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Human selection of elk behavioural traits in a landscape of fear

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Among agents of selection that shape phenotypic traits in animals, humans can cause more rapid changes than many natural factors. Studies have focused on human selection of morphological traits, but little is known about human selection of behavioural traits. By monitoring elk (*Cervus elaphus*) with satellite telemetry, we tested whether individuals harvested by hunters adopted less favourable behaviours than elk that survived the hunting season. Among 45 2-year-old males, harvested elk showed bolder behaviour, including higher movement rate and increased use of open areas, compared with surviving elk that showed less conspicuous behaviour. Personality clearly drove this pattern, given that inter-individual differences in movement rate were present before the onset of the hunting season. Elk that were harvested further increased their movement rate when the probability of encountering hunters was high (close to roads, flatter terrain, during the weekend), while elk that survived decreased movements and showed avoidance of open areas. Among 77 females (2–19 y.o.), personality traits were less evident and likely confounded by learning because females decreased their movement rate with increasing age. As with males, hunters typically harvested females with bold behavioural traits. Among less-experienced elk (2–9 y.o.), females that moved faster were harvested, while elk that moved slower and avoided open areas survived. Interestingly, movement rate decreased as age increased in those females that survived, but not in those that were eventually harvested. The latter clearly showed lower plasticity and adaptability to the local environment. All females older than 9 y.o. moved more slowly, avoided open areas and survived. Selection on behavioural traits is an important but often-ignored consequence of human exploitation of wild animals. Human hunting could evoke exploitation-induced evolutionary change, which, in turn, might oppose adaptive responses to natural and sexual selection.

Keywords: contemporary evolution; anti-predator behaviour; shy–bold continuum; hunting; elk; *Cervus elaphus*; GPS telemetry

1. INTRODUCTION

Phenotypic traits of wild vertebrate and invertebrate populations are constantly shaped and reshaped by changes in the environment and by numerous agents of natural selection, including predators [1]. Among these countless factors, modern humans have emerged as a dominant evolutionary force [2]. Humans can cause more rapid phenotypic changes than many natural agents [3]. For several animal species, Darimont *et al.* [4] suggested that rates of phenotypic change driven by human harvest could outpace those driven by other selective forces. Human influence on phenotypes also might generate large and rapid changes in population and ecological dynamics, including those that affect population persistence [5,6].

By exploiting prey at high levels and targeting fundamentally different age- and size-classes than natural predators [7,8], humans can generate rapid phenotypic and genetic changes in both morphological and life-history traits in exploited prey [9]. However, while research has focused on human-mediated selection of morphological traits in wild populations (e.g. selection of large-antlered or large-horned ungulate males [10,11]), little is known about human-mediated selection of behavioural traits. Here we predict that prey, depending on individual personality traits, can adopt anti-predator behavioural strategies in response to human hunting pressure, and thus humans directly influence prey behavioural traits. The importance of behaviourally mediated effects of humans requires greater attention in the wild, as these effects have been shown only in domesticated animals [12,13].

We tested whether elk (*Cervus elaphus*) that were eventually killed by human hunters (hereinafter referred to as harvested) had less favourable behaviours than surviving elk in southwest Alberta, Canada. Elk is a good model species because of its high degree of behavioural plasticity in response to predators [14,15]. We deployed global positioning system (GPS) satellite-telemetry collars on 122 elk. GPS-radiotelemetry provides vast quantities of high-quality relocation data that allow for disentangling spatial anti-predator strategies adopted by large mammals [16]. We investigated among-individual differences in personality traits of males ($n = 45$, age: 2 y.o.) all facing the hunting season with the same experience level but

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Table 1. Elk monitored using GPS radio telemetry in southwest Alberta and southeast British Columbia, Canada and northwest Montana, USA from 2007 to 2011. Sample size was split according to sex, individual movement strategy (migratory, disperser or resident) and individual fate during hunting season.

	males $n = 45$				females $n = 77$				
	migratory	disperser	resident	total	migratory	disperser	resident	total	grand total
harvested	11	3	1	15	8	0	2	10	25
survived	22	7	1	30	59	1	7	67	97
total	33	10	2	45	67	1	9	77	122

no longer bonded with their mothers, which can influence anti-predator strategies of calves [17,18]. At the same time, we studied females ($n = 77$) from a range of experience levels (age: 2–19 y.o.) and thus different knowledge of the environment [19].

We predict that harvested elk have higher movement rates than those that survived, thus more likely to be detected by hunters [20], particularly in less-steep terrain that is more accessible to hunters, in open areas or close to roads where there is increased detectability, and during the weekend when human activity is higher. Therefore, our general prediction is that individuals choosing to increase movements as an anti-predator strategy to avoid hunters, especially when they are more visible, have a higher probability of being harvested than animals that take a 'hiding' strategy by decreasing movement rate as an anti-predator strategy. These patterns should be more evident in males, as we studied young males with low experience levels, whereas learning could confound personality traits in older females.

In our study design, we first assessed the movement strategies of harvested elk versus those that survived before and during the hunting season. If behavioural differences between elk represent personality differences versus learning, those differences should be already present before the onset of the hunting season. We then calculated which spatial behaviour patterns affected the probability of an elk being harvested.

2. MATERIAL AND METHODS

(a) *Study area*

The study occurred within a montane ecosystem along the eastern slopes of the Rocky Mountains in southwest Alberta, Canada. Some monitored elk moved to southeastern British Columbia and northwestern Montana during study (see the electronic supplementary material, figure S1). This is a diverse landscape, from flat agriculturally developed grasslands to mixed conifer/hardwood forests and abrupt mountains.

Human activity was intense during the autumn hunting season, especially during weekends. Hunters access hunting areas using forestry roads and trails, searching at dawn and dusk until they detect prey, often using binoculars or spotting scopes. We deployed 43 trail cameras along roads and trails in the study area [21] to quantify human activity. Humans counted per day during weekends was 20.7 ± 5.7 (mean $\pm$ s.e.), and significantly lower (12.4 ± 3.3 humans per day) during weekdays (paired sample t-test: $n = 43$, $t = 3.112$, $p = 0.003$) [21].

The elk rifle hunting season was from early September until the end of November. Wolf (*Canis lupus*) cougar (*Puma concolor*) and grizzly bear (*Ursus arctos*) are the main natural predators in the area [21].

(b) *Elk data*

Male ($n = 45$) and female ($n = 77$) elk were captured (animal care protocol no. 536-1003 AR University of Alberta) during the winters of 2007–2011 using helicopter net-gunning. Males were fitted with Lotek ARGOS GPS-radiotelemetry collars, whereas females were fitted with Lotek GPS-4400 radiotelemetry collars (Lotek wireless Inc., Ontario, Canada). All collars were programmed with a 2-h relocation schedule. Satellite transmitted data of males were received weekly via email, whereas data of females were remotely downloaded in the field. A total of 635 700 GPS relocations collected from January 2007 to December 2011 were used in this study. A vestibular canine was taken using dental lifters during the capture to assess age through cementum analysis (Matson's Laboratory, MT, USA). All males were aged 1.5 y.o. during the winter capture, and consequently they faced the following hunting season at the age of 2.5 y.o. (greater than equal to three-point antlers). Age of females ranged from 2 to 19 y.o. By the last day of the hunting season, 97 elk were still alive and 25 had been harvested (table 1; see the electronic supplementary material, figure S2 for details on monitoring period). Age of females that were harvested ranged from 2 to 9 y.o. The majority (93%) of hunting mortalities occurred between early September and early November.

(c) *Ecological factors affecting elk mobility*

We calculated step length (i.e. distance between 2 h telemetry relocations, in metre) as a proxy of elk mobility [22] using ARCMAP v. 9.2 (ESRI Inc., Redlands, CA) with the Hawth's Tools extension (http://www.spatialecology.com/htools/). We report in table 2 the complete list of ecological factors that have been predicted to affect elk mobility (i.e. step length) based on previous studies on ungulates [19,20,22–31] and our own predictions (see the electronic supplementary material, table S1 for further details on GIS data). To distinguish migration from other movement behaviours, we used a single measurement, the net-squared displacement (NSD) that measures the straight line distances between the starting location and the subsequent locations for the movement path of a given individual. On the basis of shape of NSD patterns, we split the monitored sample into disperser, migratory and resident elk [32] (see table 1 and electronic supplementary material, figure S2). Dawn and dusk periods were assessed each month as the 4 h period around twilight start and twilight end (sun 6° below horizon) for which we obtained the daily occurrence using the sunrise/sunset calculator for the geographical centre of the study site (http://www.nrc-cnrc.gc.ca/eng/services/hia/sunrise-sunset.html).

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Table 2. Candidate ecological factors that influence elk mobility (step length) before and during the hunting season.

group of factors included in model selection	factors	variables associated with elk step length	predicted link with individual movement rate (step length)	supporting examples[a]
individual behaviour	hunting season fate	survived or harvested	higher movement rates are expected in elk that are eventually shot by hunters (through increased encounters with humans)	[20]
	Julian date	Julian date	elk mobility could flexibly fluctuate through time (Julian date), e.g. depending on movement behaviour, period of the year (rut) and hunting pressure	[23–25]
	movement behaviour	migratory, disperser, resident	higher movement rates are expected in dispersers or young migratory individuals owing to exploratory behaviour within unknown grounds	[26]
individual experience (age)	age	age	home ranges and, arguably, movement rates decrease with age (as a result of increased experience and/or knowledge of the habitat)	[19]
environment	day period	night, dawn, day, dusk	higher movement rates are expected at dawn and dusk as a result of crepuscular activity	[27]
	terrain ruggedness[b,c]	terrain ruggedness *r*	lower movement rates are expected as higher energy expenditure for locomotion is required due terrain ruggedness, and, consequently, elevation and snow cover.	[28]
	open areas (anti-predator behaviour)	elk step length recorded outside or inside open areas (un-forested)	higher movement rates are expected within open areas because of higher perceived risk	[29]
	open areas (foraging behaviour)		lower movement rates are expected if animals forage in open habitat	[22]
humans	land use (human disturbance on a large spatial scale)	national park, private land, public land	different movement rates are expected within national park, private and public land, but the direction of such an effect is still unclear	[20,30]
	distance from gravel roads[c] (human disturbance on a small spatial scale)	distance from the nearest gravel road d_{grv}	higher movement rates are expected close to roads	[31]
	week period (human disturbance on a temporal scale)	weekday or Sat.–Sun.	higher movement rates are expected when human disturbance increases (i.e. during the weekend)	[31]
two-way interactions	different response to humans between elk that are harvested or survive during the hunting season	two-way interactions	elk that are harvested are expected to move faster (higher detectability) when and where hunter activity is higher (i.e. flatter terrain, open areas, close to roads, during weekends)	none

[a]In ungulates.
[b]Collinear with elevation and snow cover in winter time.
[c]Computed for the telemetry relocation prior to the step length.

We modelled variation in step length (natural log-transformed, hereinafter referred to as step length) using generalized additive mixed models (GAMMs) [33] in R v. 2.14.1 [34], with individual elk fitted as a random intercept [35]. Following Burnham *et al.* [36], we constructed four sets of *a priori* GAMMs (see the electronic supplementary material, table S2–S5).

The first two sets of models (one for each sex, electronic supplementary material, table S2 and S4) were built to predict the variation of step length from January, i.e. after the end of the hunting season, through the next autumn hunting season. This approach allowed us to verify whether (i) harvested and survived elk had different movement rates before the onset of the hunting season, and (ii) elk were

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sensitized (e.g. suddenly changed their movement rate) at the onset of the hunting season. Using GAMMs allowed us to flexibly model step length through time (Julian date) by fitting smoothing splines [33]. We also fit smoothing splines for elk that survived and harvested elk separately (Julian date by hunting season fate), and smoothing splines to allow for a nonlinear effect of age on step length of females (see the electronic supplementary material, table S4).

We built two more sets of models (one for each sex, electronic supplementary material, tables S3 and S5) to predict variation in step length during the hunting season. We included four two-way interactions between hunting season fate (survived, harvested) and terrain ruggedness r, open areas (outside, inside), distance from gravel roads d_{grv} and week period (weekday, Sat.–Sun.) to verify the different individual responses to human presence between elk that survived or were harvested. To test whether experience might affect the response of females to the presence of hunters, we fit smoothing splines for the effect of age on step length for survived and harvested elk separately.

The use of AIC to select the best model could be problematic when using mixed models, given that AIC penalizes models according to the number of predictor variables [37], which is not clear because of the random effect. We thus examined our four sets of GAMMs using the deviance information criterion [38,39]. Parameters were estimated for top-ranked models.

We verified whether harvested and survived elk in our final top-ranked models were spatially autocorrelated with each other. Heterogeneity in hunting pressure could lead to spatial segregation between survived and harvested elk. Autocorrelated step length could also be expected among individuals using the same areas. We did not find any pattern in the spatial distribution of elk that survived and were harvested (see the electronic supplementary material, figure S1), nor in the distribution of residuals of top-ranked GAMMs plotted versus their spatial coordinates (see the electronic supplementary material, figure S3 [40]). Inspections of variograms allowed us to exclude spatial autocorrelation of residuals in top-ranked models (Moran's I-test: $p \geq 0.353$ in all cases; see electronic supplementary material, figure S3).

(d) *Behaviours affecting probability of being harvested during hunting season*

We investigated behavioural choices that affected the probability of an elk being harvested during the hunting season. For these analyses, we excluded those animals ($n = 4$ males, $n = 5$ females) that were partially located within National Parks during the hunting season (where no hunting is allowed) or within management units where the hunting of elk males greater than equal to three points was not allowed. For these animals, the probability of mortality was negatively affected by local harvest management restrictions. For all other animals, we fit generalized linear models (GLMs) in R v. 2.14.1 [34], with binomial error distribution with hunting season fate (survived = 0, harvested = 1) as a response variable. Following Burnham *et al.* [36], we constructed two sets of *a priori* mixed models (seven for males, 15 for females) using the following explanatory variables: mean distance from gravel roads (d_{grv}), mean terrain ruggedness (r), mean step length, elk age during the hunting season (for female models only) and selection ratios for open areas (w_{oa}). To calculate selection ratios, we generated 5000 random points within each hunting season 95 per cent kernel elk home range. We calculated selection ratios for open areas (w_{oa}) as the frequency of used locations (within open areas) divided by the frequency of random locations within open areas [41]. For each sex, parameter estimates were reported for the top-ranked model identified by minimum AIC model ranking and weighting [42].

3. RESULTS

(a) *Ecological factors affecting male mobility*

Selection and parameter estimates of the best GAMM predicting step length of males from January through the hunting season are reported in the electronic supplementary material, table S2. Males that were harvested moved faster (mean step length recorded every 2 h ± s.e.: 328.7 ± 3.1 m) than elk that survived (292.5 ± 2.0 m) the hunting season. Predictions of the top-ranked GAMM for the variation of step length of harvested versus survived elk are reported in figure 1*a*. Elk that were harvested during the hunting season moved faster before the onset of the hunting season than elk that survived (figure 1*a* and electronic supplementary material, table S2). Elk showed pronounced crepuscular activity while moving faster at dawn (474.2 ± 4.9 m) and dusk (378.1 ± 4.6 m) than during the day (273.6 ± 2.5 m) and night (175.4 ± 2.4 m). Males moved faster in areas of low terrain ruggedness and open areas (323.4 ± 2.4 m) than outside of them (287.7 ± 2.3 m). Males also moved faster when closer to gravel roads and during Sat.–Sun. (309.8 ± 3.2 m) compared with weekdays (302.3 ± 2.0 m). Movement behaviour (migratory, resident, disperser) and land use were factors retained in the best model.

Selection and parameter estimates of the best GAMM predicting step length of males specifically during the hunting season are reported in the electronic supplementary material, table S3 and table 3. Predictions of the top-ranked GAMM for variation in step length of harvested elk versus those that survived are reported in figure 2*a*. Harvested males always moved faster (321.7 ± 9.9 m) than elk that survived (269.4 ± 4.4 m) the hunting season (table 3 and figure 2*a*). In general, variation of step length in males depending on environmental and human factors (e.g. faster movements at dawn and dusk, in flatter terrain, within open areas and closer to roads) recorded during the hunting season (table 3) were similar to those recorded throughout the year. The two-way interactions between hunting season fate and environmental factors were retained by the top-ranked model (table 3). Elk that were harvested moved faster than elk that survived as terrain ruggedness decreased (i.e. flatter terrain) and when closer to roads (table 3). When located within 1 km from the closest road, harvested elk walked 58 m every 2 h more than those than survived (harvested: 333.5 ± 15.6 m; survived 275.9 ± 6.5 m). We also found a strong interaction between hunting season fate and week period in affecting elk step length (table 3). Elk that were harvested increased movement during weekends (weekday: 310.2 ± 11.2 m; Sat.–Sun. 350.0 ± 20.4 m), whereas survived elk did not (weekday: 270.7 ± 5.1 m; Sat.–Sun. 266.0 ± 8.4 m).

(b) *Ecological factors affecting female mobility*

Selection and parameter estimates of the best GAMM predicting step length of females from January through

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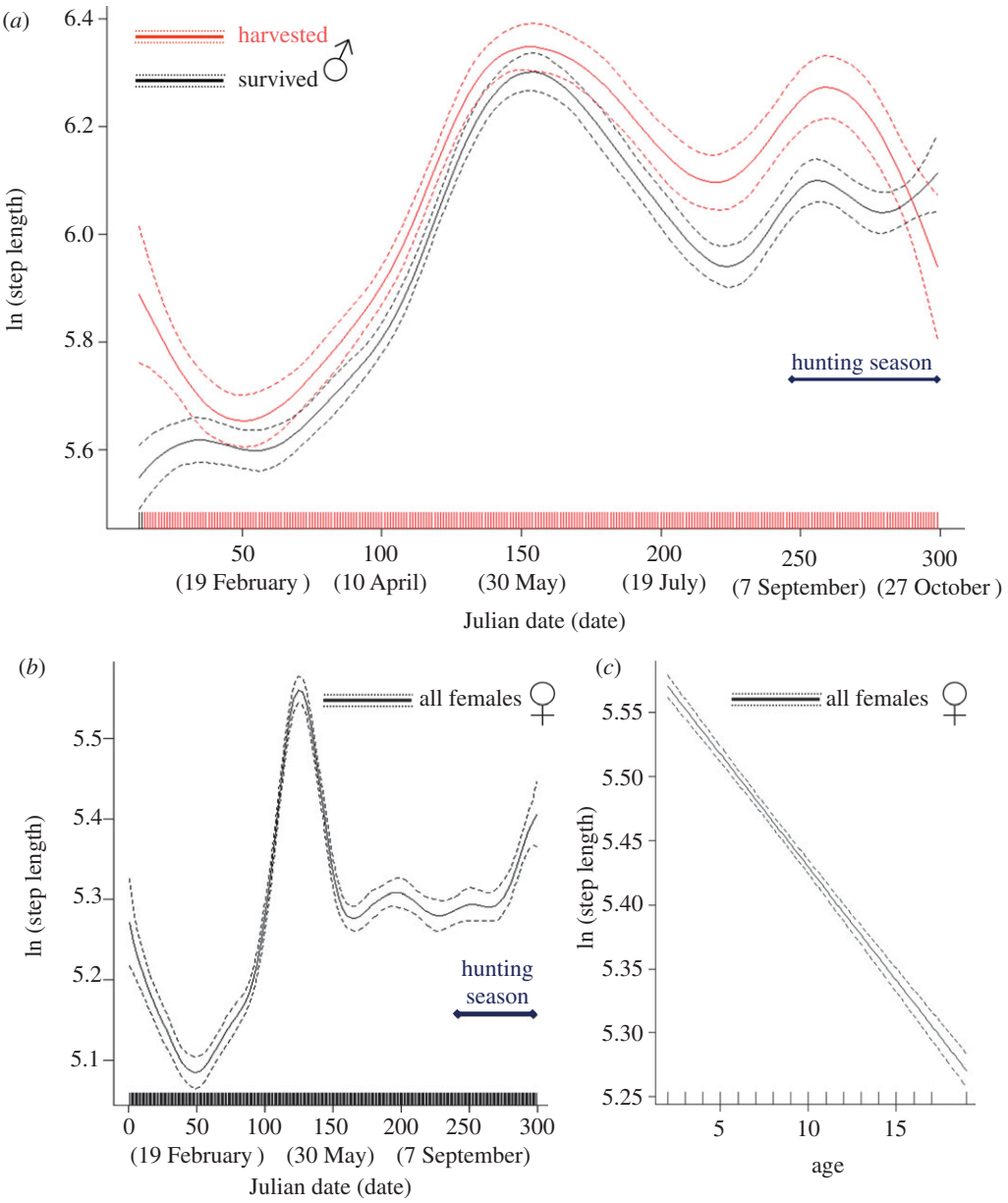

Figure 1. Predicted variation of step length over the time (from January through the hunting season) in male elk that survived or were harvested during the hunting season (*a*), in female elk irrespective of their hunting season fate (*b*), and estimated smoother predicting the effect of age on the variation of step length in female elk (*c*). Smoothed predicted values and approximate point-wise 95% CIs were calculated by adding the intercept value to the contribution of both fixed and random effects in GAMMs.

the hunting season are reported in the electronic supplementary material, table S4. Hunting season fate was not retained in the top-ranked model. Females moved faster in spring and decreased their movement rate in summer (figure 1*b*). Inter-individual variability in step length in females was higher in summer and during hunting season whether compared with earlier periods of the year (figure 1*b*). Younger females moved faster than older ones (figure 1*c*). Females showed pronounced crepuscular activity moving faster at dawn (389.2 ± 2.4 m) and dusk (309.8 ± 2.3 m) than during the day (244.3 ± 1.2 m) and night (160.9 ± 1.3 m). Females moved faster in low terrain ruggedness and open areas (281.7 ± 1.2 m) than outside of them (234.6 ± 1.2 m), and they moved faster when closer to gravel roads and during Sat.–Sun. (265.8 ± 1.6 m) compared with weekdays (256.3 ± 1.0 m). Movement behaviour (migratory, resident, disperser) and land use were factors retained in the best model.

Selection and parameter estimates of the best GAMM predicting step length of females specifically during the hunting season are reported in the electronic supplementary material, table S5. Hunting season fate was retained in the best model. Predictions for the variation of step length of harvested versus survived elk are reported in figure 2*b*. Although females that were harvested sharply decreased their movement rate at the onset of the hunting season, they moved faster (304.2 ± 8.4 m) than females that survived (242.0 ± 2.2 m) throughout the hunting season (see the electronic supplementary material, table S5 and figure 2*b*). Step length recorded during the hunting season decreased as age increased in females that survived (figure 2*c*), while this was not true for females that were harvested (figure 2*c*). Females that were harvested (age less or than equal to 9 y.o.) moved faster (304.1 ± 8.4 m) than females younger (245.5 ± 2.9 m) or older (236.7 ± 3.5 m) than 9 y.o. that survived the hunting season.

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Table 3. Coefficients (β) and standard errors (s.e.) estimated by the best general additive mixed model (GAMM) predicting step length (ln-transformed) of male elk ($n = 45$) in southwest Alberta, southeast British Columbia and northwest Montana during the hunting season.

	β	s.e.
intercept	6.464	0.390
hunting season fate (harvested)	2.189	1.220
movement behaviour (migratory)	0.095	0.086
movement behaviour (resident)	0.153	0.164
day period (day)	−0.834	0.041
day period (dusk)	−0.434	0.043
day period (night)	−1.098	0.038
terrain ruggedness r	−0.013	0.002
open areas (inside)	0.115	0.036
land use (private land)	0.184	0.086
land use (public land)	0.033	0.085
log-distance from gravel roads d_{grv}	−0.043	0.023
week period (Sat.–Sun.)	−0.055	0.033
hunting season fate (harvested) × r	−0.005	0.003
hunting season fate (harvested) × open areas (inside)	0.018	0.076
hunting season fate (harvested) × d_{grv}	−0.056	0.043
hunting season fate (harvested) × week period (Sat.–Sun.)	0.179	0.070

Two-way interactions were retained in the top-ranked model (see the electronic supplementary material, table S5) but without a clear effect in females, with the exception of distance from roads. Females that were harvested moved faster than survived elk closer to roads. When located within 1 km from the closest road, harvested females walked 55 m every 2 h more than survived elk (harvested: 317.0 ± 11.5 m; survived 262.4 ± 3.1 m).

(c) *Behaviours affecting probability of being harvested*

Selection and parameter estimates of the most parsimonious GLM predicting the probability of an elk being harvested are reported in table 4 ((*a*) males, (*b*) females). Males were more likely to be harvested if they selected open areas, increased their movement rate and used flatter terrain. Indeed, males that survived avoided open areas ($w_{oa} = 0.65 \pm 0.04$) more than harvested ones ($w_{oa} = 0.82 \pm 0.07$). Females were more likely to be harvested if they selected open areas and their movement rate increased. While harvested females selected open areas ($w_{oa} = 1.13 \pm 0.07$), survived ones avoided them ($w_{oa} = 0.87 \pm 0.05$). Younger females (effect of age) using areas closer to roads (effect of d_{grv}) had a higher chance of being shot by hunters.

4. DISCUSSION

(a) *'Shy hiders' versus 'bold runners'*

We substantiated our main prediction that individuals choosing to move faster (i.e. a 'running' strategy, thus increasing detectability *sensu* Frair *et al.* [20]) as an anti-predator strategy to escape from hunters have a higher probability of being harvested than those animals that decrease movement as an anti-predator strategy (i.e. a 'hiding' strategy). Patterns were stronger in young inexperienced males facing their first hunting season compared with females. Males with higher movement rate and weaker avoidance of open areas were eventually harvested compared with shy individuals with less conspicuous behaviour that survived. Personality clearly drove this pattern, given that inter-individual differences in movement rate were already present before the onset of the hunting season. Males that were harvested responded to hunters by moving faster than elk that survived, especially during weekends, close to roads and in flatter terrain. Flatter terrain is generally more accessible to hunters, while using sloped terrain gives an ungulate a better vantage point from which to watch for predators [43]. Thus, males that were harvested had adopted exactly the movement strategy that would increase their detectability where and when the probability of being spotted by a hunter was higher. We did not detect a significant increase in activity in males during the rut, which was likely confounded by the overlapping hunting season.

Personality traits were less evident in females, likely confounded by learning. Indeed, females adjusted their behaviour by decreasing movement rate with increasing age, perhaps as a result of increased experience and/or knowledge of the habitat [19]. However, our results showed that hunters harvested female elk based on behavioural traits. Among younger females (age 2–9 y.o.), females that moved faster and selected open areas during the hunting season were harvested, whereas females that survived moved more slowly and avoided open areas. Females that were harvested moved faster than those that survived when closer to roads, as recorded for males. Interestingly, movement rate decreased as age increased in survived females, but not among those that were eventually harvested. The latter clearly showed a lower plasticity and adaptability to the local environment. Older and more experienced females (10–19 y.o.) decreased detectability by moving slower, avoiding open areas, and consequently they all survived the hunting season.

Harvested elk could be defined as 'runners', while survived elk as 'hiders.' A noise, a car approaching or a person walking likely evoked opposite behavioural responses in eventually harvested and survived elk. Over the past few years, concepts of personality and temperament in wildlife have received increased attention [44]. In many vertebrates, including birds, fishes and rodents, individuals differ in aggressiveness, sociability, level of activity, reaction to novelty and fearfulness [45,46]. Such personality traits have been used to characterize behavioural types and gave rise to the concept of 'bold' and 'shy' individuals. The 'shy–bold continuum' is now recognized as a fundamental axis of behavioural variation in animals [44,47], and is associated with the response of an individual to risk-taking and novelty [48]. The cautious behaviour of elk that survived in our study (shy hiders) is certainly the end result of an extreme individual plasticity, resulting in the ability to adapt behaviour to more people on a weekend. An important question is whether the behavioural differences among individuals are highly repeatable (i.e. depending on personality traits) or if they are a consequence of recent experience? Hunters appear to create a 'landscape of fear' [49], but apparently individual elk respond to that stimulus very differently, significantly affecting their survival.

(b) *Humans selecting behavioural traits: three-way community-level interactions*

The occurrence of two contrasting alternative strategies (runners versus hiders) increases the probability that a

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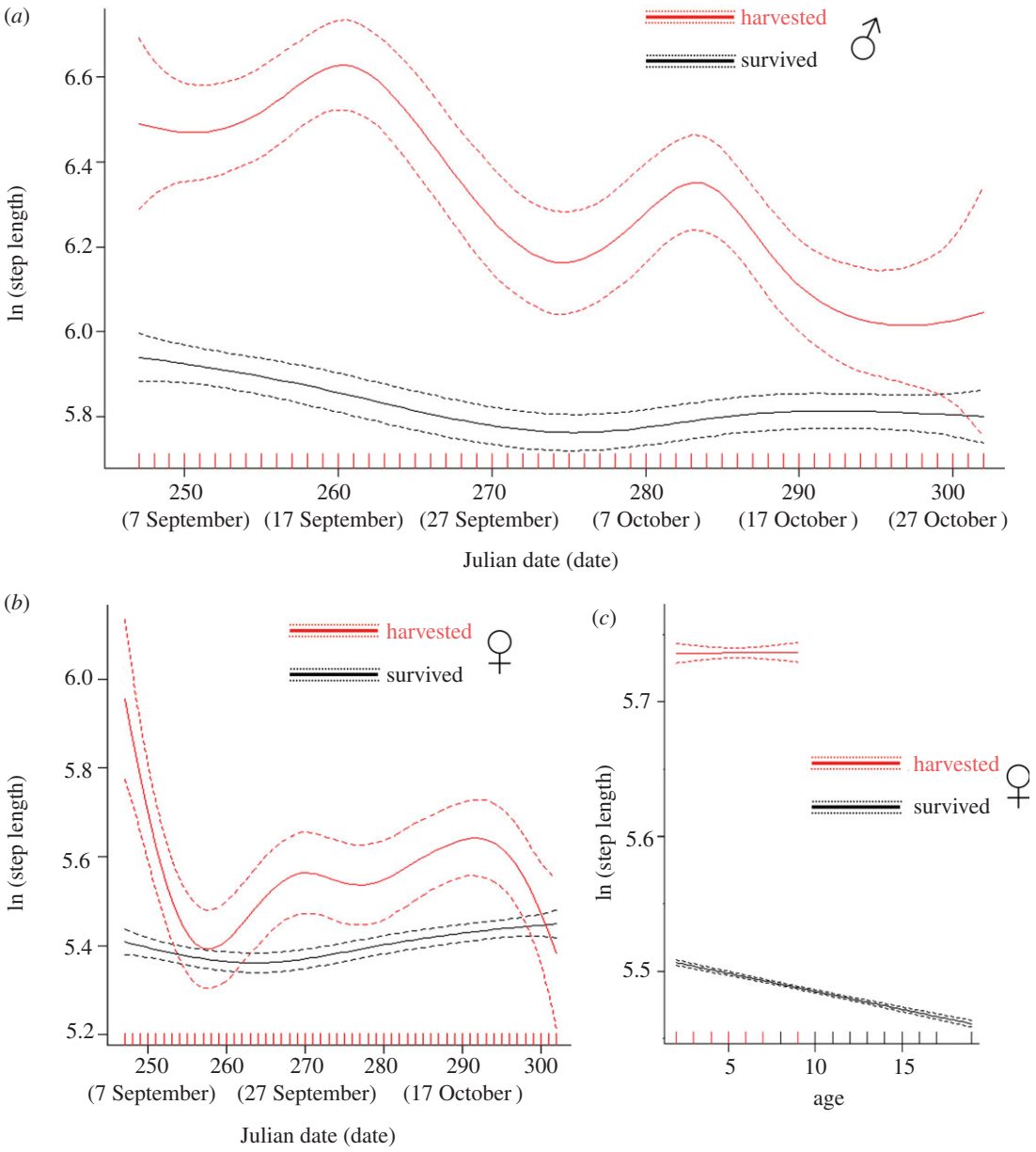

Figure 2. Predicted variation of step length in male (*a*) and female elk (*b*) that survived or were harvested during the hunting season, and estimated smoothers for the effect of age on step length in female elk depending on hunting season fate (*c*). Smoothed predicted values and approximate point-wise 95% CIs were calculated by adding the intercept value to the contribution of both fixed and random effects in GAMMs.

behavioural trait will be selected by humans. Indeed, among the most ubiquitous recent impacts on vertebrate predator–prey dynamics are the global dissemination and explosive growth of humans in all but high Arctic landscapes [50]. As a consequence, the strength of the interaction that once involved native prey and native predators is now modulated by a complex, three-way community-level interaction involving people, predators and prey [51]. Hunting mortality is often substantially higher than natural mortality for game animals [52]. Selection of behavioural traits is an important but often-ignored the consequence of human exploitation of wild animals. Adaptation to exploitation might produce undesirable evolutionary change [52]. Such a change may not be undesirable if environmental conditions and selection pressures generate new evolutionary trajectories reflecting new conditions experienced by animals. For instance, if hunters are producing shyer elk that are harder to find, it may be undesirable for the hunters but not for the elk population. However, evolutionary change could become undesirable when previous selection pressures and the new ones are antagonistic, and the combination of both pressures is leading to a decrease in population viability [2–4]. Empirical studies showed how human harvest of ungulates may drive wolf–elk or wolf–caribou population trends [53–55], with special regards to ungulate populations subjected to multiple predators [56]. Human hunters might cause even more rapid changes if they are selecting elk anti-predator strategies differently than those selected by wolves. Increases in mobility could be the natural response of elk against their natural predator [57], but this strategy is clearly not favourable for avoiding human predation, as shown by our data.

Many species such as elk have been hunted by humans for centuries [58]; so human selection on prey is not new. Hunting pressure, though, might have been increased

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Table 4. Generalized linear models (GLMs) predicting the probability of a male (*a*) or a female (*b*) elk being shot during the hunting season. The top-ranked model (in bold) selected for each sex using Akaike information criterion (AIC) was used to estimate parameters (reported below each panel). W_i are Akaike weights.

	AIC	ΔAIC	w_i
(*a*) factors included in the model (males)			
selection ratios for open areas W_{oa} + step length + ruggedness r	**11900.0**	**0**	**1.0**
selection ratios for open areas W_{oa} + step length	11924.4	24.4	0
selection ratios for open areas W_{oa} + step length + distance from gravel roads d_{grv}	11926.0	26.0	0
selection ratios for open areas W_{oa}	11934.5	34.5	0
ruggedness r	12360.6	460.6	0
step length	12387.7	487.7	0
distance from gravel roads d_{grv}	12403.9	503.9	0
parameter estimates for the top-ranked male model ($\beta \pm$ s.e.): intercept -2.520 ± 0.112, W_{oa} 1.793 ± 0.088, step length 0.046 ± 0.015, r -0.011 ± 0.002			
(*b*) factors included in the model (females)			
selection ratios for open areas W_{oa} + step length + distance from gravel roads d_{grv} + age	**20904.2**	**0**	**1.0**
selection ratios for open areas W_{oa} + step length + ruggedness r + age	21131.4	227.2	0
selection ratios for open areas W_{oa} + step length + age	21167.5	263.2	0
selection ratios for open areas W_{oa} + age	21183.0	278.8	0
distance from gravel roads d_{grv} + age	22487.1	1582.8	0
ruggedness r + age	22506.5	1602.2	0
age + step length	22579.2	1675.0	0
age	22601.2	1697.0	0
selection ratios for open areas W_{oa} + step length + distance from gravel roads d_{grv}	23215.2	2310.9	0
selection ratios for open areas W_{oa} + step length + ruggedness r	23315.0	2410.8	0
selection ratios for open areas W_{oa} + step length	23320.5	2416.3	0
selection ratios for open areas W_{oa}	23359.0	2454.8	0
distance from gravel roads d_{grv}	24239.6	3335.4	0
ruggedness r	24258.9	3354.7	0
step length	24277.7	3373.5	0
parameter estimates for the top-ranked female model ($\beta \pm$ s.e.): intercept 2.076 ± 0.078, W_{oa} 1.670 ± 0.042, step length 0.044 ± 0.012, d_{grv} -0.00020 ± 0.00001, age -0.244 ± 0.006			

where human population has exploded in the recent past. However, the main difference between the pre-Columbian era and present day is technology. Modern hunters have high-powered rifles for hunting, and this favours different behaviours than when hunters were hunting with spears or with a bow. High-technology hunting is certainly introducing very different selection pressures, and this could explain why elk have not already evolved a consistent strategy to deal with modern hunting. Wildlife managers have typically placed primary emphasis on the demographic consequences of hunting, with little consideration of potential evolutionary effects [52]. If humans are indeed becoming the most powerful evolutionary force in the environment [2–4], wildlife managers might need to modify harvest regulations and policies to ensure that hunting is sustainable. Human-mediated evolutionary changes could reduce fitness [59–61] with the potential to affect future yield and population viability [52]. Species with a relatively high degree of individual behavioural plasticity (such as elk) are more likely to survive these new human selection pressures, but there could be direct trait-mediated consequences for the population as well as indirect consequences for other species that interact with elk (e.g. wolves). Furthermore, species with little behavioural plasticity might be in greater danger of extirpation or extinction.

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