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# Did the Late Pleistocene climatic changes influence evolutionary trends in body size of the red deer? The study case of the Italian Peninsula

Luca Pandolfi [a,*], Leonardo Maiorino [a,b], Gabriele Sansalone [a,b]

[a] Dipartimento di Scienze, Università Roma Tre, Largo San Leonardo Murialdo 1, 00146, Rome, Italy
[b] Center for Evolutionary Ecology, Largo San Leonardo Murialdo 1, 00146, Rome, Italy

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ABSTRACT

Variations in the body size of red deer (*Cervus elaphus*) have been reported by several authors from several European fossiliferous localities for the Late Pleistocene and Holocene. Recently, several contributions focused on body size variation of red deer populations from the Italian Peninsula. Evolutionary trends of phenotypic traits may follow distinct tempos and modes of evolution such as Brownian, Ornstein–Uhlenbeck, stasis or random walk. Here, we investigated which evolutionary model better explained the temporal trend in body size of *C. elaphus* ssp. from the Italian Peninsula using modern statistical tools. We also tested the potential relationships between climate change and geographical variation through the Late Pleistocene. Our sample includes 1090 specimens from several peninsular Italian localities. For each specimen, we extracted the Size Variation Index calculated on postcranial elements. We found that stasis was the model better explaining the body size evolution in *C. elaphus*. We also found a nonsignificant interaction between body size and climate, whereas we detected a significant relationship with geography. We hypothesized that the red deer phenotypical plasticity was able to mitigate the selective constraints driven by climatic changes and geographical variability through the Late Pleistocene and Holocene, therefore returning a no neat variation in body size.

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## 1. Introduction

Variations in body size of European red deer populations have been reported for the Pleistocene by Lister (1984) and for the Holocene by Hornberger (1970), Riedel (1976) and Rosvold et al. (2014). Di Stefano et al. (2015) recently recorded body size variations of the red deer during the Late Pleistocene and Holocene from the Italian Peninsula. Among the Late Pleistocene large mammals of Italy, the red deer is relatively abundant in several fossiliferous localities throughout the Peninsula (Petronio et al., 2011; Di Stefano et al., 2015) allowing to evaluate geographic and temporal variations in body size. During the Late Pleistocene and the Holocene, only one species of red deer occurred in the Peninsula (Di Stefano and Petronio, 2002; Petronio et al., 2011; Di Stefano et al., 2015), whereas different haplogroups were established by Sommer et al. (2008), Banks et al. (2008) and Skog et al. (2009).

Evolutionary trends through time in mammalian species have been investigated by several authors using different statistical strategies (Piras et al., 2009, 2012; Magniez, 2010; Desantis et al., 2011; Nishioka et al., 2011; Pandolfi et al., 2011, 2013; Raymond and Prothero, 2011; Stefaniak et al., 2012; Lozano-Fernandez et al., 2013; Mazza and Bertini, 2013; Meachen et al., 2014; O'Keefe et al., 2014; van der Made et al., 2014; Sansalone et al., 2015). Several works have focused on the sequences of fossil populations in order to investigate phenotypic changes and their causes through the Pleistocene, a period characterized by dramatic climatic changes (Pandolfi et al., 2011; Mazza and Bertini, 2013; van der Made et al., 2014; Pandolfi and Tagliacozzo, 2015; Sansalone et al., 2015). However, a few works were aimed at testing the influence of geography and climate on these phenotypical variations by means of modern statistical tools (Sansalone et al., 2015).

Since 1972, paleontologists have focused on the relevance of stasis in traits evolution (Eldredge and Gould, 1972). Stasis is a central point inside the Punctuated Equilibria Theory (Eldredge and Gould, 1972; Gould and Eldredge, 1977; Gould, 2002; Eldredge et al., 2005). The major focus of this evolutionary model is that the phenotypes are stable through time and no directional trends are observable. The causes of the stasis could be (a) absence of variability; (b) balancing selection; (c) developmental constriction; (d) habitat tracking; and (e) population structure: a species being structured in semi-isolated metapopulations. Different isolated populations experienced different selective pressures thus returning a no neat phenotypic change in time (Wright, 1932; Eldredge and Gould, 1972; Gould and Eldredge, 1977; Gould, 2002; Eldredge et al., 2005).

Most paleontological studies set apart between patterns of stasis, random walk, and directional evolution. Stasis *sensu strictu* can be defined as when the variance of the total time series sample is not significantly larger than that of a single population in a time lapse

* Corresponding author. Tel.: +39 0657338000.
*E-mail address:* luca.pandolfi@uniroma3.it (L. Pandolfi).

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(Wood et al., 2007; Piras et al., 2009, 2012; Sansalone et al., 2015). Sansalone et al. (2015) recently evidenced a non-directional trend in the lower carnassials length of the Italian *Canis lupus* from the Late Pleistocene.

In this framework, we propose to investigate the evolutionary models of *Cervus elaphus* ssp. body size from Italian Peninsula in order to unveil if different trends occur with respect to wolves. We also tested the presence (if any) of relationships between climate change, geographical variation and body size through the Late Pleistocene–Holocene. We used the Size Variation Index (Di Stefano et al., 2015) calculated on postcranial elements of the red deer, from several Italian fossiliferous localities, in order to explore and better understand the factors influencing the evolutionary dynamics of body size, through time, using modern statistical tools.

## 2. Material and methods

### 2.1. Material

We considered 1090 linear measurements (mm) of the postcranial material referred to as *C. elaphus* ssp. and reported by Di Stefano et al. (2015 and references therein) and Ruiu and Tagliacozzo (in press).

Details on the sample, localities and ages are reported in Table S1.

We used the Size Variation Index (SVI) as a body size proxy. This metric allows a comparison of the size of the whole skeleton and it has been commonly used in archaeozoology and, recently, in palaeontology (Uerpmann, 1982, 1986; Meadow, 1986, 1999; Eisenmann and Kuznetsova, 2004; Di Stefano et al., 2015). Moreover, this index is particularly useful when the fossil remains are numerous but fragmented (for further details see Fig. S1 and Supplementary material). Fig. 1 summarizes the geographic distribution of our sample size. The sample was divided into three groups, which reflect three different geographic areas, Northern, Central and Southern Italy, following Di Stefano et al. (2015). The pair-wise comparison between these groups was performed considering the entire Late Pleistocene and Holocene sample for each area.

### 2.2. Methods

We applied the model-based functions available in "paleoTS" R package (Hunt, 2011) to test different evolutionary patterns. This statistical tool provides the best-fitting evolutionary model of data (maximum likelihood) after testing four main phenotypic models of evolution: unbiased random walk (URW), general random walk (GRW), stasis *s.s.* and Ornstein–Uhlenbeck (OU). URW indicates a fluctuation of the phenotype (population mean values) with no directionality, where the variance of the entire sample is larger than the individual population's variances. The GRW model indicates a phenotypic fluctuation (population mean values) with a significant directionality; the trend can be typically directional or related to a directional random walk. Stasis *s.s.* indicates an evolutionary model wherein no trend appears in time and the variance of the entire sample is not larger than that of the individual populations. OU represents a random walk evolutionary model with a central tendency to an adaptive optimum of the phenotype. However, a further case may occur when the total sample variance is larger than individual interval variance with no directionality (Sansalone et al., 2015).

We selected the best-fitting model using the Akaike Information Criterion (AIC; Akaike, 1974; Hurvich and Tsai, 1989; Anderson et al., 2000). AIC measures the relative quality of a statistical model for a given set of data. It represents the estimate of the information lost when a given model is used to represent the process that generates data. AIC offers a trade-off between the goodness of fit of the model and its complexity. The preferred evolutionary model is the one with the lowest AIC value.

Finally, we performed a permuted analysis of variance (perANOVA; in order to deal with unbalanced sample size), using the function adonis() in "vegan" R package (Oksanen et al., 2013), to investigate if any size differences occur among the red deer populations in space

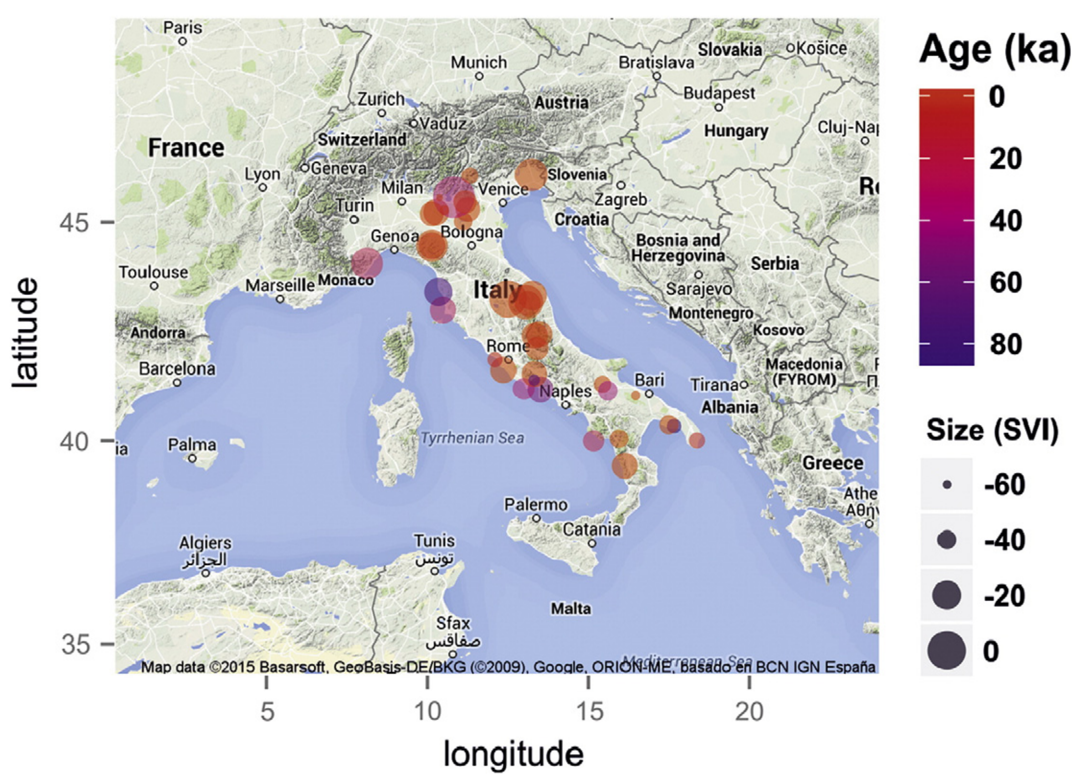


**Fig. 1.** Geographic position of the localities yielded postcranial material and considered in this work (see Table S1). The mean dimension of the SVI value for each locality and its age are also reported.

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