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Fluctuating asymmetry in Alpine chamois horns: an indicator of environmental stress

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Abstract
Developmental stability of an individual is often evaluated by means of fluctuating asymmetry (FA) in bilaterally paired morphological characters. Even though FA has been widely investigated in ungulates, its connection with the condition of individuals and their environment is still debated. In this study we investigated factors contributing to FA in horn length in the sexually monomorphic Alpine chamois. We measured right and left horn length of 1682 Alpine chamois ($N_{females} = 734$; $N_{males} = 948$) shot during 2 consecutive hunting seasons (2015 and 2016) in 7 neighbouring districts in Central-Eastern Alps (Italy). We found no consistent left or right bias. Within our study population, FA values were normally distributed around a mean value that was not significantly different from zero (Skewness = −0.107, SE = 0.06; Kurtosis = −0.055, SE = 0.119). We also found that absolute FA in horn length was affected by environmental and climatic conditions experienced by the individuals during their first year and half of life. Statistically significant differences between right and left horn length were found with higher local population density and lower forage quality (i.e., siliceous substrate). Moreover, snow cover duration during the individuals' first winter increased horn length asymmetry. No individual characteristics played a role in promoting horn length asymmetry. The associations between exposure to stressors and deviations from bilateral symmetry suggest that absolute FA can be used to identify populations whose individuals experienced stressful conditions early in life. We found in this relatively monomorphic species that both male and female horns were equally affected by climate, substrate, and local population density, thus showing that large male secondary sexual characters, such as the antlers of deer stags, are not the only traits which can be influenced by a negative environment and exhibit increasing FA.

Keywords Fluctuating asymmetry · Geological substrate · Horn · *Rupicapra rupicapra* · Secondary sexual trait · Stress condition

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Introduction

Developmental stability of an individual is often measured by means of fluctuating asymmetry (FA) in bilaterally paired morphological characters (Møller and Swaddle 1997; Palmer and Strobeck 2003; Swaddle 2003; Van Dongen 2006). FA consists of small random variations from perfect bilateral symmetry and is thought to develop either from the inability of individuals to compensate for stress related to the ecological context in which they grew up (i.e., climatic harshness, food shortage, parasitism, intra- or inter-specific competition; e.g., Van Dongen and Lens 2000; Coda et al. 2017) or from such as heterogeneity (e.g., Shadrina 2016), hybridization (e.g., Auffray et al. 1996), inbreeding (e.g., Wauters et al. 1996; Roldan et al. 1998; Gomendio et al. 2000), and mutation (e.g., Clarke and McKenzie 1987).

Given their elaborate weapons (Geist 1966; Goss 1983; Lincoln 1992, 1994), whose characteristics are ideal for evaluating departures from bilateral symmetry, FA has been widely studied in ungulates, including deer (e.g., Reindeer, *Rangifer tarandus*—Folstad et al. 1996; Roe deer, *Capreolus capreolus*—Pélabon and Van Breukelen 1998; White-tailed deer, *Odocoileus virginianus*—Ditchkoff et al. 2001; Iberian red deer, *Cervus elaphus hispanicus*—Mateos et al. 2008) and bovids (e.g., Gemsbok, *Oryx gazelle*—Møller et al. 1996; Mountain goats, *Oreamnos americanus*—Côté and Festa-Bianchet 2001). However, results pertaining to whether FA depends on the characteristics of individuals or on their ecological conditions are mixed (e.g., Smith et al. 1982; Solberg and Sæther 1993; Borges 2000). The use of inadequate sample size (e.g., Babbitt et al. 2006), the lack of using rigorous protocols to control measurement errors (e.g., Bjorksten et al. 2000; Palmer and Strobeck 2003), along with the complex relationship between FA and stress conditions are all factors that may account for the considerably heterogeneous results found to date (Van Dongen 2006).

Darwin's (1871) theory of sexual selection provides an explanation for the evolution of extravagant differences between males and females in several phenotypic traits. In this context, one of the most evident examples of secondary sexual traits in vertebrates is represented by antlers and horns of ungulates. Shape and size of male weapons are largely driven by selection operating through male–male competition over females (Geist 1966; Andersson 1994; Caro et al. 2003). In female ungulates, the primary function of weapons, when present, is linked to antipredator defence (Stankowich and Caro 2009) rather than sexual competition (Bro-Jørgensen 2007), although intrasexual selection can occasionally occur (Robinson and Kruuk 2007; Stankowich and Caro 2009). Given that symmetry in antlers and horns may be related to fitness (i.e., individuals with high survival rate and dominance status are characterized by low levels of FA and preferably selected as mates, see Møller et al. 1996; Pélabon and van Breukelen 1998) and thus carry evolutionary consequences, it is important to disentangle all factors that may affect the stable development of weapons and influence individual life histories and population dynamics in large herbivores.

Although the negative effects of developmental stressors on perfect bilateral symmetry are generally acknowledged, the scientific community is still skeptical about the widespread use of FA as a proxy for health, fitness, and behavior in response to stressors. This is largely due to the heterogeneous results pertaining to FA and its physiological and behavioral correlates (see Van Dongen 2006 and Knierim et al. 2007 for a review), indicating that the relationship between FA and stress conditions may be weaker and more complex than first thought (Van Dongen 2006). Even though a number of studies linked FA with fitness indicators (reviewed in Møller 1997) and mate choice (e.g., Møller and Thornhill 1998; Thornhill and Møller 1998), several other investigations yielded negative results and a series of reviews questioned such connection (e.g., Clarke 1998; Houle 1998; Palmer 1999; Simmons et al.1999; Bjorksten et al. 2000; Borges 2000; Kruuk et al. 2003). Given the mixed results of previous research, it is necessary to conduct further studies on different species to check for any general FA patterns. For this reason, we investigated ecological factors and individual characteristics that are related to FA in Alpine chamois, *Rupicapra rupicapra*, an ungulate in which male and female horns show limited sexual dimorphism. This study allows us to evaluate whether horn development in males and females is influenced by individual/population characteristics and environmental/climatic stressors in a similar way—an approach that is rarely applied to the study of FA.

We formulated the following predictions (P_x) regarding the different factors potentially influencing horn developmental stability:

(P1) Since about 60–70% of horn growth occurs during the first year and a half of life in both males and females (Bassano et al. 2003; Rughetti and Festa-Bianchet 2010, 2011), we expected no increase in horn length asymmetry with age;

(P2) Although the Alpine chamois is a relatively sexually monomorphic mountain ungulate, horns serve different purposes for males and females. Thus, we expected males to invest more than females in the stable development of this secondary sexual trait, as the expression of ornaments may affect their individual fitness and reproductive success (e.g., Geist 1966; Andersson 1994; Caro et al. 2003);

(P3) Since high quality individuals can sustain the cost of developmental stability, we expected a negative association between FA and individual body mass (e.g., Møller et al. 1996);

(P4) Chirichella et al. (2013) demonstrated that soil characteristics may affect horn development in Alpine chamois. Pastures on calcareous substrates have a higher grazing value than those on siliceous substrates (Rameau et al. 1993; Michalet et al. 2002; Cavallero et al. 2007). Thus, we may expect herbivores grazing on calcareous substrates to be in comparatively better condition and to exhibit higher quality secondary sexual traits. Moreover, high summer temperature and long snow cover duration can affect horn development since they account for both the decrease in meadows quality (depending on the availability of water and direct solar radiation) and the increase in energy expenditure for thermoregulation activities (e.g., Forchhammer et al. 1998). In addition, a high level of intraspecific competition (i.e., areas with high local densities) may increase environmental stress (e.g., Serrano et al. 2008). Thus, we expected FA to increase with harsh conditions, such as the maximum temperature in July during the first summer of Alpine chamois' life, snow cover duration during their first winter, low levels of pasture quality (i.e., siliceous substrate), and high local densities.

Materials and methods

Study area

This study was carried out in the Central-Eastern Alps, in the South-Western part of the Trento Province (1432.31 km^2-wide area; lat. 46° 10′ N, long. 10° 45′ E), Italy. The study area was subdivided into 7 hunting districts (Fig. 1) where chamois hunting using rifles was

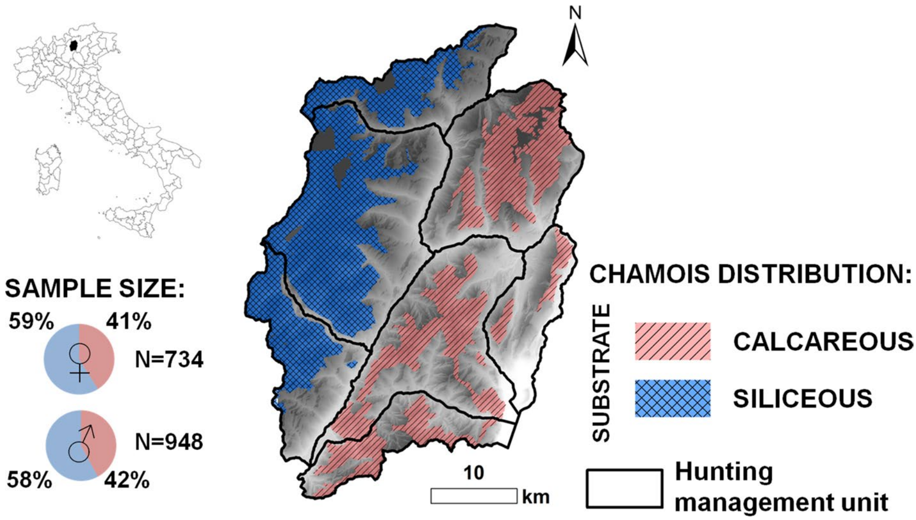

Fig. 1 Map of the study area (South-Western part of Province of Trento, Central-Eastern Alps, Italy). The 7 hunting districts where 1682 chamois ($N_{♀}=734$; $N_{♂}=948$) were legally shot during 2 consecutive years are shown in the digital elevation model of the study area (darker colours correspond to higher elevation above sea level). The species distribution was classified according to the geological substrate (Trento Province Official data; geological categories were reduced by authors)

allowed from mid-September to mid-December. The 7 hunting districts coincide with the main mountain groups and their boundaries are generally constituted by such natural barriers as the bottom of the valleys, which either prevent or strongly limit movement of animals between one area and another. We further subdivided the districts into 92 municipal reserves (hunting management units). Every summer, i.e., after the birth period and prior to the hunting season, local population density was estimated by means of block count census in all municipal reserves of the 7 hunting districts. Block count census method entailed a coordinated and simultaneous count of all individuals across the different blocks of each hunting district. Within each block of our study area, pairs of rangers with prior experience with Alpine chamois and the area to scan performed the counts from vantage points in open habitats when the weather was favourable (i.e., good visibility, lack of strong wind, rain, and snow). Each pair of observers was in radio contact with the observers of the nearby monitoring areas and had binoculars, spotting scopes, and appropriate maps. Hunting was regulated through licenses issued by local wildlife boards. Hunting quotas in each district were set for specific sex-age classes. During this study (2015–2016), hunting quota represented 12% of the estimated population and 95% of the quota was met. Wildlife managers' inspection of each chamois shot was mandatory in each municipal reserve.

Elevations range from 65 m above sea level (a.s.l.) at the Southern border around Lake Garda to 3558 m a.s.l. in the Presanella Massif. Forests cover the area up to the treeline at about 2000 m, above which it consists of Alpine meadows, rocky outcrops, scree fields, and open rock faces. Given its remarkable geological and geomorphological diversity, the area is recognised as UNESCO Global Geopark. The Eastern part of the Geopark presents a Mesozoic coverage of the Dolomites characterized by calcareous rock, while the Western one is mainly composed of Batholite with a siliceous character. Among the chamois management areas, Adamello, Destra Chiese, and Presanella are characterised by nutrient-poor siliceous vegetation, while Brenta, Cadria Altissimo, Misone-Casale, and Ledro are characterised by nutrient-rich calcareous vegetation (see Chirichella et al. 2013 for further details; Fig. 1). Chamois living in different management areas show individual genetic signatures, thus suggesting that they are independent units (Scandura et al. unpublished data). Typical meadows in siliceous areas are dominated by *Festuca scabriculmis* and *Carex curvula*, whereas those in calcareous areas are composed of *Sesleria albicans* and *Carex firma* (Adamello Brenta Nature Park—official data).

During the study period, red deer (*Cervus elaphus*) and roe deer were abundant but seldom used the areas above the tree line (2000 m a.s.l.), which were usually populated by the Alpine chamois. In contrast, mouflon (*Ovis aries*) and Alpine ibex (*Capra ibex*), which potentially used chamois areas, were limited to few small locations, the two species having been introduced and reintroduced in the recent past only.

Data collection and analyses

We measured the right and left horn length of 1682 Alpine chamois ($N_{females}=734$; $N_{males}=948$) shot during 2 consecutive hunting seasons (2015 and 2016). Date of culling, sex, age (calculated by counting horn annuli), body mass, and hunting municipal reserve were recorded for all chamois which were legally shot during the annual autumn harvest (September-December period) in the 7 hunting districts of our study area. Body mass was expressed as dressed weight (i.e., live weight minus viscera and bleedable blood). Dressed weight in all sex and age classes (1, 2, 3, 4 and 5 + y.o.) decreased during the hunting season (1st September—15th December). Hunting date was coded from 0 to 105, with 1st September as day 0. Linear regression was used to set to day 0 the dressed weight of males and females, according to different age classes in order to avoid the effect of date of data collection in our analysis. Right and left horn length was measured to the nearest 0.5 millimetres on the front side by 2 researchers by using a flexible ruler. Repeated measures (n = 3; Palmer 1994) were taken on a subsample of 50 horns in order to test (Paired-Samples *t* Test) for the effect of data collector. An error lower than 3.5% was considered negligible for secondary sexual traits in ungulates (Kruuk et al. 2003). The average measurement error was lower than 0.8% for both collectors. No difference between data collected by the 2 measurers was reported (Paired-Samples *t* Test: $t_{(2)49}=0.41$, $p=0.79$). Thus, data collector was not included in our model selection procedure as a random effect.

We calculated FA and verified its normal distribution, derived as the absolute value of the difference between right and left horn length for each animal. We analysed FA variation in relation to potential stressors for this species (see Table 1 for the complete list of predictors).

We used generalized additive mixed models (GAMM; Poisson family) to identify the factors affecting absolute FA, implemented in gamm4 package (Wood 2017; Wood and Scheipl 2017) in R software (www.r-project.org) and fitted models by means of maximum likelihood estimation (Wood 2006, 2008; Wood and Scheipl 2017). We used hunting district (N = 7) as a random factor (Machlis et al. 1985) and *z*-transformed continuous independent variables in order to compare the relative effects of predictors on the developmental stability of horn length. We modelled the effect of all continuous predictor variables as natural cubic spline functions. When the estimated degree of freedom of a predictor variable was 1 and the graphical inspection confirmed a linear relationship with the response variable, we refitted the model by omitting the smoothing function. We fitted models with all possible biologically meaningful combinations of independent variables

Table 1 Predictor variables potentially influencing fluctuating asymmetry (FA) in Alpine chamois horn length

Independent variable	Description	Prediction
Sex	[f] = female; [m] = male	Lower FA in males [P_1]
Age	Number of years by counting horn annuli	Stable FA (no age effect) [P_2]
Dressed weight	Dressed weight (i.e., live weight minus viscera and bleedable blood) to the nearest 0.1 kg	Positive correlation between FA and individual quality [P_3]
Local density[a]	Number of individuals/100 ha recorded during developmental period of each individual (mean value in the first 3 years of life)	FA negatively affected by higher local density [P_4]
July temperature[b]	Mean July daily maximum temperature during the first summer experienced	FA negatively affected by maximum summer temperature [P_4]
Now cover duration[c]	Number of days with more than 10 cm of snow on the ground from November to early May during the first winter experienced	FA negatively affected by winter harshness [P_4]
Substrate[d]	[c] = calcareous; [s] = siliceous	Lower FA on calcareous substrate [P_4]

Combined effects of factors (i.e., sex and substrate) with each covariate (i.e., age, dressed weight, local density, July temperature and snow cover duration) were tested

[a]Data availability: Trento Province Official data; period of data collection mid July-mid August (block count census)

[b]Data availability: Data from 10 weather station (Forecasts and Organization Office—Civil Protection Infrastructures Department of the Province of Trento—www.meteotrentino.it)

[c]Data availability: Five snow-gauges supplied data on snow cover duration (Forecasts and Organization Office—Civil Protection and Infrastructures Department—www.meteotrentino.it). These covariates were associated according to municipal reserve considering the weather station closest to the reserve

[d]Data availability: Trento Province Official data; geological categories were reduced by authors

(i.e., combination of factors with all covariates, see Table 1 for details). We assessed collinearity by using variance inflation factors (VIFs) and excluded all the models with VIFs > 3, as suggested by Zuur et al. (2010).

We used the Akaike Information Criterion (AIC; Burnham and Anderson 2002; Symonds and Mousalli 2011) to select the best fitting models (ΔAIC ≤ 2). We refitted the final set of models by using the restricted maximum likelihood estimation and obtained the effect of each variable included in this confidence set of models via model averaging (model.avg function in MuMIn package for R; Burnham and Anderson 2002; Symonds and Mousalli 2011; Barton 2015). We validated models by inspecting the residual plots, as described by Zuur et al. (2009). Following Magee (1990), to describe how the models fitted the data observed, we estimated R^2 as:

$$R^2 = 1 - \exp\left[-2/n \times \left(\log \mathrm{L_M} - \log \mathrm{L_0}\right)\right],$$

where n is the number of observations, $\log\mathrm{L_M}$ is the standard log-likelihood of the model (which includes fixed and random effects), and $\log\mathrm{L_0}$ is the standard log-likelihood of the intercept-only model. Statistical analyses were performed in R version 3.4.4 (R Core team 2018).

Results

We found no consistent left or right bias in horn length, that is, there was no significant difference in the number of individuals with left horns longer than right ones, and vice versa. In our samples, 685 individuals (41% of the total sample) had right horns longer than left ones, 303 individuals (18% of the total sample) had horns of equal length, and 694 individuals (41% of the total sample) had right horns shorter than left ones.

Average FA within the study area was normally distributed around a mean value that was not significantly different from zero (Skewness = −0.107, SE = 0.06; Kurtosis = −0.055, SE = 0.119; Shapiro–Wilk normally test: W = 0.98, p = 0.09; see Figs. 2 and S1).

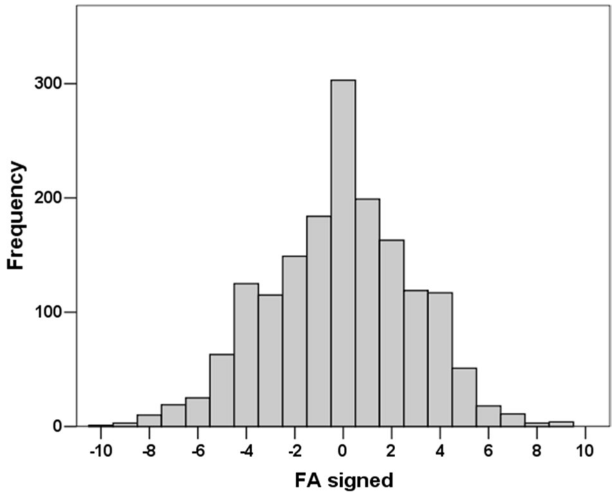

Fig. 2 Frequency of signed fluctuating asymmetry (FA) of horn length in 1862 Alpine chamois shot during 2 consecutive hunting seasons (2015–2016) in 7 hunting management units (South-Western part of Province of Trento, Central-Eastern Alps, Italy)

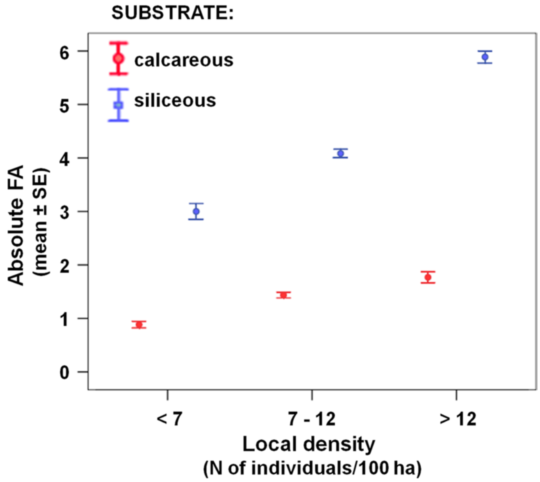

Fig. 3 Effect of local density on absolute fluctuating asymmetry (FA) of horn length in 1682 ($N_{calcareous}=700$; $N_{siliceous}=982$) Alpine chamois legally shot during 2 consecutive hunting seasons (2015–2016) in 7 hunting management units (South-Western part of Province of Trento, Central-Eastern Alps, Italy)

Table 2 Parameter estimates of the final set of generalized additive mixed models (GAMM; $\Delta AIC \leq 2$, see Table 3) predicting absolute fluctuating asymmetry (FA) in Alpine chamois horn length. The effect of each variable included in this confidence set of models was obtained via model averaging (model.avg function in MuMIn package for R; Burnham and Anderson 2002; Symonds and Mousalli 2011; Barton 2015)

Parametric coefficients	Estimate	SE	*t*	*p*
Intercept	2.499	0.0577	43.324	< 0. 001
Local density	0.152	0.067	2.286	0.022
July temperature	0.075	0.048	0.789	0.123
s (snow cover duration)[a]	–	–	–	0.046
Substrate [calcareous]	− 1.293	0.045	− 28.852	< 0. 001
Local density:substrate [calcareous]	− 0.100	0.041	− 2.432	0.015

[a]Coefficient was modelled by using a smoothing function (estimated degrees of freedom = 2.128; F = 2.169)

Absolute FA was positively affected by local population density (Fig. 3) and snow cover duration during the individuals' first winter (no linear relation; Table 2, Fig. 4). Moreover, lower level of trophic conditions (i.e., siliceous substrate) promoted the increase in unstable development in the Alpine chamois population studied (Table 2, Figs. 3, S2 in online resources). The combined effect of substrate and snow cover duration was also important (Table 2). The effect of summer temperature in shaping absolute FA reported in our best set of models was not significant (Tables 2, 3; P_4 verified) and no individual trait (i.e., sex, age, and dressed weight) was related to absolute FA (P_1, P_3 not verified; P_2 verified) (Table 2, Figs. 5, S2 in online resources).

Discussion

FA was not found to be driven by individual characteristics, but rather by climatic/environmental stressors experienced early in life. Indeed, sex, age, and dressed weight did not affect absolute FA in horn length. On the other hand, snow cover duration during the

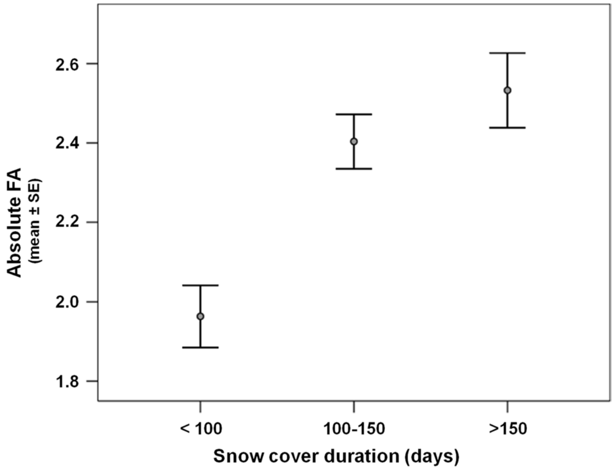

Fig. 4 Effect of snow cover duration on absolute fluctuating asymmetry (FA) of horn length in 1682 Alpine chamois legally shot during 2 consecutive hunting seasons (2015–2016) in 7 hunting management units (South-Western part of Province of Trento, Central-Eastern Alps, Italy)

Table 3 Set of the most parsimonious models showing variation in absolute fluctuating asymmetry (FA) of Alpine chamois horn length

Component models	AIC[a]	ΔAIC[b]	Wt[c]
[1] Local density + s(snow cover duration) + substrate + local density:substrate	3620.281	0.000	0.658
[2] Local density + july temperature + s(snow cover duration) +sub-strate + local density:substrate	3621.592	1.311	0.342

[a]Akaike Information Criterion

[b]AIC (respective model)-AIC (the best model). We present only the top model set containing models with ΔAIC ≤ 2

[c]Akaike weights

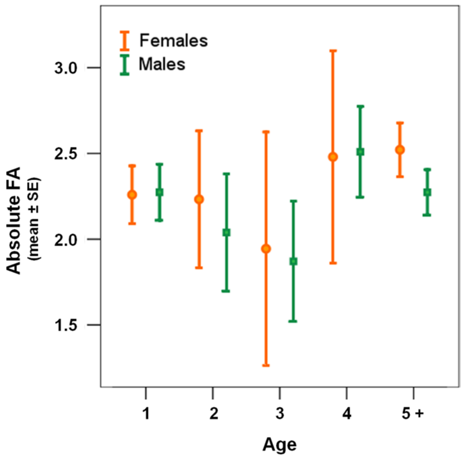

Fig. 5 Effect of sex ($N_{♀}=734$, $N_{♂}=948$) on absolute fluctuating asymmetry (FA) of horn length in Alpine chamois according to different ages. Individuals were shot during 2 consecutive hunting seasons (2015–2016) in 7 hunting management units (South-Western part of Province of Trento, Central-Eastern Alps, Italy)

individuals' first winter, low levels of trophic conditions, and high local population density influenced the increase in unstable development in the Alpine chamois population studied.

Effects of individual characteristics

FA in Alpine chamois horn length was not related to age. Unlike antlers in cervids, horn growth in bovids is a cumulative process which reflects the environmental and body conditions experienced by individuals throughout their life history (Douhard et al. 2017). Since FA neither increases nor decreases with age and evidence showed that about 60–70% of horn growth in both male and female Alpine chamois occurs during their first year and half of life (Bassano et al. 2003; Rughetti and Festa-Bianchet 2010, 2011), our study indicated that for this species bilateral symmetry in horn length was mostly achieved during the developmental period (i.e., during the early stages of the individuals' life).

In female ungulates, the primary function of weapons is usually linked to antipredator behaviour (Stankowich and Caro 2009). Thus, horn symmetry should be less evident in females than in males, in which the expression of ornaments may affect individual fitness and reproductive success. Contrary to our expectation, FA in males and females is influenced by environmental and climatic conditions in the same way. With respect to natural selection, horns supposedly provide advantages in competition during male–male combat (Lundrigan 1996). Likewise, Locati and Lovari (1991) suggested that in Apennine chamois, *Rupicapra pyrenaica ornata*, dominant males have longer horns than their competitors. Moreover, in other bovids, mating success was found to be inversely related to horn asymmetry (Møller et al. 1996; Møller and Swaddle 1997). In addition, the presence of horns is supposed to contribute to defence against predators and affect the quality and quantity of social interactions and relationships in a herd. Moreover, horns in females may be used to establish hierarchies (Barroso et al. 2000) and to gain access to resources (Robinson and Kruuk 2007). In this respect, as Côté and Festa-Bianchet (2001) reported for mountain goats, horns of dominant females are more symmetrical than those of subordinate females, thus suggesting that developmental stability (leading to low FA) may be related to an individual's ability to achieve a high social status. The same FA in horns of male and female Alpine chamois suggests that in this almost monomorphic species (Rughetti and Festa-Bianchet 2011) similar pressure is exerted on this weapon in both sexes, which is a quite peculiar finding among ungulates.

Since high quality individuals can sustain the cost of developmental stability, a negative association between FA and individual body mass was expected (e.g., Møller et al. 1996). Contrary to our prediction, FA in Alpine chamois horn length was not inversely related to dressed weight. However, given the importance of having a stable development during the early stages of life, FA may be affected by the conditions individuals experienced as yearlings. For example, a negative relationship between FA in antler length and body weight was documented in yearling white-tailed deer (Smith et al. 1982). In our dataset, dressed weight of adult individuals was recorded at the time of killing and no information about their conditions in the early stages of their life was available (i.e., the cross-sectional dataset did not allow for associating yearling body mass to each culled adult). In this respect, studies on the relationship between FA in ungulate horns and antlers and the different indicators of individual quality produced contradictory results (Arcese 1994; Malyon and Healy 1994; Folstad et al. 1996; Møller et al. 1996; Markusson and Folstad 1997; Lagesen and Folstad 1998; Pélabon and Joly 2000; Putman et al. 2000; Côté and Festa-Bianchet

2001; Ditchkoff et al. 2001; Kruuk et al. 2003). Therefore, further investigations may help understand the role of individual quality in symmetrical horn development.

Effects of environment and climate

Our results show that FA is correlated with environmental stress experienced early in life, thus supporting the prediction that it is generated by developmental instability, as proposed by Leary and Allendorf (1989). Indeed, FA increased in individuals living on siliceous substrates (i.e., in areas with low pasture quality). As Chirichella et al. (2013) reported in the same study area, regardless of sex, chamois living on a siliceous substrate had shorter horns than those living on a calcareous one, thus showing how the substrate (and the ecological conditions related to it) may affect horn growth. Likewise, meadow quality on a calcareous substrate is generally assumed to be higher than that on a siliceous one on account of (1) higher species richness (Grime 1979; Michalet et al. 2002; Cavallero et al. 2007), (2) higher nutrient availability related to higher plant productivity (Duchafour 1989, 1997; Gensac 1990; Rameau et al. 1993), and (2) the structural characteristics of the plant communities growing on siliceous substrates which can reduce digestion efficiency (Laca et al. 2001). Thus, herbivores grazing on a calcareous substrate may be positively affected in terms of energy intake and therefore exhibit larger secondary sexual traits (Chirichella et al. 2013). We showed that calcareous substrates (and the ecological conditions related to them) can promote a sustained and stable growth.

Previous studies showed that such climatic factors as winter conditions (Mysterud et al. 2005; Chirichella et al. 2013) and temperatures (Schmidt et al. 2001; Giacometti et al. 2002) can influence horn and antler growth. Moreover, as Chirichella et al. (2013) reported, horn length of chamois shot in areas with high snow cover decreases in both sexes. FA may reflect environmental stress and, accordingly, increases when environmental conditions are harsh either during the development of the horns or during early development of the individual (Hoffmann and Parsons 1991; Parsons 1992). In our study, FA increased when the individuals' first winter was harsh. Indeed, harsh winters are generally thought to affect juvenile survival and body conditions by increasing the likelihood of starvation owing to a combination of high thermoregulatory costs and low forage availability due to deep snow cover (Forchhammer et al. 1998). The height and duration of snow cover were reported to affect the costs of locomotion (Parker et al. 1984) and the availability of browsing (Post and Stenseth 1999). As for summer conditions, our results indicated that the effect of high temperature on absolute FA was not significant. Further investigations on a wider spatial and temporal scale are required and may be useful to predict the effect of climate change on the stable development of young individuals. In fact, the direct effect of high summer temperature on weapon development has not been investigated so far. However, the negative effect of this variable (owing to suboptimal nutrition) was described by Crête and Courtois (1997) on moose (*Alces alces*) population dynamics and by Chirichella et al. (2013) on chamois horn growth.

Finally, high population density causes stress by increasing intraspecific competition for food (Stewart et al. 2005). While density-dependent effects on phenotypic characters have been widely reported in many ungulates (e.g. Forchhammer et al. 2001; Chirichella et al. 2013), almost no information on the response of developmental stability to changes in population density is available. The present study found that FA in Alpine chamois horn length is a valuable indicator of their current local density condition. Our findings support previous studies showing the plasticity of skeletal growth in response to environmental challenges (e.g., Pélabon and van Breukelen 1998 for asymmetry levels in roe deer antlers; Serrano et al. 2007 for metacarpus development in fallow deer; Serrano et al. 2008 for jaw morphology).

In conclusion, the developmental environment seems to be more important than individual characteristics for FA in this species, although this might depend on the parameters being measured. The deviations from bilateral symmetry may be used as a proxy to evaluate whether a population is exposed to stressful conditions. To better understand the relationship between FA and life-history characteristics, further studies should compare individuals under conditions of resource scarcity with populations living in captivity and in high quality habitats with no negative impacts of environmental and climatic conditions. These data should be related to the dynamics of the populations studied. Moreover, further research on species with different degrees of sexual dimorphism might be useful to ascertain whether the absence of sex differences in FA in sexually monomorphic species is a general pattern or a peculiar trait of Alpine chamois.

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