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Hunting, including drive hunts, can be considered as a predation process. Although drive hunts are spatially and temporally well defined, the scale at which the hunting risk triggers anti-predator responses of prey remains poorly documented. The present study aims at 1) characterizing the delayed movement responses of female red deer *Cervus elaphus* to hunters and 2) understanding the main environmental determinants modulating these post-disturbance responses at the individual level. We hypothesized that red deer alter their movement behaviour for several days after a drive hunt by increasing their speed and exploring more space. Then, we predicted that individuals close to the hunting area would exhibit stronger responses (i.e. higher speed and larger home range size) than individuals located further away. We also expected topographic obstacles and vegetation cover to reduce the magnitude of the post-disturbance responses. We used GPS data from a large dataset collected on 91 female red deer in the National Hunting and Wildlife Reserve of La Petite Pierre (France), between 2004 and 2018. Each year, drive hunts are conducted by about 43 hunters and 6 dogs, once a week from October to February. Our results suggest that, over a 72-h period after a drive hunt, female red deer could show two contrasting strategies: 1) flight-type movements (i.e. higher maximum speed) associated with more space explored due to a temporary avoidance of the disturbed area and 2) lower movements to avoid detection and contacts with hunters. These two delayed responses are situation-specific, depending on risk proximity, landscape features, hunting conditions and individual characteristics. This study highlights that ungulate management using a 'hunting for fear' approach may be adjusted considering spatial and temporal scales of the effects of drive hunts on red deer movement patterns.

Keywords: delayed anti-predator responses, hunting, non-lethal effects, space use

Most human activities are sources of significant disturbance for wildlife (Frid and Dill 2002). Hunting is one of them and is commonly regarded as a predation process (Frid and Dill 2002). Indeed, similarly to predation, human hunting may lead to a decrease in prey densities (lethal effects) but also to a set of anti-predator behaviour strategies developed by prey to reduce the risk of predation (non-lethal effects) (Lima and Dill 1990, Lima 1998, Caro 2005, Creel and Christianson 2008). These non-lethal effects in response to the exposure to human risk have been identified in several species as behavioural responses taking the form of flights, shifts in habitat use or increase in vigilance (e.g. birds: Cresswell 2008, sea turtles: Heithaus et al. 2008, birds and mammals: Caro 2005). Such responses entail costs in terms of time and energy for other essential biological functions (e.g. energy acquisition, reproduction; Lima and Dill 1990) and can lower prey fitness (Lima 1998, Frid and Dill 2002, Creel and Christianson 2008). The lethal and non-lethal effects of hunting have been proposed as management tools and a multi-effect approach for ungulate management, combining both population abundance reduction – 'hunting to kill' – and spatial distribution and behavioural changes – 'hunting for fear', is now emphasised by scientists (Cromsigt et al. 2013). This last concept relies on the idea that non-lethal effects of human hunting can be used to reinforce the lethal effects through the fitness consequences of tradeoffs between risk and any other fitness-enhancing activities, as well as to keep ungulates away or distract them from sensitive areas (e.g. forest regeneration zones; Cromsigt et al. 2013). In this context, our study focuses on red deer movements in response to human hunting. Wildlife management could indeed benefit from a better understanding of game movement responses to human hunting risk, as they perceive it, and their variation.

Based on the processes driving natural predator–prey interactions, prey should adapt their responses to the level of perceived risk (Lima and Dill 1990, Lima and Bednekoff 1999, Creel and Christianson 2008) and are likely to exhibit stronger movement responses to human predation in a situation of high perceived predation risk (Frid and Dill 2002). Consequently, the magnitude of these movement responses and their fitness consequences may result from 1) the risk characteristics (e.g. nature and behaviours of the predator, the temporal scale of risk), 2) the environment (e.g. habitat type, distance to cover, distance to predator) and 3) prey biology (e.g. risk assessment capacities, internal state) (Liley and Creel 2007, Creel et al. 2014). These factors should be carefully studied in the context of hunting since human predation is not homogenously distributed in space and time, resulting in strong variability in the risk perceived by prey. Indeed, although drive hunts are spatially well defined, the spatial scale at which the hunting risk is perceived by prey remains poorly documented. It is unclear whether hunting disturbance occurs beyond the hunting area (i.e. zone bounded by shooters) and how it may trigger anti-predator behaviours. Landscape features may also affect the level of risk exposure at the time of the predator–prey encounter and consequently alter the magnitude of the movement responses (Hebblewhite et al. 2005, Kauffman et al. 2007). Landscape features can be divided into vegetation and topographic variables (Mysterud and Ostbye 1999, Hebblewhite et al. 2005, Kauffman et al. 2007). The magnitude of anti-predator responses has been mainly studied and interpreted in the light of habitat visibility, which affects detection of predators and ease of escape or hiding from a predator (Barja and Rosellini 2008, Valeix et al. 2009). Yet, the role of landscape features (vegetation and topography) on the magnitude of the movement responses has seldom been explored in an ungulate–human system to the best of our knowledge.

Movement responses to hunting are also likely to vary depending on the temporal scale of risk. For example, at a fine temporal scale, when prey are directly facing a predator or found cues of its presence, two immediate movement responses generally occur: fleeing or hiding (Stankowich 2008, Courbin et al. 2016). Previous studies have already studied these immediate responses of prey to natural or human predation (e.g. for zebras: Courbin et al. 2016 and red deer: Jeppesen 1987a, Sunde et al. 2009, Jarnemo and Wikenros 2014) and have shown that female red deer moved longer distances at a higher speed or changed their habitat use in response to hunters' presence. Yet, although the immediate movement responses to natural or human predation have been well documented, much less is known about the delayed effects (i.e. days after the disturbance in our study) of a drive hunt on red deer movement patterns (but see Sunde et al. 2009). It has been suggested that these immediate responses may have consequences on prey space use over several days after the predator–prey encounter (Courbin et al. 2016), but at a broader scale, spatial responses are much harder to detect (but see Jeppesen 1987a, Sunde et al. 2009, Marantz et al. 2016). Examples of remnant effects of hunting are provided by Jeppesen (1987a) who showed an increase in red deer movement patterns after they reacted to disturbance,

whereas Marantz et al. (2016) found evidence that white-tailed deer *Odocoileus virginianus* continued to decrease their total distance traveled (calculated over a two-day period) and to restrict their activities to a small area (i.e. smaller two-day range) during three days after the end of the hunting season. Finally, several studies have already assessed the role of the distance between the prey and the predator – or the source of disturbance – and the habitat on the magnitude of the immediate responses to natural predators (Liley and Creel 2007, Creel et al. 2014, Padié et al. 2015a), but very few have studied it in response to human predation and after the disturbance, over a larger temporal scale than the predator–prey encounter (i.e. the delayed responses).

Using GPS data collected on 91 female red deer in the National Hunting and Wildlife Reserve (NHWR) of La Petite Pierre (France), over a period of 14 years, we aimed at 1) characterizing the delayed movement responses of female red deer *Cervus elaphus* to hunters – their only predator in the area – after drive hunts and 2) understanding the main environmental determinants affecting the magnitude of these post-disturbance responses to hunting at the individual level. Since hunters can be perceived as predators, we hypothesized that red deer will change their movement patterns over several days after an exposure to a drive hunt (Frid and Dill 2002, Cromsigt et al. 2013). In this study, movement responses were described using a set of variables, which commonly reflect movement behaviours of female red deer. Based on previous studies, we expected female red deer to have a more alert behaviour after the drive hunt, resulting in higher movement speed (Jarnemo and Wikenros 2014). We also predicted that female red deer would either leave or increase their three-day home range in the subsequent days after a drive hunt, in response to hunting activities, in order to temporarily avoid the hunting area perceived as unsafe (Jeppesen 1987a, Sunde et al. 2009). Then, we studied the effects of two environmental factors on these post-disturbance responses: 1) the proximity to the hunting area and 2) topographic obstacles and vegetation cover. We expected that individuals close to the hunting area would exhibit stronger responses (i.e. higher speed and larger home range size after the drive hunt) than individuals located further away from the risk (Frid and Dill 2002). We also predicted that, since topographic obstacles or vegetation cover may obstruct prey detection or movements of hunters, they can reduce the risk perceived by animals at the time of the drive hunt (Mysterud and Ostbye 1999, Hebblewhite et al. 2005, Kauffman et al. 2007, Barja and Rosellini 2008), and thus the magnitude of the post-disturbance responses.

Material and methods

Study site and biological model

The study was conducted in the NHWR of La Petite Pierre (48°51′41″N, 7°19′15″E), located in northeastern France. The reserve is an unfenced 2670 ha forest area dominated by deciduous trees (mostly *Fagus sylvatica*) in the western part and by coniferous species (mostly *Pinus sylvestris* and

Abies alba) in the eastern part. It is located at a low elevation area of the Vosges mountain range, which rises up to 400 m a. s. l. The climate is continental with cool summers and mild winters (mean January and July temperatures of 1.4 and 19.6°C, respectively, data from Phalsbourg weather station, Météo France, from 2004 to 2017). Three ungulate species are present and mainly managed through hunting in the NHWR: wild boar, red deer and roe deer. The present study focuses on red deer, whose population abundance was estimated using spotlight counts (Garel et al. 2010 for details about abundance estimation) and reported in Supplementary material Appendix 1 Table A1 for the study period (2004–2018).

Regarding hunting practices on the study site, drive hunts are conducted once a week during the hunting season, from the end of October to the beginning of February (median of 12 hunting days per hunting season [first quartile: 12 – third quartile: 15] with one to four drive hunts per hunting day during the 2004–2018 period). For each drive hunt, the hunting area is defined as the area bounded by motionless shooters and traveled by beaters and dogs. The hunting effort consists of a median of 29 shooters per drive hunt [first quartile: 27 – third quartile: 33] standing on the periphery of the hunting area, 14 beaters [first quartile: 11 – third quartile: 16] – i.e. hunters who flush out the wild game in the hunting area and 6 dogs [first quartile: 5 – third quartile: 7] used by the beaters. The median hunting area is about 69 ha [first quartile: 56 – third quartile: 94] and is entirely explored by hunters during the drive hunt (Supplementary material Appendix 1 Table A1). An average of 34 (± 14) red deer have been shot every hunting season from 2004 to 2016.

Data collection

During the 2004–2018 period, 91 different female red deer were captured using either drive-netting or beet-baited live traps. The female red deer were then fitted with a GPS collar (Lotek Wireless, Ontario, Canada) and wore it for a year. The collars were set to record the individual location every two hours. We characterized the landscape structure by 1) vegetation cover using both geo-referenced aerial photographs captured in 2003, at 100 m resolution (BD ORTHO® IGN) and field observations (map actualization in 2012) and 2) topography based on a 20-m digital elevation model. We categorized the vegetation cover into different vegetation classes based on: 1) the level of detectability of an individual by hunters in a given vegetation class and 2) the possible functions (e.g. shelter, food) of a vegetation class for the animals during the hunting period. In the study site, we distinguished four vegetation classes: 'bush' for thickets and heavy bushes or bushes mixed with coppices, 'forest' for forests without understory or providing deer with weak protection, 'path' for lanes and track edges, which may also provide high food quality and facilitate both hunter movements and animal escape, and 'meadow' for open areas providing high quality forage. These different vegetation classes were chosen to represent a decreasing gradient of openness (bush < forest < path < meadow) and therefore a decrease in risk perception linked to an increase in vegetation cover.

Data processing

Eleven movement metrics commonly used in the literature (Table 1) were computed using both GPS and environmental data: animal speed (maximum SMa, mean SMe and standard deviation SSd), trajectory sinuosity (SI), 95% and 50% home range sizes (K95 and K50), Ford ratio (F = K50/K95, which reflects the concentration of activity within the home range, Ford 1983) and proportion of locations in forest (ForU), in bushes (BusU), along paths (PatU) and in meadow areas (GraU).

Then, we defined a 'hunting event' as the conjunction of the GPS monitoring of an animal and a drive hunt in the reserve. The tracked animal could be either within (direct hunting event) or outside the hunting area (indirect hunting event). Overall, 379 hunting events occurred during the 14 years of monitoring, based on the 91 individuals. We classified 26 of the 379 hunting events as direct hunting events. For each hunting event, we calculated the spatial metrics over a three-day period before and after the drive hunt, excluding the hunting day. We chose to use a time window of three days because it allows the use of an adequate number of locations to calculate each metric properly and avoid the overlap between periods of successive drive hunts (conducted every seven days). We defined the delayed response of each animal after a drive hunt for each metric as the following log ratio:

$$\text{Response} = \log\left(\frac{X_a}{X_b}\right) \tag{1}$$

where Response is the response value of metric X, X_b is the control value computed over a three-day period before the drive hunt and X_a is the value computed over a three-day period after the drive hunt, respectively. The log ratio equals 0 when no change in metric value is observed and is positive when the metric value is higher after the drive hunt and conversely.

Statistical analysis

Based on these data, we conducted a three-step analysis: 1) testing the overall significance of the delayed response of the eleven metrics using a multivariate analysis of variance (MANOVA), 2) extracting the most influential movement metrics, which best described the delayed effect of a drive hunt on the movement behaviour of animals, using a preliminary factorial analysis and 3) then, identifying the major environmental variables affecting these specific metrics based on linear mixed models. The first two steps were linked: the MANOVA tested the significance of any change in the movement behaviour of female red deer, while the factorial analysis provided additional information based on data visualisation regarding the most influential movement metrics and the direction of the change for each individual.

Delayed movement responses to direct hunting events
We first focused on the 26 direct hunting events as they were more likely to show a significant change in the spatial behaviour of individuals. Therefore, the following analyses

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Table 1. Definition of the movement variables used to characterize movement paths of female red deer in the NHWR of La Petite Pierre, France, 2004–2018. All the metrics were obtained using data from GPS collars (one location every two hours). Then, we calculated each variable over the three days preceding the hunting day and the three days following it.

Movement variable	Acronym	Description
Maximum speed (m s⁻¹)	SMa	maximum speed over the three-day period
Mean speed (m s⁻¹)	SMe	mean speed over the three-day period
Speed standard deviation (m s⁻¹)	SSd	speed standard deviation over the three-day period
Mean sinuosity	SI	cosine of the turning angle located between two successive GPS fixes over a two-hours period. Then we calculated the mean of the cosine values over the three-day period
95% three-day home range size (ha)	K95	estimation of the three-day home range size using fixed Kernel utilization distribution from the package adehabitatHR
50% three-day home range size (ha)	K50	estimation of the three-day core home range size using fixed Kernel method from the package adehabitatHR
Ford parameter	Fo	ratio (three-day home range size/three-day core home range size)
Forest use (%)	ForU	number of GPS fixes in forest patches divided by the total number of locations for the three-day period
Bush use (%)	BusU	number of locations in bush patches divided by the total number of locations for the three-day period
Path use (%)	PatU	number of locations on roadsides or paths divided by the total number of locations for the three-day period
Open area use (%)	GraU	number of GPS fixes in grassland patches divided by the total number of locations for the three-day period

tested the relevance of the chosen metrics and identified the best descriptors of red deer delayed responses to drive hunts. We performed a MANOVA on the 11 response metrics (Eq. 1) from the direct hunting events. More formally, we calculated the Wilks's λ to test whether the mean vector of response metrics differed significantly from a vector of zeros, assuming that these response metrics were distributed as a multivariate Gaussian distribution. This analysis allowed us to test the existence of an overall response of the animals to a direct hunting event, based on all movement metrics (Table 1).

Then, based on the same 26 direct hunting events, we designed a factorial analysis to identify a major axis of variation describing the changes in movement behaviour after the disturbance. Let X_1 and X_2 be the tables describing the values of the 11 movement metrics (columns) for each hunting event (rows) before and after the drive hunt, respectively. Each hunting event i is thus characterized by two points in the 11-dimensional metrics space: the i-th row of X_1 and X_2 define the position of the animal before and after the drive hunt, respectively. These two points define an 'effect vector' characterizing the effect of a drive hunt on the movement behaviour of the animal. The matrix $D = X_2 - X_1$ contains the coordinates of these vectors, which are recentred to have a common origin. We then performed a principal component analysis of this table D, which returned the direction that maximized, overall, the differences between the variables before and after the drive hunt (see Supplementary material Appendix 2 for additional details on this analysis).

Modulation of the delayed movement responses in relation to different levels of hunting disturbance

This preliminary exploratory factorial analysis, designed to identify the directions in the metrics space where the differences between before and after the drive hunt were maximized, revealed that both maximum speed and kernel three-day home range size were the best summary of the overall delayed response of the animal to the drive hunt. Therefore, we modelled the variation of these two

response metrics for all hunting events (including direct and indirect hunting events, n = 379) and tested the effects of 1) the proximity to the hunting area (Prox), 2) the size of the hunting area (HArea), 3) the topography between the individual and the hunting area (Top) and 4) the location of the individual in a refuge area at the beginning of the drive hunt (Bush) using linear mixed models. All these variables were included as fixed factors and the identities of both the animals and the drive hunts as random factors in the models.

We fitted our final model by backward elimination, starting with the model including all the candidate variables (i.e. both random and fixed effects) as follows:

$$
\begin{aligned}
\text{LogMetricAfter}_{i,j} = {} & \text{LogMetricBefore}_{i,j} + \mu \\
& + \alpha.\text{Prox}_{i,j} + \beta.\text{Prox}_{i,j}.\text{Bush}_{i,j} \\
& + \gamma.\text{HArea}_{i,j} + \delta.\text{Top}_{i,j} + u_i \\
& + v_j + \varepsilon_{i,j}
\end{aligned}
\tag{2}
$$

where $\text{LogMetricAfter}_{ij}$ is the logarithm of the variable of interest (either maximum speed or kernel three-day home range) after the drive hunt j and for the animal i; $\text{LogMetricBefore}_{i,j}$ is the logarithm of the same variable for the same animal before this drive hunt and is used as an offset; $X_{i,j}$ describes the value of a variable X (which can be either Prox, HArea or Top) for the hunting event implying animal i in the drive hunt j; μ is the intercept of the model; α is the effect of the proximity to the drive hunt on the response variable; β is the effect of the interaction between Prox and Bush (i.e. when the animal is both close to the drive hunt and in a refuge area); γ is the effect of the size of the hunting area; δ is the effect of the topography on the response variable; u_i is the random effect describing between-individual variation and v_j is the random effect describing the between-drive hunt variation; and $\varepsilon_{i,j}$ is the residual of the model. We suppose the random effects to be normally distributed: $u_i \sim N(0, \sigma_u^2)$ and $v_j \sim N(0, \sigma_v^2)$. Since the value of the logarithm of the variable of interest

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before the drive hunt is used as an offset in this model, the resulting model is mathematically equivalent to the model of the log ratio as defined in Eq. 1.

The proximity to the hunting area was computed using the following equation:

$$Prox = e^{-0.005.d} \tag{3}$$

With d the Euclidean distance in metres between the animal and the edge of the hunting area at the beginning of the drive hunt. This transformation accounts for the fact that a difference in quietness of two areas is not a linear function of the Euclidean distance (Nekola and White 1999). As field observations showed no anti-hunting response beyond 500 m, we chose the coefficient −0.005, so that Prox equals 1 for an actual Euclidean distance equal to 0 m, and approximately 0 for an actual Euclidean distance above 500 m. Top is a binary variable describing whether or not the animal was separated from the hunting area by a topographic obstacle (Mysterud and Ostbye 1999, Hebblewhite et al. 2005, Kauffman et al. 2007) at the beginning of the drive hunt. Top equals 1 when the animal was separated to the hunting area by an obstacle at least 100 m high or 0 otherwise. Finally, Bush can also take two values: 1 when the animal was located in dense cover areas (i.e. a rather inaccessible environment for the hunters) at the beginning of the drive hunt and 0 otherwise and was included as an interaction term with Prox.

We tested the removal of each fixed effect holding the same two random effects. We then selected the most parsimonious model using the Bayesian information criterion (Delattre et al. 2014), whereby the model with the lowest BIC score is selected. When the difference in BIC between two models was lower than two, we selected the most parsimonious model in terms of BIC score and discussed the other one. All analyses were performed in R ver. 3.4.2 (<www.r-project.org>) using the packages lme4 (Bates et al. 2015) and adehabitatHR (Calenge 2007).

Results

Delayed changes in movement behaviour in response to direct hunting events

A summarized overview of the metric values measured for the direct hunting events is given in Table 2. The MANOVA indicated that, overall, the 11 movement variables before hunting slightly differed from the ones after hunting (Wilks' $\lambda = 0.40$, df1 = 10, df2 = 16, p = 0.06). Then, based on the customized PCA, we observed a clear break in the decrease of the eigenvalues after the first one (PC1 accounted for 43% of the variation and PC2 for 16%), indicating that the first axis of this analysis accounted for the main structure in the data (Fig. 1a). The delayed spatial responses of female red deer to drive hunts could therefore be described by this dimension. This first axis was negatively correlated with speed parameters (standard deviation, mean and maximum), three-day home ranges and core areas, and the bush use (Fig. 1b). Being the most strongly correlated variables with the first axis of the PCA, maximum speed and three-day home range size best summarized the delayed effects of a drive hunt on red deer movement patterns and space use. In addition, among the 26 direct hunting events, 62% of the female red deer increased their three-day home range sizes and increased their speed (mean, maximum and standard deviation) after a drive hunt and 38% showed the opposite response (Fig. 1c).

Model selection

We now present our model results through inclusion/exclusion via the BIC and then the importance of each effect through effect sizes.

Response 1: variation in three-day home range size
Regarding the variation in three-day home range size (K95; Eq. 1), the model selection process resulted in the selection of three best models to explain this response metric since their ΔBIC are lower than 2 (Table 3). The three models described: 1) an increase in three-day K95 when the animal was located close to the hunting area (model 1, ΔBIC = 0),

Table 2. Range of the movement variables used to characterize movement paths of female red deer in the NHWR of La Petite Pierre, France, 2004–2018. All these metrics were obtained using data from GPS collars (one location every two hours). Mean values and standard deviations of the movement variables were then calculated for the 26 direct hunting events over the three days preceding the hunting day (before hunting) and the three days following it (after hunting), excluding the hunting day. Mean value as well as the standard deviation were computed for (a) each variable before hunting, (b) each variable after hunting, (c) the absolute difference (after–before) and (d) the log ratio (Eq. 1). The MANOVA analysis revealed that the log-ratios characterizing these variables were overall slightly different from 0 (Wilks' $\lambda = 0.40$, df1 = 10, df2 = 16, p = 0.06), suggesting a change in the mean value of these variables between the two periods.

| Movement variable	Before hunting	After hunting	Absolute difference	Log ratio
Maximum speed (m s⁻¹)	0.09 (±0.04)	0.12 (±0.08)	0.03 (±0.09)	0.18 (±0.77)
Mean speed (m s⁻¹)	0.02 (±0.01)	0.02 (±0.01)	0.004 (±0.01)	0.14 (±0.51)
Speed standard deviation (m s⁻¹)	0.02 (±0.01)	0.03 (±0.02)	0.007 (±0.02)	0.17 (±0.74)
Mean sinuosity	0.04 (±0.17)	0.07 (±0.14)	0.03 (±0.20)	0.03 (±0.20)
95% 3-day home range size (ha)	179 (±208)	335 (±495)	156 (±530)	0.46 (±1.27)
50% 3-day home range size (ha)	46 (±60)	74 (±129)	28 (±141)	0.30 (±1.26)
Ford parameter	4.24 (±0.70)	4.95 (±0.80)	0.71 (±1.16)	0.15 (±0.25)
Forest use (%)	46 (±24)	40 (±20)	−5.8 (±20)	−0.04 (±0.15)
Bush use (%)	39 (±26)	45 (±28)	5.5 (±28)	0.04 (±0.2)
Path use (%)	4.5 (±4.5)	3.9 (±4.2)	−0.7 (±6.1)	−0.01 (±0.06)
Open area use (%)	9.9 (±21)	11 (±16)	0.8 (±23)	0.01 (±0.17)

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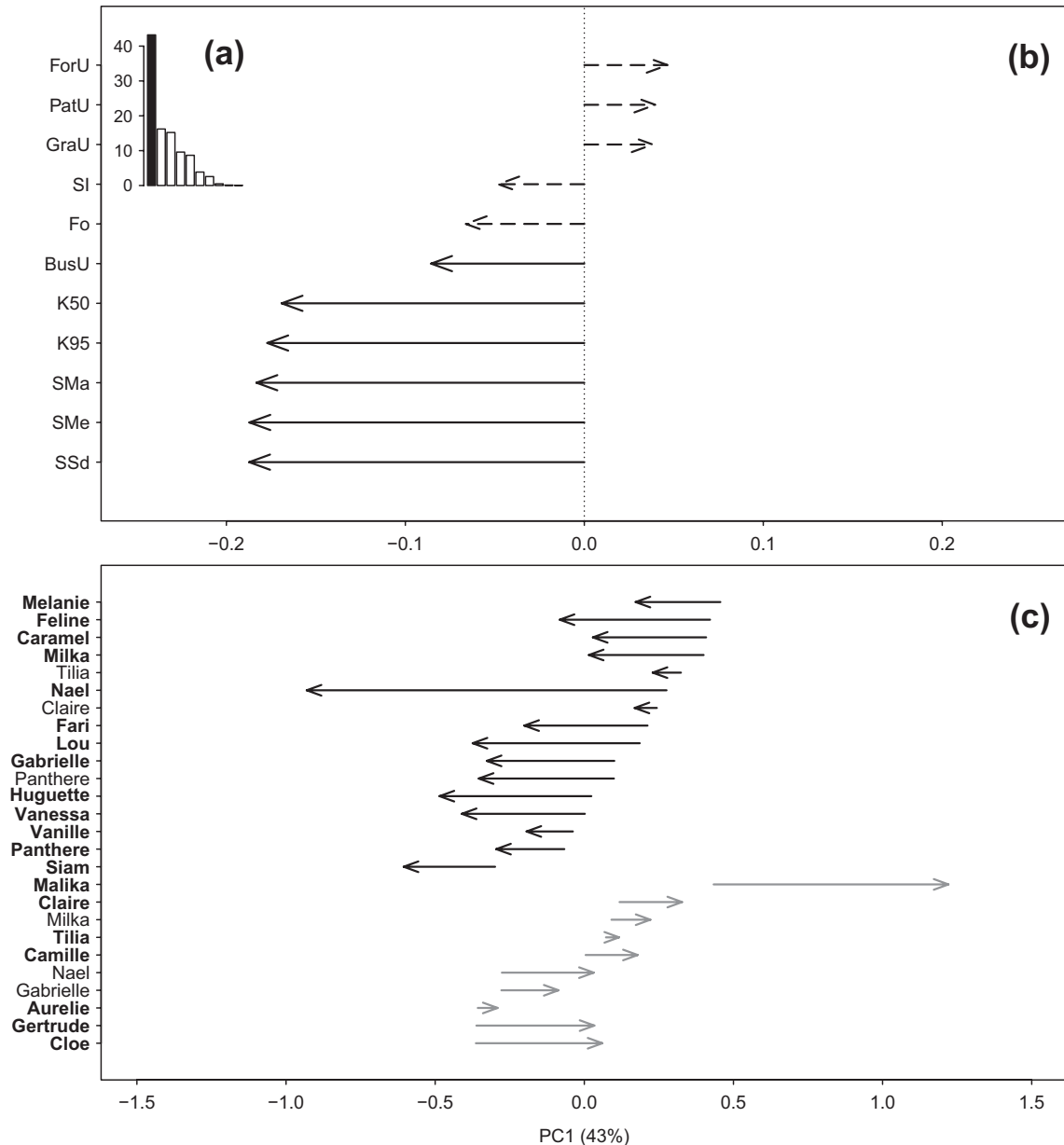
Figure 1. Principal component analysis performed to identify the effect of drive hunts on female red deer movement patterns in the NHWR of La Petite Pierre, France, 2004–2018. (a) Eigenvalues histogram displaying the amount of variation accounted for by each principal component. (b) Representation of the 11 movement variables' vectors along the first axis (black vertical bar in the histogram of eigenvalues). Vectors indicate the intensity and direction of each movement variable to the overall distribution of the hunting events. Solid arrows correspond to the variables that are significantly correlated with the first axis. The movement metrics are those described in Table 1. (c) Non recentred drive hunt effect vectors (n = 26 hunted animals) in the space defined by the spatial describers, along the first PCA axis. The basis of the vector corresponds to the score of the animal before the drive hunt and the top of the vector corresponds to the score of the animal after the drive hunt. Vectors indicate the intensity of the drive hunt effect and the variables that have changed the most in response to the drive hunt. Black arrows correspond to individuals characterized after the hunt by larger spatial describers and grey arrows correspond to individuals with the opposite characteristics. The individuals identified in bold have been located within a hunting area at the time of the drive hunt only once during a given hunting season.

2) an increase in three-day K95 when the animal was located within or close to the hunting area and outside a refuge area but no effect when the animal was inside a refuge area and close to the hunting area (model 2, ΔBIC = 1.84) and 3) no fixed effect (model 3, ΔBIC = 1.94; Table 3). On the other hand, we found little support for the role of topography and hunting area size on the response of three-day K95 (Table 3).

Response 2: variation in maximum speed
Similarly, we selected two models to explain the variation in maximum speed (SMa; Eq. 1): 1) the proximity fixed effect and its interaction with the refuge area fixed effect (model 1, ΔBIC = 0) and 2) three fixed effects: topography, proximity and its interaction with refuge areas (model 2, ΔBIC = 1.73; Table 3). Thus, the two models described an increase in maximum speed when the animal was located outside a refuge

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Table 3. Model selection among the set of candidate models exploring the effects of human hunting on changes in female red deer movement behaviour (quantified using three-day home range size (K95) and maximum speed (SMa)) between pre and post hunt in the NHWR of La Petite Pierre, France, 2004–2018. The model structure only described the fixed effects: 1) the proximity to the hunting area (Prox), 2) the size of the hunting zone (HArea), 3) the topography between the individual and the hunting area (Top) and 4) the presence/absence of the individual in a refuge area at the beginning of the drive hunt (Bush) on before/after changes in female red deer movement behaviour (R). All the models were fitted with two random effects: individual identity and the date of the drive hunt. The best model was then selected using Bayesian information criterion (BIC, bolded), $\Delta BIC = BIC - BIC_{min}$ for each model.

Model structure	Hypothesis	BIC K95	ΔBIC K95	BIC SMa	ΔBIC SMa
R ~ 1	Null model	1194.58	1.94	767.53	2.6
R ~ Prox	**Disturbance**	**1192.64**	**0**	767.68	2.75
R ~ HArea	Hunting effort	1200.34	7.7	773.46	8.53
R ~ Top	Topography	1199.33	6.69	770.64	5.71
R ~ Prox + HArea	Disturbance and hunting effort	1198.57	5.93	773.53	8.6
R ~ Prox + Top	Disturbance and topography	1196.28	3.64	769.34	4.41
R ~ Top + HArea	Topography and hunting effort	1205.11	12.47	776.57	11.64
R ~ Prox + Prox:Bush	**Disturbance and refuge areas**	1194.48	1.84	**764.93**	**0**
R ~ Prox + HArea + Prox:Bush	Hunting effort and refuge area	1200.39	7.75	770.74	5.81
R ~ Prox + Top + Prox:Bush	Topography and refuge area	1198.12	5.48	766.66	1.73
R ~ Prox + Top + HArea + Prox:Bush	Full model	1204.02	11.38	772.39	7.46

area and close to the hunting area and conversely, a decrease when the animal was separated from the hunting area by a topographic obstacle or located within a refuge area even if close to the hunting area.

A home range size increase in close proximity to the hunting area

The best model explaining the response of K95 only included the proximity fixed effect (Table 3). The response of three-day K95 was positively correlated with the proximity to the hunting area ($\alpha = 0.66$, SE $= 0.23$; Table 4). Thus, the closer the animal was to the hunting area, the larger its three-day home range would be after the hunt in comparison to the preceding days. Overall, nearly as many animals increased their three-day K95 between the two periods (before and after hunting) when they were located close to the hunting area (61%) as when they were located far away from it (i.e. >500 m; 52%). However, among these animals increasing their three-day K95 between the two periods, those located within or close to the hunting area (interquartile range of the three-day home range size ratio: [2.2–5.12]) showed a stronger response than the ones located further away from the hunting action (interquartile range: [1.28–2.8]). In addition, almost half of the animals showed the opposite response. This first model

appeared to be relatively simple, but the following ones may suggest more complex responses.

Increase in speed and home range size when the animal is close to the hunting area and outside a refuge area

One of the selected models explained the variation in both SMa and K95 with the proximity to the hunting area at the beginning of the drive hunt and its interaction with the presence/absence of the animal in a refuge area (Table 3). Therefore, the changes in SMa and K95 between pre and post hunt were positively correlated with the proximity effect for individuals located outside a refuge area at the beginning of the hunt (for this model, speed: $\alpha = 0.51$, SE $= 0.15$ and K95: $\alpha = 0.89$, SE $= 0.26$). However, in situations where the animal was located in a refuge area at the beginning of the drive hunt, the change in SMa was negatively correlated with the proximity (for this model, $\alpha + \beta = -0.34$, SE $= 0.28$), while the response of K95 was not affected (for this model, $\alpha + \beta = -0.15$, SE $= 0.45$; Table 4).

An effect of the topography on the maximum speed

Regarding SMa, in the second best model, the response was similar to the previous one: it was positively correlated with

Table 4. Estimated coefficients with their standard errors in the best models explaining the variations in female red deer movement behaviour (quantified using three-day home range size (K95 model 1, 2 and 3) and maximum speed (SMa model 1 and 2)) between pre and post hunt in the reserve of La Petite Pierre, France, 2004–2018. In addition to the two random effects, the three best models explaining the response of K95 included: 1) the effect of the proximity to the drive hunt, 2) the effect of the proximity to the drive hunt and its interaction with the refuge area and 3) any fixed effect. Similarly, two best models were selected for the SMa response, including: 1) the effect of the proximity to the drive hunt and its interaction with the refuge area and 2) the two previous fixed effect and the effect of the topography. The upper part of the table presents the estimates of the fixed effects (μ, α, β, γ, δ, Eq. 2) in the model (with their standard error) and the lower part presents the standard deviation (SD) of the random-effects (RE) included in the model, as well as the residual standard deviation.

Effects	K95 model 1	K95 model 2	K95 model 3	SMa model 1	SMa model 2
Intercept	$\mu = -0.08\ (\pm0.07)$	$\mu = -0.07\ (\pm0.07)$	$\mu = -0.01\ (\pm0.07)$	$\mu = -0.08\ (\pm0.04)$	$\mu = 0.10\ (\pm0.10)$
Proximity	$\alpha = 0.66\ (\pm0.23)$	$\alpha = 0.89\ (\pm0.26)$	–	$\alpha = 0.51\ (\pm0.15)$	$\alpha = 0.54\ (\pm0.15)$
Topography	–	–	–	–	$\delta = -0.21\ (\pm0.10)$
Proximity: Bush	–	$\beta = -1.04\ (\pm0.51)$	–	$\beta = -0.85\ (\pm0.28)$	$\beta = -0.83\ (\pm0.28)$
SD of Individual RE	0.15	0.12	0.14	0.01	6.2×10^{-8}
SD of Drive hunt RE	0.21	0.21	0.25	0.15	0.15
Residual SD	1.10	1.10	1.11	0.62	0.61

the proximity when the animal was located within a refuge area (for this model, $\alpha = 0.54$, SE = 0.15) and negatively correlated if the animal was located outside a refuge area at the beginning of the drive hunt (for this model, $\alpha + \beta = -0.29$, SE = 0.26; Table 4). However, this model also included a topographic fixed effect. Thus, animals separated from the hunting area by a topographic obstacle had a lower maximum speed response after the drive hunt as compared to before ($\delta = -0.21$, SE = 0.10; Table 4).

Individual heterogeneity in the behavioural response to hunting

Finally, the third model explaining the response of K95 included no fixed effect. This result highlighted the strong inter-individual and inter-drive hunt variability (Table 4). Indeed, the relationship between the two response metrics and the fixed effects in the previous models was very noisy: even our best model accounted for a small amount of the variation in these response metrics (K95: $R^2 = 0.02$; SMa: $R^2 = 0.04$), as well as the second one (K95: $R^2 = 0.03$; SMa: $R^2 = 0.05$), suggesting that other factors were involved in these changes. Therefore, both individual and drive hunt random effects appeared to explain a part of the observed variance in K95 and SMa. The model highlighted that response of individuals depended on drive hunt and differ markedly from one individual to another, as shown by the PCA (Fig. 1c).

Discussion

Our results showed that female red deer responded to human predation over a 72-h period after a drive hunt by an overall alteration in their movements. Overall, the perception of a human threat triggered an alteration of female red deer movements over several days after the disturbance. This response may reflect a strategy to avoid risk associated with hunting. We predicted that female red deer would increase movement speed and increase their three-day home range after a drive hunt due to a more alert behaviour and the need to avoid the hunting area perceived as unsafe. However, hunters appeared to induce two contrasting strategies: 1) lower movements in a restricted area, associated with a decreasing use of bush after the drive hunt and 2) an increase in speed, space exploration and bush use after the disturbance. These anti-predator strategies of game species are likely to result from individuals' characteristics or internal state, and surrounding conditions.

In our study, maximum speed and three-day home range size were used as markers of movement patterns and space use. We showed that the post-disturbance responses of female red deer are linearly related to the proximity of the danger area. Our prediction of stronger responses from the individuals located close to the hunting area was thus supported. The predation risk perceived by the red deer at the time of the drive hunt appears to modulate delayed responses and animals exposed to a direct risk of predation (i.e. in close proximity with hunters) increase their speed and their three-day home range size after the disturbance.

Most of the tracked individuals seemed to adjust their movement patterns over several days after a drive hunt proportionally with the level of risk perceived during the hunting event. This could be explained by the costs of anti-predator behaviours implying a tradeoff for the animals between anti-predator behaviour and any other vital activity (Lima and Dill 1990). Therefore, female red deer may be able to scan their environment using sensory cues in order to assess the human predation risk and properly respond to the situation. A few studies have already pointed out the role of risk assessment on the decision-making process and survival of a prey (Ydenberg and Dill 1986, Lima and Dill 1990) and more are needed to generalize these results, particularly in the context of human predation. Indeed, hunters differ from natural predators in terms of hunting mode, success rate, prey selectivity or sensory cues of their presence (Darimont et al. 2015). Therefore, we could expect both immediate and delayed anti-hunting responses of female red deer and natural predator–prey relationships to be different.

We also highlight the role of the vegetation cover on red deer delayed responses to hunting, discriminating two responses after the drive hunt: 1) lower movements when the animal is located within a refuge area and 2) higher speed in a larger area when the animal is located outside a dense cover area. Increase in maximum speed is generally interpreted as the result of flight responses. In our case, it suggests flight-type movements within the three-day period after a drive hunt, which could be due to a more alert behaviour after the drive hunt, resulting in higher movement speed (Jarnemo and Wikenros 2014). Similarly, a larger home range size during the hunting season has been explained by the need to temporary avoid or escape from hunters and explore more space to search for safer areas (Calenge et al. 2002, Davidson et al. 2011, Grignolio et al. 2011, Fattebert et al. 2017). At our three-day temporal scale, it may also reflect longer distance movements of the animals in a larger exploration area. These reaction patterns are consistent with previously described red deer delayed responses to hunting (Jeppesen 1987a, Sunde et al. 2009, Jarnemo and Wikenros 2014) and to natural predators (e.g. wolves: Proffitt et al. 2009). Indeed, past studies have shown that red deer experiencing a hunt flee away from the hunting area in the following days (Jeppesen 1987a, Sunde et al. 2009, Jarnemo and Wikenros 2014) towards refuges or alternative undisturbed feeding sites. Similar results have been found for other ungulates (e.g. for wild boar: Keuling et al. 2008, Scillitani et al. 2010) or other game species (e.g. for waterbirds: Madsen and Fox 1995, Fox and Madsen 1997). Conversely, reduced movements have also been described as an alternative delayed response to hunting developed by other deer species such as white-tailed deer (Marantz et al. 2016) or roe deer (Jeppesen 1987b). These response patterns can be explained by a more static behaviour used to minimize detection and contacts with hunters (Marantz et al. 2016).

Speed responses also appeared to be conditional on the topography. Therefore, our findings supported our prediction of reduced post-disturbance responses when animals are separated from the hunting area by a topographic obstacle. Several studies have already shown that landscape

features can affect the level of risk perception and consequently alter anti-predation responses (Hebblewhite et al. 2005, Kauffman et al. 2007, Barja and Rosellini 2008, Courbin et al. 2016). Indeed, topographic features are known to impact noise propagation: sound may be attenuated when reaching a hill (Embleton 1996), while it could propagate further across valleys (Piercy et al. 1977). A topographic obstacle may also obstruct prey detection and movements of hunters (Mysterud and Ostbye 1999).

Finally, the significant between drive hunt variability in our models also suggests that anti-hunting delayed responses of female red deer vary widely depending on hunting conditions. The number of hunters, beaters and dogs, as well as the size of the hunting area – which were not measured in our study – may affect the risk perceived by the animals and, therefore, their movement responses. Our results also suggest that anti-hunting delayed responses of female red deer differ from one individual to another. One of the sources of this variability appeared to be the presence/absence of the animal in a dense cover area during the hunting action. In addition, several studies have investigated risk management tactics depending on the individual's internal state (Beale and Monaghan 2004, Lea and Blumstein 2011, Bonnot et al. 2015, Padié et al. 2015b). The intensity of immediate responses to risk is linked to prey's sex (Stankowich and Blumstein 2005, Saïd et al. 2012), body condition (Beale and Monaghan 2004), previous risk exposure (Thurfjell et al. 2017) and personality (Bonnot et al. 2015). Thus, many factors are likely to be involved in red deer delayed responses to hunting and may also account for the large variability of individual responses we reported here.

Conclusion

This study brings new insights to the understanding of the delayed effects of a drive hunt on red deer movement patterns. Our results suggest that, over a 72-h period after a drive hunt, female red deer may adopt two strategies: 1) flight-type movements associated with more space explored due to a temporary avoidance of the disturbed area and 2) lower movements to avoid detection and contacts with hunters. These delayed responses are situation-specific and may be modulated by risk proximity, landscape features, hunting conditions and individual characteristics. Hunting for fear has been proposed as a management tool to reduce ungulate damage since it is supposed to reduce the fitness of animals through non-lethal effects. We showed that movement patterns of animals were altered over several days after a drive hunt, suggesting changes in the allocation of time and energy for their biological activities. Further investigations should now focus on determining the link between movement pattern alteration and individual fitness to properly test this hypothesis underlying the 'hunting for fear' theory.

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Supplementary material (available online as Appendix wlb-00545 at <www.wildlifebiology.org/appendix/wlb-00545>). Appendix 1–3.