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Morphometric characterization of Mesola red deer *Cervus elaphus italicus* (Mammalia: Cervidae)

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Abstract
The red deer of the Bosco Mesola Nature Reserve (northern Italy) constitute a population with relevance for zoogeography, genetics and conservation. We have analysed morphometrics of Mesola red deer (body weight, craniometry, stature, antler conformation and size) over a *c.* 30 year period (1980–2012), to (i) describe in detail their physical traits, (ii) compare them with those of other European populations and (iii) assess the effects of conservation actions on biometric measures of individuals. Mesola red deer were on average 15–50% lighter and at least 8–15% smaller than other European red deer. The sexual size dimorphism was low and significant only for adults. Body growth rate was also slower than that of the other European populations. While the average relative production of antler bone tissue appeared not to be different from that of other European red deer, antlers of Mesola stags were small and scarcely branched, with short trez tines. Bez tine and crown were rare and present almost exclusively in fully mature stags (2.2 and 3.6% of antler beams in adult stags, respectively). Environmental improvements led to significant favourable effects on antler size and complexity. All observed individuals had a distinct but slight spotting of the summer coat. These morphological characteristics, coupled with genetic peculiarities, make the Mesola red deer unique, deserving special protection.

Keywords: *Antlers,* Cervus elaphus*, conservation, morphometrics, ungulates*

Introduction

Morphometrics can give a detailed description of the physical characteristics of a population, which can be influenced by genetic and/or environmental factors (Anderson et al. 1974; Feldhamer et al. 1984; Terada et al. 2012). The long-term analysis of morphometric measures of a population can also help to assess changes in traits, which could be determined by e.g. variation of autoecological/sinecological or climatic factors (see Moyes et al. 2011 for birth weight and antler weight changes over time in Scottish red deer). In populations with conservation relevance, the monitoring of morphometrics could help to assess how individuals react to conservation measures (e.g. increase in body size).

The Western red deer *Cervus elaphus* Linnaeus, 1758 is among the most investigated mammal species, with a very large distribution range, encompassing Europe, North Africa and western and central Asia (Mattioli 2011). However, studies on its morphometry are rare (cf. Ingebrigsten 1924; Beninde 1937a; Mystkowska 1966; Lowe & Gardiner 1974 for craniometric investigations). If we exclude research derived from the routine monitoring of body weights and antler size on harvested individuals of hunted populations (Isakovic 1969; Drechsler 1980; Radler & Hattemer 1982; Bečejac et al. 1984; Mysterud et al. 2001), very few investigations have reconstructed the morphological and biometric characteristics of a red deer population (cf. Langvatn 1986). In particular, while some studies have been carried out on populations from central-northern Europe, information is scarce for red deer living in southern Europe (Mattioli 1993; Azorit et al. 2002; Mattioli et al. 2003; Martínez et al. 2005; Torres-Porras et al. 2009). Thus, the variability of this species in morphological and biometric features still remains poorly known.

The red deer *Cervus elaphus italicus* (Zachos et al. 2014) inhabiting the Bosco Mesola Nature Reserve

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(northern Italy) constitute a population with relevance for zoogeography, genetics and conservation (Lovari & Nobili 2010; Zachos & Hartl 2011). They are the only native red deer of peninsular Italy (Castelli 1941; Mattioli 1990; Mattioli et al. 2001) and show a mitochondrial DNA genotype with a sequence significantly different from those of all other populations of red deer (Lorenzini et al. 2005; Hmwe et al. 2006). Previous studies on morphometry of antlers, and some biometric measures, have suggested that these deer show some morphological peculiarities (small body size, reduced sexual dimorphism, persistent spotting in the summer coat, small antlers of simplified design, low reproductive performance; Mattioli 1990, 1993; Mattioli et al. 2003). Mesola red deer are threatened, because of (i) their very small distribution range (*c.* 1000 ha) and numbers (less than 200 individuals, in 2010; Ferretti & Mattioli 2012), (ii) their very low genetic variability and (iii) the impact of a dense population of sympatric fallow deer *Dama dama* on their natural food resources (Lorenzini et al. 1998; Mattioli et al. 2003; Zachos et al. 2009; Lovari & Nobili 2010; Zachos & Hartl 2011). In the last 15 years, conservation measures have been implemented (e.g. culling of fallow deer, recurrent mowing in the pastures, reseeding of pastures and winter supplementary feeding; Mattioli et al. 2003), which should be expected to have led to environmental improvements for red deer. In turn, physical conditions of red deer should improve (Mattioli et al. 2003), resulting in an increase of e.g. body weight, antler size and complexity.

Here we have collected and analysed all the available data on morphometrics of Mesola red deer, over a *c.* 30 year period (1980–2012), to (i) describe in detail the physical traits of Mesola red deer, (ii) compare them with those of other European populations and (iii) assess the effects of conservation actions on biometric measures of individuals.

Methods

Study area

The Bosco della Mesola Nature Reserve (1058 ha) is an enclosed area located in the Po river delta (Ferrara Province, northern Italy; Figure 1). This reserve is composed of woodland (93%, mainly holm oak *Quercus ilex* with manna ash *Fraxinus ornus*, hornbeam *Carpinus* spp., Caucasian ash *Fraxinus oxycarpa*, pedunculate oak *Quercus robur*, aspen *Populus* spp. and elm *Ulmus* spp.), wetland (4%) and grassland (3%: dry and wet meadows, glades and artificial pastures; Mattioli et al. 2003). Fallow deer were introduced first in the 16th century and again between 1957 and 1965, after having been exterminated during World War II (Mattioli et al. 2003).

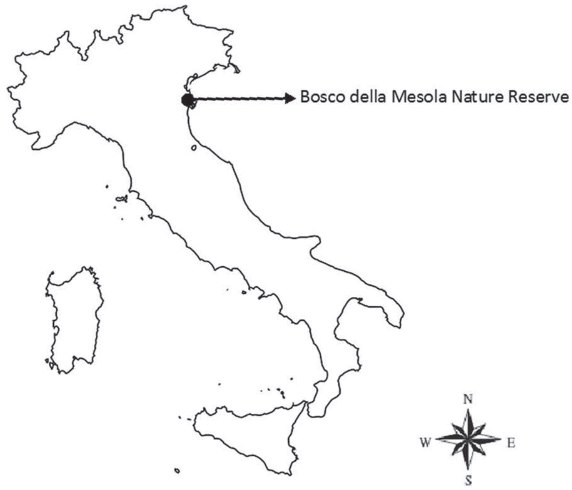

Figure 1. Location of our study area.

Morphometric analyses

To assess the morphometric characteristics of Mesola red deer, we used several datasets. Body weights were gathered during the capture sessions (1980–1991 and 1995–1999). Ratios of height at withers:head-trunk length and hind foot:head-trunk length (taken following Langvatn 1977, 1986; Mattioli & De Marinis 2009) were collected in 1995–1999 (see Mattioli et al. 2003 for descriptive statistics of the main somatic measures). Antler conformation (number and kind of tines per antler pair and antler beam) of the total stag population was recorded from 1982 to 2012. Every year (1980–2012), cast antlers were collected in late winter and spring and measured according to the CIC (Conseil International de la Chasse) rules (Trense et al. 1981), except for the bez tine (not included among the traits of the CIC formula), which was measured as the trez tine. Antler measurements were performed also for captured stags and animals found dead. Skulls were measured with a digital caliper to 0.01-mm precision according to von den Driesch (1976). Red deer age was determined exactly for individuals captured and marked when calves or yearlings. For other captured individuals, the age was estimated on the basis of tooth eruption, replacement and wear patterns (Wagenknecht 1984). For the other stags, age was estimated through visual assessment of body shape (body size and proportions, neck size and posture, head traits, length of pedicles; cf. Drechsler 1988). We recognized five biologically meaningful age classes of stags: calves, yearlings, subadults (2–4 years old), young adults (5–9 years old) and fully mature adults (> 9 years old) (Drechsler 1988), and four of hinds: calves, yearlings, young adults (2–4 years old) and fully mature adults (> 4 years old). Besides ear tags of captured animals, individual recognition was based on skin scars and coat colour patterns.

In 1996, environmental improvements (culling of fallow deer, recurrent mowing in the pastures, reseeding of pastures and winter supplementary feeding) were introduced, leading to favourable effects on physical conditions and population dynamics of the deer (Mattioli et al. 2003; Ferretti & Mattioli 2012). Thus, for the morphometric characterization of antlers we considered two sub-periods (Period 1: 1982–1996, before the conservation measures; Period 2: 1997–2012, i.e. after the beginning of conservation measures). We could not test the differences of body weights and somatic linear dimensions between periods, as our sample of captured deer was small for Period 2.

Body weights of adults, yearlings and calves of both sexes were normally distributed (Kolmogorov-Smirnov test: Z = 0.390–0.652; P = 0.790–0.982). For adults, yearlings and calves, sexual differences in body weights were tested through the t-test (Sokal & Rohlf 1995). For each age class and period, all biometric measures were normally distributed (Kolmogorov-Smirnov test: Z = 0.391–1.107; P = 0.172–0.998), except for the number of tines/antler beam (Z = 1.735–3.726; P < 0.006). We used linear models (Crawley 2007) to assess the effects of (i) age class, period and interaction age class × period on antler beam length, brow tine length, circumference at the burr, lower and upper circumference and antler beam weight, in adult stags; (ii) period on antler length, brow tine length and circumference at the burr, in subadult stags; (iii) period on antler length, in yearling stags. Simple and interactive effects of age class and period on the number of tines/antler beam of adult stags, as well as effects of period on number of tines/antler beam of subadult and yearling stags, were assessed through generalized linear models with Poisson errors (Crawley 2007).

Relationships between antler characteristics (antler beam length, antler beam weight, circumference at the burr and log-transformed number of tines per beam) were analysed through linear regressions (cf. McCullough 1982; Sokal & Rohlf 1995). Somatic ratios were compared between Mesola and those derived from a dataset on an Apennine red deer population of Alpine origin (S. Mattioli unpublished) by means of Mann-Witney U-tests (Sokal & Rohlf 1995).

Results

Body size

We collected 136 live body weights of Mesola red deer (1980–1999; Table I). Yearling stags reached 46% and yearling hinds achieved 63% of the adult weight, and the maximum mass was attained only after the age of 4 years for hinds and 9 years for stags. Adult stags were on average 43% heavier than adult hinds (t = –10.115, df = 72, P < 0.001). The heaviest recorded stag was 132 kg; the heaviest hind was 100 kg. Sexual size dimorphism was not apparent for yearlings (t = –0.336, df = 18, P > 0.05) and calves (t-test: t = –1.891, df = 27, P > 0.05).

Craniometry

The scanty material could only give a rough idea of skull size variability of Mesola red deer (Table II). Scandinavian and central European red deer (mean = 388.6 mm for stags and 339.0 mm for hinds; n = 6 populations) have skulls on average about 10% larger than the Mesola ones (Table III), the same order of magnitude found for the external somatic measures (Mattioli et al. 2003). Eastern European populations (mean = 417.8 mm for stags; n = 6) have on average skulls $c.$ 20% larger than those of Mesola red deer. Mesola skulls are of about the same size as the Iberian and the Scottish

Table I. Body weights of Mesola red deer, divided by sex and age classes (data collected from 1981 to 1999) (enlarged sample compared with that in Mattioli et al. 2003).

Age class	Weight (kg): mean ± s.d.
Adult stags	108.7 ± 15.5 n = 18
Mature adult stags	122.8 ± 8.0 n = 7
Young adult stags	99.7 ± 11.8 n = 11
Subadult stags	71.54 ± 6.7 n = 13
Yearling stags	49.7 ± 10.6 n = 13
Male calves	34.2 ± 7.1 n = 14
Adult hinds	76.2 ± 10.5 n = 56
Mature adult hinds	78.4 ± 9.3 n = 48
Young adult hinds	63.1 ± 7.4 n = 48
Yearling hinds	48.3 ± 4.0 n = 7
Female calves	30.2 ± 4.0 n = 15

Table II. Craniometry of adult Mesola red deer.

	Measure (mm): mean ± s.d.	
Measure	Adult stags	Adult hinds
Mandible length	280.2 ± 7.5 n = 7	254.6 ± 18.0 n = 4
Lower tooth row length	112.8 ± 3.9 n = 7	109.7 ± 2.6 n = 4
Total length of the skull	361.6 ± 12.8 n = 7	316.1 ± 16.2 n = 4
Condilo-basal length	349.0 ± 11.7 n = 7	307.5 ± 14.8 n = 4
Zygomatic width	121.7 ± 4.0 n = 7	107.9 ± 9.5 n = 4
Ectorbital width	155.6 ± 5.4 n = 7	134.3 ± 8.3 n = 3
Mastoid width	117.3 ± 4.0 n = 7	96.0 ± 7.9 n = 4
Interorbital width	103.2 ± 4.5 n = 7	83.9 ± 6.1 n = 3
Rostral length	212.5 ± 11.2 n = 4	184.0 ± 7.0 n = 4
Nasal length	110.9 ± 10.4 n = 7	88.3 ± 7.1 n = 4
Upper tooth row length	106.5 ± 2.3 n = 5	100.3 ± 1.3 n = 4

Table III. Condylobasal length (mean in mm) of different populations of red deer, in Europe.

Population	Stags	Hinds	Reference
Sardinia	322.5	–	Toschi (1965)*
Scotland (UK)	332.0	310.0	Szunyoghy (1963), Lowe & Gardiner (1974)
Spain	–	312.0	Lowe & Gardiner (1974)
Mesola	349.0	307.5	this study
Denmark	364.0	340.9	Ahlén (1965)
Norway	366.1	327.9	Ahlén (1965)
Norway	368.3	325.5	Røskaft (1978)
Sweden	381.3	344.0	Ahlén (1965)
Germany	396.5	339.4	Bützler (1986)
Poland, lowland	395.6	356.2	Mystkowska (1966)
Poland, Carpathians	421.3	–	Wierzbowska (1999)
Slovakia	400.2	–	Hell & Herz (1972)
West Belarus	404.0	376.0	Danilkin (1999)
Slovakia	414.4	–	Bališ (1959)
Hungary	431.2	385.9	Szunyoghy (1963)**
Bulgaria	435.4	375.3	Markov (1998)

*Averaged from a range of values.
**Reconstructed from the greatest length of the skull, which is 1.05% higher than the condylo-basal length (S. Mattioli, unpubl.).

ones and only slightly larger than those of the Tyrrhenian red deer *Cervus elaphus corsicanus* (Table III). The mean length of the upper tooth row (106.5 mm in stags and 100.3 mm in hinds) is similar to that of other European populations (cf. Beninde 1937a).

Stature

All the measures considered were significantly greater in Apennine red deer (AD) than in Mesola red deer (MD; medians, torso length, MD stags and hinds: 186.9–167.3 cm, AD stags and hinds: 198.4–178.0 cm; height, MD: 108.6–94.4 cm, AD: 128.0–113.0; hind foot-length, MD: 48.9–45.1 cm, AD: 57.0–53.0 cm; height:torso length ratio, MD: 0.58–0.57, AD: 0.64; hind foot-length:torso length ratio, MD: 0.26–0.27, AD: 0.29–0.30; Mann-Whitney U test, females: $Z = -7.333/-4.524$; $P < 0.001$; $n = 122$; males: $-4.112/-3.223$, $P \leq 0.001$, $n = 106$).

Antler conformation

We observed 642 sets of cranial appendages. The mean number of tines/antler pair of adult stags was 6.2 ± 1.7 (s.d., $n = 392$). The number of tines/antler pair was significantly greater in fully mature stags (7.0 ± 1.6, $n = 183$) than in young adults (5.6 ± 1.4, $n = 209$; $B = 0.239$, s.e. = 0.041, $P < 0.001$) and was significantly greater in Period 2 (all adults: 6.7 ± 1.6, $n = 248$, young adults: 6.0 ± 1.4, $n = 136$, mature adults: 7.6 ± 1.4, $n = 112$) than in Period 1 (all adults: 5.4 ± 1.5, $n = 144$, young adults: 4.9 ± 1.2, $n = 73$, mature adults: 6.1 ± 1.4, $n = 71$; $B = 0.218$, s.e. = 0.043, $P < 0.001$; Figure 2). The mean number of tines/antler pair was much lower in Mesola stags than in stags of other European populations of red deer (Table IV).

Antler beams with three tines prevailed (42.1% out of $n = 783$ antler beams; one tine: 2.2%, two tines: 22.0%, four tines: 28.9%, five tines: 4.7%, six tines: 0.1%, only one case). Only 2.2 and 3.6% of adult antler beams had a bez or a crown tine, respectively, and only 3.3% of young adults had a bez tine or a crown. Frequencies of occurrence of crown and bez tine were much lower than those observed in other European populations of red deer except for those from Corsica (Table V).

Among subadults, 10.9% were antlerless, mostly with bony buttons (Figure 2). Antlered subadults were mainly spikers and three- to four-pointers (Figure 2). Among yearlings 45.5% were antlerless and the antlered ones were all spikers (Figure 2).

Antler biometry

We measured 353 antler beams (Tables VI and VII). Linear regressions among antler characteristics of adults were highly significant (r^2 = 0.281–0.794,

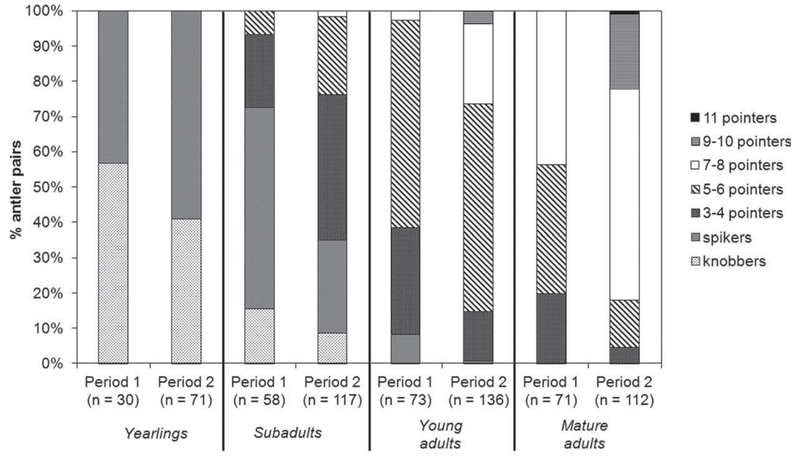

Figure 2. Number of tines/antler pairs in Mesola red deer stags of different age classes, in Period 1 and Period 2.

Table IV. Mean number of tines per antler pair in adult red deer of different European populations. I: Italy; UK: United Kingdom; CH: Switzerland; D: Germany; PL: Poland. Other abbreviations: L. Saxony: Lower Saxony; N. Apennines: Northern Apennines.

Area	No. of tines	Reference
Mesola, I	6.2	this study
Glenfeshie, UK	6.6	Mitchell et al. (1986)
Sardinia, I	7.8	Mattioli, Caboni, Murgia unpubl.
Ticino, CH	9.4	Salvioni (1999)
L. Saxony, D	9.8	Drechsler (1980)
Carpathians, PL	9.8	Wierzbowska (1999)
Norway	10.0	Mysterud et al. (2005)
Norway	10.7	Røskaft (1978)
Slovenia	10.7	Hafner (2008)
Masuria, PL	11.0	D. Zalewski, pers. comm. 2006
N. Apennines, I	13.0	Mattioli (1996)
Latvia	13.0	Danilkin (1999)
Lithuania	13.8	Danilkin (1999)

P < 0.001, n = 190–247). For adult stags, all the measures were significantly greater in fully mature adults than in young ones (B = 0.180–392.910, s.e. = 0.074–26.680, P < 0.05) and in Period 2 than in Period 1 (B = 0.264–109.370, s.e. = 0.080–29.880, P < 0.01), except the upper circumference, which did not differ significantly between periods (P > 0.05). The interaction age class × period was significant only for antler length (B = –5.181, s.e. = 2.233, P = 0.021), which increased significantly in Period 2 only for young adults (t-test: t = –3.692; df = 40.599; P < 0.001) but not for mature ones (t = –1.574; df = 60.539; P = 0.121). In adults, brow tine length was on average *c.* 32% of the main beam while the trez tine length was *c.* 18% of the beam. The bez tine was relatively short, on average *c.* 15% of the main beam length. The longest antler beam measured 92 cm, the heaviest 1366 g.

Table V. Percentage of occurrence of crown and bez tine in adult stag antlers from some European populations. F: France; I: Italy; CH: Switzerland; D: Germany; SLO: Slovenia; PL: Poland; SK: Slovakia; RO: Romania; HR: Croatia.

Area	Crown	Bez tine	Reference
Corsica, F	0	0	Vigne & Marinval-Vigne (1988)
Mesola, I	3.6	2.2	this study
Sardinia, I	14.0	7.3	Mattioli, Caboni, Murgia unpublished
Grison, CH	32.4	/	Buchli (1992)
Vosges, F	55.0	/	Klein (1987)
Harz, D	/	50.0	Drechsler in Mattioli (1993)
Slovenian Alps, SLO	67.0	53.0	M. Haffner (pers. comm. 2013)
Masuria, PL	70.8	/	D. Zalewski, (pers. comm. 2006)
Carpathians, PL, SK, RO	/	71.5	Isakovic (1969)
Lublin, PL	72.0	/	Dziedzic et al. (1999)
Allier, F	77.5	/	Hartl et al. (1991)
N. Apennine, I	82.0	82.5	Mattioli (1996)
Slavonia, HR	/	94.5	Isakovic (1969)

/ = not available.

For subadult stags, antler length and brow tine length increased significantly in Period 2 (B = 4.154–12.139, s.e. = 1.427–3.174, P < 0.006). There was a not-significant increase of circumference at the burr and of the number of tines/antler beam in Period 2 (B = 0.899–0.356, s.e. = 0.200–0.468, P = 0.060–0.075). Trez tine length did not differ significantly between periods (B = 1.333; s.e. = 1.464; P = 0.377).

For yearling stags, antler beam length was significantly greater in Period 2 than in Period 1 (B = 8.790; s.e. = 2.070; P = 0.001). The number

Table VI. Morphometric characteristics (linear measures: cm; weight: g; means ± s.d.) of antler beams of Mesola red deer, in 1981–2012.

	Mature adults	Young adults	Subadults	Yearlings
Antler length	76.2 ± 7.8 *n* = 182	57.9 ± 9.0 *n* = 89	41.1 ± 13.4 *n* = 59	11.4 ± 5.9 *n* = 16
Brow tine length	25.7 ± 4.1 *n* = 177	17.1 ± 5.4 *n* = 86	11.0 ± 4.4 *n* = 39	–
Bez tine length	11.7 ± 5.3 *n* = 10	–	–	–
Trez tine length	13.4 ± 4.0 *n* = 157	8.6 ± 3.3 *n* = 58	5.2 ± 1.9 *n* = 17	–
Circumference at the burr	16.3 ± 1.5 *n* = 171	13.4 ± 1.8 *n* = 85	10.9 ± 1.7 *n* = 53	–
Lower circumference	11.1 ± 1.9 *n* = 168	9.3 ± 1.3 *n* = 66	7.6 ± 1.0 *n* = 24	–
Upper circumference	9.9 ± 1.1 *n* = 105	8.2 ± 1.0 *n* = 17	6.1 ± 0.4 *n* = 8	–
Antler beam weight	751.2 ± 202.6 *n* = 162	358.0 ± 112.0 *n* = 61	170.1 ± 64.5 *n* = 39	24.9 ± 8.9 *n* = 8
Number of tines per beam	3.6 ± 0.8 *n* = 182	2.9 ± 0.9 *n* = 89	1.9 ± 0.8 *n* = 59	0.9 ± 0.3 *n* = 16

Table VII. Antler beam length (mean) of different populations of red deer in Europe. I: Italy; E: Spain; D: Germany; PL: Poland; SLO: Slovenia; HR: Croatia.

Area	Antler beam length (cm)	Reference
Sardinia, I	63.0	Caboni et al. (2006)
Mesola, I	70.2	this study
Sierra Morena, E	75.5	Azorit et al. (2002)
Norway	72.5	Røskaft (1978)
Harz, D	82.9	Drechsler (1980)
Hohenbucko, D	85.5	Neumann 1968
Masuria, PL	84.6	D. Zalewski (pers. comm. 2006)
Carpathians, PL	88.2	Wierzbowska (1999)
E. Alps, SLO	89.5	Hafner (2011), M. Hafner (pers. comm. 2013)
N. Apennine, I	92.0	Mattioli 1996
Slavonia, HR	96.8	Bečejac et al. (1984)

of tines/antler beam did not differ between periods (B = 0.182; s.e. = 0.548; P = 0.739).

Antler investment

For Mesola adult stags, the average antler investment was 11.8 g of net weight/kg of body weight. Adult stags invested 73.9 g of gross antler weight (antlers plus 1.2 kg of skull)/kg of metabolic weight or 4.4 gr/kg $BW^{1.35}$ (Geist 1987, 1998). The best stags, with the highest body weight and the highest antler mass, have a production of 5.5 g of gross antler mass per kg $BW^{1.35}$ (2.7 kg of antlers plus skull for stags of 130 kg). By comparison with other European populations, the mean relative antler mass of Mesola red deer falls within the general pattern (Table VIII).

Coat spotting

The totality of adult Mesola red deer had a distinct slight yellowish spotting of the summer coat, especially on the haunches. The colour patterns of the rump patch and tail are the same as those of the central European populations (cf. Dolan 1988; Geist 1998).

Discussion

Morphometrics is mostly unsuitable for differentiating genetic, epistatic, environmental and true statistical variation (cf. Geist 1991), but certainly can be used to give a detailed description of the physical characteristics of a population. Our data show that Mesola red deer are among the smallest red deer in Europe. Mean adult body weight is 30–35% (stags) and 15–30% (hinds) lighter than that of central European populations (Dauster 1940; Radler & Hattemer 1982; Bützler 1986; Wagenknecht 1986; von Raesfeld & Reulecke 1988) and 45–50% (stags) and 35–40% (hinds) lighter than that of eastern European ones (Szunyoghy 1963; Paller & Csányi 1999). Mean external linear dimensions were reduced by 8–15% compared with Swiss, German, Norwegian or Croatian populations (Buchli 1979; Drechsler 1985; Langvatn 1986; von Raesfeld & Reulecke 1988; Tucak 1997; Tucak et al. 1999). The sexual size dimorphism was low and apparent only for adults: stags have about 10% longer linear dimensions and are on average 43% heavier than females. Usually, size dimorphism is already apparent in newborn calves (Albon, Guinnes & Clutton-Brock 1983), and European red deer adult stags are on average 12–15% larger and 70–90% heavier than

Table VIII. Antler mass production per unit of body weight in average adult stags (cf. Geist 1987, 1998). I: Italy; UK: United Kingdom; D: Germany; PL: Poland.

Area	Antler weight with skull (kg)	Lean body weight (kg)	g/BWkg1.35	Reference
Sardinia, I	2.0	105	3.7	Mattioli, Caboni, Murgia unpubl.
Mesola, I	2.5	110	4.4	Mattioli (1993), this study
Glenfeshie, UK	2.2	115	3.6	Mitchell et al. (1986)
Rum, UK	2.4	115	4.0	Lowe in Mattioli (1993)
L. Saxony, D	3.5	160	3.7	Drechsler (1980)
Norway	3.7	165	3.8	Røskaft (1978)
Słowinski N.P., PL	3.7	170	3.6	Dzięciołowski et al. (1996)
Masuria, PL	4.5	170	4.4	D. Zalewski, pers. comm. (2006)
N. Apennine, I	5.8	180	5.2	Mattioli (1996), S. Mattioli unpubl.

hinds (Radler & Hattemer 1982; Bützler 1986; Geist & Bayer 1988; von Raesfeld & Reulecke 1988). Dimorphism in size decreases as a consequence of the greater sensitivity of males to food limitation (Clutton-Brock et al. 1982; Leberg & Smith 1993; Ashley et al. 1998; LeBlanc et al. 2001).

Body growth rate of the Mesola red deer was slower than that of the other European populations. The ratio of yearling to adult mass was 26–29% lower than that observed in other populations (Radler & Hattemer 1982; von Raesfeld & Reulecke 1988). Young adult (i.e. 2–4 years old) hinds were on average 15 kg lighter than fully mature ones, which may contribute to explain the low birth rate (Mattioli et al. 2003; Ferretti & Mattioli 2012), since in hinds ovulation and pregnancy are related to the attainment of threshold body mass (Albon et al. 1983; Langvatn et al. 1996). The retarded body growth is also responsible for the delay in antler development of juvenile stags. Pedicles, which usually begin to grow at 8–10 months of age, in Mesola Wood did not start before 11–13 months, and sometimes later. When pedicles grew at 11–13 months, Mesola yearlings produced short spikes. When pedicles grew at 14–16 months, yearlings failed to produce true antlers and were true knobbers, with skin-covered pedicles, or "buttons" with small, bony outgrowths. When the pedicle fails to develop until 16–20 months of age, the first vestigial antlers, consisting of just two bony buttons, appear only in 2-year-old stags, whereas spikes arise in 3-year-old animals. Pedicle initiation is associated with the attainment of a threshold body weight and the growth of the first antler set is possible only when the pedicle reaches a critical length (Suttie & Kay 1983; Fennessy & Suttie 1985; Gaspar-López et al. 2008).

Mesola red deer fall within small-bodied red deer populations, like the Tyrrhenian *Cervus e. corsicanus*, the Barbary stag *C. e. barbarus*, the Iberian *C. e. hispanicus* and the Scottish populations *C. e. scoticus* of the Highlands. They are all clear adaptations to poorly productive habitats (i.e. Mediterranean woods and scrubs or Scottish open moorlands). Reduced sexual size dimorphism, slow body growth and delay in antler initiation of stags are typical traits of resource-restricted deer populations. Mesola red deer, together with Tyrrhenian, Iberian, North African and Scottish populations are often defined as "maintenance phenotypes" (cf. Geist 1987, 1998). It remains to be determined just to what extent in the Mesola red deer body size is genetically fixed and what instead is related to phenotypic plasticity. Habitat improvements in the Nature Reserve of Mesola Wood have caused a statistically significant slight increase in size (Mattioli et al. 2003; this study), which reflects a certain plasticity.

Western Red Deer are characterized by great size flexibility, as demonstrated by Scottish red deer transferred into English parks or New Zealand (Mitchell et al. 1977), or by the low-performance Silesian red deer subjected to a high nutrition plane in the experiments by F. Vogt in the 1920s and 1930s of the 20th century (Vogt 1937, 1947; Geist 1986). When reared with a high-quality diet, Iberian red deer attain the body weights of central European populations. Iberian stags, which normally weigh about 125 kg (Martínez et al. 2005), in farm can reach an average body mass of 150–200 kg (Gaspar-López et al. 2010).

The low stature of Mesola red deer, already observed by Perco (1984) and caused by a slight leg shortening, is particularly noteworthy. The adult height at the withers is about 57–58% of the head-trunk length, against a standard of 62–64%, and the hind foot length is 26–27% of the head-trunk length against a standard of about 30% (cf. Langvatn 1986; Raesfeld & Reulecke 1988). It is not clear if this shrinking of limbs is simply a by-product of body size reduction, a consequence of genetic drift, an effect of malnutrition or an adaptive change (related for example to the locomotion needs in sandy and swampy terrain). Metapodial length tends to vary in several deer species with habitat and body condition.

Populations in high-quality environments have relatively longer legs than those in poor habitats. Changes in leg proportions have been observed in a single population after only three decades of nutritional stress (Klein 1964; Terada et al. 2012; Putman & Flueck 2013). An evident shortening of limbs has been documented for the Tyrrhenian red deer *C. e. corsicanus* (Vigne & Marinval-Vigne 1988; Banwell 1998; Geist 1998).

The length of the upper tooth row is similar to that of other European red deer (cf. Mystkowska 1966), regardless of the smaller body size, as expected with a high-priority tissue like teeth, which tends to develop irrespective of environment (Geist 1998).

Antlers were relatively small, with a narrow spread and typically with a short trez tine. For a full array of the types of cranial appendages in Mesola Wood see Cortesi (2012). Mean antler length was 2.0 times the condylo-basal length of the skull, in substantial accord with other European populations (Geist 1998). The average relative antler mass was not very different from that of other European red deer (Table VIII), while the antler investment of the largest Mesola stags (5.5 g/kg $BW^{1.35}$) was rather lower than that of the best trophy stags in free conditions (6.5–9 g/kg $BW^{1.35}$) (cf. Geist 1998). If the sizes of antlers of Mesola red deer are simply in line with the small body size, their antler conformation is quite peculiar. The structure is oversimplified, with a low and scarcely variable number of branches, a very low frequency of bez tine and crown and a short trez tine (Tables III and IV). While the brow tine length is comparable to that observed in other red deer populations (*c.* 30–35% of the beam), the trez tine on average is short (18% of the main beam) with respect to other red deer populations (30–35% of the beam) (Bečejac et al. 1984; Mattioli 1996; Hafner 2011). The infrequent bez tine is short too (on average 15% of the main beam against a standard of 18–20%) (Mattioli 1996; Hafner 2011). The rare crown is rudimentary, three-pointed and short-tined. It can be cup-like, the classical shape in Europe (Beninde 1937b), or fan-like, a peculiar configuration of Mesola, with the three tines (a short dagger and a terminal fork) arising transversally and medially from different points of the main beam. This last crown type resembles the upper parts of wapitoid antlers (Geist 1998).

Scottish adult stags may reach a maximum of 14–16 tines per antler pair (Mitchell et al. 1986; V.P.W. Lowe 1986, pers. comm. to S.M.) and Sardinian stags 12 tines (Beccu 1989; Mattioli pers. obs.). The highest number of antler tines recorded in Mesola Wood over 30 years was 11 (only once). It is remarkable that from 1957 to 1996, bez tine and crown, typical traits of the European-type *Cervus elaphus* taxa, were totally absent and that for all the first part of the 20th century they both were only very rarely recorded (Mattioli 1993). Habitat enhancement measures carried out in the Reserve led to a significant improvement of antlers: the mean number of tines increased by 30%, the frequency of eight-point antlers grew from 9.0 to 24.6%, (Figure 2), and bez tine and crown began to appear, mostly in fully mature stags. Antlers of young adults were 14.0% longer and 13.7% heavier in Period 2 than in Period 1, whereas those of mature stags showed a 20.8% increase in weight and only a not-significant 3.0% increase in main beam length. These results suggest that, when environmental conditions improved, the investment of mature and young adults favoured different antler characteristics. While the latter allocated energy to increase the main beam length, the weight and the branching of antlers, the former particularly favoured the rearrangement of the antler bone structure and the complexity of their cranial appendages. Thus, in antler growth, the main beam length seems to have priority, followed by the weight (through the increase of the more compact cortical bone at expense of spongiosa) and then by the development of tines. Also, Tyrrhenian red deer have small antlers, with a relatively simple antler design and a peculiar tendency to slight palmation in fully mature stags (Caboni et al. 2006).

The slight spotting of the summer coat is a common trait of all Mesola red deer. A speckled coat is very frequent in the Caucasian and Iranian *C. e. maral* and in yearlings and subadults of the North African *C. e. barbarus* (Meyer 1972; Dolan 1988) but is generally absent in *C. e. corsicanus* (Mattioli pers. obs.). Some spotting was observed in some Tyrrhenian red deer by Banwell (1998). Spotted individuals can sometimes be present in European red deer populations but their frequency is normally low. In Hohenbucko, a research area in eastern Germany, spotting occurred in about 10% of animals (Wagenknecht 1986).

Our morphometric study, together with a genetic one, could also help to understand the taxonomic status of this population (Zachos et al. 2014), already considered a potential independent conservation unit (Lovari & Nobili 2010). Their morphological characteristics, coupled with genetic peculiarities (Lorenzini et al. 2005; Hmwe et al. 2006; Zachos et al. in press) make the Mesola red deer unique, deserving special protection (Lovari & Nobili 2010; Zachos & Hartl 2011; Ferretti & Mattioli 2012).

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