

An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season



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Hunting by humans can be a potent driver of selection for morphological and life history traits in wildlife populations across continents and taxa. Few studies, however, have documented selection on behavioural responses that increase individual survival under human hunting pressure. Using habitat with dense concealing cover is a common strategy for risk avoidance, with a higher chance of survival being the payoff. At the same time, risk avoidance can be costly in terms of missed foraging opportunities. We investigated individual fine-scale use of habitat by 40 GPS-marked European red deer, *Cervus elaphus*, and linked this to their survival through the hunting season. Whereas all males used similar habitat in the days 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. This habitat switch also involved a trade-off with foraging opportunities on bilberry, *Vaccinium myrtillus*, a key forage plant in autumn. Moreover, deer that use safer forest habitat might survive better because they make safer choices in general. The lack of a corresponding pattern in females might be because females were already largely using cover when hunting started, as predicted by sexual segregation theory and the risk of losing offspring. The behavioural response of males to the onset of hunting appears to be adaptive, given that it is linked to increased survival, an important fitness component. We suggest that predictable harvesting regimes with high harvest rates could create a strong selective pressure for deer to respond dynamically to the temporal change in hunting risk. Management should consider the potential for both ecological and evolutionary consequences of harvesting regimes on behaviour.

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Harvesting by humans is a major source of mortality and a potent force of 'unnatural' selection in many wildlife populations (Darimont et al., 2009). The pattern of mortality from harvesting is rarely random and often differs from patterns of natural mortality (Allendorf & Hard, 2009). Thus, recently, there has been much interest in potential evolutionary effects of harvesting on life history attributes and morphological traits such as horns, antlers and body size (Allendorf & Hard, 2009; Festa-Bianchet, 2003). Systems dominated by human harvesting outpace systems dominated by natural selection or other anthropogenic agents in the rate of phenotypic change (Darimont et al., 2009). Harvested populations have shown substantial alteration of morphological and life history traits with net documented changes in these types of traits

averaging 18% and 25%, respectively (Darimont et al., 2009). Yet, distinguishing between ecological and evolutionary causes is neither a trivial nor a simple matter (Bunnefeld & Keane, 2014; Fenberg & Roy, 2008) and, in one recent study, demographic changes resulting from hunting explained observed phenotypic changes that were earlier attributed to evolution (Traill, Schindler, & Coulson, 2014). Still, potential evolutionary impacts of harvesting deserve consideration in applied management and conservation efforts, not least because they can be difficult to reverse (Bunnefeld & Keane, 2014; Coltman et al., 2003; Darimont et al., 2009; Fenberg & Roy, 2008). 'Unnatural' selection from hunting can potentially also affect heritable behavioural traits (Allendorf & Hard, 2009), but there is still limited knowledge of the link between harvesting by humans and animal behaviour.

Behavioural responses to human or natural predators are widespread, diverse and generally carry some cost (Lima & Dill, 1990; Peacor, Peckarsky, Trussell, & Vonesh, 2013). One widespread response to reduce predation risk is to shift habitat use away from

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areas with high predation risk (Creel, Winnie Jr, Maxwell, Hamlin, & Creel, 2005; Valeix et al., 2009). Across a range of taxa, such a habitat shift involves a trade-off between access to resources and safety (Breviglieri, Piccoli, Uieda, & Romero, 2013; Embar, Raveh, Burns, & Kotler, 2014; Heithaus, Wirsing, Burkholder, Thomson, & Dill, 2009; Nonacs & Dill, 1990). A typical situation for large grazing mammals is that individuals have to choose between open habitats with good foraging opportunities, but where they are visible to predators, and habitats that provide more cover from potential dangers but which might limit foraging efficiency (Godvik et al., 2009; Werner, Gilliam, Hall, & Mittelbach, 1983). Individuals can differ substantially in how they respond to such a trade-off (Bonnot et al., 2014). The shy–bold continuum is one of the most studied personality axes in animals and characterizes inherent tendencies in how an individual responds to novelty, innovation and risk taking (Quinn & Cresswell, 2005; Wolf & Weissing, 2012). Nevertheless, there has been less focus on individual differences in behaviour and trade-offs in situations in which humans are the predator (Ciuti et al., 2012; Madden & Whiteside, 2014).

Risk varies in space and time, and studies should ideally incorporate both elements (Creel, Winnie Jr, Christianson, & Liley, 2008; Latombe, Fortin, & Parrott, 2014). Prey responses can be constant (also called 'chronic' in the terminology of Latombe et al., 2014; e.g. as assumed in Laundré, Hernández, & Ripplé, 2010), or temporary, varying at characteristic spatiotemporal scales in response to cues (Latombe et al., 2014; Valeix et al., 2009). North American wapiti, *Cervus elaphus canadensis*, respond to wolf, *Canis lupus*, predation by a combination of constant and temporary responses at different scales (Latombe et al., 2014). Whether animals tend to respond constantly or temporarily, and at what temporal and spatial scales, depends on the context, with the costs and benefits of alternative strategies varying with factors such as predator mobility, resource needs, risk patterns and the ability of prey to assess risk reliably (Brirot, Bateson, Nettle, Whittingham, & Read, 2012; Lima & Bednekoff, 1999; Lone et al., 2014). A constant response could be favoured if prey have incomplete knowledge of the whereabouts of predators or if switching between behaviours is costly or simply not feasible. Conversely, if risk varies strongly at certain timescales (such as between seasons or between day and night), temporary behavioural responses during high-risk periods could be favoured. Hunting by humans is often strongly structured temporally (Cromsigt et al., 2013), and can elicit behavioural shifts in game species between the open and closed hunting seasons (Proffitt et al., 2010; Tolon et al., 2009). Nevertheless, although hunting is an ideal and controlled way to test for dynamic responses, few

studies have examined immediate responses to the onset of the hunting season (Ciuti et al., 2012; Ordiz et al., 2012).

By definition, antipredator behaviour should be effective in reducing mortality, but few empirical studies have explicitly linked individual behaviour with survival (DeCesare et al., 2014; Leclerc, Dussault, & St-Laurent, 2014; Van Moorter et al., 2009). Previous studies have found that higher hunting pressure and hunter accessibility negatively affect wapiti survival at the scale of seasonal home ranges, but that there are no significant associations between cover and survival at this scale (McCorquodale, Wiseman, & Marcum, 2003; Unsworth, Kuck, Scott, & Garton, 1993). Nor are there significant associations between wapiti survival and the amount of cover at the scale of weekly home ranges (Webb et al., 2011). In contrast, a finer-scale analysis has revealed that bold wapiti individuals, with higher rates of movement, weaker response to human activity and greater use of open terrain, are more likely to be harvested than shy individuals (Ciuti et al., 2012).

To determine whether and how behaviour influences hunting season survival, and to identify potential trade-offs, we investigated habitat use by European red deer, *Cervus elaphus elaphus*, at spatial and temporal scales likely to shape their responses to hunting. Red deer populations in central Norway occur at high densities and are heavily hunted by humans; there are no other major predators present (Langvatn & Loison, 1999). We compared the use of fine-scale cover and forage habitat between 10 surviving and 10 shot deer of each sex shortly before and soon after the onset of the hunting season. We tested four competing hypotheses (Table 1) to identify whether individual differences in habitat use affect survival (H2, H3 or H4), whether deer respond dynamically to the onset of the hunting season (H1, H3 or H4) and whether the strength of these dynamic responses influences survival (H4). We expected differences in the use of cover because it presents a gradient of risk, and differences in the use of forage habitat as this would arise from spatial behaviour that traded off the risk of mortality against access to food.

METHODS

Ethical Note

Permits to capture and mark animals were granted by the Norwegian Animal Research Authority (NARA; ref no. s-2006/28799; permit no. FOTS ID 4863), and the Norwegian Environment Agency (ref no. 2006/5393). Three veterinarians, assisted by eight other field personnel approved by NARA, marked the animals. Animals were

Table 1
Null and alternative hypotheses relating the fate of red deer during the hunting season to their risk avoidance behaviour, along with associated predictions about the individuals' habitat use with respect to sighting distance (and the inverse pattern expected for concealing cover) and forage availability (forage opportunities forgone, a potential cost of responding spatially to predation)

Alternative hypotheses	Temporal pattern	Pattern of survivors vs shot individuals	Model structure
<i>H0: No response to onset of the hunting season and survivors and shot individuals use habitat with the same characteristics</i>	<i>No</i>	<i>No</i>	<i>-1 (intercept only)</i>
<i>H1: Dynamic response to onset of the hunting season that either is exhibited by all animals equally or does not affect survival</i>	<i>Yes, decreasing</i>	<i>No</i>	<i>Period</i>
<i>H2: No dynamic response to onset of the hunting season, but individual differences in habitat use affect survival</i>	<i>No</i>	<i>Survivors have lower mean values than shot animals</i>	<i>Fate</i>
<i>H3: All individuals respond dynamically to the onset of hunting, but survival is determined by pre-existing and ongoing individual differences</i>	<i>Yes, decreasing by similar amounts for both groups</i>	<i>Survivors have lower mean values than shot animals</i>	<i>Period+Fate</i>
H4: Individuals differ in their dynamic response to the onset of hunting, and the strength of this response influences survival	Yes, decreasing by different amounts	Survivors respond more strongly than shot animals	Period×Fate

The males in our study were found to conform to the model in bold and the females to the model in italics.

captured under cover of darkness using spot lights at feeding sites from January to early April each year. Deer were immobilized by dart injection of xylazine–tiletamine–zolazepam from a distance of 10–30 m, in accordance with standard procedures (Sente et al., 2014). When animals were recumbent, they were approached slowly, blindfolded and kept lying down. The main physiological side-effects of immobilization were mild hypoxemia and hypercapnia. Animals were closely monitored during immobilization and through recovery (12 ± 7 min) after drug reversal with atipamezole (Sente et al., 2014). Of the 132 captures, there were two capture-related mortalities. One female died within a few days of marking and one male became asphyxiated during weighing, after which safer specialized weighing equipment was developed and used to avoid a recurrence. All animals were marked with ear tags (Allflex Super Maxi Tag, 75×97 mm, Allflex, Denmark) in one ear, and were fitted with GPS collars suitable for red deer females and males, respectively (Tellus from Followit, Sweden, and GPS ProLite from Vectronic, Germany; collar weight: ca. 850 g, 0.5–1.0% of animal body weight). Collars were set to provide one location every hour for up to 2 years and most collars supported wireless download of data over the GSM telecommunications network, thus not requiring collar recovery. None the less, many collars had the capacity to drop off when data collection ended. Two collars malfunctioned at the time of deployment, and some others stopped collecting data prematurely. Animals whose collars were not designed to drop off or that malfunctioned or stopped working were recaptured whenever possible to remove the collars. These animals were either shot as normal during the hunting season, shot during winter (under special

permit from municipalities), or recaptured by darting at a feeding site during winter. This collar retrieval could take between 1 and 4 years, and some collared deer were never recovered. The collars caused minor hair loss or slight chafing around the neck in some deer, but no severe adverse effects of the tags or collars were observed during the study.

Study Area

The study was carried out on a partially migratory population of red deer in central Norway ($62^{\circ}36'–63^{\circ}30'N$, $8^{\circ}48'–10^{\circ}6'E$). The study area was approximately 6000 km² and included coastal to inland areas with diverse topography, land use and cover (Fig. 1). The landscape included agricultural areas in the valleys, but was dominated by forested and montane areas. Natural forests that were not intensively managed, but in which some harvesting occurred, were dominated either by deciduous species (mainly *Betula pubescens*, *Betula pendula*, *Salix caprea*, *Alnus incana*, *Alnus glutinosa* and *Sorbus aucuparia*) or by Scots pine, *Pinus sylvestris*. Dense plantations of Norway spruce, *Picea abies*, were scattered across the study area. The patchy mixtures of dense spruce plantations and other forest types of varying age and density of understory created strong heterogeneity in sighting distance within the forests.

Red Deer Population

Absolute density estimates were not available, but from hunting statistics we know that, on average across the study area, 6.2

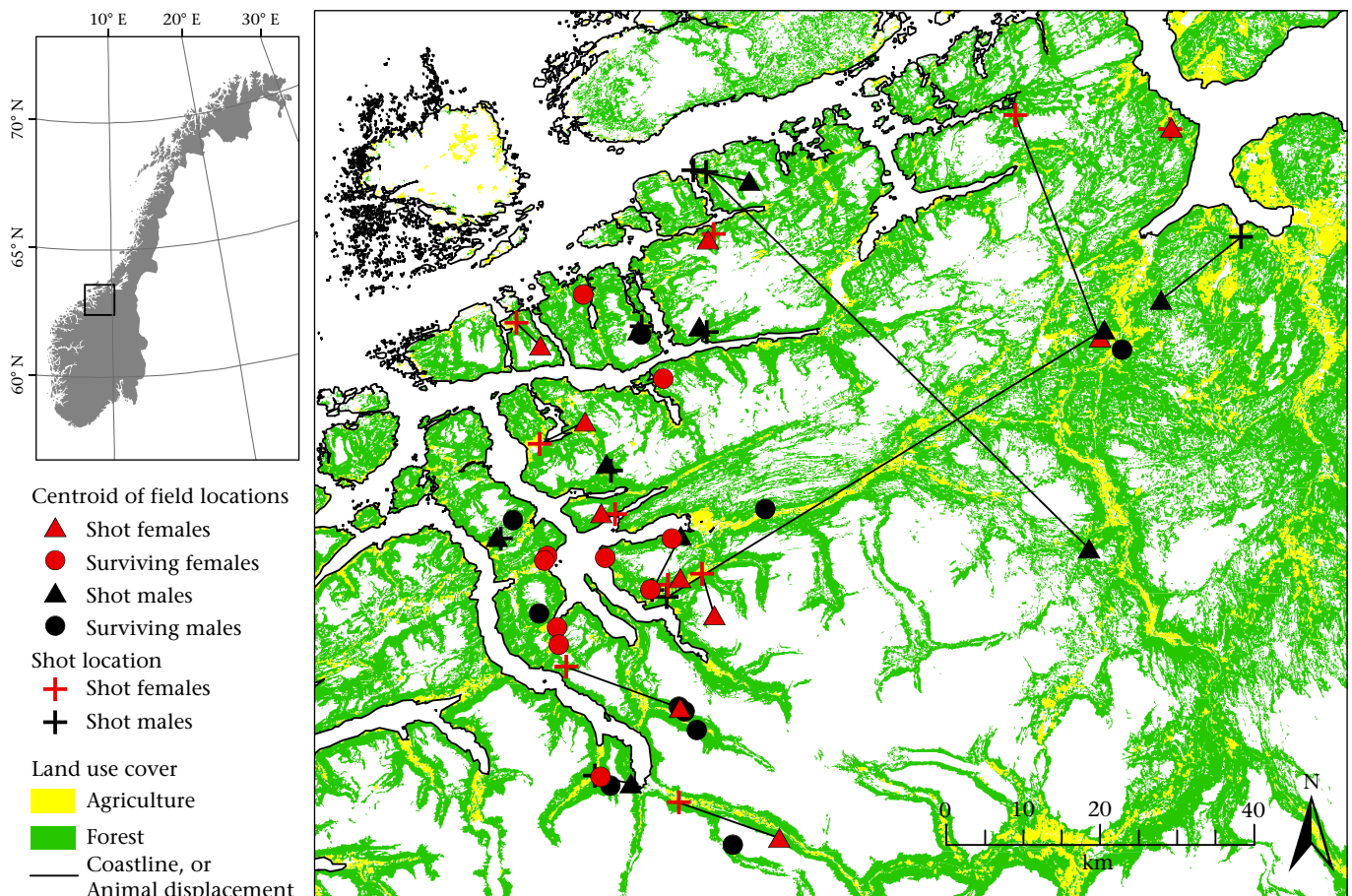


Figure 1. Study area and spatial distribution of studied red deer (centroid position of the 12 field plots for each individual). Black lines connect the centroids of the field plots with the location where each individual was shot. In some cases, deer were shot close to the areas used at the onset of hunting; in other cases they were shot some distance away.

deer were harvested annually per 10 km² during the study period (Statistics Norway, 2014). Red deer are the dominant large mammal in the region. Their primary habitat is forest, but they also use agricultural areas intensively for foraging, mainly at night (Godvik et al., 2009). Red deer associate in small matrilineal family groups (two to seven individuals) during most of the year, whereas juvenile and older males are generally solitary (Bonenfant et al., 2004). During the rutting season, however, animals form mixed-sex groups and males compete for the right to defend a harem of females. Males defend a group of females and not a territory. Young or otherwise subordinate males are typically found near the harems and are, on occasion, able to secure a mating undetected by the dominant male (Clutton-Brock, Guinness, & Albon, 1982). In winter, deer occur in larger groups because they congregate at food sources. The hunting season coincides with the rutting season, which peaks in early to mid-October (Loe et al., 2005). The rutting season begins gradually. The sexes generally start associating around 19 September (95% CI: 14–23 September), with the earliest roaring male being heard on 17 September (305 instances of roaring males across 16 years: Loe et al., 2005). Females that are 2 years or older typically reproduce every year (Langvatn, Bakke, & Engen, 1994; Langvatn, Mysterud, Stenseth, & Yoccoz, 2004). The migratory segment of the population move between their summer and winter ranges at some point during the hunting season, usually in September (Mysterud, Loe, Meisingset, et al., 2011).

Hunting Regime

Hunters hunt for meat and recreation rather than for trophies (Milner et al., 2006); offtake is limited by locally set age- and sex-specific quotas (Andersen, Lund, Solberg, & Saether, 2010). Harvest mortality has been strongly male biased for many years (1977–1995), with the risk of mortality to males increasing slightly during the 1980s, before stabilizing in the 1990s (Langvatn & Loison, 1999). Recent cohort modelling of data from three areas in Norway (one of them within our study area) confirmed this pattern and quantified the annual mortality risk from harvesting to be around 45% for adult males (≥ 2 years old) and around 15% for adult females (Veiberg, Nilsen, & Ueno, 2010). The strong male bias contrasts with harvesting practices in the rest of Europe, where there is generally low or no sex bias, and, if anything, a slight female bias (Milner et al., 2006). Note, however, that females typically have a calf at heel, and calves are also targeted by hunters (annual mortality risk around 15%; Veiberg et al., 2010). For several decades up until 2011, the hunting season started on 10 September, but in 2012 it was advanced to 1 September. During our study (2007–2012), the hunting season was open until 23 December. Deer are harvested throughout, but there is a strong burst of hunting activity when the season opens, with around 27% of all animals being shot during the first week (www.hjorteviltregisteret.no). Both adult males and females are targeted with similar percentages of the total harvest for each sex, 23% and 26%, respectively, being taken during the first week. Hunters access all parts of the red deer's habitat and use a variety of hunting methods (stand hunting, still hunting, call hunting and drive hunting with and without dogs) to target all ages and sexes, although call hunting is used mainly for males during the rutting season and comprises a small percentage of the total harvest. Although open agricultural land makes up only a small proportion of the landscape, it is the riskiest per unit area, with around 50% of all hunting mortality occurring there (Rivrud, 2013). Hunting occurs around the clock, with distinct peaks during twilight hours at dusk and dawn. Night hunting is only undertaken during strong moonlight. All hunting is done with rifles, requiring a free line of sight between the hunter and the animal.

The spatial distribution of risk should thus be directly related to vegetation density and sighting distance.

During the study, hunters and local residents were informed that there were no restrictions on harvesting marked deer. In other populations, harvest rates of radiocollared deer were found to be representative of the population, despite differing hunter attitudes towards shooting radiocollared animals (Buderman, Diefenbach, Rosenberry, Wallingford, & Long, 2014). We therefore assume that marked deer were subject to a similar pattern of risk as unmarked deer, and because we compared only marked animals, any slight bias would probably be similar among them. Nevertheless, any discrimination against marked animals should favour the survival of marked deer in open areas, where they can be observed for longer and the collar noticed. A tendency to move in groups could cause the same pattern, because marked deer could be spared at the expense of another group member in open environments, whereas in denser forest a hunter might not even realize that the deer is a member of a group. Neither of the two potential sources of bias would predict a lower probability of an individual being shot when using denser habitat. On the contrary, both these relationships could be expected to weaken (or reverse) the predicted relationship between sighting distance and survival hypothesized in Table 1. Because we predicted the opposite patterns to those expected from hunter bias, our analysis is therefore a conservative test of the hypotheses about how individual behaviour influences survival. Furthermore, it is difficult to see how this potential hunting bias could account for the predicted shift to using habitat with denser cover once hunting begins.

GPS-tracking Data and Selection of Animals

This study is based on an existing data set of 130 GPS-collared red deer (82 females, 48 males) marked and monitored during 2007–2012 in Møre-og Romsdal and Sør-Trøndelag counties in central Norway (Bischof et al., 2012; Mysterud, Loe, Zimmermann, et al., 2011). Hourly GPS position data were screened for outliers visually and with an automated technique based on movement characteristics (Bjørneraas, Moorter, Rolandsen, & Herfindal, 2010), removing less than 0.05% of the locations. Median location error had earlier been calculated to be 12 m (Godvik et al., 2009). Limited by logistics and time, we restricted field investigations to locations from 40 adult deer (≥ 2.5 years old) with sufficiently complete track logs during the period of interest and known either to have been shot by hunters or to have survived the entire hunting season. We chose 10 animals of each sex and fate because a balanced sampling design maximizes the statistical power for a given sample size. Further details of how these animals were selected and what efforts were taken to avoid biases in this are given in Appendix 1. The estimated ages of shot and surviving deer were similar (female means 6.8 and 5.2 years, respectively, unpaired t test: $t_{18} = 1.43$, $P = 0.17$; male means 4.2 and 4.9 years, respectively, unpaired t test: $t_{18} = 0.66$, $P = 0.52$). Age is closely connected to social status in males; thus there is no indication of any systematic differences in social status between shot and surviving males. Shooting dates for the females ranged from 24 September to 11 December with a mean date of 8 November; shooting dates for the males ranged from 25 September to 15 November (mean date: 15 October).

Study Design

We compared habitat use between 10 surviving and 10 shot deer of each sex in a short period around the start of the hunting season. For each individual, we surveyed the habitat at six locations it had visited before, and six locations it had visited after the onset of the hunting season. The 12 locations for each animal were

selected as follows. We sampled the last Monday–Wednesday (3 days) before the hunt started ('before onset', 1–9 days before the onset, depending on the year concerned), and the first Monday–Wednesday after the first weekend of the hunting season ('after onset', 2–8 days after onset), so we could expect some hunting to have taken place in all hunting areas. The sample periods were selected to be as close together in time as possible (consecutive weeks for two-thirds of the animals) to identify immediate responses and to minimize any confounding effect of season on our results. Importantly, all points were sampled before the rutting season so any change in habitat use could not be attributable to rutting activities rather than behavioural responses to hunters.

Within each sampled day two positions were selected: the first position after sunrise and the last position before sunset, times when deer are expected to be active and the light levels are sufficient for hunting. We restricted the locations to two times of day to ensure that the deer had moved some distance between the positions and to avoid diurnal patterns in habitat use inflating the variance when comparing shot and surviving animals. Our data do not show habitat use throughout the 3-month hunting season, but are a snapshot of what happens at the start of the hunting season in early- to mid-September. Locations on pastures were excluded so as to focus on within-forest variation in habitat use. The use of different habitat types by red deer has been contrasted in other studies (Godvik et al., 2009). Gaps in the GPS track logs and the exclusion of pasture locations (initially thought to be in forest, based on GIS maps) caused some individuals to be represented by fewer than 12 but never fewer than 10 locations. The final data set consisted of 458 surveyed deer locations. Only two of the females and five of the males in our study were shot in forest; the remaining eight females and five males were shot on agricultural land (based on locations reported by hunters and GIS maps).

Habitat Surveys

To characterize the habitats used by deer before and after the onset of hunting, we surveyed habitat cover and forage availability at the deer locations between 18 June and 20 August 2013. An individual had used a given location up to 6 years prior to the habitat survey (Table A1), but the habitats were likely to have remained similar throughout this period. In the field we evaluated whether any changes in habitat state had occurred since the year when the animal used that location, for example tree harvests, avalanches, recent drought or successional stages or young plantations likely to have grown radically in a few years, but did not find grounds for excluding any plots. We measured the distance at which a cover board 30 cm wide and 80 cm high could be sighted in all four cardinal directions at a single point at the GPS location; the mean value reflected the visual screening provided by cover at the plot as a function of topography and vegetation (Lone et al., 2014). A concave densiometer was used to estimate the proportional canopy cover directly above the plot, as an average of four measurements in the cardinal directions. Available forage was characterized in three 2 × 2 m quadrats located 10 m apart. Percentage ground cover was calculated as the mean of the three quadrats for each of three functional groups, the three potentially important forage resources for red deer in September: grasses, herbs and the ericoid species bilberry, *Vaccinium myrtillus*. Of these, bilberry has the highest quality this late in the growing season (Albon & Langvatn, 1992).

Statistical Analysis

We modelled these field-measured habitat characteristics as responses to the crossed effects of fate (shot or surviving) and

period (before or after the onset of hunting) in a linear mixed model with a random intercept for animal identity. This was to identify the relationship between survival and habitat use, and to test for expected differences between deer that were shot and those that survived, including different temporal patterns (Table 1). Separate mixed models were constructed for each sex for each of the response variables: (1) sighting distance of cover board, (2) canopy cover and forage availability measured as percentage cumulative cover of (3) grasses, herbs and bilberry, (4) grasses and herbs, or (5) bilberry alone. Because preliminary data analysis showed that males and females differed in their responses, we chose to analyse male and female data separately so the alternative scenarios could be tested for each sex. All proportions were arcsine square-root transformed and sighting distance was log transformed to meet the assumption of a homogeneous and normal error structure when modelled using the function lme from the package nlme (Pinheiro, 2014) in the software R 2.14.1 (R Development Core Team, 2011). For each response variable, the five candidate models corresponding to the alternative scenarios in Table 1 were compared on the basis of Akaike's information criterion, AIC (Burnham & Anderson, 2002). All models with $\Delta AIC \leq 2$ and lower AIC than simpler nested models (thereby avoiding uninformative parameters) were considered to have some support (Arnold, 2010). We report Ω^2 and Ω_0^2 as measures of explained variation by the fixed effects and fixed and random effects, respectively (Xu, 2003). They give the proportional reduction in residual sum of squares of the model compared with the residual sum of squares of a null model that included only random effects (Ω^2) or a fixed intercept (Ω_0^2).

RESULTS

The best models, based on AIC, differed for males and females (Table 2). With respect to habitat openness and forage availability, the contrast between survivors and shot individuals was in line with H4 for males (Table 1). Hypothesis H4 states that there are individual differences in the dynamic response to the onset of hunting, and the strength of this response influences survival. The males that ultimately survived the hunting season had shifted to using areas with 29% shorter sighting distances after the onset of hunting compared with those used before the hunt, whereas the males that were shot during the hunting season did not change their use of concealing cover (Table 3, Fig. 2a). The male patterns were also similar when the analysis was run using only individuals shot in forests or on agricultural land, and were actually stronger when considering only the males shot on agricultural land. In males, there was support for the hypothesis of a trade-off between forage availability and survival (Table 2). In line with H4, surviving

Table 2
Summary of ΔAIC values for the candidate models fitted to male and female data

Model	df	Sighting distance	Canopy cover	Grasses and herbs	Grasses, herbs and bilberry	Bilberry
Males						
~1	3	12.6	1.9	0.2	2.3	9.3
Period	4	6.0	0.0	0.0	4.0	3.5
Fate	4	12.5	3.9	2.2	4.1	10.4
Period+Fate	5	5.9	2.0	2.0	5.8	4.5
Period×Fate	6	0.0	1.8	1.2	0.0	0.0
Females						
~1	3	0.2	0.4	0.0	0.0	0.0
Period	4	2.2	2.8	2.0	2.0	1.4
Fate	4	0.0	0.0	2.0	1.8	2.0
Period+Fate	5	1.9	2.0	3.9	3.8	3.3
Period×Fate	6	3.4	3.3	3.3	4.5	5.3

Models with $\Delta AIC \leq 2$ without uninformative parameters are shown in bold.

Table 3
Parameter estimates from the best models relating red deer use of cover and forage (cover of grasses (G), herbs (H) and/or bilberry (B)) to hunting season fate and time period (before and after the onset of hunting)

Sex	Response	Fixed effect	Estimate	SE	Ω^2	Ω_0^2	Random intercept SD	Residual SD
Male	Sighting distance	(Intercept)	0.19	0.20	0.07	0.36	0.51	0.83
		Survive vs shot	-0.04	0.28				
		After vs before	-0.02	0.16				
		Survive vs shot: After vs before	-0.62	0.22				
Male	Canopy cover ^a	(Intercept)	-0.11	0.15	0.02	0.39	0.58	0.81
		After vs before	0.21	0.11				
Male	G+H ^a	(Intercept)	-0.08	0.15	0.01	0.36	0.56	0.83
		After vs before	0.16	0.11				
Male	G+H+B	(Intercept)	-0.11	0.17	0.04	0.19	0.36	0.93
		Survive vs shot	0.28	0.24				
		After vs before	0.28	0.18				
		Survive vs shot: After vs before	-0.69	0.25				
Male	Bilberry	(Intercept)	0.13	0.19	0.07	0.31	0.47	0.86
		Survive vs shot	0.08	0.27				
		After vs before	-0.03	0.16				
		Survive vs shot: After vs before	-0.59	0.23				
Female	Sighting distance ^a	(Intercept)	-0.21	0.20	0.000	0.38	0.57	0.81
		Survive vs shot	0.40	0.28				
Female	Canopy cover ^a	(Intercept)	-0.19	0.18	0.000	0.32	0.51	0.85
		Survive vs shot	0.39	0.26				

Response variables were arcsine transformed (except sighting distance, which was log-transformed) and standardized for each analysis. In cases where null models (intercept only) were selected as the best model, parameter estimates are not shown (female forage models).

^a Best models with only limited support as they were within 2 AIC units of the null model.

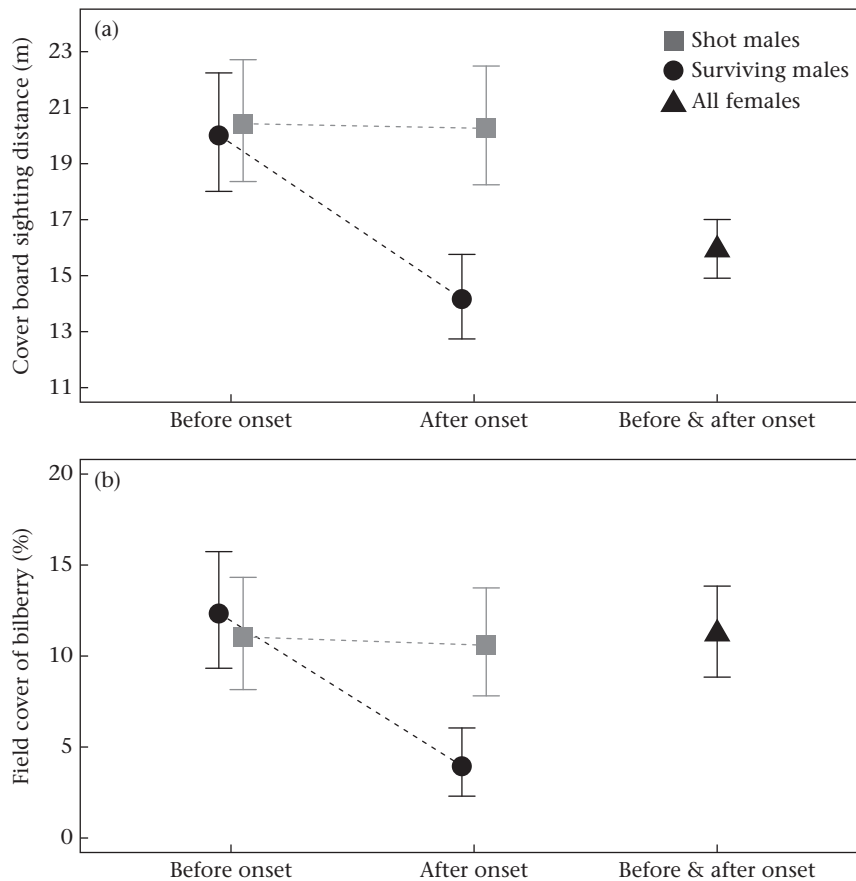


Figure 2. Red deer use of (a) cover and (b) forage habitat depending on sex, individual fate at the end of the hunting season (shot versus surviving) and time (immediately before and/or after the onset of the hunting season). Fitted estimates of cover board sighting distance \pm SE and field-layer cover of bilberry \pm SE from the best models for males and females as identified by AIC.

males switched to areas with 68% less bilberry cover after the onset of the hunting season compared with the pre-hunting season, and in contrast to shot males (Fig. 2b). Lower bilberry cover was the main contributor to the reduced cover of grasses, herbs and bilberry

combined in habitats used by surviving males (Table 3, Fig. A1). Neither canopy cover nor the cover of grasses and herbs alone differed statistically between sites used by shot and surviving deer (Table 2). The patterns identified are also visible in the raw data

despite wide variation in habitat used by different individuals as well as large heterogeneity between sites used by the same individual (Fig. A1).

There was no support for the hypotheses that females responded to the onset of hunting or that differences between individual females influenced their survival (H1–4) relative to the null hypothesis (H0, Tables 1, 2). Indeed, the degree of habitat cover was similar in shot and surviving females and was not affected by the onset of hunting (Table 2). Note that females used habitat with 21% shorter sighting distance (more cover) than males before the onset of the hunting season (linear mixed model: $t_{38} = 2.05$, $P = 0.047$; Fig. A1). There was no correlation between bilberry availability and survival that could indicate a similar trade-off in females as seen in males (Table 2).

Overall, at the plot level, horizontal and vertical measures of cover were themselves only weakly correlated (canopy cover: range 0–96%; sighting distance: range 6–144 m; Pearson correlation coefficient $r = -0.28$). Second-order linear models relating forage availability with measures of cover revealed only weak correlations, the strongest being a humped relationship between bilberry cover (range 0–73%) and canopy cover, which nevertheless explained only 9% of the variation in bilberry cover (other correlation statistics are reported in Fig. A2 and Table A2).

There was no support for using Julian date in addition to or instead of the onset of hunting as a predictor variable for either sex. In the best models, replacing the time period contrast with the linear effect of Julian date always resulted in $\Delta AIC > 2$. Including the Julian date did not alter the parameter estimates of the other predictor variables. Thus, the data support the notion that the changes at the onset of the hunting season are abrupt rather than gradual.

DISCUSSION

Hunting is the main cause of mortality in many managed ungulate populations (Langvatn & Loison, 1999). Deer should therefore avoid humans in space and time, in line with general predator–prey theory. Previous studies have shown that individual deer using open habitat have a higher risk of mortality from hunting (Ciuti et al., 2012). But our study is the first to show that deer that survived and those that were shot during the hunting season differed in their immediate response to the onset of hunting, and that this survival strategy involved a trade-off with access to a key forage plant species. Our results show that managed ungulate populations in human-dominated landscapes, such as red deer in Norway, potentially experience strong selection pressure for the ability to respond to the risk of mortality associated with human presence in space and time.

We have linked a plastic response in behaviour at the onset of the hunting season to reduced hunting mortality in wild red deer. Surviving males shifted from using habitat with longer sight lines to habitat with 29% shorter sight lines within days of the start of the hunting season. Because it was a dynamic response to the hunting season we identify it as a deliberately employed spatial strategy in response to hunting, and from the differences between surviving and shot individuals, we infer that it successfully managed risk. That such an immediate response correlated with overall hunting season survival suggests that we measured a general response that is sustained by the individuals in question throughout the hunting season.

There are several plausible mechanisms for how the red deer in our study were able to perceive the onset of the hunting season. Deer probably assess predation risk using a variety of sensory cues, and presumably detect people and dogs using a combination of auditory, visual and olfactory inputs (Kluever, Howery, Breck, & Bergman, 2009; Kuijper et al., 2014; Lynch et al., 2014). Deer could be alerted by the heightened off-track human activity and the

first gunshots. Ravens, *Corvus corax*, are known to react to gunshots (White, 2005), showing the potential for animals to react to such cues. The time of year could also play a role, as the timing of the hunt has been relatively fixed for several decades. The behavioural plasticity of responding to cues about hunting by adopting safer behaviour is central to explaining the pattern we documented in males. Whereas the deer's use of more open forests does not necessarily mean they are more likely to be shot in a forest, it does mean they are more likely to be shot in general (indeed most individuals were shot on agricultural pasture in our study). This dynamic spatial response to the onset of hunting could correlate with other risk management behaviours such as increased vigilance (Bonnot et al., 2014) or the tendency to hide rather than run when encountering humans (Ciuti et al., 2012). In contrast to our study, Ciuti et al. (2012) found that individual differences in behaviour existed before the hunting season started, and highlighted that this reflected personality traits. Personality traits have been found to be moderately heritable (Wolf & Weissing, 2012). Behavioural plasticity can also have a hereditary basis (Snell-Rood, 2013). The behavioural shift by males at the start of the hunting season appears to be adaptive, indicating that selection for risk avoidance behaviour probably also operates in our system.

Linking individual survival with field-measured sighting distance corroborates earlier findings relating habitat selection to habitat visibility in coarse GIS-based land use classes (Ciuti et al., 2012; Godvik et al., 2009), and extends them to fine-scale variability in horizontal visibility within a forested environment. Our results contrast with those of Kuijper et al. (2014) who found no link between risk-reducing behaviour by either deer or wild boar, *Sus scrofa*, and fine-scale horizontal visibility. They attributed the lack of response to visibility being relatively homogeneous in a dense forest, and a poor indicator of predation risk by wolves in that environment. Moreover, their study area had other predators, with deer being subjected also to predation by lynx, *Lynx lynx*, an ambush predator that hunts most efficiently in dense cover (Lone et al., 2014). Visibility is more variable in our study area, and the risk is undoubtedly biased towards open areas (Rivrud, Meisingset, Loe, & Mysterud, 2014) because humans are the only significant predator (Langvatn & Loison, 1999). Indeed, horizontal visibility and other characteristics of the habitats used by our deer differed substantially within and between individuals (Fig. A1), a typical feature of such small-scale habitat measures. Nevertheless, the mixed modelling framework allowed us to account for these inter- and intra-individual differences and extract the maximum information possible on the overall differences between shot and surviving deer, thereby providing clear support for some of our hypotheses about the associations between habitat use and survival.

The decreased use by survivors of habitats with substantial bilberry cover is indirect evidence of a cost associated with a successful spatial strategy for avoiding risk. Bilberry is probably the most important forage species during autumn. Herbs and grasses are higher quality and preferred forage during summer, but their crude protein content decreases exponentially through summer (outside of agricultural fields), and deer switch to bilberry from the end of July onwards (Albon & Langvatn, 1992). Surviving males that decreased their use of bilberry-dominated sites were consequently trading off higher survival against the use of the best forage resources. It is not clear whether the associated cost comes from moving into denser vegetation, as the correlation between sighting distance and bilberry cover was weak at our measurement scale, or is incurred because of another underlying spatial strategy (e.g. avoiding bilberry-dominated communities because hunters prefer such sites). The magnitude of the cost to the surviving animals of using less profitable habitats is also not clear, nor the degree to which they can compensate by increasing foraging time or being

more selective in these other vegetation communities. None the less, finding the same pattern of decline in forage quality and sighting distance (Fig. 2) strengthens the overall conclusion that some males survive because they respond dynamically to hunting cues, even at the expense of foraging opportunities.

Whereas individual male survival depended on the strength of a dynamic response to the risk of predation through habitat use, females did not show the same response, nor did their survival depend on persistent individual differences in habitat use. The sex difference in response to the onset of hunting that we observed could be explained by females with calves already being more cautious prior to the start of the hunting season. Indeed, females used denser cover than males. Previous studies have shown that female red deer with offspring segregate from males, and also use denser habitat prior to the hunting season (Bonenfant et al., 2004), a common phenomenon in ungulates (Ruckstuhl & Neuhaus, 2005). That females apparently use persistent risk avoidance in a setting in which risk varies temporally suggests that it could be a strategy adapted to past patterns of predation rather than current human hunting ones. In the adult female red deer of our study population there is a strong tendency to reproduce every year (Langvatn et al., 2004). Their response to the onset of hunting might be small because the reproductive females have already exhausted much of their potential to shift habitats earlier in the summer.

Conclusions and Perspectives

We have found that survival of male red deer was related to responding dynamically to the risk of predation by shifting habitats at the onset of the hunting season, showing that hunters can influence wildlife behaviour directly in ecological processes. These results also highlight the hunters' potential role in selecting for risk avoidance behaviour. Other recent research has also shed light on how harvesting can unintentionally target 'bold' over 'shy' individuals (Ciuti et al., 2012; Madden & Whiteside, 2014). Nevertheless, even important fitness components such as adult survival might not always relate well to overall fitness (Lind & Cresswell, 2005). For example, do more risky adult males gain access to more females during the coming rutting season, thus enhancing their reproduction? A priority for the future should be to relate behaviour with measures of overall fitness. Such an integrative endeavour could provide a better understanding of the ecological and evolutionary mechanisms of risk avoidance interacting with other aspects of animal ecology.

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APPENDIX 1. FURTHER DETAILS ON THE SELECTION OF SHOT AND SURVIVING ANIMALS

For the sake of analysis, we chose to have a balanced number of individuals and observations per individual. We selected 10 surviving and 10 shot deer of each sex, disregarding three shot males and seven surviving females that we could have potentially surveyed. Which of the candidate deer to leave out at this stage were chosen so as to have as even a geographical spread between categories as possible. Where there were several candidate deer in one municipality, of which we were to retain one or two, these were chosen randomly. We always used data from the first year of monitoring, except in six cases in which deer were monitored for 2 years and shot in the second year. These three female and three male deer were thus classified as 'shot' and we used the GPS data from the year in which they were shot, rather than classifying them as 'surviving' and using data from the first year. This could influence the results by reducing differences between shot and surviving deer, but excluding these animals did not notably alter parameter estimates.

Table A1
Distribution of the data from the study animals across years

Year	Males		Females	
	Shot	Surviving	Shot	Surviving
2007	0	4	1	1
2008	4	0	4	1
2009	2	3	2	2
2010	3	1	2	3
2011	1	1	1	3
2012	0	1	0	0

APPENDIX 2. RAW DATA

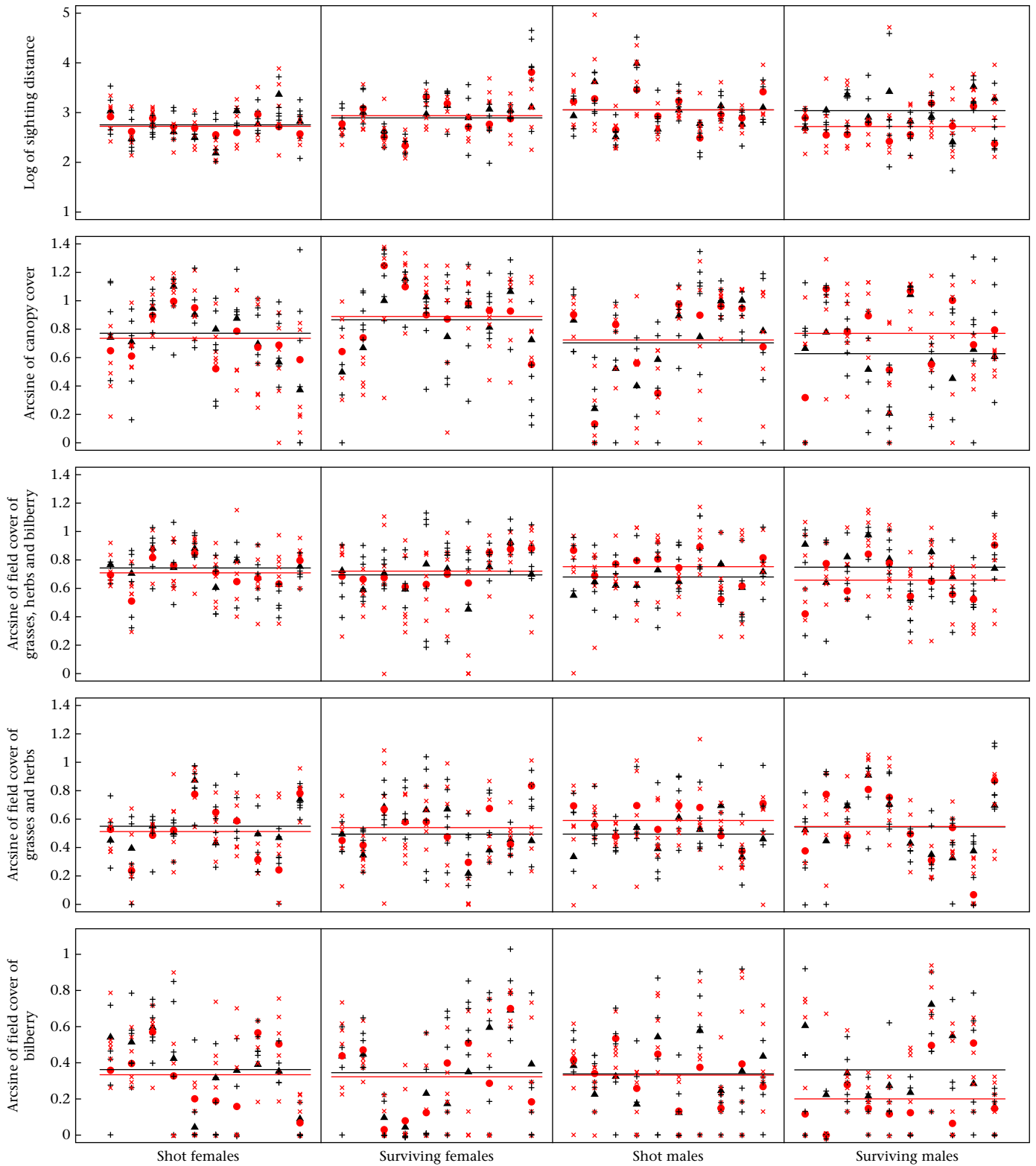


Figure A1. Raw data showing intra- and inter-individual variation and group differences in habitat characteristics. Vertical scatterplots ($N = 10\text{--}12$) represent each individual deer ($N = 40$, balanced across each combination of sex and fate). Locations visited before the onset of the hunting season (+), their mean for each individual (filled triangle) and the mean of the individual means for each combination of sex and fate (line) are shown in black. Locations visited after the onset of hunting (\times), their mean for each individual (filled circle) and overall mean of individual means (line) are shown in red. Original data were in m (sighting distance) and proportions.

APPENDIX 3. CORRELATIONS BETWEEN HORIZONTAL AND VERTICAL COVER AND FORAGE MEASURES

Table A2

First- and second-order relationships between forage availability (cover of grasses (G), herbs (H) and/or bilberry (B)) and horizontal and vertical measures of cover

	Estimate	SE	<i>t</i>	<i>P</i>	Adjusted <i>R</i> ²	Variation explained (%)
Bilberry						
Intercept	-0.45	0.31	-1.44	0.151	0.009	0.9
Sighting distance	0.51	0.20	2.49	0.013		
Sighting distance²	-0.08	0.03	-2.48	0.014		
G+H						
Intercept	1.03	0.29	3.54	<0.001	0.002	0.2
Sighting distance	-0.33	0.19	-1.74	0.083		
Sighting distance ²	0.05	0.03	1.75	0.081		
G+H+B						
Intercept	0.74	0.27	2.74	0.006	-0.004	-0.4
Sighting distance	-0.01	0.17	-0.05	0.960		
Sighting distance ²	0.00	0.03	0.01	0.991		
Bilberry						
Intercept	0.13	0.04	3.24	0.001	0.091	9.1
Canopy cover	0.84	0.13	6.64	<0.001		
Canopy cover²	-0.64	0.09	-6.90	<0.001		
G+H						
Intercept	0.61	0.04	15.79	<0.001	0.009	0.9
Canopy cover	-0.30	0.12	-2.44	0.015		
Canopy cover²	0.21	0.09	2.40	0.017		
G+H+B						
Intercept	0.65	0.04	18.19	<0.001	0.011	1.1
Canopy cover	0.29	0.11	2.55	0.011		
Canopy cover²	-0.22	0.08	-2.67	0.008		

Significant first- or second-order relationships between a measure of cover and forage are shown in bold.

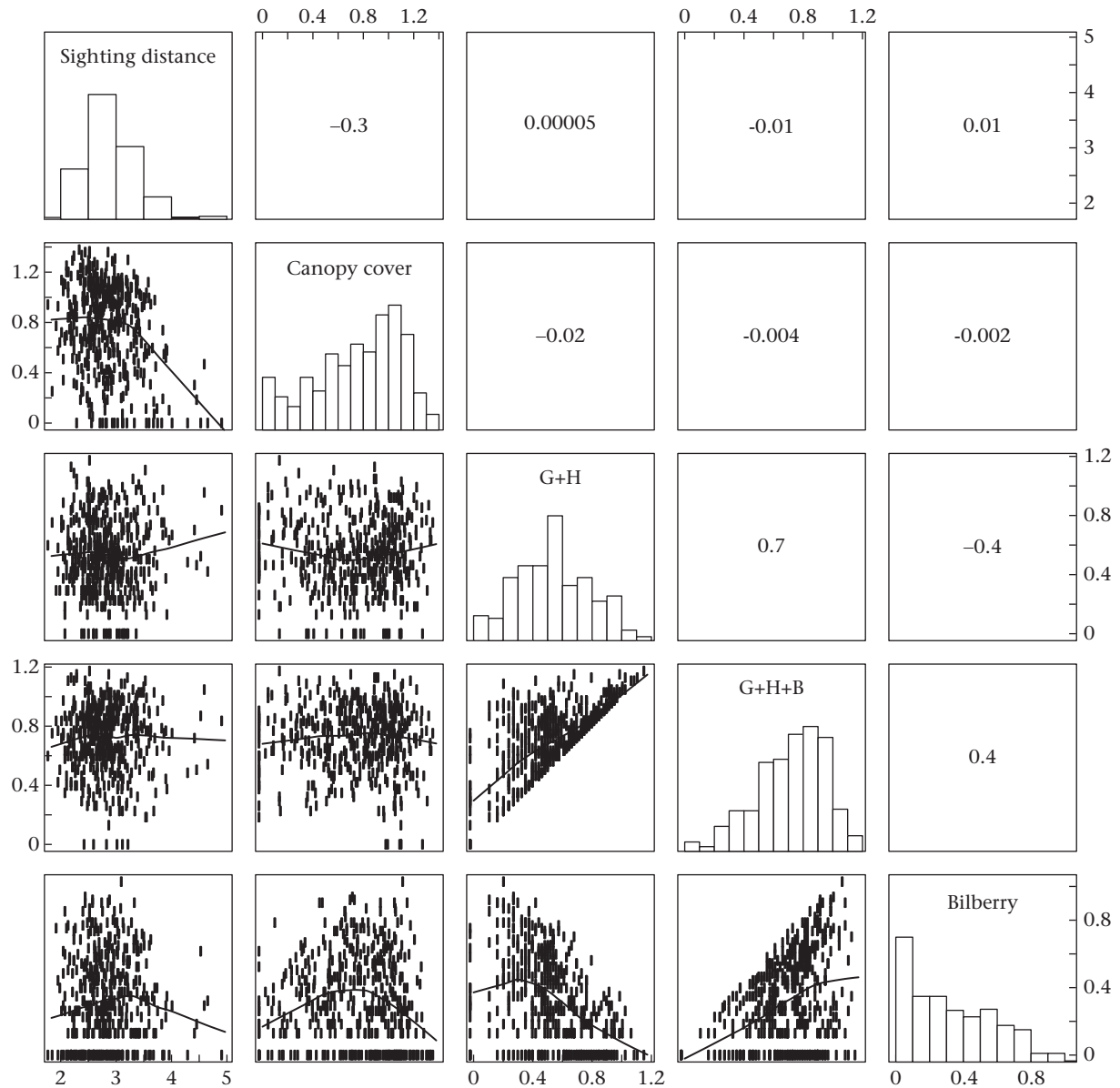


Figure A2. Correlations between sighting distance, canopy cover and forage availability (cover of grasses (G), herbs (H) and/or bilberry (B)). Proportions have been arcsine transformed and sighting distance log-transformed. Panels on the diagonal show the histogram distribution of each variable. For each combination of two variables, a scatterplot is shown below the diagonal and the Pearson correlation coefficient is printed above the diagonal.