Body mass change over winter is consistently sex-specific across roe deer populations

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Abstract:

In polygynous vertebrates, males must allocate energy to growing the secondary sexual characteristics, such as ornaments or weapons, that they require to attract and defend potential mates, impacting body condition and potentially entailing fitness costs.

We investigated sex differences in over winter body mass change across five intensively monitored populations of roe deer with markedly contrasting environmental conditions. At winter onset, males weighed, on average, 8.5% (from 4.5% in the most northerly population to 12.3% in the most southerly one) more than females. However, across all populations, males fared worse over the winter than females, losing more (Sweden) or gaining less (France) mass, so that sexual mass dimorphism was virtually absent prior to the onset of spring.

Our findings reveal that the direction of over-winter change in mass of roe deer depends on winter severity, but that males are consistently more sensitive to this environmental constraint than females. As a result of this sex-specific change in body mass, sexual mass dimorphism is lowest at the onset of the territorial season. We suggest that allocation to antler growth and territory establishment drives this pattern, providing a likely explanation to account for the lower rates of male adult survival that are consistently reported in this weakly dimorphic species.

Introduction

Although the difference in body mass of males and females is often considered as a fixed quantity for a given species, in reality, body mass of large herbivores varies seasonally in relation to resource abundance (Douhard et al. 2018) and the sex-specific schedule of allocation to reproduction (Apollonio et al. 2020). First, because of the greater energy requirements to sustain their larger body size, males are generally more susceptible to lose mass during periods of resource restriction, notably over winter in temperate areas (Clutton-Brock et al. 1982). Second, body condition is expected to fluctuate asynchronously between the sexes in relation to their different schedules of reproductive allocation (Stephens et al. 2009). In species that lack male parental care, females pay the costs of rearing offspring, notably during late gestation and early lactation, which generally coincide with the period of peak resource availability during late spring-early summer. Mothers can therefore offset this marked increase in energy expenditure by either increasing foraging activity (income breeder, sensu Jönsson 1997) or by mobilizing previously accumulated body reserves (capital breeder, sensu Jönsson 1997). In contrast, males must engage in contest competition to ensure access to mates, for example, through tending receptive females (Hogg 1984) or by defending a mating territory (Vanpé et al. 2009), and may lose substantial body condition as a result (Apollonio et al. 2020). In addition, to maximise their competitive ability, males must allocate substantial energy to developing secondary sexual traits including weapons such as antlers, which are regrown annually as a prerequisite to successful reproduction. Because allocation to these elements of male-

male competition occurs earlier, typically prior to or during winter, when resources are less abundant in temperate areas, males are expected to adopt a capital breeder tactic (sensu Jönsson 1997), accumulating fat reserves during the season of highest resource abundance to offset the subsequent costs of reproduction (Williams et al. 2017).

The roe deer is a weakly polygynous species (Vanpé et al. 2008) with a low level of sexual size dimorphism (Hewison et al. 2011) and relatively short antlers (Lemaitre et al. 2018), but where males are strongly territorial from late winter until the end of the summer (Vanpé et al. 2009). Unusually, roe deer males cast their antlers in late autumn which then regrow immediately over the following two to three months, so that the costs of allocation to antler growth are levied during the heart of winter. In contrast, roe deer females are not territorial, but are considered income breeders (Andersen et al. 2000), with very few fat reserves (Hewison et al. 1996), that breed every year irrespective of previous reproductive status (Andersen et al. 2000, Hewison and Gaillard 2001) and offset the annual costs of gestation and lactation during spring and summer through concurrent intake.

While we previously showed that immature juvenile roe deer of both sexes continued to gain mass at a similar rate over winter (Hewison et al. 2002 for two populations at 46-48°N latitude), no study has yet analyzed how sexual mass dimorphism of mature adults is impacted by winter harshness at a broad spatial scale. We addressed this knowledge gap by investigating how this unusual schedule of allocation to secondary sexual traits in males shapes sex differences in body mass change over the winter and, hence, the degree of sexual size dimorphism. We used body mass data derived from the intensive (> 7000 individuals), long-term (> 20 years) capture-mark-recapture monitoring of five roe deer populations living under markedly different ecological conditions to test the following predictions. First, because males have to allocate to antler growth during the winter months, loss of body mass should be greater (or mass gain should be lower) in males than females so that sexual mass dimorphism is lowest at the onset of spring. Second, roe deer in the two Swedish populations should lose more body mass than those in the three French populations because of the much harsher winter conditions in the north of the species' range.

Materials & Methods

Study sites

We focused on five intensively monitored populations of roe deer, three in France and two in Sweden, living on study sites with markedly different environmental conditions (Table 1). The two Swedish study sites are situated towards the northern limit of the species' range, with harsh winter conditions, whereas the French study sites are within the southern part of the roe deer core range and have relatively mild winters. Otherwise, the study sites differ in terms of available habitat types, landscape structure and population density (Table 1).

Table 1: Study site characteristics of the roe deer populations. Sample size indicates the number of body mass measurements and the number of unique individual roe deer (i.e. the ratio indicates the mean number of measures per individual). Julian date indicates when body mass was measured where 1 = Jan 1st.

	Bogesund (Sweden)	Grimsö (Sweden)	Aurignac (France)	Chizé (France)	Trois Fontaines (France)
Latitude, Longitude	59°38′N, 18°28′E	59°73′N, 15°47′E	43°13′N, 0°52′E	46°11’N, 0°34’W	48°43’N, 4°55’E
Surface area (ha)	2 600	8 000	7 500	2 614	1 360
Habitat type	Mixed agricultural	Boreal coniferous forest	Mixed agricultural	Deciduous forest	Deciduous forest
Snow cover (days)	80	130	5	<15	<15
January temperature (°C)	3.7	- 1.3	4.9	5.6	3.1
Years monitored	1989-2016	1974-2017	2001-2021	1978-2015	1976-2015
Sample size: observations (individuals)	2432 (463)	1498 (531)	442 (321)	5571 (3297)	3887 (2564)
Julian date: (start, end)	2-93	1-99	5-74	4-84	4-73

Body mass data

We collected data for all animals caught during routine capture-mark-recapture operations that took place each winter (January to March) over two to four decades depending on the study site (see Table 1). Animals were caught either in baited box traps (Sweden) or drive nets (France). They were subsequently manipulated by experienced handlers who recorded each individual’s sex, body mass (to the nearest 0.1 kg) and age (as either juveniles in their first winter i.e. around 8 months old, or adult i.e. older than 1.5 years old when both sexes have attained >90% of their asymptotic body mass, Hewison et al. 2011). Juveniles can be easily distinguished from older animals on the basis of the presence of a milk tooth at the third pre-molar (Ratcliffe & Mayle 1992). Animals were marked with individually numbered ear tags and, in some cases, collars, before being released on site.

Ethical statement

All capture and marking procedures were done in accordance with local and European animal welfare laws. For Aurignac-VCG: prefectural order from the Toulouse Administrative Authority to capture and monitor wild roe deer and agreement no. A31113001 approved by the Departmental Authority of Population Protection. For Bogesund and Grimsö: the marking and handling of roe deer were approved by the Ethical Committee on Animal Experiments, Uppsala, Sweden (Current approval Dnr: C302/2012). For Chizé and Trois Fontaines, the capture protocol for roe deer under the authority of the Office Français de la Biodiversité (OFB) was approved by the Director of Food, Agriculture and Forest (Prefectoral order 2009-14 from Paris). All procedures were approved by the Ethical Committee of Lyon 1 University (project DR2014-09, June 5, 2014).

Data analysis

We analysed individual body mass of adult animals only in relation to sex and capture date defined as the number of days after 1st January (hereafter, Julian date 1). Although captures occasionally took place during October, November or December in the French study sites, we excluded these few data so as to consider a common winter start date across all five populations. However, because a given Julian date cannot be considered strictly equivalent between France and Sweden from a phenological point of view (e.g. different dates for spring vegetation green-up), we performed the analysis separately for each population. Hence, while the analysed range for Julian date started from 1 (i.e. January 1st) in all populations, the end date differed somewhat among populations (see Table 1). Preliminary analysis indicated that body mass change over winter was adequately modelled as a linear function of date in all populations (little or no improvement in model fit when looking for non-linearity using quadratic, cubic, logarithmic or smoothing functions, see Table S6 in Appendix), and that including exact age did not influence the outcome (analyses restricted to known aged individuals, results not presented). Therefore, to evaluate sex-specific body mass trajectories over winter, we built linear mixed models with the lme4 (Bates et al. 2015) package in R where the full model contained sex, Julian date and their two-way interaction. We included individual identity (to control for repeated measures) and year (to control for annual variation in conditions) as random intercepts in all models. Finally, for the Aurignac-VCG population only, we included the spatial sector of capture as a two-modality fixed factor (mixed vs. open habitat) to control for body mass differences in relation to landscape structure at this study site (i.e. roe deer heaviest in open areas, Hewison et al. 2009); note, we did not include animals caught in the strict forest sector because of systematic differences in capture date among sectors). We performed model selection in relation to AIC values and weights for the candidate model set. For each population, we retained the model with the lowest AIC value as long as it differed by at least 2 points from any simpler competing model (see Arnold 2010).

Results

In all five populations, the best supported model describing over-winter variation in body mass consistently included the sex*date interaction (for all five populations, ΔAIC > 3.5 compared to the second-best model), showing that average change in body mass over winter differed between males and females (see Tables S1-S5). More specifically, in the two Swedish populations, body mass of males decreased by 24.5 g (± 5.4, Bogesund) and 20.2 g (± 6.7, Grimsö) per day between 1 January and the end of the winter, while this decrease was much less marked for females (7.2 ± 3.6 g and 11.3 ± 4.4 g /day, respectively). In contrast, in the three French populations, female body mass increased by between 14.3 g (± 5.7, Trois Fontaines) and 32.7 g (± 12.5, Aurignac-VCG) per day over winter, while that of males remained more or less constant (from -1.9 ± 5.9 g/day at Chizé to 6.8 ± 18.8 g/day at Aurignac-VCG). As a result, while males were clearly heavier, on average, than females at the onset of winter in all five populations, albeit more pronounced in France (Chizé: 23.0 kg for males vs. 20.7 kg for females; Trois Fontaines: 25.0 kg for males vs. 22.8 kg for females; Aurignac-VCG: 23.8 kg for males vs. 21.2 kg for females, i.e. a sexual mass dimorphism of about 10%) than in Sweden (Bogesund: 25.0 kg for males vs. 23.7 kg for females; Grimsö: 26.3 kg for males vs. 25.1 kg for females, i.e. a sexual mass dimorphism of about 5%), by the March equinox (Julian date = 79), males did not weigh substantially more than females in all populations except Trois Fontaines (Fig. 1). Finally, at Aurignac-VCG only, the best supported model included an additive effect of sector, indicating that deer weighed, on average, 0.57 kg (± 0.22) more in the open sector than those in the partially wooded sector.

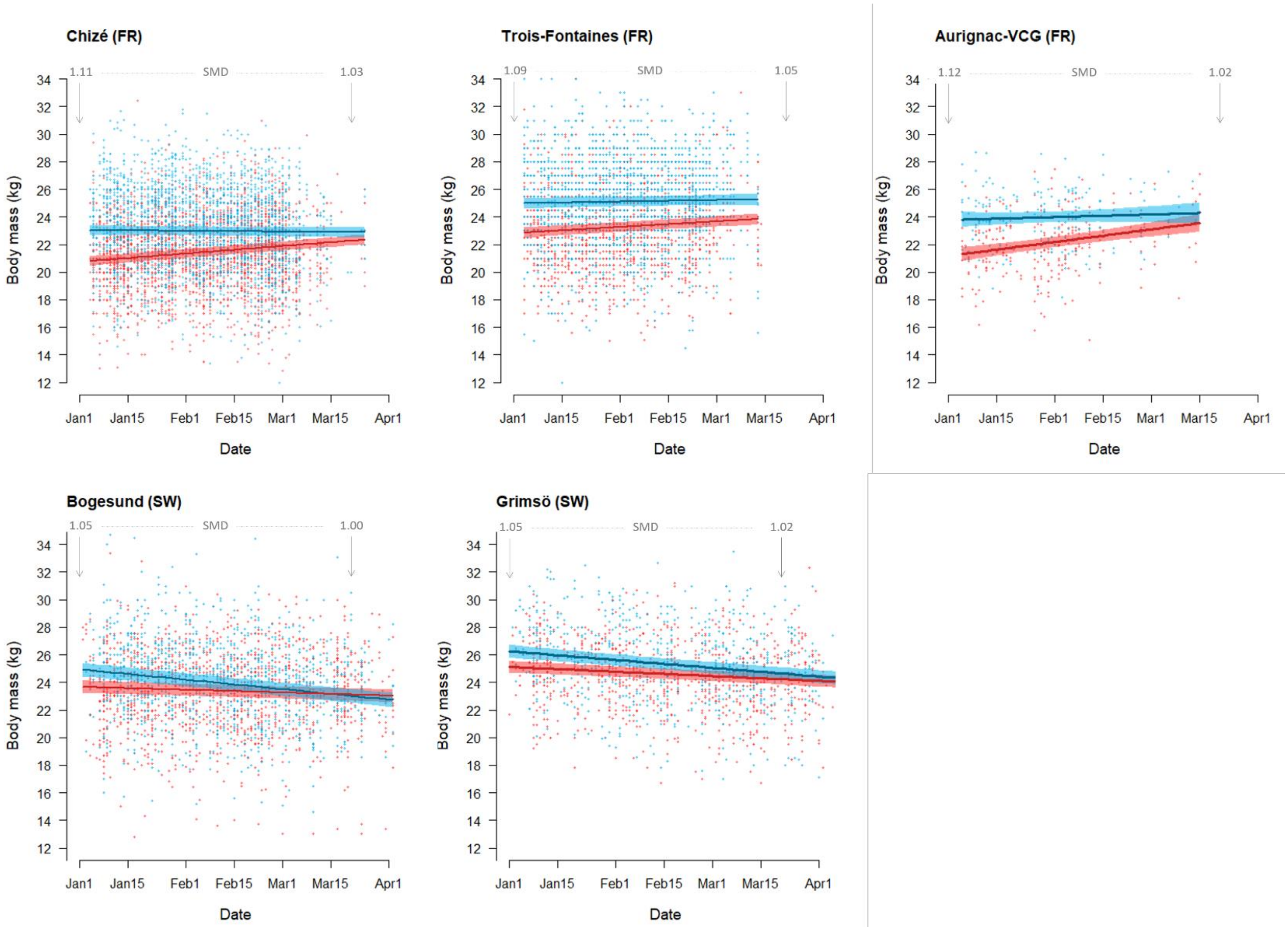

Fig. 1: Body mass (kg) of male (blue) and female (red) adults (>1.5 years old) in five intensively monitored populations of roe deer situated in France (Chizé, Trois Fontaines, Aurignac-VCG) and Sweden (Bogesund, Grimsö) in relation to date over winter. Sexual mass dimorphism (SMD) calculated as the ratio of predicted male mass to female mass at the start (1st January) and end (21st March) of the winter period is indicated for each population.

Discussion

From the analysis of the body mass of over 7000 individual roe deer living along a gradient of ecological conditions in terms of winter harshness, from near the northern-most extreme to the southern part of their core geographical range, we found strong support for both our predictions, i/ that over-winter body mass change was sex-specific whereby males lost more (or gained less) than females, so that sexual dimorphism in mass was virtually absent by the end of the winter; ii/ but that this pattern was strongly modulated by winter severity such that while roe deer in Sweden lost mass, on average, those in France gained mass. The costs of allocation to sex-specific reproductive schedules likely drive seasonal variations in the degree of sexual mass dimorphism in this weakly polygynous ungulate.

On the energetic cost of allocation to secondary sexual traits during winter

In polygynous mammals, reproductive effort during the mating season can lead to considerable loss of body mass in males (Apollonio et al. 2020; e.g. in red deer: Yoccoz et al. 2002; in elephant seals: Deutsch et al. 1990; in moose: Mysterud et al. 2005a). Indeed, reproductive males often abstain from feeding while they court and defend females or a mating territory (Mysterud et al. 2008). Similarly, although information on the costs of allocation to secondary sexual traits is sparse, antlers are smaller during less favourable years (Mysterud et al. 2005b), suggesting that growing these secondary sexual traits is costly. Here, we showed that male roe deer were consistently more constrained by winter resource restriction than females, losing around two to three times more mass in Sweden, while gaining up to five times less mass in France. As a result, by the onset of territorial season at the end of March (Hewison et al. 1998), sexual dimorphism in mass was virtually absent, with the average male only weighing about half a kilogram more than the average female across all five populations. While gestation in roe deer females begins in late December or early January following approximately 4.5 months of diapause (Aitken 1974), substantial allocation to foetal growth is concentrated in the latter third (April-May) so that fetuses weigh no more than a few grams during the winter period studied here. We suggest that this pattern is likely due to sex differences in the schedule of reproductive effort, in particular, the energetic costs to males of growing weapons and establishing a mating territory during the most resource-limited season (Williams et al. 2017).

On the impact of winter severity for body mass change

While roe deer are consistently heavier in Sweden than France at winter onset, the severity of conditions during the Scandinavian winter caused an average body mass loss of between 0.65 (females at Bogesund) and 2.2 (males at Bogesund) kg. Note that these figures are likely conservative, as resource scarcity during winter may begin well before the New Year in northern environments depending on the annual timing of snowfall. For an animal of around 20-25 kg this loss is clearly considerable and indicates that the capacity to store fat reserves and, therefore, seasonal fluctuations in body mass, are much greater in the north of its range than previously documented for this medium-sized income breeder (Kjellander et al. 2006). This is likely an adaptation to buffer against severe winters, as further south, in the heart of its range, over-winter body mass is generally stable and may even increase slightly (Hewison et al. 1996, 2002). Larger body size (Linstedt & Boyce 1985) and the capacity to store fat (Trondrud et al. 202, Denryter et al. 2022) have been widely interpreted as adaptations which increase fasting endurance in response to the dramatic fluctuations of resource availability in highly seasonal environments.

On the life history implications of annual body mass loss during winter

The repeated annual cycles of fat accumulation and depletion that underpin a capital breeding tactic are predicted to carry life history costs (Houston et al. 2006). While there is clear evidence to indicate that roe deer females adopt an income breeder tactic relative to other large herbivores (Andersen et al. 2000), our results imply that males must accumulate body condition prior to winter to offset the energetic costs of antler growth and subsequent territory establishment and, in this sense, can be considered capital breeders relative to females (Apollonio et al. 2020). In polygynous mammals, allocation to traits that confer an advantage in contest competition for females are predicted to impose costs in terms of survival (Clinton & Leboeuf 1993). Previous work has established that, despite the low level of polygyny in roe deer (Vanpé et al. 2008), the sex difference in annual survival of adults is equivalent to that of more polygynous and size dimorphic ungulates (Gaillard et al. 1993). We suggest that the repeated energetic cost of allocating to secondary sexual traits every winter is a proximal driver that, together with the direct costs of territorial defense and male-male competition for mates, contributes to the survival deficit for males in this weakly dimorphic ungulate. Most deer species cast and re-grow antlers during spring, when resources are plentiful (Mysterud et al. 2005b). However, because of their unusual schedule of allocation to reproduction, roe deer males are repeatedly faced with a trade-off between maintaining accumulated mass to offset the costs of establishing and defending a mating territory in spring, a full four months prior to the rut, and growing antlers during the winter season of food scarcity. The relative importance of antler size, body mass and territory quality for determining male reproductive success has yet to be established.

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Appendix

Model selection:

Table S1: Model fit and selection (fixed and random effects, difference in AIC score compared to the best model, AIC weight,) describing sex-specific over-winter variation in body mass in the Bogesund population. The best and second-best models, all models with ΔAIC < 10 compared to the best model, plus the constant model are displayed; the selected model is indicated in italics.

Fixed effects	**Random effects - Intercept**	**Delta AIC**	**weight**
*Sex*Julian date*	*ID + Year*	*0.0*	*1.00*
Sex + Julian date	ID + Year	36.9	0
null	ID + Year	140.3	0

Table S2: Model fit and selection (fixed and random effects, difference in AIC score compared to the best model, AIC weight,) describing sex-specific over-winter variation in body mass in the Grimsö population. The best and second-best models, all models with ΔAIC < 10 compared to the best model, plus the constant model are displayed; the selected model is indicated in italics. population.

Fixed effects	**Random effects - Intercept**	**Delta AIC**	**weight**
*Sex*Julian date*	*ID + Year*	*0.0*	*0.92*
Sex + Julian date	ID + Year	4.83	0.08
null	ID + Year	85.58	0.00

Table S3: Model fit and selection (fixed and random effects, difference in AIC score compared to the best model, AIC weight,) describing sex-specific over-winter variation in body mass in the Aurignac-VCG population. The best and second-best models, all models with ΔAIC < 10 compared to the best model, plus the constant model are displayed; the selected model is indicated in italics. population.

Fixed effects	**Random effects - Intercept**	**Delta AIC**	**weight**
*Sex*Julian date + Sector*	*ID & Year*	*0.0*	*0.48*
Sex*Julian date	ID & Year	4.6	0.08
Sex + Julian date + Sector	ID & Year	5.0	0.07
Sex + Julian date	ID & Year	9.4	0.01

null	ID & Year	84.9	0.00

Table S4: Model fit and selection (fixed and random effects, difference in AIC score compared to the best model, AIC weight,) describing sex-specific over-winter variation in body mass in the Chizé population. The best and second-best models, all models with ΔAIC < 10 compared to the best model, plus the constant model are displayed; the selected model is indicated in italics. population.

Fixed effects	**Random effects - Intercept**	**Delta AIC**	**weight**
*Sex*Julian date*	*ID + Year*	*0.0*	*1.00*
Sex + Julian date	ID + Year	48.6	0
null	ID + Year	429	0

Table S5: Model fit and selection (fixed and random effects, difference in AIC score compared to the best model, AIC weight,) describing sex-specific over-winter variation in body mass in the Trois Fontaines population. The best and second-best models, all models with ΔAIC < 10 compared to the best model, plus the constant model are displayed; the selected model is indicated in italics. population.

Fixed effects	**Random effects - Intercept**	**Delta AIC**	**weight**
*Sex*Julian date*	*ID + Year*	*0.0*	*0.862*
Sex + Julian date	ID + Year	3.66	0.138
null	ID + Year	343.3	0.00

Test for non-linear variation in over-winter body mass

In preliminary analysis, in addition to a linear function, we modelled body mass change over winter with quadratic, cubic or smoothing functions of date using the lme4 and mgcv packages in R. All models included sex, Julian date and their two-way interaction, as well as individual identity (to control for repeated measures on individuals) and year (to control for annual variation in conditions) as random factors. In four out of five cases, the linear function provided a satisfactory fit (Table S6), whereas the cubic model provided a somewhat better fit in the Grimsö population. Because this improvement was marginal from a biological point of view, and to facilitate comparison among populations, we present results from linear models in the main text, i.e. assuming that the rate of change in body mass during winter is constant over the entire study window.

Table S6: Comparison of model fit (AIC values) for the best supported model describing sex-specific over-winter variation in body mass in five roe deer populations (i.e. mass ~ sex * Julian date, with an additive effect of sector for the Aurignac-VCG population only, see main text) when the relationship between body mass and date was modelled as either a linear effect, a quadratic effect, a cubic effect or a logarithmic effect, or as a smoothing spline in a General Additive Mixed Model framework). The selected model is indicated in bold italics.

Population	**linear**	**quadratic**	**cubic**	**logarithmic**	**GAMM**
Bogesund	***9551.6***	9551.7	9553.9	9585.1	9568.5
Grimsö	6284.8	6277.9	***6274.7***	6289.3	6299.4
Aurignac-VCG	***1791.4***	1791.6	1795.5	1798.9	1860.1
Chizé	***24094.2***	24095.8	24100.7	24114.9	24438.4
Trois Fontaines	***17773.6***	17774.6	17780.2	17776.6	18107.1