



Land cover and weather jointly predict biometric indicators of phenotypic quality in a large herbivore

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ABSTRACT

Body size and body mass are key indicators of individual phenotypic quality and predictors of important life-history traits such as survival and reproductive success. In wild herbivores, individual responses to changing environmental conditions influence morphometric traits over temporal scales and between populations. However, little research has assessed joint effects of weather and land use on body size/mass at finer, intra-population scale. We used data collected on female and juvenile red deer *Cervus elaphus* shot over a 17-year period (2001–2017) along two sides of a mountainous ridge largely differing in land cover and habitat productivity, to investigate how fine-scale land use patterns and weather influenced multiple morphometric indicators of phenotypic quality. Accounting for weather, body mass of all sex/age classes increased with increasing proportion of cultivated areas in the landscape and, for young females and calves, that increase was stronger or occurred only in the “low-quality” site. Other biometric traits such as mandible length and hind foot length showed the same pattern in young and calves, suggesting that body mass/size reflects individual responses especially in the early life-stage. Accounting for land use, body mass of adult females and calves was enhanced by increasing rainfall and decreasing temperature in spring-summer, i.e. favourable conditions for vegetation growth. This result also supports late gestation- and lactation-mediated effects of vegetation productivity on offspring quality. Additionally, in male calves, body mass and several other traits increased with decreasing severity of the previous winter, suggesting that quality of male offspring - but not that of females - could depend on winter conditions experienced *in utero*, likely due to higher maternal costs. Our findings emphasise how land cover and weather jointly affect indicators of phenotypic quality in a large mammal, helping to predict size responses of herbivores under the ongoing climatic- and anthropogenic land use-changes.

1. Introduction

Phenotypic quality is a pivotal indicator of health, fitness and viability of animal populations. Morphology is a key component of phenotype, and it can be influenced by both genetic and environmental factors to which individuals are exposed. In vertebrates, climate and habitat quality are major causes of evolutionary changes in morphometric traits, mainly via effects on metabolic constraints or food resources which impact individual growth rate and, therefore, population

age structure and dynamics (fish: e.g. Daufresne et al. 2009; amphibians: Connette et al. 2015; birds: Weeks et al. 2020; mammals: Ozgul et al. 2009). Within species, variation in food availability/quality can influence body growth, which may later contribute to differentiate populations, if phenotypic responses are adaptive (Gortázar et al., 2000; Yom-Tov et al., 2007). Individuals living in habitats with a low productivity of food resources have usually smaller size and lower body mass than those living in “rich” habitats, and the latter can thus invest more in body growth and in storing fat reserves (e.g. Power, 1983;

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Hinsley et al., 2008; Rugheri and Festa-Bianchet, 2012). Recent global changes in climatic conditions and habitat cover have altered the quality/availability of food resources for vertebrates. Whilst morphometric responses to climatic changes have been suggested (Gardner et al., 2011; Sheridan and Bickford, 2011, for reviews), it is still unclear the extent by which anthropogenic land use changes may influence traits indexing phenotypic quality.

In mammals, body mass and body size are important drivers of individual fitness and development (rodents: Boyce 1978; carnivores: MacNulty et al. 2009; ungulates: Festa-Bianchet et al. 1997), and depend upon the annual productivity pulse duration, i.e. the availability of nutrients and energy during the growing season (Geist 1987). Body mass is a key indicator of phenotypic quality (e.g. Pettoelli et al., 2001; Ozgul et al., 2009; Toigo et al., 2006, for herbivores). Individuals with a low phenotypic quality are usually smaller, reproduce later and with a lower reproductive success than high quality individuals (Clutton-Brock, 1988; Pettoelli et al., 2001). Besides body mass, skeleton size can also index individual quality and performance (e.g. Morellet et al., 2007; Santos et al., 2013; Garel et al., 2014; Risco et al., 2018). Investigating physical factors affecting variation of these somatic traits across individuals would be important to understand environmental determinants of phenotypic quality, providing clues about individual responses to ongoing environmental changes. Furthermore, in wild herbivores, biometrical measurements are indicators of population health status and have been implemented in monitoring and management plans (Morellet et al., 2007; Santos et al., 2013; Garel et al., 2014; Risco et al., 2018). Our work aims to identify whether such indicators are environmentally-mediated and to show how they can be used to evaluate spatial, temporal and environmental correlates of key life history traits related to phenotypic quality. Although earlier studies considered effects of habitat diversity and heterogeneity (Hewison et al., 2009; Herfindal et al., 2014), little research has so far investigated the potential joint effects of weather and the extent of land use variations on multiple mammalian morphological traits. Moreover, while relationships between land cover features and indicators of phenotypic quality have been well assessed at a broad geographical scale, information is scanty on spatial patterns at a small, intra-population spatial scale and their interaction with habitat quality at larger scale.

Here, we investigated how fine-scale variations in land use and weather influenced morphological traits in a large herbivorous mammal, the red deer *Cervus elaphus*, which is a highly flexible species in terms of phenotypic plasticity (Mitchell et al. 1977; Geist, 1998). Over 17-years, we compared morphometrics across individuals living in two sectors covering neighbour slopes of a mountainous ridge characterised by comparable density but different land cover (Mattioli et al. 2021). Among deer species, spatiotemporal variation in resource availability can influence skeletal development, body mass and specific reproductive rates per age in the cohort (e.g. Klein, 1964; Sæther and Heim, 1993), which in turn are key predictors of individual survival and reproductive success (Clutton-Brock et al., 1982; Langvatn et al., 1996). Additionally, further morphometric indicators can index phenotypic quality in deer (hind foot length: Zannese et al., 2006; Toigo et al., 2006; mandibular measurements: Bertouille and De Crombrughe, 1995; Hewison et al., 1996; thoracic circumference: Gómez et al., 2006; Gaspar-López et al., 2011; shoulder height: Fruzinski et al. 1982).

Ungulate numbers and particularly those of cervids are increasing worldwide (Putman et al. 2011a), with a growing overlap with anthropised areas such as agricultural landscapes. Cultivated areas mainly include herbaceous crops, which usually have a great nutritional value for wild ungulates and are easily accessible (Abbas et al. 2011). We focused on the potential effect that this highly rewarding resource may have on body mass and size of red deer at the intra-population scale, whereby deer accessing to more nutritious patches would be expected to develop greater size and reach heavier body mass (Langvatn and Albon, 1986; Albon and Langvatn, 1992; Mysterud et al., 2002; cf. Brisbin and Lenarz, 1984; Michel et al., 2016, for white-tailed deer

Odocoileus virginianus; Hewison et al., 2009; De Marinis et al., 2019; Zini et al., 2019, for roe deer *Capreolus capreolus*). Effects of crop cover on biometric measurements may also be conditional to habitat heterogeneity occurring at a larger-scale. However, there is a general lack of research conducted at multiple spatial scales, which makes it an ideal investigation where various hypotheses are plausible.

Land use is not the only environmental player affecting body growth in wild herbivores. Owing to the influence on food resources, weather is a major driver of ungulate body mass/size, especially in strongly seasonal habitats such as those located at high latitudes or on mountains (e.g. Rugheri and Festa-Bianchet 2012). During the cold months, when energy consumption is higher and resource availability/accessibility is limited by snow cover, a decrease of body mass is usually observed (Renecker and Samuel, 1991; Festa-Bianchet et al., 1996). Conversely, favourable weather during the growing season of the vegetation, e.g. appropriate quantity of rainfall, triggers the development of high-quality resources. Access to adequate resources in spring-summer is particularly important for females, increasing their investment in maternal care/lactation (Côté and Festa-Bianchet, 2001; Therrien et al., 2007; Scornavacca et al., 2016) and, in turn, body growth and winter survival of offspring (Côté and Festa-Bianchet, 2001; Pettoelli et al., 2005; Ferretti et al., 2019). Unfavourable spring-summer weather has been also suggested to negatively affect fecundity in female herbivores by worsening body condition (Corlatti et al. 2018). In various ungulate species, body mass is permanently affected by the environmental conditions experienced during the early life-stage (particularly the weather experienced in the first year of life), a pattern belonging to the so-called 'cohort effects' (e.g. Post et al., 1997; Gaillard et al., 2003; Pérez-Barbería et al., 2020; but see also Hamel et al. 2016). Thus, we expect that body mass and other biometric traits of red deer would vary in relation to weather conditions experienced during both the cold months and the growing season of vegetation.

According to the above hypotheses, we predict that (i) deer living in the sector with greater availability of cultivated crops would show heavier body mass and larger skeletal traits, than those living in the one with less crops; (ii) at the individual level, there would be a positive relationship between availability of cultivated crops and body mass/skeletal traits for deer living in both study sectors; (iii) juvenile deer experiencing more favourable weather conditions at birth, i.e. greater rainfall during the growing season of the vegetation, and milder winter conditions *in utero*, would show higher phenotypic quality, i.e. heavier body mass and larger skeletal traits.

2. Methods

2.1. Study area and red deer population

We conducted our study in two sectors embraced within a c. 1400 km² area where red deer is distributed, laying onto the two opposite slopes of the northern Apennine, Italy (North slope, province of Bologna, hereafter Bologna: c. 900 km²; South slope, province of Pistoia, hereafter Pistoia: c. 500 km²; Fig. 1a). Both sectors include mountainous terrain (highest peak: 1945 m a.s.l.), as well as hilly areas and valleys within a human-dominated landscape. However, the two sectors are substantially different in land cover. Bologna is characterized by higher environmental heterogeneity, with relatively vast forest tracts, small woods, shrubs, meadows and cultivated areas: woods and open habitats cover 52.8% and 39.5% of the red deer distribution, respectively (Table S1). Pistoia is made up of large, rather compact forests with a few restricted and clumped open habitats (abandoned crops, small pastures): woods and open areas cover 80% and 11.5% of red deer range, respectively (Table S1). Thus, availability of meadows and fields is more than three times greater in Bologna than in Pistoia.

The area lies in the temperate ocean bioclimate, and supratemperate thermotype (Pesaresi et al. 2014). Winter is relatively mild (mean \pm SE in November-February, averaged over 2000–2017; daily temperature:

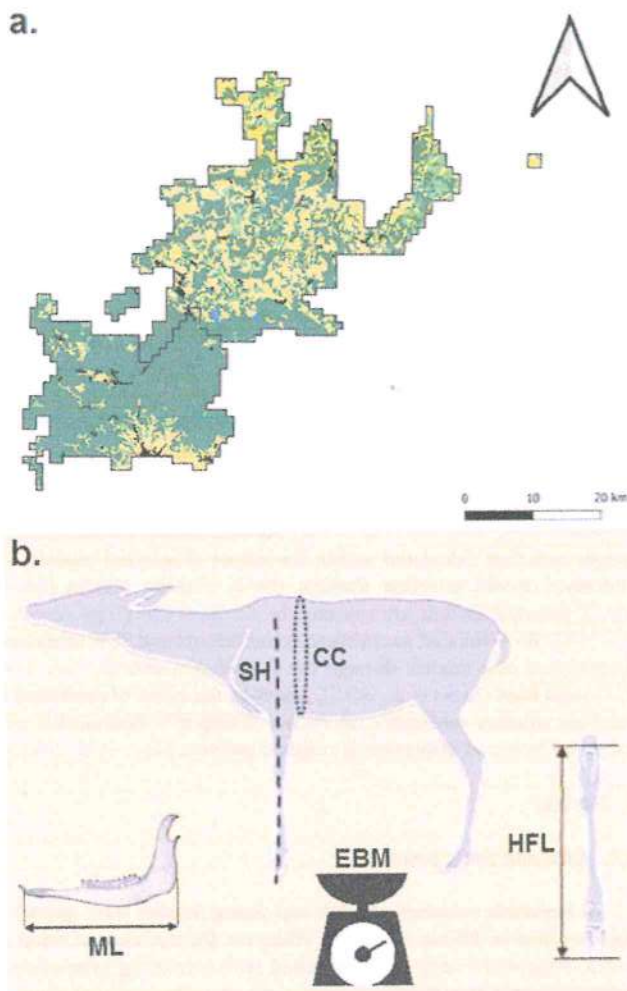


Fig. 1. a. Map showing the distribution range of red deer in the two study sectors (North sector: Bologna; South sector: Pistoia) and land use according to Corine Land Cover 2006 Project (dark green: woodland; light green: shrubs and sparse vegetation; yellow: agricultural areas; blue: water bodies; black: human settlements). b. Biometrical variables measured in red deer and considered in our analyses (EBM: eviscerated body mass; SH: shoulder height; CC: chest circumference; ML: mandible length; HFL: hind foot length). Figure was modified from Mattioli and De Marinis (2009). Formal definitions of biometrical variables are reported in Table S2 (Supplementary Material). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.14 ± 0.18 °C; no. days with mean daily temperature below 0 °C, out of 120 winter days: 19.58 ± 1.63), with scarce snowfall. In our study period (2000–2017), daily rainfall was greater in Pistoia than in Bologna (Bologna: 3.47 ± 0.11 mm, Pistoia: 4.46 ± 0.14 mm; paired sign test: $r = 2298$, $p < 0.001$, $n = 6575$ days; for details on weather data, see below). Conversely, mean daily temperature was greater in Bologna than in Pistoia (mean \pm SE; Bologna: 11.98 ± 0.09 °C, Pistoia: 11.21 ± 0.09 °C; paired sign test: $r = 6218$, $p < 0.001$, $n = 6575$ days; for details on weather data, see below).

Red deer were reintroduced to the area in 1958–1965 (Mattioli et al. 2001). Since 2000, regular harvest takes place between August–March, mainly through selective hunting and, for a limited number of cases, through population control. Moreover, on the last decades, counts of roaring males and other surveys have been used to monitor population trends, indicating that in both sectors the autumn density has been kept relatively constant at low levels (Figure S1, Supplementary Material), which correspond to spring densities of about 2 individuals/km²

(Nicoloso et al., 2010; Mattioli et al., 2016, for details). No supplemental feeding is implemented. Wild boar *Sus scrofa*, roe deer *Capreolus capreolus*, fallow deer *Dama dama* and wolves *Canis lupus* also occur in the area.

2.2. Biometrical measurements

Biometrical measurements were collected from females and calves shot from January to March, over 17 hunting seasons (2001–2017). Upon harvesting, deer were sexed and aged through tooth eruption and wear (De Marinis 2015). Age assessment was conducted by two of us (SM and SN) and dubious cases were discarded. As the age of adults may still have not been determined with a yearly precision, we adopted precautions to strengthen age reliability. First, we used a conservative approach and discarded data concerning 2 years old-females to avoid assigning a young female to the ‘adult’ category. Thus, we considered adult females (≥ 3 years old), young females (1 year old) and calves of both sexes (< 1 year old). Finally, we pooled adult females in age classes (3–4, 5–6, 7–8, ≥ 9 years old), which should further minimise potential mistake in age assessment (e.g. Flajsman et al. 2017, Putman et al. 2019).

Two of us (SM and SN) implemented an intense biometric monitoring of the hunted animals. Despite most measurements were taken by several different operators, they were trained together and followed the same, standardised procedure (Mattioli and De Marinis, 2009; Mattioli, 2019). Six biometrical variables were measured (Fig. 1b; see Table S2, Supplementary Material, for definitions): whole body mass (kg), eviscerated body mass (kg), shoulder height (cm), chest circumference (cm), mandible length (mm) and hind foot length (cm). As whole body mass strongly correlated to eviscerated body mass ($r = 0.97$, $p < 0.001$, $n = 2562$ individuals; see Supplementary Material, for sex/age-specific conversion factor), we only considered the eviscerated body mass, as customarily when investigating ungulate biometry (e.g. Radler and Hattermer, 1982; Loison and Langvatn, 1998, for red deer). We could not measure all biometrical variables for each individual, therefore sample size slightly differed within sex/age classes (Table S2, Supplementary Material). However, within each sex/age class, sample size was consistent across months and study sectors (Figure S2, Supplementary Material).

2.3. Land use and climatic data

Locations and dates of shooting were recorded; then, we centred a circular buffer in each shooting location to assess the relative availability of land cover in an area including the approximate yearly home range of adult/young female and juvenile red deer. Buffer size (300 ha) was defined according to data relevant to a red deer population living in a mountainous area c. 250 km far from ours (Bocci et al. 2009). Previous knowledge on female philopatry (e.g. Porter et al., 1991; Aycrigg and Porter, 1997; Mattioli 2003) and preliminary local information (Crocetti et al. 2010) support our assumption. We obtained land cover data from the Corine Land Cover (CLC) 2006 project (European Environmental Agency, 2006). We used Quantum Gis 2.18.23 (Quantum Gis Development Team 2015) to calculate the percentage of cultivated areas within each individual buffer, by the following steps: (i) we drew a circular buffer of 300 ha around each shooting location; (ii) we overlapped it with the CLC layer and intersected them; (iii) we calculated the percentage of cultivated areas in each buffer. We did not consider other land cover types because, in each circular buffer, cultivated areas are strongly collinear with woodland areas ($r = -0.9$, $p < 0.001$), and these habitat types cover together most of our study area (c. 85%; Table S1). Spatial resolution of CLC layer was 25 ha (minimum mapping unit) and 100 m (minimum linear element width), which is unlikely to affect estimation of cultivated areas in 300 ha buffers (SM and SN, pers. obs.).

Local weather data were obtained for each study sector: we used mean daily temperature and daily rainfall recorded, processed and

provided by Servizio Idrologico Regione Toscana and Arpa Emilia-Romagna (Dext3r). Weather data were spatially interpolated using raw data recorded across a net of several neighbouring meteorological stations, to refer them to each specific spatial grid cell. For each study sector, we used weather data interpolated in the central grid cell, which was located at a comparable mean elevation, thus being representative of each sector (Bologna: Camungnano Nord, c. 690 m a.s.l.; Pistoia: Treppio, c. 700 m a.s.l.). For each study sector, we calculated in each year: i) the mean temperature and the total rainfall experienced by deer during the favourable season, i.e. from the onset of green-up until the senescence of vegetation (March–October, Primi et al. 2016); ii) the mean temperature experienced during the previous unfavourable season (i.e. November–February).

2.4. Statistical analyses

We modelled biometrical measures using linear models and linear mixed models (LMs and LMMs; Zuur et al. 2009). For each sex/age class, we analysed five response variables: eviscerated body mass (EBM, in kg), shoulder height (SH, in cm); chest circumference (CC, in cm), mandible length (ML, in mm), hind foot length (HFL, in cm). For adult females, whose year of birth was estimated with unknown accuracy, we analysed only EBM, as adult skeletal measurements should not be influenced solely by environmental conditions in the previous year, but also by factors over longer time-lags (e.g. cohort-specific conditions; Klein, 1964; Bertouille and De Crombrughe, 1995). Conversely, body mass of adult females should be relatively less driven by conditions at birth than skeletal variables, still reflecting the conditions experienced by deer in the previous year (e.g. Loison and Langvatn 1998).

For each response variable, we included seven fixed effects in the global model: (1) study sector (categorical; reference category: Bologna); (2) proportion of cultivated areas within the 300 ha buffer (continuous, as %); (3) number of days elapsed from 1st January (continuous, as days), to account for temporal changes in biometrics between January–March (e.g. mass losses, in all/sex age classes, and growth in skeletal traits for young females and calves); (4) mean temperature of the previous unfavourable season (continuous, in °C), as a proxy for winter severity experienced by deer in the preceding year (Figure S3, Supplementary Material) which, for calves, corresponds to *in utero* conditions; (5) weather PCA (continuous), as an index reflecting climatic conditions experienced by deer during the latest favourable season, whereby higher values represented warmer/drier spring-summer, and lower values indicated the reverse (Figure S4, Supplementary Material). We also included as predictors the interactive effects between (6) study sector and percentage of cultivated areas in the buffer, to test sector-specific effects of land use in affecting biometrics, which can be investigated because the proportion of cultivated areas in 300 ha-buffers overlapped between study sectors (Figures S4–S8, Supplementary Material); (7) study sector and number of days elapsed from 1st January, to test for sector-specific changes in biometrics from January to March. We did not include interactions between sector and weather variables because weather data were only available at the coarser, sector-scale. In the model fitted on adult females, assuming that all age classes responded similarly to different environmental variables, we accounted for age variation in body mass (e.g. Putman et al. 2019, for female red deer) by treating age classes as random intercepts. Our sample size (Table S2, Supplementary Material) allowed including seven fixed effects in our models because, as a rule of thumb, 10–20 observations per predictor are required (Bolker et al. 2009). We found no multicollinearity ($r < |0.5|$) between explanatory variables. Covariates were scaled to improve model convergence and interpretability of interactive terms.

Statistical analyses were conducted according to the information-theoretic approach (Burnham and Anderson 2002) through the evaluation of multiple competing *a priori* hypotheses, for each indicator. Multi-model selection has become invaluable when multiple hypotheses are

plausible as it determines the combination of predictors which best contribute to empirical data by selecting the model(s) with the lowest uncertainty (Harrison et al., 2018). Once a subset of candidate models has been generated, selected models can be used to predict the measured indicator by estimating the effects of predictors. We could not discard in advance any combination of the explanatory variables included in the full model, as all the underlying hypotheses could be meaningful biologically. In particular, interactive effect of crop cover with the overall habitat heterogeneity at a wider scale need to be evaluated in association with other predictors. Consequently, for each response variable, in each sex/age class, we performed a model selection to fit all the possible models with different combinations of predictors, each one representing a specific *a priori* hypothesis (Harrison et al. 2018). The null model was also included in model selection, to allow for an assessment of model performance relative to a fixed baseline (Mac Nally et al. 2018). Model selection used Akaike's Information Criterion corrected for small sample sizes (AICc) and followed the 'nesting rule' to avoid retain overly complex models: models were retained if they had $\Delta AICc \leq 2$, and if their AICc value was lower than that of any simpler alternative (Burnham and Anderson, 2002; Harrison et al. 2018). For each model, the standardised weight was thus calculated within the subset of selected models. We performed model selection through the R package *MuMIn* (Barton 2012). Selected models are reported in Tables S3–S7 (Supplementary Material). We estimated parameters (β coefficients and 95% confidence intervals) of best models through the R packages *stats* (R Core Team 2013) and *lme4* (Bates et al. 2015), assessing the effect of predictors by checking whether confidence intervals overlapped 0. Best models were validated by visual inspection of residual patterns (Zuur et al. 2009).

3. Results

3.1. Adult and young females

All biometric variables of adult and young females were greater in Bologna than in Pistoia (Table 1). Whatever the age class of adult females, eviscerated body mass increased with increasing proportion of cultivated areas in individual buffers, with an average gain of about 10 kg at 90% crops cover compared to absence of crops (Table 1a; Fig. 2a). In both sectors, eviscerated body mass also decreased from January to March (Table 1a), and increased with higher rainfall/lower temperature of previous spring-summer (Table 1a; Fig. 3a).

In young females, eviscerated body mass increased with increasing proportion of cultivated areas only in Pistoia, where deer gained approximately 15 kg at 90% crops cover compared to areas without crops (Table 1b; Fig. 2b). Mandible length and hind foot length also showed an increase with increasing proportion of cultivated areas (Table 1b; Fig. 2b). We also found, only in Pistoia, an increase in mandible length between January and March (Table 1b).

3.2. Female calves

For female calves, all biometrical variables were greater in Bologna than in Pistoia (Table 2a). Eviscerated body mass increased with increasing cultivated areas in the buffer only in Pistoia, where they gained about 8 kg in areas with 90% crops cover compared to areas without crops (Table 2a; Fig. 2c). Mandible length and hind foot length also increased with increasing cultivated areas in the buffer, but only in Pistoia (Table 2a; Fig. 2c). We found a positive effect of greater rainfall/lower mean temperature in the green-up season on eviscerated body mass and chest circumference (Table 2a; Fig. 3b). Eviscerated body mass also decreased from January to March, only in Pistoia (Table 2a). Mandible length and, only in Bologna, shoulder height and hind foot length, increased between January and March (Table 2a).

Table 1

Coefficients (β) and 95% confidence intervals (95% CIs) estimated for the top-ranked models predicting biometrical measurements from (a) adult and (b) young females. For the LMM, variance of random intercepts (σ) is also shown. Asterisks mark the 95% confidence intervals which do not include 0.

Sex/age class	Response variable	Predictor	β	95% CI
a. ADULT FEMALES	EBM (kg) $\sigma_{\text{age class}} = 0.813$	Intercept	82.712	81.395; 84.029*
		Study sector (Pistoia)	-11.188	-12.813; -9.564*
		Cultivated areas	1.238	0.313; 2.161*
		Days from 1st Jan	-0.632	-1.159; -0.104*
		Weather PCA	-0.737	-1.403; -0.072*
		Study sector (Pistoia) \times Cultivated areas	1.207	-0.176; 2.589
	SH (cm)	Intercept	70.675	69.545; 71.805*
		Cultivated areas	-1.149	-2.466; 0.167
		Study sector (Pistoia)	-11.816	-14.494; -9.137*
		Study sector (Pistoia) \times Cultivated areas	4.625	2.295; 6.954*
		Intercept	109.217	108.566; 109.868*
		Study sector (Pistoia)	-2.478	-4.104; -0.852*
		Cultivated areas	0.221	-0.539; 0.982
		T previous winter	0.448	-0.058; 0.953
		Study sector (Pistoia) \times Cultivated areas	1.002	-0.361; 2.366
	CC (cm)	Intercept	116.114	115.163; 117.064*
		Study sector (Pistoia)	-5.802	-7.971; -3.632*
		Cultivated areas	0.396	-0.726; 1.519
		Study sector (Pistoia) \times Cultivated areas	1.402	-0.483; 3.288
	ML (mm)	Intercept	266.993	265.619; 268.368*
		Study sector (Pistoia)	-8.966	-13.091; -4.842*
		Cultivated areas	-0.935	-2.495; 0.625
		Days from 1st Jan	0.692	-0.499; 1.883
		Weather PCA	0.982	-0.239; 2.204
		Study sector (Pistoia) \times Cultivated areas	4.222	1.098; 7.346*
b. YOUNG FEMALES	EBM (kg)	Intercept	4.548	1.951; 7.145*
		Study sector (Pistoia) \times Days from 1st Jan	51.888	51.659; 52.117*
		Study sector (Pistoia)	-0.961	-1.560; -0.363*
		Cultivated areas	-0.098	-0.360; 0.163
		Weather PCA	0.145	-0.051; 0.341
		Study sector (Pistoia) \times Cultivated areas	0.601	0.133; 1.068*

3.3. Male calves

For male calves, all biometrical variables were greater in Bologna than in Pistoia (Table 2b). We found a positive effect of the proportion of cultivated areas in the buffer on eviscerated body mass, which was stronger in Pistoia, where it increased by nearly 10 kg in areas with 90% crops in respect to areas without crops. Chest circumference, mandible length and shoulder height also increased with increasing crops cover in individual buffers, which was respectively stronger or occurred only in Pistoia for the last two traits (Table 2b; Fig. 2d). Eviscerated body mass increased also with higher quantity of rainfall/lower temperature in the green-up season (Table 2b; Fig. 3c) and with increasing mean temperature in previous winter (Table 2b; Fig. 3d). Less severe winter in previous year had a favourable effect also on chest circumference and mandible length (Table 2b; Fig. 3d). Furthermore, we found an increase of shoulder height, mandible length and hind foot length from January to March (Table 2b).

4. Discussion

We reported significant fine-scale spatial variations in body mass/size of female and calf red deer, matching differences in land cover composition between two sides of a mountain ridge. As expected (prediction i), at a broad scale heavier and larger individuals occurred in the northern slope, characterised by higher habitat heterogeneity and greater availability of cultivated crops than the southern slope (see also Mattioli et al. 2021, for investment in sexually-selected traits by male red deer). Nevertheless, in contrast with our expectations (prediction ii), at a finer scale this positive relationship between availability of crops and biometric responses was not ubiquitous, being it only observed in the "poor" sector but not in the "rich" one. These results emphasise the role of environmental heterogeneity in influencing small scale variations of key life history traits in a highly polygynous species (Pettorelli et al., 2005, for the weakly polygynous roe deer).

4.1. Crop cover effects on biometric indicators

Cultivated areas represent high-quality, energetic and easily accessible food patches for wild herbivores, by which individuals can increase resource allocation, favouring early growth and development of physical characters (Hewison et al., 2009; Zini et al., 2019). Our work shows that the extent of this particular class of land use influenced biometric indicators of phenotypic quality, leading to heavier and larger individuals in the "rich" sector, at a broad scale. However, our results indicate that the potential for access to cultivated fields to shape inter-individual variation in biometric indicators was not consistent across study sectors, being significant only in the sector where the overall habitat quality is low. Indeed, we found a remarkable spatial variation of the effects of crops on body size in young and juvenile red deer, as this effect only occurred or was stronger for deer inhabiting the relatively low-quality area than for those in the rich-area. Most likely, in Pistoia, i.e. the sector characterised by greater forest cover and lower occurrence of cultivated lands, high-quality food was a limiting factor for deer in the early life-stage. Individuals in areas with locally abundant cultivated fields/open areas were heavier and larger than those found in densely wooded patches, emphasising the phenotypic plasticity of this species (see also Mitchell et al. 1977; Geist, 1998). Conversely, in Bologna, all individuals had probably access to abundant food resources, taking advantage of feeding on higher quality patches throughout the area, i.e. cultivated lands, possibly explaining why the proportion of crops in their home ranges influenced body mass to a relatively lesser extent. Previous research on land use classes conducted at multiple scales has concentrated on multi-grain effects on habitat selection or distribution range (for deer, see Laforge et al., 2016, 2017), whereas studies concerning biometric indices are not available. Here, in contrast to our prediction (ii), the relationship between crop cover and body mass seems chiefly

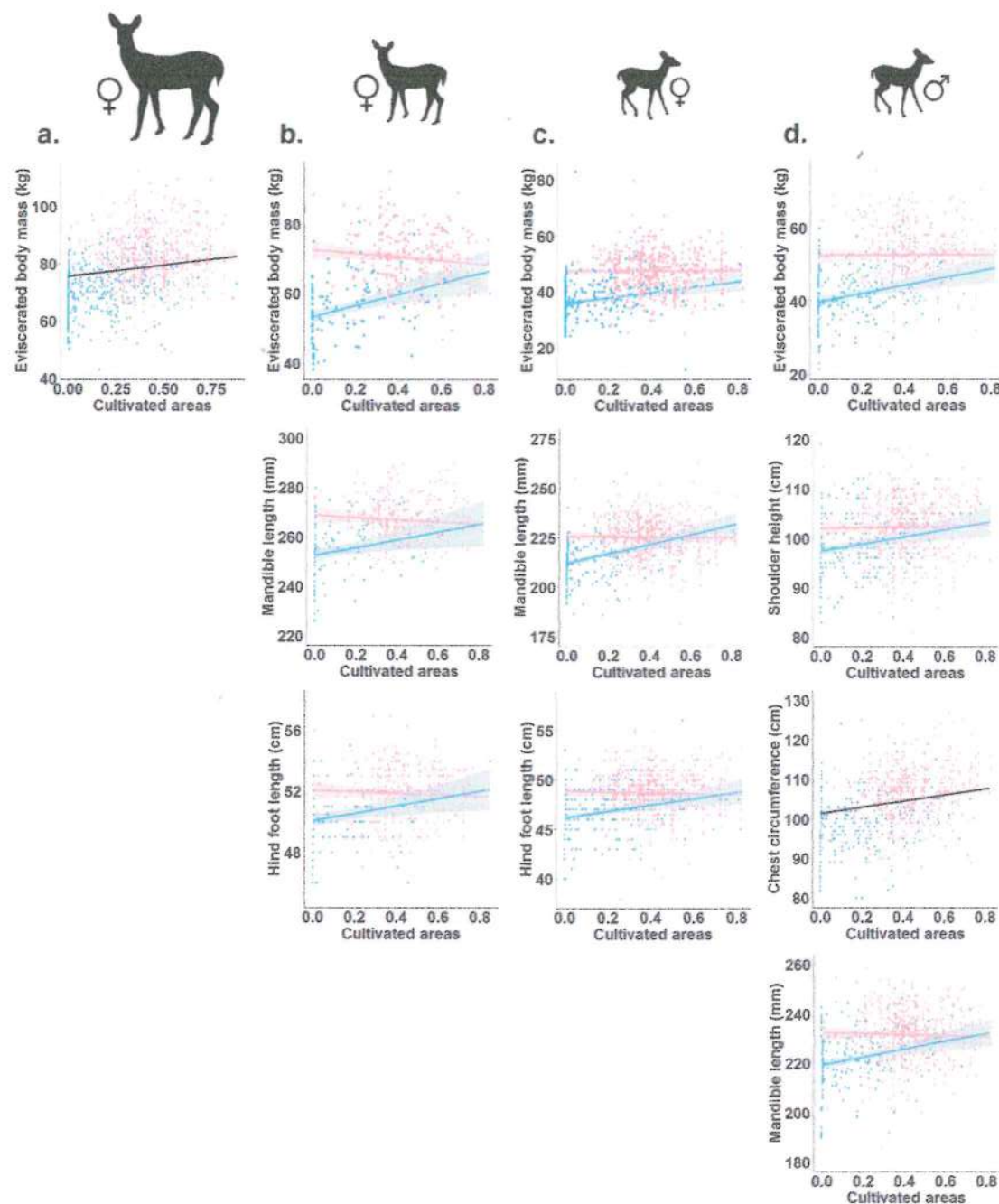


Fig. 2. Predicted biometrical variables in red deer (a: adult females; b: young females; c: female calves; d: male calves) in relation to proportion of cultivated areas. Lines: predicted values; bands: 95% confidence intervals; dots: observed values; red items: Bologna (higher habitat heterogeneity); blue items: Pistoia (lower habitat heterogeneity); grey items: both sectors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

conditional to the local environmental complexity, thus providing evidence that fine-scale variation in crop availability also depends on habitat quality at a higher spatial level.

Unlike body mass, skeletal measurements are not influenced by the amount of fat reserves, therefore their variation can provide an index of individual growth. Generally, individuals living in highly productive environments tend to develop a more robust skeletal structure (e.g. Bertouille and De Crombrughe, 1995; Gaillard et al., 1996, for deer). As young and juvenile deer using home ranges/areas with a greater extent of cultivated lands developed larger mandibular traits, we suggest that even the skeletal growth of young individuals may benefit from the occurrence of agricultural areas (cf. Yom-Tov et al. 2007, for carnivores;

Hewison et al. 2009, for herbivores). In particular, size measurements of immature deer showed a pattern similar to that observed for body mass, i.e. with crop cover having a conditional effect on skeletal responses depending on the overall habitat heterogeneity.

4.2. Weather effects on biometric indicators

Weather fluctuations and climate conditions can synchronize life-history traits of different animal populations over large distances, and this synchronization is mirrored especially by juvenile body mass (Herfindal et al. 2020). We observed that weather effects occurred on calves, disappearing in yearling and being less pronounced in adult

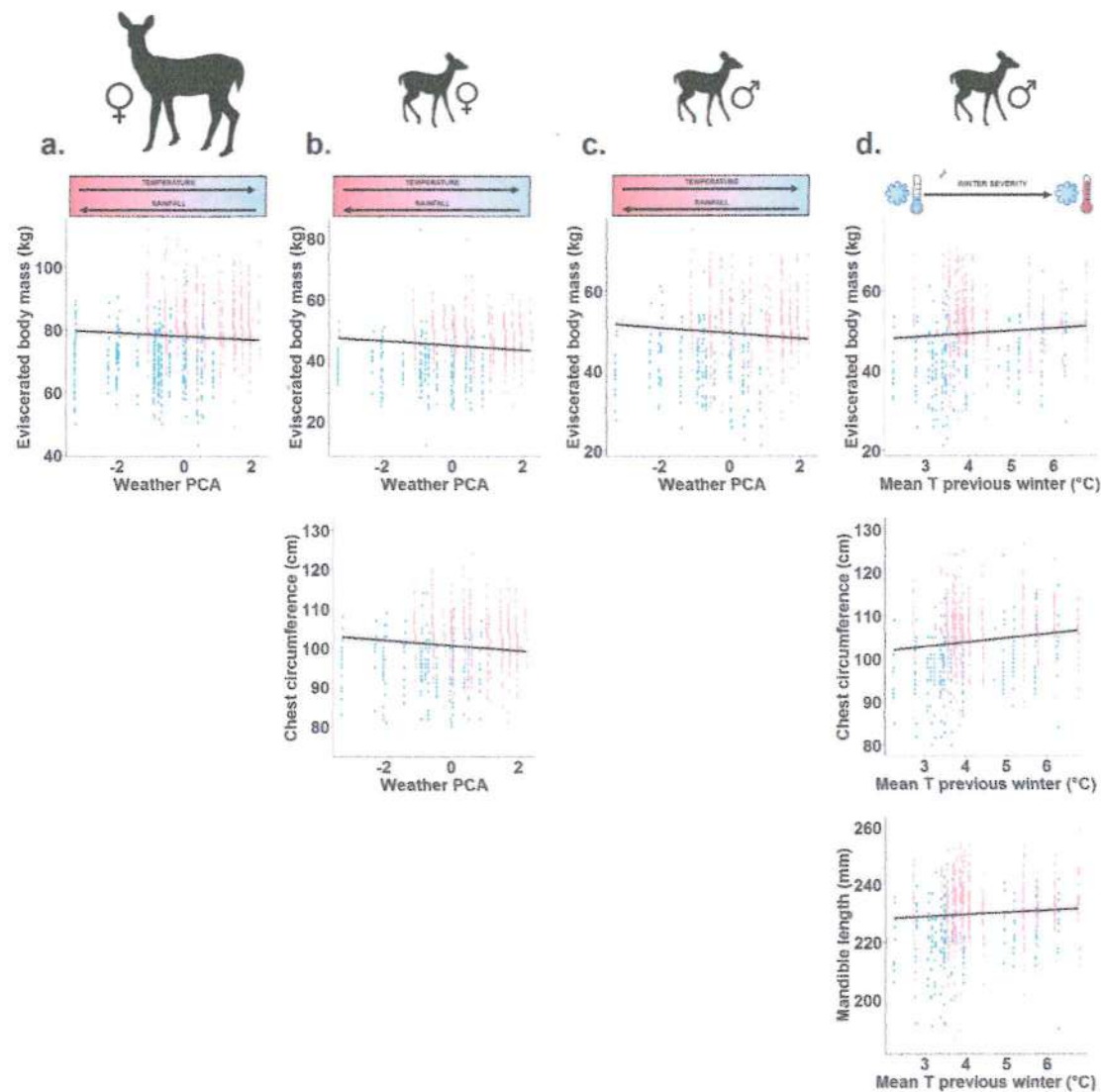


Fig. 3. Predicted biometrical variables in (a) adult females, female (b) and (c) male calves in relation to weather during the previous spring-summer and in (d) male calves in relation to severity of the previous winter. Lines: predicted values; bands: 95% confidence intervals; dots: observed values; red items: Bologna (higher habitat heterogeneity); blue items: Pistoia (lower habitat heterogeneity); grey items: both sectors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

females, supporting our prediction (iii). This result confirms that meteorological factors have mainly cohort-specific effects, acting especially at birth (Post et al., 1997; Gaillard et al., 2003; Pérez-Barbería et al., 2020; Hamel et al., 2016). With higher rainfall and lower temperature in spring-summer, newborns responded with a faster body growth (Pérez-Barbería et al. 2020). In mountain environments, higher rainfall/lower temperature in the growing seasons are associated to a higher vegetation productivity, with positive effects on female ungulates (e.g. on fecundity: Coriatti et al. 2018; foraging efficiency: Ferretti et al. 2019). Conversely, higher temperatures/lower rainfall decrease pasture quality by increasing fibrous/less digestible material, ultimately affecting offspring growth and survival (Festa-Biancher et al., 1996; Ferretti et al., 2019). The growth potential of newborns thus depends on both pre- and post-birth environmental conditions, which influence body condition and milk quality/quantity of their mothers (Pérez-Barbería et al. 2020). Interestingly, whereas spring-summer weather influenced body size in calves of both sexes, the harshness of previous winter only affected that of male offspring. Such difference may be explained by maternal costs of gestation. For ungulates, giving birth to a male is more expensive in

terms of energy allocation (Clutton-Brock et al., 1981; Landete-Castillejos et al., 2004, for red deer), supporting a conservative maternal strategy during harsh winters, after which hinds gave birth to smaller males. As cohort-effects of climatic conditions could not be evaluated for adult females, future studies based on adult age estimated with a known accuracy would be necessary to investigate meteorological variables at different time-lags, achieving a better understanding of weather effects on adult body mass. Additionally, here we considered climatic conditions as 'control' predictors to investigate its joint effect with land use, the latter being our primary focus; however, finer-scale weather data is needed to evaluate the potential occurrence of interactive effects with habitat quality at a larger scale.

4.3. Sector-specific effects on biometric indicators

Regardless weather and fine-scale variations in land use, our findings also show an overall difference in body size between the two sectors, with higher metrics in red deer from Bologna than those from Pistoia. Herfindal et al. (2014) have shown that, in a large cervid, higher habitat

heterogeneity increases the opportunity to optimise forage in all seasons, increasing body mass, as well as that regional variation in biometry is partly explained by genetic structure. Red deer were reintroduced to our study area in 1950–60 s, with a few individuals translocated from a population inhabiting north-eastern Italian Alps. That Alpine area is characterized by harsher winter conditions than the Apennines and includes vast coniferous forests offering low quantity/quality of food. Accordingly, red deer living in that area are characterised by a relatively small body size/mass (SM, unpublished data). When translocated to the Apennines, they originated a population including progressively larger/heavier individuals, most likely thanks to a milder climate, greater availability/quality of food resources and a low population density (SM, unpublished data for 1970–80 s). Over the last 25 years, population

Table 2

Coefficients (β) and 95% confidence intervals (95% CIs) estimated for the top-ranked models predicting biometrical measurements from (a) female and (b) male calves. Asterisks mark the 95% confidence intervals which do not include 0.

Sex/age class	Response variable	Predictor	β	95% CI
a. FEMALE CALVES	EBM (kg)	Intercept	47.364	46.623; 48.106*
		Study sector (Pistoia)	-8.454	-10.151; -6.757*
		Cultivated areas	0.060	-0.751; 0.871
		Weather PCA	-0.980	-1.591; -0.369*
		Days from 1st Jan	0.266	-0.320; 0.852
		Study sector (Pistoia) × Cultivated areas	1.972	0.601; 3.342*
		Study sector (Pistoia) × Days from 1st Jan	-1.379	-2.494; -0.263*
	SH (cm)	Intercept	99.681	99.222; 100.140*
		Study sector (Pistoia)	-5.089	-6.054; -4.123*
		Days from 1st Jan	0.677	0.253; 1.100*
		Weather PCA	-0.325	-0.760; 0.110
		Study sector (Pistoia) × Days from 1st Jan	-1.303	-2.168; -0.438*
	CC (cm)	Intercept	102.670	101.967; 103.372*
		Study sector (Pistoia)	-7.308	-8.885; -5.731*
		Cultivated areas	0.597	-0.061; 1.254
		Weather PCA	-0.842	-1.445; -0.239*
	ML (mm)	Intercept	225.289	224.359; 226.220*
		Study sector (Pistoia)	-5.062	-7.559; -2.566*
		Cultivated areas	-0.138	-1.238; 0.961
		Days from 1st Jan	2.745	2.035; 3.455*
		Study sector (Pistoia) × Cultivated areas	5.111	3.057; 7.165*
	HFL (cm)	Intercept	48.678	48.461; 48.896*
		Study sector (Pistoia)	-1.427	-1.948; -0.906*
		Cultivated areas	-0.088	-0.345; 0.168
		Days from 1st Jan	0.318	0.131; 0.505*
		Study sector (Pistoia) × Cultivated areas	0.741	0.297; 1.185*

Table 2 (continued)

Sex/age class	Response variable	Predictor	β	95% CI
b. MALE CALVES	EBM (kg)	Study sector (Pistoia) × Days from 1st Jan	-0.577	-0.959; -0.195*
		Intercept	52.536	51.604; 53.469*
		Study sector (Pistoia)	-9.079	-10.991; -7.167*
		Cultivated areas	0.050	-0.935; 1.035
		Weather PCA	-0.869	-1.611; -0.128*
		T previous winter	0.717	0.103; 1.331*
		Study sector (Pistoia) × Cultivated areas	2.374	0.779; 3.970*
	SH (cm)	Intercept	102.273	101.672; 102.874*
		Study sector (Pistoia)	-2.421	-3.830; -1.012*
		Cultivated areas	0.157	-0.510; 0.824
		Days from 1st Jan	0.585	0.158; 1.012*
		Weather PCA	-0.480	-0.987; 0.028
		T previous winter	0.407	-0.029; 0.844
		Study sector (Pistoia) × Cultivated areas	1.298	0.182; 2.415*
	CC (cm)	Intercept	105.871	105.152; 106.590*
		Study sector (Pistoia)	-5.858	-7.423; -4.294*
		Cultivated areas	1.560	0.910; 2.210*
		Weather PCA	-0.510	-1.129; 0.109
		T previous winter	1.074	0.547; 1.601*
	ML (mm)	Intercept	231.661	230.647; 232.676*
		Study sector (Pistoia)	-6.848	-9.324; -4.373*
		Cultivated areas	-0.386	-1.562; 0.790
		Days from 1st Jan	2.459	1.676; 3.242*
		T previous winter	0.808	0.010; 1.606*
		Study sector (Pistoia) × Cultivated areas	3.624	1.554; 5.694*
	HFL (cm)	Intercept	50.106	49.893; 50.318*
		Study sector (Pistoia)	-1.437	-1.885; -0.988*
		Cultivated areas	0.201	-0.004; 0.406
		Days from 1st Jan	0.194	0.030; 0.358*

density remained relatively stable, whereas in the southern slope (Pistoia) forest cover increased at the expense of more nutritious, open habitats (cf. Falcucci et al. 2007; Camarretta et al., 2018; Vacchiano et al. 2017). Furthermore, the ageing of coppice woods and the consequent progressive closure of the canopy have negatively affected the undergrowth, with a gradual decrease of food availability for deer, especially in Pistoia. Conversely, forest cover has not increased significantly in Bologna, which should have contributed to differentiate the size of deer living in the two slopes (cf. Mattioli et al. 2021, for biometric differences in male red deer). We suggest that when individuals of the “poor” area can use sites characterized by higher availability of cultivated lands, they show a plastic phenotypic response, i.e. greater allocation in body growth, leading to larger biometrical indices. If so, fine-

scale land use would be a key driver of phenotypic responses, though we still suggest that such plasticity may not be widespread, as it also depends on habitat characteristics at larger scales.

4.4. Future responses

Considering the effects of both land use and weather variations, our work may therefore help to predict plastic responses in body size by wild herbivore populations under future environmental changes. Recent studies have investigated the effect of climatic changes on morphological traits across different animal classes, suggesting how the general response to global increase of temperature should be a reduction in body size, as predicted by the Bergman's rule (e.g. Gardner et al., 2011; Sheridan and Bickford, 2011; but see Teplitsky and Millien 2014). Whereas body mass and size of Alpine ungulates has remained relatively stable during the last decades (Büntgen et al., 2020), our results on Apennine red deer are consistent with such predictions. Yet, along with weather, we further suggest that land use variations will jointly affect body size because of energetic-mediated investment in body growth and the store of fat reserves as plastic responses. Both land use and climatic changes are expected at Mediterranean latitudes, over the coming decades. In Europe, increase of shrub cover and woody plant expansion (+35% on average, in the last 70 years; Espunyes et al. 2019) triggered by rural land abandonment and by the decline of agro-pastoral activities can imperil the extent of mountain grasslands and threaten wild ungulates living on them (Espunyes et al. 2019). As to our geographical zone, the Apennines, forest cover nearly doubled (c. +80%) over the last 50–70 years, with a strong reduction of open habitats, including anthropised patches such as cultivated lands (up to c. –50%; Falcucci et al., 2007; Riviello et al., 2017; Malandra et al., 2018). On the next decade, woodlands in central Apennines have been predicted to increase further at the expense of open habitats such as grasslands, pastures and cultivated areas (e.g. up to 12–17%, locally; Cimini et al., 2013). At the same time, reduction in spring-summer rainfall and increase in duration of dry season are expected (Giannakopoulos et al., 2009; Cramer et al., 2018), shifting the pluviometric regime towards more arid conditions. If so, with other things being equal (e.g. under similar population density), ongoing environmental changes may trigger future phenotypic adjustments in wild herbivores which, based on our results, would be likely to occur towards a smaller body size. Based on our results, we should also note that the response to land cover changes may vary across areas with different habitat heterogeneity.

4.5. Conclusions

Density-dependence plays a key-role in shaping energy store in wild herbivores (Bonenfant et al. 2009), due to intraspecific competition for resources, potentially affecting biometrics (Bonardi et al., 2017; Putman et al., 2019, for red deer). In our study area, red deer density was low compared to other sites (from 2- to 10-fold differences: e.g. Langvatn et al., 1996; Kruuk et al., 1999; Bonardi et al., 2017; Putman et al., 2011b; 2019), suggesting that density dependence should have played a minor role. At higher densities, effects of weather and land cover on body size may be expected to interact with those of intraspecific competition, potentially exacerbating the negative consequences of living in a poor habitat or experiencing harsh climatic conditions (Bowyer et al., 2014; Bonardi et al., 2017). Future research on populations living at different levels of density is needed to test this hypothesis. Our findings strongly suggest that some biometric indicators are finely tuned to small-scale habitat quality and climatic conditions in a low density-population of deer, with responses of young and juveniles being conditional to environmental heterogeneity at a wider scale. Whether increasing density would improve or limit the reliability of such environmentally-mediated indicators is yet to be investigated through long-term studies on fluctuating populations and changing ecological contexts.

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CRediT authorship contribution statement

CV: Conceptualization, Data curation, Writing - original draft, Writing - review & editing. NF: Conceptualization, Formal analysis, Writing - original draft, Writing - review & editing. SM: Conceptualization, Data curation, Supervision, Writing - review & editing. SN: Conceptualization, Data curation, Supervision, Writing - review & editing. FF: Conceptualization, Data curation, Supervision, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.107818>.

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