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Antler Size Provides an Honest Signal of Male Phenotypic Quality in Roe Deer

Cécile Vanpé,[1,2,*] Jean-Michel Gaillard,[3,†] Petter Kjellander,[2,‡] Atle Mysterud,[4,§] Pauline Magnien,[3,‖] Daniel Delorme,[5,#] Guy Van Laere,[5,**] François Klein,[5,††] Olof Liberg,[2,‡‡] and A. J. Mark Hewison[1,§§]

1. Laboratoire Comportement et Ecologie de la Faune Sauvage, Institut National de la Recherche Agronomique, BP 52627, F-31326 Castanet-Tolosan Cedex, France;
2. Department of Conservation Biology, Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, S-73091 Riddarhyttan, Sweden;
3. Laboratoire de Biométrie et Biologie Evolutive, Unité Mixte de Recherche 5558, Université Claude Bernard Lyon 1, 43 boulevard du 11 novembre 1918, F-69622 Villeurbanne Cedex, France;
4. Department of Biology, Center for Ecological and Evolutionary Synthesis, University of Oslo, P.O. Box 1066 Blindern, N-0316 Oslo, Norway;
5. Office National de la Chasse et de la Faune Sauvage, Centre National de Recherches Appliquées sur les Cervidés-Sanglier, 1 Place Exelmans, F-55000 Bar-le-Duc, France

Online enhancements: appendixes with figure and tables.

* E-mail: cecile.vanpe@toulouse.inra.fr.

† E-mail: gaillard@biomserv.univ-lyon1.fr.

‡ E-mail: petter.kjellander@nvb.slu.se.

§ E-mail: atle.mysterud@bio.uio.no.

‖ E-mail: pauline.magnien@inapg.fr.

E-mail: d.delorme@oncfs.gouv.fr.

** E-mail: g.vanlaere@oncfs.gouv.fr.

†† E-mail: f.klein@oncfs.gouv.fr.

‡‡ E-mail: olof.liberg@nvb.slu.se.

§§ E-mail: mark.hewison@toulouse.inra.fr.

abstract: Identifying factors shaping secondary sexual traits is essential in understanding how their variation may influence male fitness. Little information is available on the allocation of resources to antler growth in territorial ungulates with low sexual size dimorphism. We investigated phenotypic and environmental factors affecting both absolute and relative antler size of male roe deer in three contrasting populations in France and Sweden. In the three populations, we found marked age-specific variation in antler size, with an increase in both absolute and relative antler size between yearling and prime-age stages, followed by a decrease (senescence) for males older than 7 years. Antler size increased allometrically with body mass. This increase was particularly strong for senescent males, suggesting the evolution of two reproductive tactics: heavy old males invested particularly heavily in antler growth (potentially remaining competitive for territories), whereas light old males grew small antlers (potentially abandoning territory defense). Finally, environmental conditions had little effect on antler size: only population density negatively affected absolute antler size in one of the three populations. Antler size may therefore provide an honest signal of male phenotypic quality in roe deer. We discuss the implications of these results in terms of territory tenure and mating competition.

Keywords: allometry, *Capreolus capreolus*, climate, population density, secondary sexual trait, senescence.

Antlers and horns of ungulates have been subject to great interest since Darwin (1859, 1871) developed his theory of sexual selection, as they represent one of the most spectacular examples of male secondary sexual traits in vertebrates. Several hypotheses have been put forward to explain the evolution of horns and antlers (see reviews by Geist [1966]; Clutton-Brock [1982]; Andersson [1994]; Lincoln [1994]), most of which relate to the framework of male-male competition over mates. Horns in bovids and antlers in cervids are used as weapons for attack and defense against rival males during the mating season. Closely related to this, they may also function as indicators of male strength and fighting ability in display toward other males. In addition, females may use the traits as reliable signals reflecting sexual vigor and genetic quality when choosing mates. In all cases, a large trait is advantageous and, if heritable, will evolve, as there may thus be positive feedback between the effects of intrasexual combat among males and female choice (Wong and Candolin 2005). These behavioral advantages of large horns and antlers should translate into reproductive success, with larger-horned/antlered males siring more offspring, irrespective of age and body size (in reindeer *Rangifer tarandus* [Espmark 1964], bighorn sheep *Ovis canadensis* [Coltman

et al. 2001], red deer *Cervus elaphus* [Kruuk et al. 2002], and Soay sheep *Ovis aries* [Preston et al. 2003]).

According to the conditional handicap theory (Zahavi 1977; Pomiankowski 1987; Iwasa et al. 1991), secondary sexual traits such as antlers, to serve as honest signals of male quality for choosy females, are expected to be strongly condition dependent and costly to produce and maintain, particularly for males in poor condition (e.g., Kotiaho 2000). While several studies have shown a correlation between antler size or shape and body size or mass (e.g., in roe deer *Capreolus capreolus* [Pélabon and Van Breukelen 1998] and red deer [Mysterud et al. 2005]), condition dependence has rarely been fully demonstrated (for a general review on sexual ornaments, see Cotton et al. 2004). There is also some evidence that antlers are costly sexual traits. Mohen et al. (1999) estimated that energy requirements for antler growth by moose (*Alces alces*) were half as much as energy requirements for summer fat and protein deposition. Hence, if we assume that antlers are honest quality traits, choosing a male with large weapons might lead to short-term direct benefits for females, such as access to good-quality territories, paternal care, or male sexual vigor (Price et al. 1993), or long-term indirect benefits, such as high genetic quality of offspring, to the extent that these benefits are heritable (Fisher-Zahavi's handicapped sexy son model, combining both Fisherian runaway and good-genes processes; Fisher 1915; Møller and Alatalo 1999; Eshel et al. 2000; Kokko et al. 2003). Recently, antler size in red deer stags has been shown to be heritable (Kruuk et al. 2002), positively related to the probability of becoming a harem holder in stags (Bartos and Bahbouh 2006), and positively related to relative testes size and sperm velocity (Malo et al. 2005). This suggests that antler size in red stags is an honest signal of male quality, which may be used by females to choose mates.

Identifying the factors shaping antler and horn size is therefore essential for a better understanding of how weapon size variation may influence male fitness in ungulates (Prichard et al. 1999), but studies of variation in secondary sexual traits are comparatively scarce. Previous studies have mainly focused on nonterritorial species with a high level of sexual size dimorphism (e.g., in moose [Solberg and Saether 1994], red deer [Schmidt et al. 2001; Mysterud et al. 2005], bighorn sheep [Festa-Bianchet et al. 2004], and reindeer [Weladji et al. 2005]). Few studies have investigated age-dependent variation in antler size in territorial species and/or in species with low sexual size dimorphism. Yet, these species are particularly interesting because they are expected to be only weakly polygynous, with reduced potential for sexual selection by male-male competition, compared to species with high sexual size dimorphism and harem-holding or lekking mating systems (e.g., Wade 1979; Andersson 1994), and the opportunity

for female mate choice may also be higher because females have greater, unimpeded access to assess either the male or his territory (Min 1997).

In this study, we therefore analyzed variation of antler size in roe deer, a medium-sized territorial deer with a low level of sexual size dimorphism (Andersen et al. 1998), using individual-based long-term data of known-age males from three contrasting populations. We analyzed how male age, population density, climate, habitat quality, and resource abundance influenced absolute and relative antler size (i.e., before and after controlling for the allometric relationship between antler size and body mass, respectively) to test the following predictions.

1. *Age-specific changes of absolute and relative antler size.* Age is known to structure markedly most life-history traits of vertebrate populations (Charlesworth 1994). In large mammals, three main life cycle stages are generally recognized: a juvenile stage, a prime-age stage, and a senescent stage (Gaillard et al. 2000). Individual performance typically peaks during the prime-age stage (for reviews on birds and large herbivores, respectively, see Bennett and Owens 2002; Gaillard et al. 2000), as reported for survival (e.g., Caughley 1966; Loison et al. 1999) but also for antler size (e.g., in red deer; Mysterud et al. 2005). We therefore expected to find larger antlers in prime-age males than in younger and older males (prediction 1*a*). While senescence (i.e., a decline in performance with increasing age) has been documented in several large herbivores for body mass (e.g., on red deer; Mysterud et al. 2001), reproduction (e.g., on moose; Ericsson et al. 2001), and survival (for a review, see Gaillard et al. 2003*b*), clear evidence of senescence in sexually selected traits such as antler size or horn growth are comparatively scarce (but see in ibex *Capra ibex* [Von Hardenberg et al. 2004], moose [Saether and Haagenrud 1985], and red deer [Mysterud et al. 2005]). We therefore tested for senescence in antler size in roe deer (prediction 1*b*). Because large, costly traits can be physiologically afforded only by individuals of superior condition, we expected antler size to be strongly condition dependent (e.g., Andersson 1994; Mysterud et al. 2005), predicting a positive allometric relationship between antler size and body mass (prediction 1*c*; e.g., Huxley 1931).

2. *Responses of absolute and relative antler size to environmental factors.* Because antlers are cast and regrown each year and are costly to produce, we should expect a strong relationship between energy allocation to antler growth and current environmental conditions (Andersson 1994). Several studies of ungulates have reported a negative effect of increasing population density and harsh climatic conditions on antler size or horn growth (e.g., in white-tailed deer *Odocoileus virginianus* [Ashley et al. 1998], bighorn sheep [Jorgenson et al. 1998], red deer [Schmidt et al. 2001; Mysterud et al. 2005], and roe deer [Pélabon and

Van Breukelen 1998]). These effects may reflect the impact of environmental factors on overall body size or, alternatively, their impact on energy allocation to antler growth. Few studies have distinguished between these two possibilities (but see in red deer; Mysterud et al. 2005). We investigated the effects of environmental conditions on antler size, predicting that both absolute and relative antler size should decrease under harsh conditions, that is, with increasing population density (prediction 2*a*) and summer dryness (prediction 2*b*). The negative effects of harsh environmental conditions on antler size or horn growth are commonly interpreted as resulting from decreased forage availability and quality (e.g., Skogland 1983; Fowler 1987; Weladji et al. 2005). Several studies have demonstrated a direct relationship between antler size or horn growth and food quantity or quality (e.g., Schmid 1955), but these studies have been commonly based on experimental manipulation of food (but see Festa-Bianchet et al. 2004), which may not replicate food stress typical of natural conditions (see Cotton et al. 2004; Putman and Staines 2004). Here, we investigated the influence of spatiotemporal variation in habitat quality on antler size by looking at the effects of natural variations in acorn mast abundance and habitat quality. We expected to find larger antlers, in both absolute and relative terms, in favorable years when acorn mast production was high (prediction 2*c*) and in the richest habitats (prediction 2*d*).

Material and Methods

Study Species

The European roe deer is a small-sized cervid (adults weigh about 20–30 kg) with low sexual size dimorphism (males are less than 10% heavier than females; Andersen et al. 1998). In this species, only males carry antlers, and in contrast to most other deer species, male roe deer grow antlers during the winter (i.e., during the period of food restriction), mainly from December to early March. The antler cycle is controlled mainly by testosterone secretions (Sempéré 1982), and males are territorial from early spring to the end of the rut (late August–early September). While buck kids first develop a small button on top of their pedicle before growing small antlers at 1 year old, classically with two spikes, subadult and adult bucks usually develop a four-point and five-point/six-point head, respectively. However, there are large individual differences in antler size and shape, even within an age class, and antler size is generally considered as an unreliable indicator of age (e.g., Prior 2000).

Study Sites and Roe Deer Populations

We used data from three contrasting populations of European roe deer: Chizé, a 2,614-ha enclosed forest located in western France (46°06′N, 0°26′W); Trois Fontaines, a 1,360-ha enclosed forest located in eastern France (48°43′N, 2°61′E); and Bogesund, a 2,600-ha area of fragmented habitat (with 65% forest) located in the central eastern part of Sweden (59°23′N, 18°15′E). While Chizé has a temperate oceanic climate, with mild winters and hot and dry summers, and Trois Fontaines has a continental climate characterized by moderately severe winters, with low temperatures and rainy summers (Gaillard et al. 1997), Bogesund has a continental climate under the influence of the Baltic Sea, with relatively harsh snowy winters and mild and dry summers (Kjellander 2000). More details can be found in articles by Gaillard et al. (1997) and Kjellander et al. (2006). The three populations have been monitored for more than 16 years on the basis of annual capture-mark-recapture sessions involving known-age animals. Because a high proportion of roe deer were marked each year in all three sites, reliable estimates of annual population size were available (for Chizé and Trois Fontaines, see Gaillard et al. 2003*c*; for Bogesund, see Kjellander 2000). Experimental manipulation of density through hunting and/or removals took place in all three study areas, so marked between-year differences occurred in population density (see fig. B1 in the online edition of the *American Naturalist*; for further details, see Gaillard et al. 1993, 2003*c*; Kjellander 2000; Kjellander et al. 2006).

Morphometric Measurements

We used data from annual winter captures (January–March) in each site. Antler length was measured to the nearest 0.5 cm along the external side of the main beam, from the base of the antler to the top of the main beam. When both antlers were measured, the average length was retained. Measurements from cleaned antlers were removed from the analyses ($N = 124$ at Chizé and $N = 96$ at Trois Fontaines) so that we considered only antlers still in velvet (i.e., still growing). Antler length was considered as a proxy for antler size. Note that strong allometric relationships generally occur among morphometric traits; hence, antler length is expected to reliably index antler size. We used body mass (measured to the nearest 0.1 kg) to assess relative antler size. Note that roe deer are income breeders with few fat reserves (see Andersen et al. 2000); hence, body mass has been reported to be a better measure of phenotypic quality than body condition (Toïgo et al. 2006).

When an individual was caught more than once in a given year, only the latest measures of antler length and

body mass were used. All roe deer included in our analyses were first caught within their first year of life, when tooth eruption patterns enable young-of-the-year and older animals to be discriminated without error (Flerov 1952). The analyses included 451 measurements of 216 roe deer at Chizé, 271 measurements of 158 roe deer at Trois Fontaines, and 130 measurements of 56 roe deer at Bogesund.

Climatic Data

We obtained meteorological data from Météo France and from the Swedish Meteorological and Hydrological Institute. We calculated a monthly Gaussen (1954) summer hydric index (June–August) as the amount of precipitation minus twice the mean temperature (for previous applications to ungulates, see Gaillard et al. 1997; Garel et al. 2004; Toïgo et al. 2006). This index has been widely used in plant biogeography and climatology (e.g., Walter and Lieth 1960) because of the strong correspondence with plant distributions. The hydric index measures the water available for vegetation (Dajoz 1973), and the summer hydric index is known to influence the duration of green forage, as well as its quality (Becker et al. 1994). We calculated a yearly summer hydric index as the average of the monthly indexes for June, July, and August. The summer hydric index of the year i was expected to affect antler growth from January to March of the year $i + 1$. We did not use measures of winter climate in the present analyses because we did not find any effect of winter conditions on various roe deer life-history traits in previous work (for Chizé and Trois Fontaines, see Gaillard et al. 1996; for Chizé and Bogesund, see Kjellander et al. 2006) or on roe deer antler size in preliminary analyses of the present data at Bogesund.

Resource Availability and Habitat Quality

Acorn mast production was recorded by a commercial seedling producer (Svenska Skogsplantor AB) at several different locations in southern Sweden but not at Bogesund itself. However, mast years occur concomitantly across the entire Swedish range of oak (G. Hamilton, Swedish National Board of Forestry, unpublished data). From the recorded data, we distinguished two types of mast years: in poor years, mast harvest varied between 0 and 500 kg, while in true mast years, it varied between 1.5 and 4 t (Kjellander et al. 2006). The effect of acorn mast years on antler size at Bogesund was investigated by fitting this parameter as a two-modality factor (poor vs. true mast year) in the models. A positive effect of mast on fawn body mass has been previously reported at Bogesund (Kjellander et al. 2006).

At Chizé, we distinguished two main habitats of con-

trasting quality within the reserve (see, e.g., Pettorelli et al. 2005). The northern area is covered by a 1,397-ha oak forest in which the preferred food plants of roe deer in spring and summer occur more frequently and have a higher nitrogen content than in the southern part of the reserve, which is covered by a 1,143-ha limestone beech forest (Pettorelli et al. 2001). We therefore included habitat quality at Chizé as a two-modality factor (poor vs. rich) in the models. To attribute a habitat type to each roe deer captured, we used its capture site (for further details, see Pettorelli et al. 2003). Adult roe deer living in forests in continental Europe are highly sedentary (Strandgaard 1972; Pettorelli et al. 2003), so we can reliably assume that individuals were captured in the habitat type where they lived at this scale. Habitat quality has been previously shown to affect several life-history traits at Chizé (Pettorelli et al. 2001, 2002, 2003).

Statistical Analyses

Because the antler size measurements were taken during the period of antler growth and because we considered only antlers still growing, we first controlled for capture date (as the Julian date, with January 1 as day 1) by adjusting antler size to February 14 (i.e., the median date of the whole capture period) in the three sites. Although antler growth is a nonlinear process (Goss 1983; for roe deer, see Rörig 1908), in this study, data collection was restricted to a quite short period of time for which the relationship between antler length and date was well described by a linear model (correlation between residuals from linear models and residuals obtained including a quadratic function; Bogesund $R^2 = 0.996$; Chizé $R^2 = 0.966$; Trois Fontaines $R^2 = 0.937$). We did not adjust body mass to a standard date at Bogesund and Trois Fontaines because we did not find any significant change of body mass with Julian date (common slope of the linear regression between body mass and Julian date $\pm$ SE = -0.0014 ± 0.0134, $t = -0.107$, $P = .92$ and 0.0030 ± 0.0087, $t = 0.348$, $P = .73$, for Bogesund and Trois Fontaines, respectively). Such an adjustment was necessary, however, at Chizé (slope = -0.0248 ± 0.0073, $t = -3.413$, $P < 10^{-3}$). The standardized measures of antler size and body mass were ln transformed to fit homoscedasticity requirements.

We used linear models to assess the factors influencing antler size. The mean number of measures per individual ($\pm$ SD) was 2.08 ± 1.60 (range = 1–9) at Chizé, 1.72 ± 1.06 (range = 1–6) at Trois Fontaines, and 2.32 ± 1.25 (range = 1–6) at Bogesund. To control for repeated measures of the same individuals over the study period, male identity was entered as a random factor in mixed models. While fitting random effects may be prob-

lematic when only one measure is available for some individuals (see Crawley 2002), it was not a problem in our case because we fitted random effects only on the intercept, not on the slope. To check this empirically, we redid the analysis, excluding individuals for which we had only one measure. Because we obtained nearly identical results, we chose to present the analysis of the full data set here. Model selection was performed using the Akaike Information Criterion (AIC), as recommended by Burnham and Anderson (2002). A smaller AIC value corresponds to a better fit of the model to the data (i.e., the best compromise between accuracy and precision). However, when the difference between AIC values of two competing models was less than 2, we used the criterion of parsimony, selecting the simpler of the two models (Burnham and Anderson 2002). We used a backward procedure by fitting first the more complicated model, then removing interactions, and, last, removing the main effects of factors. All the analyses were performed using the R 2.2.1 statistical package (R Development Core Team 2004). We used the "lme" function (included in the "nlme" R package) for fitting mixed-effects models (Pinheiro and Bates 2000), using the maximum likelihood estimation procedure.

We first fitted several age-dependent models (for details, see table A1) to determine the pattern of age-specific changes of antler size. We then determined the allometric relationship between antler size and body mass by testing the effect of body mass, population, and age on antler size, as well as all their two-way and three-way interactions. For comparisons among populations, we restricted the analysis to a common range of body mass (i.e., ln-transformed values from 2.94 to 3.47; $N = 436$ at Chizé, $N = 271$ at Trois Fontaines, and $N = 117$ at Bogesund). For each age class within each population, we then estimated (i) the annual mean absolute antler size and (ii) the annual mean of the residuals from the selected allometric model as a measure of relative antler size. We investigated the effects of environmental variables on age-specific variation across years in both absolute and relative antler size in each site. At Chizé and Trois Fontaines, we tested the main effects of age (three age classes), population density (estimated in March–April of the year of antler growth), and the summer hydric index (of the previous year), as well as their two-way and three-way interactions. At Bogesund, for both yearlings and prime-age males (senescent males were eliminated because of low sample size; for details, see table C1 in the online edition of the *American Naturalist*), we tested the main effects of population density, the summer hydric index, and acorn mast abundance (of the previous autumn), as well as their two-way and three-way interactions. To be able to compare the effects of these three factors among and between populations, we standardized all the environmental variables

within each population so that they had a mean of 1 and a standard deviation of 1. The summer hydric index and population density were not correlated at Chizé ($r = 0.186$, $P = .18$) or Bogesund ($r = -0.031$, $P = .45$). However, a negative correlation between the summer hydric index and population density occurred at Trois Fontaines ($r = -0.45$, $P = .01$), which may complicate interpretation if both variables appear in the selected model. Finally, we tested the influence of habitat quality on antler size at Chizé by comparing the selected age-specific model with and without the additional effect of habitat quality. The details concerning model selection for environmental effects are provided in table C2 in the online edition of the *American Naturalist*.

Results

Antler Growth Models

Antler growth was investigated in each of the three sites from the beginning of January to the end of March. The linear model selected to standardize antler size data explained 4.2%, 34.1%, and 43.5% of the variation in antler size at Chizé, Trois Fontaines, and Bogesund, respectively. The low value for Chizé was expected because the data collection period occurred toward the end of antler growth in this population, when antler size no longer increased over time. Indeed, antler size increased over the winter capture period with different speed among sites. Growth rate was five times lower at Chizé (mean $\pm$ SE $= 0.4 \pm 0.1$ mm/day; fig. 1) than at Bogesund and Trois Fontaines, which had similar growth rates (2.1 ± 0.2 and 2.0 ± 0.2 mm/day, respectively). However, standardized antler size on February 14 was much higher at Chizé (mean $\pm$ SE $= 195.6 \pm 1.4$ mm) and Trois Fontaines (199.6 ± 2.7 mm) than at Bogesund (98.6 ± 4.1 mm).

Age-Specific Variations in Absolute Antler Size

A three-age-class model best accounted for age-specific changes of standardized antler size in all three study populations (see table A1). Antler size increased from yearlings to prime-age males, peaked for prime-age males, and then decreased in senescent males (fig. 2), as predicted in prediction 1*a*. We therefore detected a general senescence process in roe deer antler size in all populations, from 8 years onward, as predicted in prediction 1*b*. However, the magnitude of senescence markedly differed among populations. Between prime-age and senescent stages, absolute antler size decreased by only 6.1% at Chizé but by 23.2% and 46.0% at Trois Fontaines and Bogesund, respectively. Indeed, while senescent males had larger antlers than year-
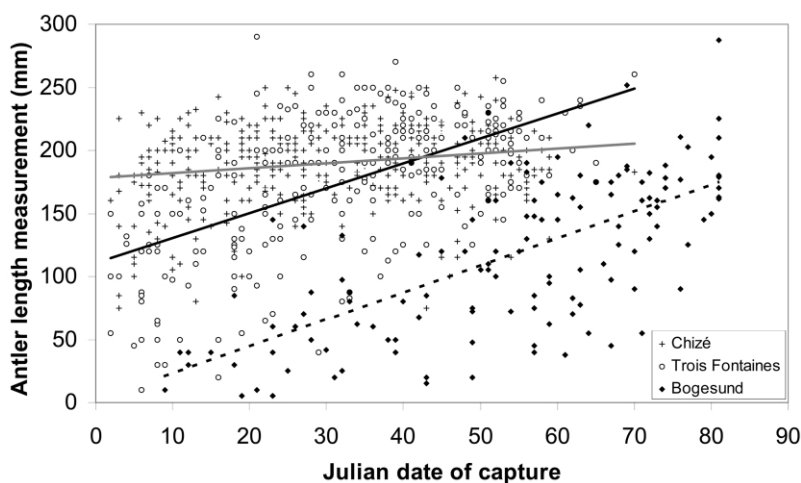
Figure 1: Antler growth models at Chizé (*crosses*, *gray line*), Trois Fontaines (*circles*, *black line*), and Bogesund (*diamonds*, *dashed line*).

lings at Chizé, they had shorter ones at Trois Fontaines and Bogesund (fig. 2).

### Allometric Variation in Antler Size

The best model describing allometric variation in antler size was the full model (AIC = 44.80 vs. 65.86 when removing the population × age class × body mass three-way interaction), which included the effects of body mass, age (three age classes), and population, as well as all their two-way and three-way interactions. As predicted (prediction 1a), within a given population, prime-age males had larger antlers for a given body mass than did yearlings and senescent males (fig. 3). In addition, as predicted (prediction 1c), a positive allometric relationship occurred between antler size and body mass in the three sites and for all age classes (fig. 3).

Within a given population, the slope of the allometric relationship did not differ between prime-age males and yearlings in all three populations ($t = 0.218$, $P = .83$ at Chizé; $t = 0.275$, $P = .78$ at Trois Fontaines; and $t = -0.614$, $P = .54$ at Bogesund; fig. 3). However, interestingly, antler size at Bogesund increased significantly more strongly with increasing body mass in senescent males than in younger males (mean slope difference ± SE between senescent males and yearlings: 5.052 ± 1.025, $t = 4.930$, $P < 10^{-4}$; between senescent males and prime-age males: 5.351 ± 0.975, $t = 5.487$, $P < 10^{-4}$; fig. 3). Although not significant, the same trend occurred at both Chizé (mean slope difference ± SE between senescent males and yearlings: 0.253 ± 0.372, $t = 0.680$, $P = .50$; fig. 3) and Trois Fontaines (1.077 ± 0.611, $t = 1.763$, $P = .08$; fig. 3). That is, light senescent males had smaller antlers than both

yearlings and prime-age males, but the antlers of the heaviest senescent males were of similar size to those of prime-age males.

Effects of Environmental Conditions on Antler Size

At Chizé, the best model accounted for 40% of the variation in absolute antler size across years and included the additive effects of age (three age classes), the summer hydric index, and population density, as well as the two-way interaction between age and the hydric index (AIC = -147.3 vs. -144.9 for the same model without the two-way interaction; see table C2). Age accounted for 27.5% and environmental drivers for 12.4% of the variance (including 6.7% by population density). Antler size significantly decreased with increasing population density (as expected in prediction 2a) to the same degree for all age classes (slope ± SE = -0.02 ± 0.01, $t = -2.36$, $P = .02$; table 1). The effect of the summer hydric index on absolute antler size was slight and age specific, that is, a nonsignificant negative trend in yearlings (slope ± SE = -0.03 ± 0.02, $t = 1.76$, $P = .08$; table 1) and no effect in prime-age and senescent males (slope ± SE = 0.0009 ± 0.016, $t = 0.58$, $P > .1$ and 0.03 ± 0.02, $t = 1.64$, $P > .1$, respectively; table 1), contrary to prediction 2b. Finally, the additive effect of the habitat factor (AIC = -423.6) did not improve the selected model at Chizé (three age classes; AIC = -431.9). Hence, contrary to our prediction 2d, individual habitat quality did not affect absolute antler size at Chizé. By comparing the retained model (AIC = -147.3) with the retained model plus an additive effect of year (fitted as a factor; AIC = -144.5), we estimated that the proportion of annual var-
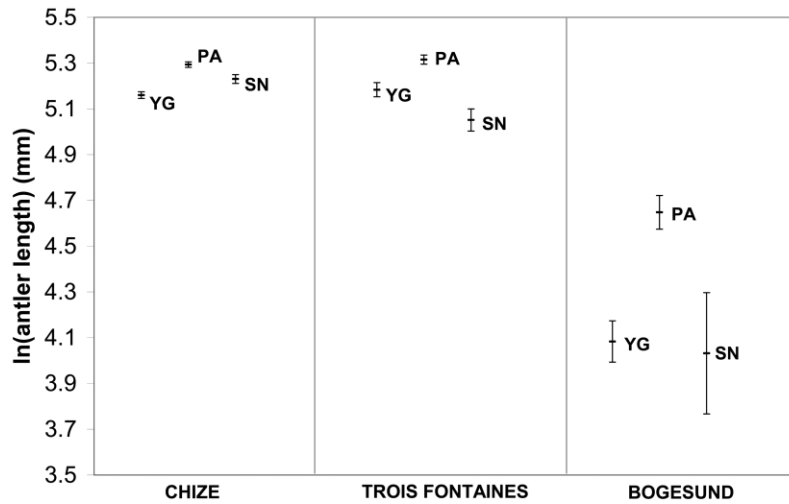
Figure 2: Differences of mean ln-transformed antler size (in mm) between yearlings (*YG*), prime-age males (*PA*), and senescent males (*SN*) in the three studied populations at Chizé, Trois Fontaines, and Bogesund. Estimates are based on the model with three age classes that was selected in each population. Error bars represent standard errors of the estimates.

iation in absolute antler size accounted for by the environmental drivers (12.4%) was lower than the proportion that remained unexplained (28.1%).

At Trois Fontaines, the best model explaining annual variation in absolute antler size was the constant model without any effect of environmental factors (see table C2). Hence, contrary to predictions 2*a* and 2*b*, neither population density nor the summer hydric index influenced absolute antler size. Similarly, at Bogesund, for both yearlings and prime-age males, the best model accounting for annual variation in absolute antler size was the constant model without any effect of environmental factors (see table C2). Hence, contrary to predictions 2*a*, 2*b*, and 2*c*, the summer hydric index, population density, and acorn mast abundance did not influence absolute antler size at Bogesund.

The best models explaining variation in relative antler size across years at Chizé, Trois Fontaines, and Bogesund were the constant models without any effect of environmental factors, except for prime-age males at Bogesund, where the best model accounted for 43% of the annual variation in relative antler size and included the effect of population density only (AIC = −12.5 vs. −8.4 for the constant model; see table C2). Thus, contrary to predictions 2*b*, 2*c*, and 2*d*, the hydric index, acorn mast abundance, and the habitat quality had no effect on relative antler size in all three populations. There was also little support for prediction 2*a* because at Chizé, Trois Fontaines, and Bogesund, for yearlings, relative antler size was not affected by population density, although relative antler size did decrease with increasing density at Bogesund

for prime-age males (slope ± SE = −0.11 ± 0.04, $t = -2.58$, $P = .03$).

Discussion

Our results indicate that changes in age and body mass were more influential than changes in environmental factors in shaping the variation observed in roe deer antler size in all the three populations we studied, as expected in general for deer (e.g., Clutton-Brock 1982; Andersson 1994). In accordance with our prediction 1*a*, prime-age males had larger antlers and allocated more energy to antler growth than yearling and senescent males. These results provide support for the mating strategy–effort hypothesis (Yoccoz et al. 2002), which predicts that reproductive effort peaks in prime-age males, because they are most often harem holders or territory owners, compared to young and senescent males. Our results are also in agreement with prediction 1*b* because males from 8 years of age onward grew smaller antlers than prime-age males, demonstrating, for the first time, clear evidence of senescence in antler size of roe deer. Previous studies have been unable to document this phenomenon because of the lack of data from known-age animals (e.g., Pélabon and Van Breukelen 1998), given the large errors obtained when aging roe deer from tooth wear (see Hewison et al. 1999). A similar decrease of absolute antler size in old males has previously been reported in dimorphic species of large herbivores such as moose (Saether and Haagenrud 1985), white-tailed deer (Scribner et al. 1989), and red deer (Mysterud et al. 2005), although not consistently (in red deer, see, e.g.,
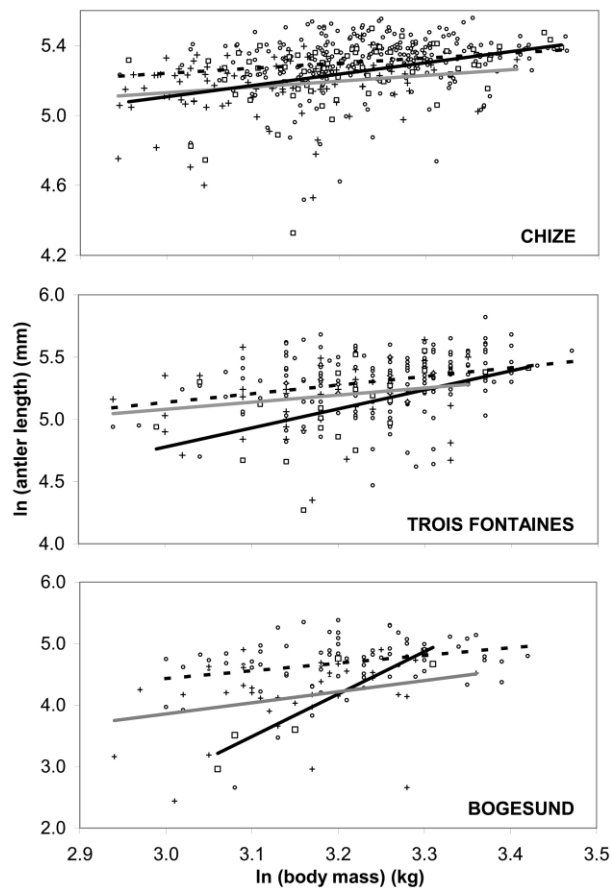
Figure 3: Allometric relationships between ln-transformed antler size (in mm) and ln-transformed body mass (in kg) in yearlings (*crosses, gray line*), prime-age males (*circles, dashed line*), and senescent males (*squares, solid line*) in the three studied populations at Chizé, Trois Fontaines, and Bogesund.

Kruuk et al. 2002). Interestingly, the onset of senescence in antler size of roe deer occurs at the same time as the onset of senescence in survival rate (Gaillard et al. 1993, 2004), suggesting that antler size may be an honest signal of male health and quality. In line with prediction 1*c*, we also found that antler size increased with increasing body mass in all the three populations and for all age classes. This suggests that antler size in roe deer is condition dependent because only the heavy males can afford long, costly antlers. Finally, contrary to predictions 2*a*, 2*b*, 2*c*, and 2*d*, our results suggest that environmental variables have little influence on antler size. Of the tested environmental variables, only population density had any significant influence on antler size. The absence of an effect of climate on antler size might be due to the low variation in conditions, notably at Bogesund, and/or the lack of food

stress related to harsh climatic conditions over the study period.

While these results underline the general importance of age and body mass over environmental factors for determining roe buck antler size, comparison of the three contrasting populations highlights some further interesting patterns. First, standardized antler size (on February 14) was much higher at Chizé and Trois Fontaines than at Bogesund, while antler growth rate was much lower at Chizé than at Trois Fontaines and Bogesund. This is because data collection occurred toward the end of the antler growth period at Chizé, while it occurred in the middle and at the beginning of antler growth at Trois Fontaines and Bogesund, respectively. These results highlight the contrasting phenology in antler growth between the three populations. In the more southerly French populations, antler growth occurs earlier than at Bogesund, presumably linked to the earlier onset of spring and the territorial and sexual cycle of roe deer males. Similarly, but to a lesser extent, spring is somewhat later in the harsh continental climate of Trois Fontaines compared to Chizé, which is under oceanic influences; hence, antler growth is later.

Second, we found that the magnitude of senescence on antler size was much higher at Trois Fontaines than at Chizé and much higher at Bogesund than in the two French populations. From the ranking of senescence rate in our three populations, it seems that the magnitude of senescence increases with winter severity. Similarly, Gaillard et al. (1993) have previously reported a stronger senescence for roe deer survival at Trois Fontaines compared to Chizé. Furthermore, in the three populations, antler size tended to increase more strongly with increasing body mass for senescent males than for yearling and prime-age males. This general pattern was especially marked at Bogesund, where the difference in slope between senescent males and younger males was statistically significant, possibly because the marked senescence rate at Bogesund provided the necessary conditions to trigger a contrasting pattern of allocation in antler growth between light and heavy senescent deer, whereas the lower senescence rate at Trois Fontaines and Chizé did not. Indeed, in the two French populations, when we restricted the analysis to very old deer (10 years of age and older), the slope of the antler size–body mass relationship was steeper (mean slope difference $\pm$ SE between males 10 or more years old and yearlings: 0.319 ± 0.243 at Chizé and 1.434 ± 0.870 at Trois Fontaines) than when considering the whole senescent age class (mean slope difference $\pm$ SE between males 8 or more years old and yearlings: 0.253 ± 0.372 at Chizé and 1.077 ± 0.611 at Trois Fontaines). These results show that while the heaviest senescent males allocated as much energy to antler size as did prime-age males of similar body mass, light senescent males allocated much less than

Table 1: Best models describing the response of antler size to environmental variables

	LS estimate	SE	t	P
Absolute antler size at Chizé:				
Intercept	5.1827	.0161	322.289	.000
Age PA − YG	.1232	.0227	5.421	.000
Age SN − YG	.0698	.0250	2.797	.007
Density	−.0249	.0105	−2.357	.021
HI	−.0287	.0163	−1.755	.084
Age (PA − YG) × HI	.0380	.0228	1.666	.100
Age (SN − YG) × HI	.0616	.0260	2.374	.021
Relative antler size at Bogesund in PA:				
Intercept	−.0097	.0349	−.279	.786
Density	−.1087	.0421	−2.582	.030

Note: Parameter estimates are shown as least square (LS) estimate and standard error (SE) and test statistics as *t* and *P*. The best model describes the response of absolute ln-transformed antler size to environmental variables at Chizé and relative ln-transformed antler size to environmental variables at Bogesund in prime-age males. YG = yearlings, PA = prime-age males, SN = senescent males. HI = summer hydric index. Parameters for the terms including age PA − YG and age SN − YG are given as the differences between the given age level (PA and SN, respectively) and the reference age level YG.

did light younger males. This suggests that for senescent males, antler growth is more costly for poor-condition males than for good-condition males, as assumed by the handicap theory (e.g., Kotiaho 2000). We suggest that two alternative reproductive tactics may have evolved among senescent males, who are particularly sensitive to harsh environmental conditions (e.g., Clutton-Brock et al. 1982; Clutton-Brock and Albon 1983; Albon et al. 1983). First, heavy (i.e., high-quality) senescent males may exhibit a risk-prone tactic by investing heavily in antler growth in order to develop antlers of sufficient size to remain competitive against younger males, thereby allowing them to continue to defend their territory so as to maximize mating opportunities and hence lifetime reproductive success. Second, light (i.e., low-quality) senescent males may exhibit a conservative tactic, being unable to divert a large amount of energy to antler growth and so having inferior competitive ability than heavier and/or younger males. We speculate that these light old males might find it difficult to successfully defend a territory that may preclude them from mating. In support of this idea, Johansson (1996) observed that three of the five senescent males that she monitored in Sweden during their last rutting season before death were still actively territorial, were involved in male-male conflicts, and also courted and mated females, whereas the two others were evicted from their territory by younger males, subsequently remaining in restricted areas, and did not participate in any rutting activities at all (see also Liberg et al. 1998).

Third, the only effects of population density were on absolute antler size at Chizé and relative antler size at Bogesund in prime-age males (i.e., antler size decreased with increasing density). This was, in part, expected because the Chizé population has experienced substantial density variation over the study period (range = 6.2–20.7 deer/km^2), and density-dependent responses have been previously reported for several life-history traits (Boutin et al. 1987; Gaillard et al. 1992, 1996, 1997; Pettorelli et al. 2002; Kjellander et al. 2006), while no evidence of density dependence has so far been reported in the highly productive population of Trois Fontaines (see Gaillard et al. 1993, 1996, 1997, 2003a). The absence of an effect on relative antler size at Chizé suggests that the observed effect of population density on absolute antler size simply translated an effect on body mass. At Bogesund, while density-dependent responses have also been reported (Kjellander 2000; Kjellander et al. 2006), the absence of any density effect on absolute antler size here may be due to the weak density variation and low number of years for this study (see fig. B1; table C1). The significant effect of density on relative antler size in prime-age males was due to one exceptional high-density year (1992) when relative antler size was particularly low. Because sample size for this year was particularly low (see table C1), no firm conclusions can yet be drawn.

While most studies dealing with sexual selection have focused on highly sexually dimorphic ungulate species with a dominance-based mating system, such as red deer or Soay sheep, little is known about male mating tactics in territorial species with low sexual dimorphism, such as roe deer. We suspect that antler size in roe deer, as a major sexually selected trait, may play a crucial role in determining male mating success. A common view is that antlers, as weapons that can potentially inflict serious injury, may allow males to successfully defend their territory and so to control an area within which they may mate females without being harassed by rival males (e.g., Andersen et al. 1998). However, although they are monoestrous, female

roe deer may be courted and mated by several males because their ranges may overlap several male territories (Strandgaard 1972; Andersen et al. 1998), and a significant proportion (up to one-third) may make short (less than 48 h) rut excursions outside their normal home range, potentially mating with a nonneighboring male (see anecdotal observations in Norway [Linnell 1994; Andersen et al. 1995], Sweden [Liberg et al. 1998], Italy [San José and Lovari 1998], and France [M. Pellerin, S. Said, and J.-M. Gaillard, unpublished data]). Hence, territorial males may not be able to fully monopolize females during rut, and female mate choice probably also greatly influences male mating success in this species. Furthermore, in territorial species, dominance between males is generally location dependent, with males dominant inside their territory but subordinate outside (Owen-Smith 1977; for roe deer, see Hewison et al. 1998). In support of this idea, a very recent article on roe deer convincingly showed that territory holders consistently won male-male fights within their territories but not outside (Hoem et al., forthcoming). The authors concluded that roe deer territoriality was a low cost–low benefit process, which could be a tactic to reduce the frequency of potentially dangerous fights. Contrary to fights in harem-holding or lekking species, direct male-male fights are rather infrequent in territorial species. Even in the case of an intrusion of a rival male inside a territory, display behaviors (e.g., parallel walk, head shaking, scraping) often allow males to resolve conflicts without resorting to fighting (Liberg et al. 1998; Hoem et al., forthcoming). Hence, we suggest that in territorial species such as the roe deer, antler size may be a major cue in male display and female mate choice, acting as a reliable and honest signal of individual male phenotypic quality (our results). In support of this, Hoem et al. (forthcoming) showed that male-male fights escalated more and were more complex when the difference in antler size between combatants was smaller. Wahlström (1994) also found a positive correlation between yearling antler size and testicle

size in roe deer, indicating that antler size may reflect male fertility and sexual vigor, because testes size determines sperm production rate (Møller 1989). Furthermore, it seems that territorial males may evaluate the potential threat of yearlings, in terms of mating competition, by using yearling antler size as an honest indicator of phenotypic quality (Strandgaard 1972): yearlings with large antlers and large testes are more frequently victims of aggressive acts from territorial males and hence tend to disperse more (Strandgaard 1972; Wahlström 1994). Linking studies of antler size variation, territorial behavior, female choice, and genetic paternity in roe deer should provide a better understanding of how and why reproductive success varies in this weakly dimorphic territorial ungulate.

APPENDIX A

Model Selection for the Effects of Age on Antler Size

Table A1: Model selection for age-specific changes in absolute ln-transformed antler size in the three studied populations

	Null	Age	Age^2	Age^3	Full classes	**Three classes**	Four classes
Chizé:							
df	3	4	5	6	15	**5**	6
AIC	−376.7	−367.4	−396.4	−396.0	−366.9	**−431.9**	−423.9
ΔAIC	55.1	64.4	35.5	35.8	64.9	**.0**	8.0

Table A1 (*Continued*)

	Null	Age	Age^2	Age^3	Full classes	**Three classes**	Four classes
Trois Fontaines:							
df	3	4	5	6	15	**5**	6
AIC	15.9	22.6	11.8	21.1	31.2	−5.5	.4
ΔAIC	21.4	28.1	17.3	26.6	36.7	**.0**	5.9
Bogesund:							
df	3	4	5	6	12	**5**	6
AIC	251.2	255.2	240.8	251.2	239.4	**227.0**	231.2
ΔAIC	24.2	28.3	13.9	24.2	12.4	**.0**	4.2

Note: Model selection was performed using the Akaike Information Criterion (AIC) as recommended by Burnham and Anderson (2002). ΔAIC is the AIC difference between the given model and the best model. The selected model appears in bold. Null = constant model. Age = model with age fitted as a covariable. Age^2 = model with age fitted as a quadratic function. Age^3 = model with age fitted as a cubic function. Full classes = model with age fitted as a factor with as many age classes as observed different ages. Three classes = model with age fitted as a factor with three age classes (i.e., 1, 2–7, 8+ years). Four classes = model with age fitted as a factor with four age classes (i.e., 1, 2, 3–7, 8+ years).

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