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Elevational range shifts in four mountain ungulate species from the Swiss Alps

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Abstract. Warming-induced range shifts along elevational and latitudinal gradients have been observed in several species from various taxa. The mobility and behavioral plasticity of large endothermic mammals, however, complicate the detection of climatic effects on their spatial distributions. Here, we analyzed 230,565 hunting locations of the four most abundant ungulate species in the European Alps: ibex, chamois, red deer, and roe deer. Year-to-year and inter-decadal range shifts toward higher elevations in Switzerland coincided with warmer, snow-free, and thus more favorable autumn conditions in the same area. The average harvest elevation of ibex, chamois, and red deer significantly increased between 1991 and 2013. Although this trend is anticipated to continue, behavioral plasticity may allow the Alpine ibex and other mountain ungulates to buffer some of the associated consequences of climate change. Our results demonstrate the utility of well-replicated hunting archives to supplement shorter but more precise monitoring data. This study also provides independent evidence of animal range shifts in response to environmental change at interannual and multi-decadal time-scales.

Key words: animal ecology; behavioral plasticity; climate change; elevational gradient; European Alps; hunting inventory; range shifts.

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INTRODUCTION

Climate-induced elevational and latitudinal range shifts have been reported for many plant and animal species around the world (Parmesan and Yohe 2003, Thomas et al. 2004, Lenoir et al. 2008, Harsch et al. 2009, Chen et al. 2011, Gottfried et al. 2012, Pauli et al. 2012). Although range shifts observed in alpine and arctic ecosystems have mainly been toward higher elevations and latitudes (Parmesan and Yohe 2003, Thomas et al. 2004, Lenoir et al. 2008, Harsch et al. 2009, Post et al. 2009, Johnson et al. 2010, Chen et al. 2011, Gottfried et al. 2012, Pauli et al. 2012), these changes tend to be complex and difficult to explain from a single factor alone (Parmesan 2006, Mason et al. 2014).

In contrast to most plant and ectotherm animal species, linkages between climate change and range shifts in large endothermic mammals are often obscured by the high mobility and lack of long-term observational data for most species (Inouye et al. 2000, Bolger et al. 2008, Sunday et al. 2012, Seebacher and Post 2015). Large herbivores with pronounced behavioral plasticity often move over long distances (Middleton et al. 2013, Mysterud 2013, Mason et al. 2014). Moreover, there are wide ranges of potential biotic and abiotic drivers of large herbivore spatial distributions (Senft et al. 1987). Several niche-related habitat features may modulate range shifts; these include, for instance, forage abundance, availability, and accessibility (Larter and Gates 1994, McLoughlin and Ferguson 2000, Nilsen et al. 2005, Schradin et al. 2010, van Beest et al. 2011), landscape structure (Tufto et al. 1996, Anderson et al. 2005, Lamberti et al. 2006), seasonality (McLoughlin et al. 2000), predator abundance (Creel et al. 2005), hunting intensity (Vercauteren and Hyngstrom 1998, Scillitani et al. 2010, Ciuti et al. 2012), as well as combinations of these factors (Borger et al. 2006, Bolger et al. 2008).

The most common approaches for monitoring space use by large mammals are visual observation, radio and satellite telemetry, as well as tracking via Global Positioning System (GPS) sensors, an emerging technology over recent years (Signer et al. 2010, Scillitani et al. 2012, Filli 2013, Mason et al. 2014, Kays et al. 2015, Brivio et al. 2016). High-resolution animal tracking data can contribute valuable insight into various aspects of individual and group behavior, life history, as well as ecophysiology (Signer et al. 2010). Most tracking data are, however, restricted to a few individuals rather than an entire population (Cagnacci et al. 2010, Gaillard et al. 2010, Hebblewhite and Haydon 2010). The focus of many such tracking studies has been quantification of space use across geographical scales varying from home ranges to migratory routes, but sampling has generally not permitted observation of distributional changes over long time-scales and large populations. Hunting data refer to the in situ recording of harvest-specific details such as date, location, and elevation, as well as different parameters of animal weight and size, as well as its overall condition (Appendix S1: Table S1). Such harvesting inventories may extend continuously over several decades, and thus describe an abundant source of information for many game species. Although they may have a multitude of limitations, systematically aggregated and well-replicated hunting/harvesting records can provide a particularly useful supplement for the estimation of large vertebrate spatial distribution dynamics (Fischer et al. 2016).

Here, we analyze 230,565 hunting locations of the four most abundant mountain ungulate species in the European Alps: ibex, chamois, red deer, and roe deer. Licensed hunters of the Swiss canton Grisons contributed these data, which were compiled over the last decades by the government wildlife agency. Interannual variation and multidecadal trends in the average harvest elevations of the four ungulate species from 1991 to 2013 are compared with meteorological measurements and other environmental observations. Emphasis is placed on year-to-year relationships between the autumnal harvest locations of each species and environmental factors. A simple split period approach is further used to detect inter-decadal range shifts toward higher elevations, while non-metric multidimensional scaling (NMDS) techniques and multiple linear regression models were applied to detect and unravel the direct and indirect effects of possible abiotic drivers of spatial distribution changes.

MATERIALS AND METHODS

To quantify elevation distribution dynamics of the four most abundant wild ungulate species in the European Alps, we assessed the harvesting locations of 230,565 ibex (*Capra ibex*), chamois (*Rupicapra rupicapra*), red deer (*Cervus elaphus*), and roe deer (*Capreolus capreolus*) individuals. Each animal was legally hunted between 1984 and 2013 in the eastern Swiss canton Grisons. All data were collected outside of the Swiss National Park and wildlife sanctuaries. Our study is located between 260 and 4059 m asl. The region is topographically heterogeneous and comprises meadows (mainly used for hay), pastures (mainly used for grazing), various forest types, alpine tundra, cliffs, permanent snow, and ice fields, as well as areas of permanent and temporal settlement. The hunting seasons for chamois, red deer, and roe deer are restricted to September, whereas ibex are hunted throughout October (Büntgen et al. 2014). Autumnal hunting locations for each species correspond with the altitude of their summer ranges. The cantonal hunting system is only permitted to residents of Grisons. There is no trophy hunting in the area and the use of motor vehicles is heavily restricted. Since stalk hunting in Grisons is not accompanied by any type of supplementary feeding, ungulates can be considered as free roaming populations, especially between their summer and winter ranges.

Registered hunters must report every harvested animal as specified by the official management protocol of Grisons' Department of Wildlife and Fishery Service (www.jagd-fischerei.gr.ch). Hunters are required to record biological, ecological, and geographical information for each harvested animal (Appendix S1: Table S1). These data are compiled and used for the canton's sustainable management of natural resources (www.jagd-fischerei.gr.ch). The autumnal hunting quota is re-calculated each year based on standardized spring surveys and regional population reports. As a result, the hunting intensity is well adapted to interannual population fluctuations. Although the wildlife survey data from spring tend to slightly underestimate true autumnal population sizes, the well-established and professional survey organization provides reliable minimum values of population sizes that can be used for year-to-year comparisons and long-term trend analyses. Grisons' protocols are designed to maintain population sizes at approximately stable levels and to harvest a fixed proportion of the population. With the exception of females with offspring, authorized hunters target both sexes and all age-classes. The official hunting management protocol and the total number of hunters remained relatively stable during the period of this study (Appendix S1: Table S2).

To assess possible effects of sexual segregation, the harvesting datasets for each species were analyzed with respect to male and female hunting elevations. Additional separation into ≤4- and >4-yr-old ibex and chamois, and circa ≤2- and >2-yr-old red deer and roe deer, further allowed comparison of harvest locations between juvenile and adult individuals. The two-year age separation actually refers to animals that are younger and older than ~14–16 months. The herein applied age-class splitting resulted in fairly robust and equivalent sample sizes for each subgroup. Associated error ranges were expected to be larger for cervids in contrast to bovids and almost negligible for ibex.

The common interval of hunting records among all four ungulate species was 1991–2013. A Wilcoxon test was used to assess differences in the autumnal mean harvest elevation of each species between two equally long periods before and after 2002 (1991–2002 and 2002–2013). A Wilcoxon test was also performed to test for differences in the harvesting elevation of sex (male and female)- and age (juvenile and adult)-specific subgroups in each species. Monthly mean temperatures (as well as maximum and minimum values), monthly total precipitation, and snow cover data were compiled from a high-resolution, gridded (0.25° × 0.25°) dataset of surface measurements (E-OBS v10.0; Haylock et al. 2008), which were averaged over the study area (9.5°–10.5° East and 46.0°–47.0° North). Measurements from local meteorological stations in the eastern Swiss Alps were used for validation of the gridded product (Büntgen et al. 2014). Monthly mean temperatures, recorded at high-elevation stations in Grisons, were highly correlated ($r > 0.9$) with the temperature indices from the E-OBS grid cell at the same location. The gridded dataset was further used for a European-wide assessment of spatial field correlations between the species-specific time-series of ungulate harvest elevations and climate fluctuations between 1991 and 2013 (Büntgen et al. 2014). This assessment was used to provide additional insight into the prevailing climate dynamics of the European/North Atlantic sector, which are most relevant for the eastern Swiss Alps. Moreover, the normalized differenced vegetation index (NDVI) was used for comparison against the harvest elevation changes for each species. Ten-day averages from National Oceanic and Atmospheric Administration's (NOAA; "advanced very high resolution radiometer" Swinnen et al. 2007) were available for the period 1982–2014. Spatially homogeneous information of the October mean NDVI was averaged from 1 km resolution grid boxes over Grisons' study area.

Non-metric multidimensional scaling, canonical correlation coefficients, and multiple regression analyses were applied to assess, visualize, and quantify relationships between harvest elevation and meteorological variation. These three different statistical approaches were applied to provide insight into the behavior of and associations within the different datasets, as well as to confirm the robustness of the observed patterns. Nonmetric multidimensional scaling is an explanatory ordination method with the main purpose of providing a simplified representation of patterns of proximities (i.e., similarities or distances) among a set of variables (Rabinowitz 1975). More related or similar variables are depicted near to each other, while dissimilar variables are found further apart. In our case, NMDS helped identify relationships between monthly resolved precipitation totals as well as minimum, mean, and maximum temperatures between August and December, and the harvesting data of ibex, chamois, red deer, and roe deer, with their additional classification into adult, juvenile, male, female individuals. In addition, canonical correlation coefficients and multiple regression analyses were applied to determine the relationships between hunting elevation and climate variation, with all data being normally distributed (Lilliefors normality test; $P > 0.05$). To avoid biases from multicolinearity, analyses were restricted to monthly mean temperatures and monthly total precipitation, and performed separately for the subgroups of sex and age within each species. Canonical correlations were used to quantify the fraction of variance in hunting elevation that can be explained by climatic variation along one or more axes, that is, using orthogonal linear combinations of variables within each dataset best explaining variability within and between datasets. Multiple linear regression models were calculated to quantify the link between climate variation predictors (i.e., potential explanatory variables are September and October temperature) and hunting elevation responses (i.e., dependent variables are ibex, chamois, red deer, and roe deer hunting elevation). These models were based on normalized time-series (with a mean of zero and a standard deviation of one) to obtain more information on the relative contribution of each variable than would be obtained from correlation coefficients alone. Results of the correlation coefficient approach described above were validated against the output from a linear mixed-effects model. This model tested the response of the autumnal ibex hunting elevation to changes in October mean temperature, snow cover, and NDVI, with time considered as a random effect (Zuur et al. 2009). Statistical analyses were carried out using the R software (R Development Core Team 2013).

RESULTS

A total of 85,306 chamois, 68,588 red deer, 59,034 roe deer, and 17,637 ibex were harvested between 1991 and 2013 in the Swiss canton of Grisons. Autumnal harvest locations were spread across ~7000 km^2 of montane–subalpine–alpine habitat between 280 and 3600 m asl (Fig. 1a). Ibex were mainly harvested at high elevations, whereas the three other ungulate species were generally hunted at lower elevations (Fig. 1b). The widest elevational range in hunting locations is found for chamois. For ibex and chamois, the elevational harvesting zones are largely comprised of alpine tundra and pastures above the upper treeline. For roe deer, harvesting is mainly restricted to forest habitats, pastures, and meadows situated between valley bottoms and the treeline ecotone. The harvesting range of red deer corresponds to a mostly intermediate forest area. Although long-term trends were not detected for red deer and roe deer from 1991 to 2013 (Mann-Kendall; $P > 0.05$), harvest amounts declined slightly for ibex and chamois (Fig. 1c).

Interannual fluctuations in autumnal mean harvest elevations of the four ungulate species are superimposed on long-term elevation increases from 1991 to 2013 (Fig. 2a). After normalization of each harvest time-series to have a mean of zero and standard deviation of one (1991–2013), it is obvious that the hunting elevation of all four ungulate species not only exhibits strong year-to-year fluctuations but also uniformly describes a positive trend from the early 1990s to at least ~2006 (Appendix S1: Fig. S1). High-frequency variability is most pronounced in the ibex data, which is further reflected in the lowest first-order autocorrelation coefficient of the four ungulate mean harvest elevation time-series (ACF1; $r = 0.12$). Higher ACF1 values were found in the mean elevation series of the three other ungulate species (chamois, red deer, and roe deer), with ACF1 values ranging between 0.42 and 0.76. A significant ($P < 0.001$) positive correlation coefficient between the harvesting time-series of chamois and red deer ($r = 0.71$) suggests a common external factor that predominantly synchronizes their elevational distribution during September when hunting takes place (Fig. 2a inset cross-correlation matrix). Cross-correlation coefficients of annual mean ibex and roe deer hunting

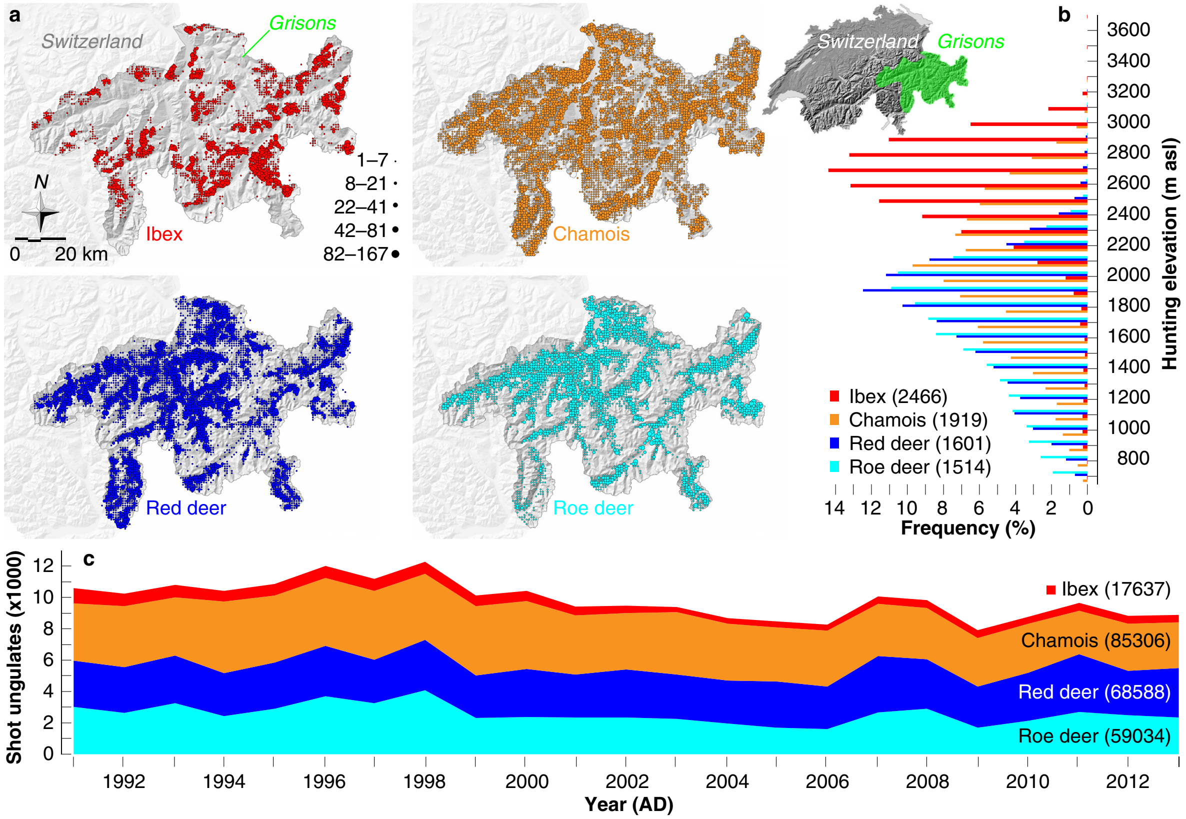


Fig. 1. (a) Spatial, (b) elevational, and (c) temporal distribution of 230,565 ungulates that were harvested in the eastern Swiss canton Grisons, between 280 and 3600 m asl, and during the common 1991–2013 period. (a) The individual points refer to hunting locations of each species (red = ibex, orange = chamois, dark blue = red deer, light blue = roe deer). (b) The green shading superimposed on the Swiss map shows the geographical extent of the Grisons canton, and the numbers in parentheses indicate the average harvesting elevation of each species (m asl). Note that the lowest elevation class refers to all animals harvested ≤600 m asl (six ibex, 208 chamois, 481 red deer, and 1136 roe deer). (c) Numbers in parentheses provide the total amount of harvested animals per species.

elevation data with the other ungulate harvesting records are overall lower. Linear regression slopes of the trend from 1991 to 2013 reveal statistically significant ($P < 0.05$) upward trends for the mean autumnal hunting elevations of ibex, chamois, and red deer (with mean elevation changes from 1991 to 2003 of 135, 95, and 79 m; Fig. 2a, Table 1). Simple early/late periods of equal window length (≤/≥ 2002) indicate small, though significant positive (Wilcoxon test; $P < 0.05$) mean elevational upward shifts of 61, 52, 43, and 19 m for the ibex, chamois, red deer, and roe deer populations, respectively. Differences in the autumnal harvest elevation of the early and late periods show significant upward shifts not only of the mean but also of the whole distributions of ibex, chamois, and red deer (Fig. 2b). Normalized harvest data reveal a steady increase for all species from 1993 to 2006 (Appendix S1: Fig. S1b), but less positive trends afterward. Consistent increasing trends are evident across all age-classes and sexes (Appendix S1: Fig. S2, Table S3), as the juvenile and adult, as well as male and female subgroups, resemble the species-specific trends. On average, adult ibex, chamois, and roe deer were hunted at higher elevations compared to juveniles, whereas juvenile red deer were hunted at higher elevations than adult red deer. Differences in harvest elevations between adults (higher) and juveniles (lower) are largest for chamois. Male ibex, red deer, and roe deer were generally harvested at higher elevations compared to females,

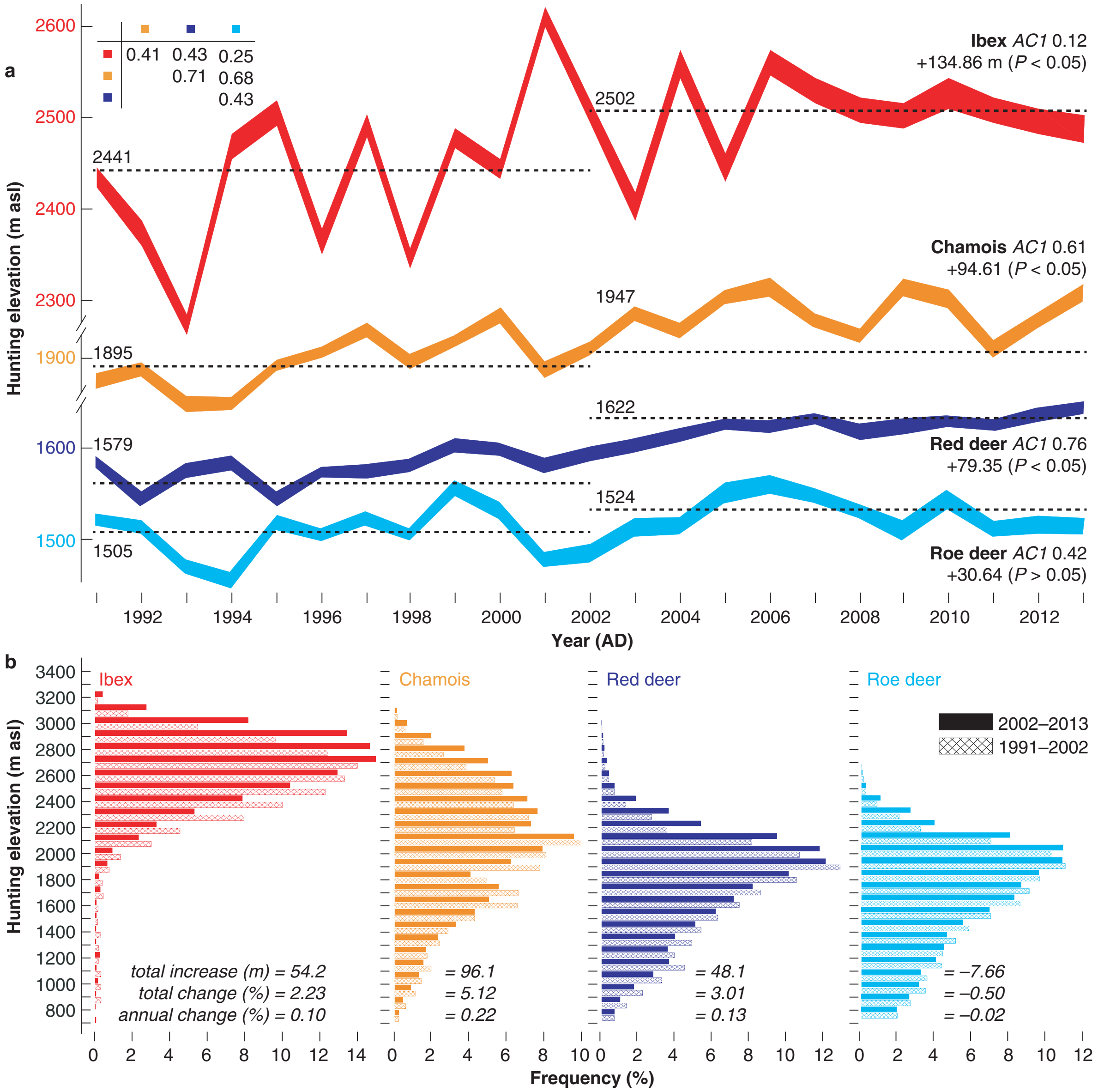


Fig. 2. (a) Annual variation in mean harvest elevation (±1 standard error as independently calculated each year from 1991 to 2013) of 17,637 ibex, 85,306 chamois, 68,588 red deer, and 59,034 roe deer, with the horizontal dashed lines referring to early/late split period means (≤/≥ 2002 to ensure equal window length). Inset shows cross-correlation coefficients between the four ungulate time-series (1991–2013). First-order autocorrelations (ACF1) as well as long-term trends based on linear regression slopes (1991–2013) are provided for each species on the right side. All differences in harvest elevation means between the two sub-periods are significant (Wilcoxon test; $P < 0.05$), and the linear regression slopes indicate significant increases for the ibex, chamois, and red deer time-series. (b) Differences in harvest elevation classes calculated for the early and late split periods for each species, with values on the bottom referring to differences between 1991 and 2013.

Table 1. Species- and subgroup-specific differences in harvest elevation calculated as the difference between the early/late split periods (1991–2002 and 2002–2013), using linear regression slopes between 1991 and 2013, and considering the simple difference between the first and last year (1991 and 2013).

Species	Group	Mean elevation 1991–2002 (m asl)	Mean elevation 1991–2002 (m asl)	*P* value (*t*-test)	Linear regression slope 1991–2013 (m asl)	Increase 1991–2013 (m asl)	*P* value	Difference 1991–2013 (m asl)
Ibex	Male	2495	2545	0.085	4	98	0.052	26
	Female	2395	2458	0.056	7	148	0.008	66
	All	2438	2502	0.036	6	135	0.009	54
	Juvenile	2410	2462	0.100	5	114	0.034	7
	Adult	2471	2542	0.016	7	146	0.003	98
Chamois	Male	1853	1905	0.001	5	101	<0.001	83
	Female	1933	1995	<0.001	5	113	<0.001	124
	All	1899	1950	<0.001	4	95	<0.001	96
	Juvenile	1813	1882	<0.001	6	125	<0.001	112
	Adult	1998	2039	<0.001	4	79	<0.001	87
Red deer	Male	1625	1669	<0.001	4	79	<0.001	62
	Female	1528	1567	<0.001	3	72	<0.001	24
	All	1581	1625	<0.001	4	79	<0.001	48
	Juvenile	1594	1637	<0.001	4	80	<0.001	50
	Adult	1557	1604	<0.001	4	81	<0.001	54
Roe deer	Male	1537	1552	0.108	1	18	0.281	−11
	Female	1467	1491	0.055	2	37	0.001	−9
	All	1506	1528	0.029	1	31	0.095	−8
	Juvenile	1490	1517	0.009	1	33	0.084	−10
	Adult	1526	1547	0.064	2	38	0.054	16

whereas female chamois were harvested at higher elevations compared to male chamois. Differences in harvest elevations between males (higher) and females (lower) are smallest for ibex and largest for red deer.

Fluctuations in mean annual (i.e., using the original as well as 10-yr high-pass time-series) and decadal (using the 10-yr low-pass time-series) ungulate harvest elevations correlate with variation in monthly mean temperatures as well as subsequent changes in plant phenology and snow cover during the corresponding hunting months (Figs. 3 and 4). Since 1991, both September and October mean temperatures increased by 1.3°C (Appendix S1: Fig. S3a). Correlation between the two meteorological time-series is, however, not significant ($r = -0.02$) and thus considerably lower than the correlation between September (chamois, red deer, and roe deer) and October (ibex) harvest elevations. Moreover, the ACF1 values of the monthly mean temperatures in autumn are not statistically significant, whereas the ACF1 values in hunting elevation are.

Year-to-year changes in the mean autumnal harvest elevation of Alpine ibex correlate significantly positively with fluctuations in October mean temperature ($r = 0.65$), snow cover ($r = -0.74$), and the NDVI ($r = 0.53$; Fig. 4a; Appendix S1: Fig. S4). All of these significant relationships persist on the corresponding 10-yr high- and low-frequency domains of the individual datasets (Fig. 4b). Moreover, the strong relationship with temperature was also found when using the ibex sex and age subsets, as well as when using minimum, mean, and maximum temperatures (Fig. 3a; Appendix S1: Fig. S5). Non-metric multidimensional scaling, canonical correlation analyses, and multiple linear regression models support this association (see also *Methods* section). Similar relationships were found between September temperature and the elevation of all other ungulate species. Monthly mean temperatures and monthly total precipitation before and after the species-specific hunting seasons had no effects on the animals' elevational distribution (Fig. 3a, b; Appendix S1: Fig. S6).

While ibex harvest elevations track year-to-year variation in October temperature (Fig. 3c; Appendix S1: Fig. S3b), elevational variation in the other three ungulate populations is linearly related to September temperatures and this coincides with their earlier hunting period (Fig. 3c;

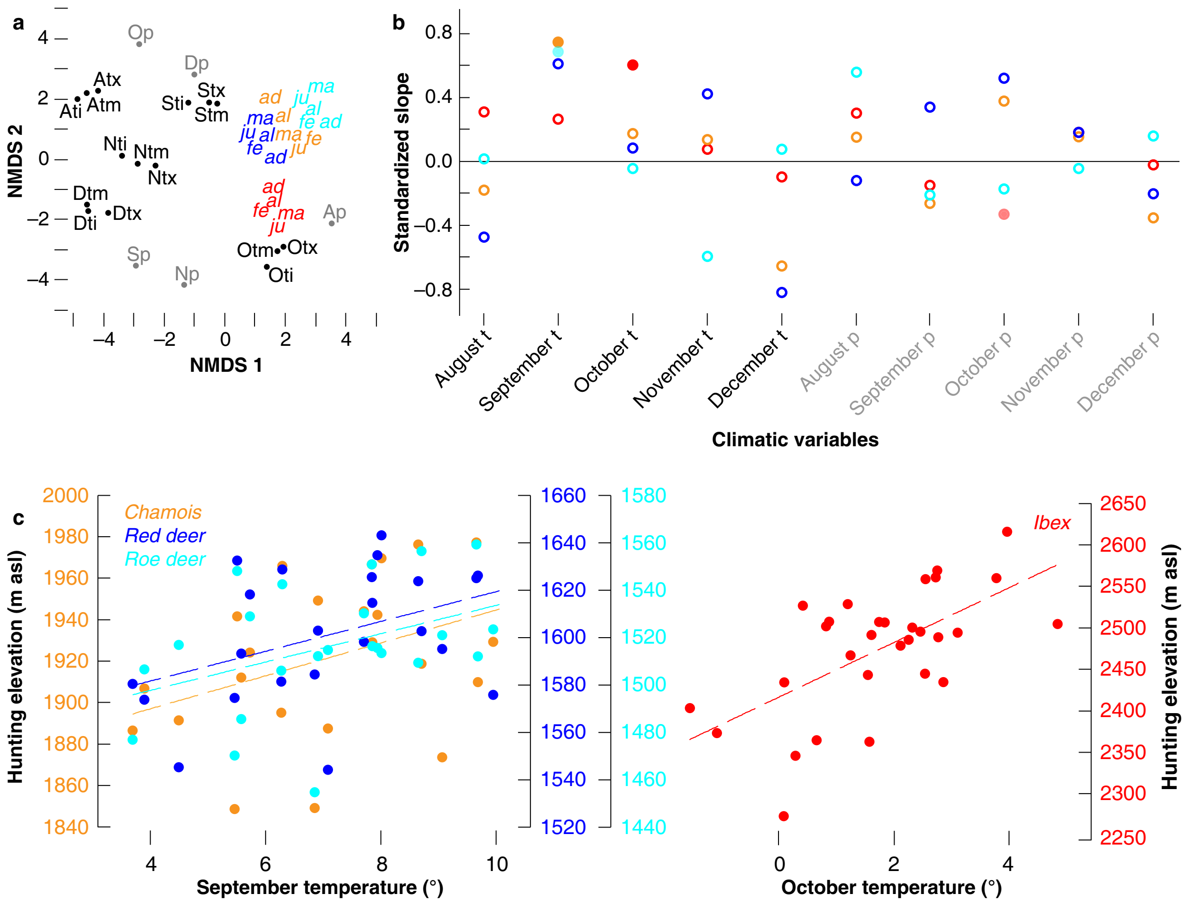
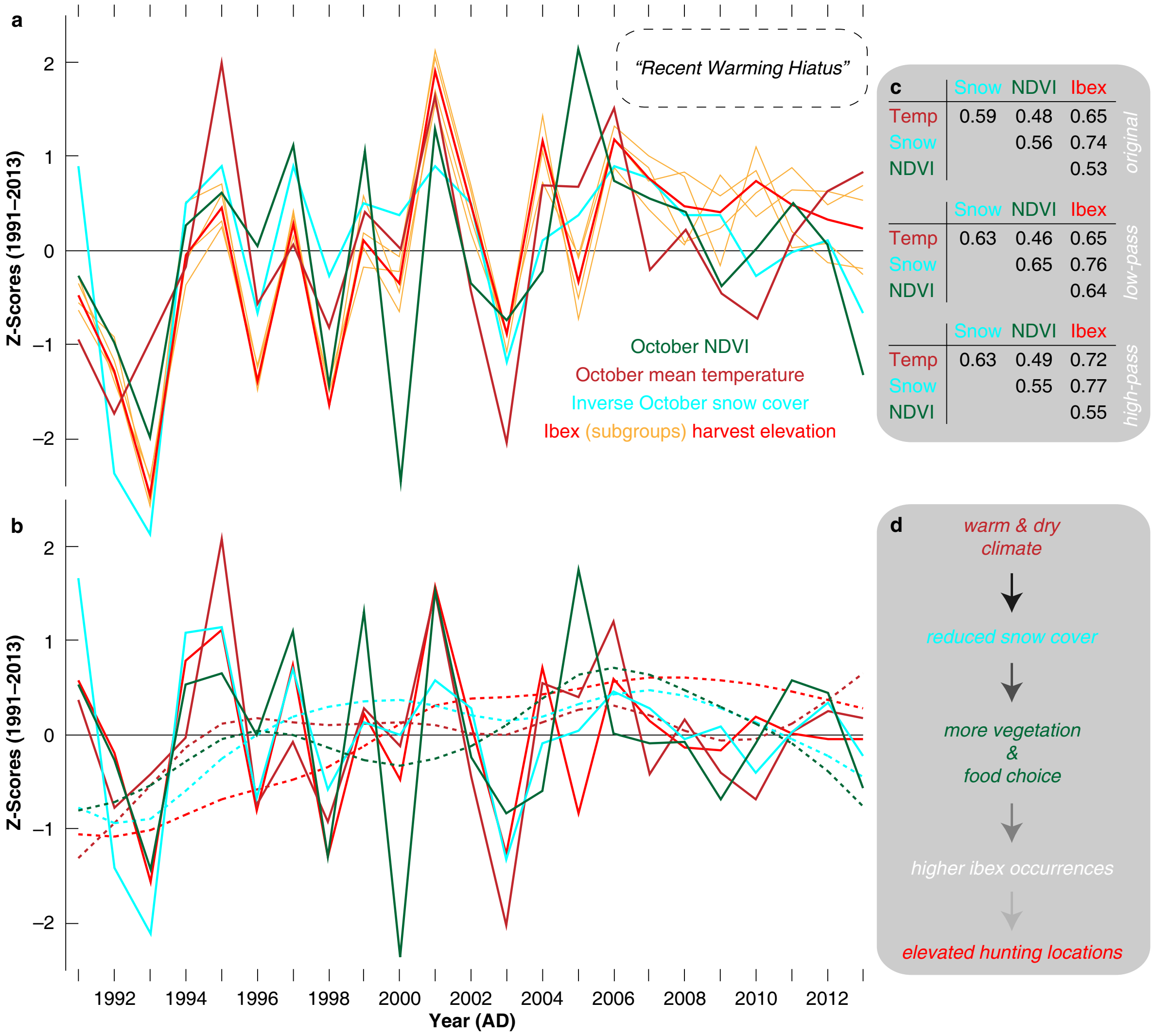


Fig. 3. (a) Non-metric multidimensional scaling, which characterizes similarities or distances among annual changes in ungulate harvest elevations and meteorological variables. Gray refers to precipitation (p) and black to minimum, mean, and maximum temperature (ti, tm, tx), while the first letter abbreviates either August, September, October, November, or December (A, S, O, N, D). Ibex, chamois, red deer, and roe deer are indicated by red, orange, blue, and light blue, with additional classification into adult, juvenile, male, female, and all individuals (ad, ju, ma, fe, al). (b) Standardized coefficients of multiple linear regression models, with the harvest elevation of each species set as the dependent variable, and the meteorological variables set as explanatory variables. Circles filled dark (light) indicate significant coefficients with $P < 0.01$ (<0.05) between ibex (red), chamois (orange), red deer (blue), and roe deer (light blue) and monthly resolved August–December temperature (t) and precipitation (p). (c) Relationship between hunting elevation and September (chamois, red deer, and roe deer) and October (ibex) mean temperatures. All linear regressions are significant (ibex: $R^2 = 0.62$ and $P < 0.001$; chamois: $R^2 = 0.38$ and $P = 0.046$; red deer: $R^2 = 0.41$ and $P = 0.030$; roe deer: $R^2 = 0.41$ and $P = 0.030$).

Appendix S1: Fig. S7). It should be noted that September and October mean temperatures are statistically independent ($r = -0.02$). Correlation coefficients between the mean autumnal harvest elevation records of the four ungulate species and monthly resolved, high-resolution gridded August to December mean temperatures over the European landmass confirm the strong positive relationship between year-to-year temperature variations and elevational changes in hunting locations (Appendix S1: Fig. S6). These patterns in the correlation maps show not only that the influence of temperature is indeed restricted to the hunting period, but also indicate the importance of prevailing maritime air masses. The spatial domains of significantly positive correlation coefficients between the time-series of harvest elevations for each species and monthly resolved, gridded



c — original

	Snow	NDVI	Ibex
Temp	0.59	0.48	0.65
Snow		0.56	0.74
NDVI			0.53

low-pass

	Snow	NDVI	Ibex
Temp	0.63	0.46	0.65
Snow		0.65	0.76
NDVI			0.64

high-pass

	Snow	NDVI	Ibex
Temp	0.63	0.49	0.72
Snow		0.55	0.77
NDVI			0.55

Fig. 4. (a) Annual variation in the mean autumnal harvest elevation of all Grisons ibex populations (red), compared to the October mean temperature (dark red), the inverse accumulated October snow cover at Passo del Bernina (46°24′ N, 10°01′ E and 2307 m asl; light blue), and the October normalized differenced vegetation index spatially averaged over all ibex colonies (green). The orange lines refer to age- and gender-specific ibex subsets. All data were normalized over the 1991–2013 common period. (b) The individual time-series after 10-yr high- and low-pass filtering (solid and dashed lines, respectively). The ibex subgroups have been excluded for a better visual inspection. (c) Cross-correlation coefficients of all relevant time-series (1991–2013). (d) The putative interplay of various environmental factors, resulting in more favorable autumn conditions that allow the Grisons ibex populations to utilize habitats at higher elevations, and subsequently elevate their October hunting locations (see also Appendix S1: Table S4).

August to December maximum temperatures across the European landmass reflect the main west–northwest flow direction of the so-called westerlies (Appendix S1: Fig. S6), which are typically associated with warm and wet autumn conditions in the Swiss Alps. The combination of the later ibex hunting season with the higher elevational distribution of this species indicates a distinct temperature effect on Grisons' ibex populations. Statistically significant ($P < 0.05$)

influences of October snowfall totals and long-term snowfall accumulation rates during this month on ibex harvest elevations further highlight the driving force of climate variability (Fig. 4). A clear relationship between interannual variation in ibex harvest elevation and October snowfall ($r = -0.68$) was evident. The statistical agreement between the mean ibex harvest elevation and October snowfall accumulation rates was even more pronounced ($r = -0.74$). Year-to-year variability and a positive trend in ibex harvesting elevation were most distinct between 1993 and 2001 (Fig. 4b), whereas less coherency and even declining values were found after 2006 (see *Discussion* for possible explanations). These relationships were confirmed by a linear mixed-effects model (Appendix S1: Table S4): Snow cover was found to be the most important predictor variable ($P < 0.02$), whereas temperature was found to be less important ($P < 0.10$), and NDVI had no statistical significance ($P < 0.53$). October snowfall totals and snow cover rates from 1991 to 2013 in the eastern Swiss Alps correlate at 0.89, whereas October snowfall (cover) and mean temperatures correlate at −0.62 (−0.59) over the same period. No impact of monthly snowfall totals or accumulation rates between August and December was found on the elevational distribution of ibex in October. Moreover, no such relationships were evident for the three other ungulate species and autumnal snow conditions.

DISCUSSION

Although recent advances in GPS technology (Brivio et al. 2016) allow the detailed tracking of large mammal movements (Cagnacci et al. 2010, Kays et al. 2015), results obtained from such approaches are typically inadequate to detect long-term species distribution dynamics. Taking advantage of the multi-decadal recording of spatial locations of harvested ungulates in the eastern Swiss Alps, our study is unique with respect to the detection of year-to-year and longer-term elevational range shifts of large, mobile vertebrates from different montane–alpine habitats in response to autumnal temperature changes and other environmental factors. We found that the average hunting elevation of Grisons' ibex, chamois, and red deer populations increased from 1991 to 2013, with the strongest upward movement, independent of sex and age, between 1993 and 2001. However, only moderate changes were found for roe deer, a browsing species showing a close relationship to forest habitats (Schröder and Schröder 1984, Hofmann 1989, Bonenfant et al. 2007, Storms et al. 2008, Filli 2013). Roe deer are dependent on fibrous and easily digestible nutrients from forbs (Hofmann 1989). Nevertheless, the species is regularly switching to a higher proportion of browsing during autumn and winter (Gebert and Verheyden-Tixier 2001). During this time of the year, roe deer prefer to be located near meadows in valley bottoms. In contrast, chamois primarily prefer alpine regions, and red deer range widely in between. Red deer, ibex, and chamois are all mixed feeders with grasses comprising large portions of their diet (Hofmann 1989). A recent study found significant differences in plant biomass and plant nitrogen content between the core foraging areas of these three species (Schweiger et al. 2015). Overlapping niches delineated by habitat use and food choice have been reported for red deer and chamois (Bertolino et al. 2009). Red deer further prefer forest habitats and show complementary niche utilization with roe deer (Petrak 1993). Nevertheless, red deer frequently switch to open habitats for foraging, in particular during night hours (Godvik et al. 2009), because the species can move further from daytime cover than roe deer. In consequence, the three species with distinct upward trends in their hunting locations are those known to frequently inhabit open terrain, including areas above the upper treeline, as well as avalanche tracks spanning large elevational gradients. For all four ungulate species, we found slower increases in hunting elevations during the last few years, which coincided with a so-called hiatus in recent warming (Fyfe et al. 2016).

Elevational habitat use of different ungulate species might be influenced by sex-dependent behavior (Ruckstuhl and Neuhaus 2005). Such patterns are most pronounced in sexually dimorphic ungulates (Mysterud 2000). Adult males often segregate from females, because their larger body size leads to a different activity rhythm (Ruckstuhl 1998), and sexes often also differ in their choice of diet, which further results in habitat segregation (Clutton-Brock et al. 1987). Similar to the behavior of bighorn sheep (*Ovis* *canadensis*; Ruckstuhl 1999), juvenile ibex herd with their mothers during their first circa 3–4 yr, however, later on segregate when they outgrow their mothers' size (Bon et al. 2001). The autumnal ibex hunting locations were found to be lower for females compared to males, while chamois exhibited the reverse pattern. In addition to the different forms of sexual elevational segregation, females with offspring are known to be more sensitive to risk, and thus often choose safer habitats (Main 2008). Male red deer often inhabit open, less-protected higher-elevation forests in contrast to their female counterparts (Bonenfant et al. 2004), which are particularly reclusive with offspring. The hunting protection of females with newborn offspring affects our findings, as it excludes any data from the most influential component of ungulate population demography.

The responses of large herbivores to climatic changes are often mediated through plant quality and quantity (Mysterud et al. 2001, 2008). Although elevational shifts in ungulates harvested from Grisons cannot be explicitly linked to changes in forage accessibility, quality, or quantity, this is the most likely causal explanation for the observed interannual and decadal variability in their autumnal distributions. Snow cover is usually considered the main driver of seasonal shifts in northern ungulate populations as they track nutritional resources in spring and early summer (Mysterud and Austrheim 2014). Mule deer winter survival was linked to both spring and autumn conditions (Hurley et al. 2014), and onset of autumn migration in red deer was weakly associated with changes in plant phenology (i.e., NDVI), as well as abrupt weather fluctuations at the beginning of the autumnal hunting season (Rivrud et al. 2016). However, much less is known about plant phenology and the subsequent quality and quantity of diets toward the end of the plant growing season. Autumn has thus been referenced to as the neglected season in climate change ecology (Gallinat et al. 2015).

It should be further noted that for some species (particularly ibex), insect and/or heat avoidance behavior might be additional drivers of elevational movements (Aublet et al. 2009), especially in summer. Since ibex not only seek shade but also frequently congregate on north-exposed snow patches, snow cover probably influences the distribution of this species independently of its effect on plants. This argument, however, might be of minor importance during October, when temperatures at higher elevations are often below zero. Although large, free-ranging north-temperate mammals seasonally adjust thermoregulation and energy expenditure (Signer et al. 2011), such factors are possibly less important than those related to forage quality, as previously demonstrated for elk (Cook et al. 1998). The role of thermoregulation, especially for mountain ungulates that can readily adjust their altitude over short time-scales, however, requires more research, particularly in autumn and winter.

Changes in plant phenology and the accessibility of diets at the end of the vegetation period can influence trophic interaction, animal vigor, species migration, as well as their spatial distribution (Parmesan and Yohe 2003, Festa-Bianchet et al. 2004, Ozgul et al. 2009, Loehr et al. 2010, Sheridan and Bickford 2011, Mysterud 2013, Büntgen et al. 2014, Plard et al. 2014). Moreover, ungulates may respond to hunting pressure by altering their seasonal habitat use (Ciuti et al. 2012). Therefore, despite its large sample size, caution must be advised when interpreting our results. Nevertheless, we consider the year-to-year signals in the Grisons' archive of ungulate harvest locations unaffected by systematic long-term modifications in the regulated hunting system, minor fluctuations in the number of hunters and livestock (Appendix S1: Table S2, Fig. S8), as well as by any of the small variation in animal population densities, human-induced land-use/land-cover changes, and/or climate-induced vegetation shifts.

Hunting pressure (Appendix S1: Table S2) and competition with livestock (Appendix S1: Fig. S8) remained fairly stable in the study area since at least 1990. Possible effects of large predators, such as wolf and lynx during the last decades, can be excluded from this region as well (Breitenmoser et al. 2016). The potential strength of inter-specific interactions within and between the four ungulate species is also unlikely to have changed sufficiently to drive the observed patterns, because size and density in Grisons' ungulate populations remained fairly stable over time (www.jagd-fischerei.gr.ch). Expansion of ranges and utilization of more marginal habitats are predicted with increased population density. In our case, small fluctuations in animal population densities are unlikely to explain the elevational range shifts in

September and October, especially as ibex and chamois population sizes have been slightly declining and would imply shrinking of range utilization rather than upward movements. The size of a strictly protected ibex population in the Swiss National Park also did not rise since the early 1990s (Filli 2013). Although human disturbance cannot be fully ignored, it is most unlikely that anthropogenic influence, as well as all of the other factors mentioned, exhibits pronounced year-to-year fluctuations to explain the observed interannual changes in species-specific ungulate harvest elevation. Although the hunting season for chamois, red deer, and roe deer experienced a one-week shift in 2007 toward the beginning of September (Appendix S1: Fig. S7), this systematic change did not result in an abrupt upward shift in the corresponding harvest elevations. Moreover, the strongest elevational upward shift in hunting locations was found in Grisons' ibex populations, for which the hunting season did not change since 1991.

Our study emphasizes the value of well-replicated, long-term animal hunting inventories to supplement wildlife monitoring programs. Joining methodological forces and combining different datasets will further strengthen our ability to capture seasonally constrained spatial distribution dynamics of large animals across a wide range of spatiotemporal scales. Despite its strengths, future research should be directed toward calibrating citizen science-based hunting inventories against higher-resolution records of animal tracking programs (Cagnacci et al. 2010, Signer et al. 2010, Scillitani et al. 2012, Mason et al. 2014, Kays et al. 2015).

The observed direct and indirect linkages between autumn temperature variation and hunting elevation for the most abundant mountain ungulate species in the European Alps are in line with independent evidence from protected ibex and chamois populations in the Swiss National Park (Filli 2013), as well as with previously reported elevational range shifts in many other taxa from different habitats and regions around the world (Parmesan and Yohe 2003, Thomas et al. 2004, Lenoir et al. 2008, Harsch et al. 2009, Post et al. 2009, Johnson et al. 2010, Chen et al. 2011, Gottfried et al. 2012, Pauli et al. 2012). Agreement between short-term (interannual) and long-term (multi-decadal) variability in autumn temperatures and ibex and chamois harvest elevations is indicative in part of the behavioral plasticity that characterizes these species and their ability to possibly mitigate direct and indirect effects of a warmer climate.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1761/full