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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.

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, & Ripple, 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 (Brilot, 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
H0: No response to onset of the hunting season and survivors and shot individuals use habitat with the same characteristics	*No*	*No*	*~1 (intercept only)*
H1: Dynamic response to onset of the hunting season that either is exhibited by all animals equally or does not affect survival	Yes, decreasing	No	Period
H2: No dynamic response to onset of the hunting season, but individual differences in habitat use affect survival	No	Survivors have lower mean values than shot animals	Fate
H3: All individuals respond dynamically to the onset of hunting, but survival is determined by pre-existing and ongoing individual differences	Yes, decreasing by similar amounts for both groups	Survivors have lower mean values than shot animals	Period+Fate
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.