0.30 and 0.15 in Models 1 and 2, respectively.

TABLE 2 The selected mixed models linking (1) probability of moving out of home range and (2) time out of home range of red deer after the approach to several predictors in the two regions in Norway, 2015–2019.

Variable	Estimate	SE	Lower 95% CL	Upper 95% CL
(1) Probability of moving out of home range				
Intercept	−10.421	2.136	−14.607	−10.421
log(Escape distance)	**1.522**	**0.317**	**0.902**	**2.143**
log(Home range size)	**−0.484**	**0.168**	**−0.814**	**−0.154**
(2) Time out of home range				
Intercept	−0.529	1.465	−3.482	2.396
Season (pre-hunt vs. hunt)	**0.557**	**0.274**	**0.011**	**1.117**
log(Escape distance)	**0.401**	**0.195**	**0.013**	**0.792**

Note: Model terms with estimates, standard error (SE), lower and upper 95% confidence limit (CL) from the selected mixed-effect model are displayed. Random effect of individual red deer (ID): Model 1 (ID, $n = 28$): variance = 0.161, SD = 0.402; Model 2 (ID, $n = 27$): variance = 0.528, SD = 0.726. Parameters with 95% CIs not overlapping zero appear in boldface. Conditional R^2 was 0.40 and 0.45 in Models 1 and 2, respectively.

TABLE 3 The selected mixed models linking (1) sighting distance (in meters) (2) tree density, (3) canopy cover (in percentage), (4) bilberry cover (in percentage), and (5) grass cover (in percentage), at the escape positions for red deer and control sites in the two study regions in Norway (2015–2019).

Variable	Estimate	SE	Lower 95% CI	Upper 95% CI
(1) Sighting distance				
Intercept	2.459	0.057	2.345	2.574
Season (pre-hunt vs. hunt)	**0.109**	**0.046**	**0.019**	**0.200**
Population (low density vs. high density)	**−0.323**	**0.068**	**−0.467**	**−0.188**
Site (animal vs. control)	**0.198**	**0.045**	**0.109**	**0.286**
(2) Tree density				
Intercept	2.806	0.128	2.554	3.058
Season (pre- vs. post-hunt)	**0.087**	**0.038**	**0.013**	**0.161**
Experiments within season	**0.155**	**0.038**	**0.081**	**0.228**
Approaches within day	**0.118**	**0.027**	**0.066**	**0.171**
Population (low density vs. high density)	0.248	0.143	−0.031	0.528
Sex (female vs. male)	**−0.598**	**0.175**	**−0.941**	**−0.255**
Site (animal vs. control)	−0.088	0.047	−0.181	0.004
Site (animal vs. control) × experiments within season	**0.211**	**0.053**	**0.108**	**0.315**
Site (animal vs. control) × approaches within day	−0.082	0.053	−0.185	0.022
(3) Canopy cover				
Intercept	4.269	0.056	4.159	4.387
Season (pre- vs. post-hunt)	−0.004	0.020	−0.042	0.035
Experiments within season	0.022	0.019	−0.017	0.060
Approaches within day	**0.070**	**0.014**	**0.043**	**0.098**
Sex (female vs. male)	**−0.629**	**0.093**	**−0.822**	**−0.455**
Site (animal vs. control)	**−0.168**	**0.024**	**−0.215**	**−0.122**
Site (animal vs. control) × season (pre- vs. post-hunt)	**0.101**	**0.028**	**0.047**	**0.156**
Site (animal vs. control) × experiments within season	**−0.057**	**0.028**	**−0.112**	**−0.003**
(4) Bilberry cover				
Intercept	0.164	0.035	0.095	0.233
Approaches within day	0.021	0.028	−0.034	0.078
Population (low density vs. high density)	**−0.118**	**0.043**	**−0.202**	**−0.035**
Site (animal vs. control)	0.011	0.028	−0.044	0.065
Site (animal vs. control) × approaches within day	**−0.078**	**0.039**	**−0.155**	**−0.001**
(5) Grass cover				
Intercept	0.180	0.034	0.113	0.248
Season (pre- vs. post-hunt)	0.020	0.028	−0.034	0.074
Population (low density vs. high density)	0.081	0.042	−0.002	0.164
Site (animal vs. control)	0.030	0.026	−0.021	0.081
Site (animal vs. control) × season (pre- vs. post-hunt)	0.072	0.039	−0.003	0.148

Note: Model terms with estimates, standard error (SE), lower and upper 95% confidence limits (CLs) from the selected mixed-effect model are displayed. Random effect of individual red deer ($n = 26$): Model 1, variance = 0.164, SD = 0.128; Model 2, variance = 0.188, SD = 0.434; Model 3, variance = 0.062, SD = 0.249; Model 4, variance = 0.009, SD = 0.097; Model 5, variance = 0.009, SD = 0.097. Parameters with 95% CIs not overlapping zero appear in boldface. Conditional R^2 was 0.25, 0.83, 0.89, 0.30, and 0.31 in Models 1–5, respectively.

Population had the strongest effect on FID of the predictor variables (Table 1), and FID was overall 77% longer in the high-density population compared with the low-density population. Red deer increased their FID by 15% by the start of the hunting season. FID was reduced by increasing terrain ruggedness around the animal's site

(Table 1). On the other hand, red deer in the low-density population had a 41% longer escape distance than the high-density population (Table 1). However, approaches within day had the strongest effect on escape distance (Table 1) and after the second approach they increased the escape distance by 49%. Even though hunting season entered the best model for escape distance, the effect was not significant (Table 1).

Spatial behavior

The red deer moved out of their weekly HR after 52% ($n = 159$) of the approaches, with a mean time spent out of their prior HR of 34.6 ± 49.29 h (range = 0.87–243 for those who returned [$n = 80$]). After three of the approaches (4% of the approaches), the deer did not return to its prior HR but initiated its autumn migration. Probability to move out of HR was higher with increasing escape distance and higher with smaller weekly HRs (Table 2; Appendix S1: Table S3). The selected model for time spent outside the HR showed that after the onset of hunting, time spent outside the HR increased by about 89%, from 24.8 to 45.5 h (Table 2; Appendix S1: Table S4). Lastly, time spent outside increased with escape distance (Table 2).

Habitat characteristics

The selected models for tree density and canopy cover included the interactions between animal/control site and season, and animal/control site and experiments within season (Appendix S1: Tables S6 and S7), indicating that the difference between animal sites and control sites changed with season after the disturbance (Table 3). Compared with animal sites, the sighting distance was 24% longer at control plots, suggesting that red deer preferred denser resting sites. Sighting distance increased slightly by onset of hunting season, but the increase was equal at both animal and control sites (Table 3; Appendix S1: Table S5). Tree density was quite equal between animal sites and control sites, but increased at the onset of hunting season, and increased between approaches within a day and between experiments within season (Table 3; Appendix S1: Table S6). Further, canopy cover was larger at animal sites, and canopy cover increased at the onset of the hunting season (Table 3; Appendix S1: Table S7). Canopy cover also increased between the first and second approach within day and with replicated experiments within season. The sites in the high-density population had 43% shorter sighting distance compared with those in the low-density population, but tree density was higher in the high-density population

(Table 3). The cover of bilberry was different across the populations, with higher bilberry cover in the low-density population (Table 3; Appendix S1: Table S8). Bilberry cover was higher at red deer resting sites compared with the control sites, but just at the second site within a day (Table 3). The selected model for grass cover gave no considerable effects (Table 3; Appendix S1: Table S9).

DISCUSSION

Flight response

There has been an increasing focus on how human hunting affects wildlife population also indirectly through risk sensitivity (Cromsigt et al., 2013). Whereas the direct and lethal impact of hunting on deer population dynamics has been documented (Langvatn & Loison, 1999; Solberg et al., 1999), less is known about its disturbance effects on deer behavior. We showed that red deer increased FID at the onset of the hunting season, whereas they increased escape distance after consecutive approaches within the same day independent of season. There is a strong burst of hunting activity at the onset of the hunting season, and about 27% of the annual harvest is shot during the first week of the hunting season in Norway. This probably leads to an increase of the perceived risk from humans. Behavioral responses to human activity, such as increased FID and escape distance, are found in studies in various species (Austin & Ramp, 2019; de Boer et al., 2004; Holmern et al., 2016). However, few studies have shown direct effect on flight behavior of onset of hunting season. In his review, Stankowich (2008) found that ungulates in areas with hunting activity generally had greater flight responses than in non-hunted areas. Other studies have shown that red deer vigilance was greater during the hunting season than during preseason (Benhaiem et al., 2008; Jayakody et al., 2008).

An adjusted antipredator behavior was evident in our study for consecutive approaches within a day, as it gave considerably longer escape distances. Our results therefore indicated no short-time habituation, similar to in a study of bears (*Ursus arctos*) in Sweden (Ordiz et al., 2019). In a German study, red deer did not show a spatiotemporal reaction to recreational on-trail hiking, but were sensitive to off-trail hiking that always induced flight (Westekemper et al., 2018). However, not all cervid species respond similarly when encountered by off-trail hiking humans. Norwegian wild reindeer (*Rangifer tarandus*) showed that both FID and escape distance decreased per consecutive approach during the same day (Reimers et al., 2012). A meta-analysis on ungulates showed an overall significant effect of habituation to

repeated human exposure, but the interspecies variation was high (Stankowich, 2008). The same meta-analysis showed that sexual differences were non-consistent regarding FID and escape distance across ungulate species. In our study, we found no difference in flight response between males and females, similar to results reported for black-tailed deer (*Odocoileus hemionus*) (Stankowich & Coss, 2007). However, in a study of mouflon (*Ovis orientalis musimon*), females with calves had a greater flight response than males and females without calves (Ciuti et al., 2008). Unfortunately, we had no systematic overview of calf at heel for the females in our study.

Even though there is a different history of hunting in our two populations, hunting pressures over the last two decades have been comparable. However, flight response differed between the populations likely related to differences in population density. While red deer in the high-density population had longer FID and shorter escape distance, the low-density population showed shorter FID and longer escape distance. Larger groups of individuals or denser populations have a higher detection rate of predators due to collective detection (Bednekoff & Lima, 1998; Lima & Zollner, 1996). As red deer are shown to form social feeding groups (Clutton-Brock et al., 1982) and group size tends to increase with higher population density (Hebblewhite & Pletscher, 2002), collective detection could be an explanation for the longer FID in the high-density population, as more individuals could potentially detect the approaching threat and thus start the escape earlier (Stankowich, 2008). With an early escape, the stress level might be lower as with a late escape, which again could explain the shorter escape distance in the high-density population. Our analyses also showed that increasing terrain ruggedness decreased FID. Other studies have shown that topography can affect both alert distance and assessment time, and thereby flight response (Taraborelli et al., 2014). A rugged topography might limit the ability to detect the approacher at longer distances (Frid, 2003).

Spatial behavior

We showed that red deer moved out of their prior week HR after 52% of the approaches, and probability to leave its HR increased with longer escape distances and decreased with larger HRs. This rate was quite equal to what was found in Denmark, where 53% of driven hunts caused red deer to move out of their HR (Sunde et al., 2009), but higher than that found among female red deer in a Swedish study (28%; Jarnemo & Wikenros, 2014). The severity of the disturbance might be proportional to the

return time (Jarnemo & Wikenros, 2014). We show that return time to their initial HR increased considerably after the onset of the hunting season. This shows that deer adjust their behavior to the perceived risk and that human disturbance might be more invasive during the hunting season. We further observed that three approaches lead to no return to their prior HRs, a pattern found among red deer males in Sweden (Jarnemo & Wikenros, 2014). These deer initiated autumn migration to winter ranges and all occasions happened after onset of hunting season. Sudden changes in human behavior in red deer-occupied habitats may thus cause significant changes in space use. Human disturbance might cause animals to change the location of their HR (Arlettaz et al., 2015). Several studies have shown that ungulates can respond to hunting by increasing movement rate (Stankowich, 2008), altering habitat use (Lone et al., 2015; Thurfjell et al., 2017), decreased foraging time (Ciuti et al., 2012), and initiating migratory behavior. In fact, onset of hunting in red deer was shown to be the largest triggering factor on autumn migration, with a marked increase in risk of migration during the first days of the hunting season (Rivrud et al., 2016). Also, timing of elk (*C. elaphus*) departure from summer range and arrival on winter range was influenced by exposure to hunting (Rickbeil et al., 2019) and elk moved to protected areas prior to or by the onset of the hunting season (Conner et al., 2001; Mikle et al., 2019).

Habitat characteristics

The spatial distribution of risk for many hunted animals is not equal between habitats. Rifles are the only allowed weapon for red deer hunting in Norway. Densely forested habitats are often avoided by hunters as rifles require free line of sight (Lone et al., 2015), and the risk of being shot is undoubtedly higher in open areas (Rivrud et al., 2014). We show that after disturbance, red deer did seek habitats with more concealing cover than the surroundings, a pattern documented on a variety of species such as brown bear (Moen et al., 2012; Ordiz et al., 2011), wolf (*Canis lupus*) (Wam et al., 2012), and wild boar (*Sus scrofa*) (Thurfjell et al., 2013). We also found that red deer seek more densely forested habitats in the hunting season compared with pre-hunting season. Such habitat switch has earlier been found among surviving red deer males (Lone et al., 2015). Whereas all males used similar habitat before the hunting season, the onset of hunting induced an immediate switch to habitat with more concealing cover in surviving males, but not in males that were later shot (Lone et al., 2015). By contrast, a study in Poland found that mortality risk during hunting season did not

change red deer habitat use (Fattebert et al., 2019). They reported that nonlethal human disturbance does affect red deer habitat selection, but with no differences between seasons. However, denser forested areas are used as a refuge for the red deer and they seek these areas to avoid upholding their vigilance when disturbed by humans (Benhaiem et al., 2008; Jayakody et al., 2008; Sibbald et al., 2011). We were unable to detect a clear food–cover trade-off in selection of habitat. Locations of deer after the disturbance had denser cover than the initial locations, but the availability of bilberry and grass was similar. The availability of forage was measured at a very local scale (2×2 m^2), not considering quality per se, and it is therefore uncertain whether it reflects the relevant foraging decision of deer.

CONCLUSIONS

Human disturbance in the form of hunting might be a driver for space use and habitat selection in general. Our study has improved knowledge about flight responses and habitat use of red deer after human approaches. Most importantly, we showed that onset of hunting initiates stronger fear responses in red deer, which may in turn affect red deer distribution and harvesting efficiency. With a rapidly increasing red deer population in Norway, maximizing hunting output in a sustainable way is an important management approach for both population control and local economic income.

AUTHOR CONTRIBUTIONS

Erling L. Meisingset designed the study and did the project administration. Øystein Brekkum and Erling L. Meisingset organized and did the red deer marking and the data collection. Joar Gusevik and Atle Skjørestad did the fieldwork and approached the red deer, as a part of their master thesis. Erling L. Meisingset analyzed the data and wrote the first draft of the manuscript. All authors contributed substantially to the final version.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Meisingset, 2022) are available from NIBIO: https://doi.org/10.21350/iw216516.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.