

1 **Body mass change over winter is consistently sex-specific across roe deer (*Capreolus capreolus*)**  
2 **populations**

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19

## 20 **Abstract:**

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

24 We investigated sex differences in over winter body mass change across five intensively monitored populations  
25 of roe deer (*Capreolus capreolus*) with markedly contrasting environmental conditions. At winter onset, males  
26 weighed, on average, 8.4% (from 4.7% in the most northerly population to 11.6% in the most southerly one) more  
27 than females. However, across all populations, males fared worse over the winter than females, losing more  
28 (Sweden) or gaining less (France) mass, so that sexual mass dimorphism was virtually absent prior to the onset  
29 of spring.

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

## 36 **Introduction**

37 Although the difference in body mass of males and females is often considered as a fixed quantity for a given  
38 species, in reality, body mass of large herbivores varies seasonally in relation to resource abundance (Douhard  
39 et al. 2018) and the sex-specific schedule of allocation to reproduction (Apollonio et al. 2020). First, because of  
40 the greater energy requirements to sustain their larger body size, males are generally more susceptible to lose  
41 mass during periods of resource restriction, notably over winter in temperate areas (Clutton-Brock et al. 1982).  
42 Second, body condition is expected to fluctuate asynchronously between the sexes in relation to their different  
43 schedules of reproductive allocation (Stephens et al. 2009). In species that lack male parental care, females pay  
44 the costs of rearing offspring, notably during late gestation and early lactation, which generally coincide with  
45 the period of peak resource availability during late spring-early summer. Mothers can therefore offset this  
46 marked increase in energy expenditure by either increasing foraging activity (income breeder, sensu Jönsson  
47 1997) or by mobilizing previously accumulated body reserves (capital breeder, sensu Jönsson 1997). In  
48 contrast, males must engage in contest competition to ensure access to mates, for example, through tending  
49 receptive females (Hogg 1984) or by defending a mating territory (Vanpé et al. 2009), and may lose substantial  
50 body condition as a result (Apollonio et al. 2020). In addition, to maximise their competitive ability, males must  
51 allocate substantial energy to developing secondary sexual traits including weapons such as antlers, which are

52 regrown annually as a prerequisite to successful reproduction. Because allocation to these elements of male-  
53 male competition occurs earlier, typically prior to or during winter, when resources are less abundant in  
54 temperate areas, males are expected to adopt a capital breeder tactic (sensu Jönsson 1997), accumulating fat  
55 reserves during the season of highest resource abundance to offset the subsequent costs of reproduction  
56 (Williams et al. 2017).

57  
58 The roe deer (*Capreolus capreolus*) is a weakly polygynous species (Vanpé et al. 2008) with a low level of  
59 sexual size dimorphism (Hewison et al. 2011) and relatively short antlers (Lemaitre et al. 2018), but where  
60 males are strongly territorial from late winter until the end of the summer (Vanpé et al. 2009). Unusually, roe  
61 deer males cast their antlers in late autumn which then regrow immediately over the following two to three  
62 months, so that the costs of allocation to antler growth are levied during the heart of winter. In contrast, roe deer  
63 females are not territorial, but are considered income breeders (Andersen et al. 2000), with very few fat reserves  
64 (Hewison et al. 1996), that breed every year irrespective of previous reproductive status (Andersen et al. 2000,  
65 Hewison and Gaillard 2001) and offset the annual costs of gestation and lactation during spring and summer  
66 through concurrent intake.

67  
68 While we previously showed that immature juvenile roe deer of both sexes continued to gain mass at a similar  
69 rate over winter (Hewison et al. 2002 for two populations at 46-48°N latitude), no study has yet analyzed how  
70 sexual mass dimorphism of mature adults is impacted by winter harshness at a broad spatial scale. We  
71 addressed this knowledge gap by investigating how this unusual schedule of allocation to secondary sexual  
72 traits in males shapes sex differences in body mass change over the winter and, hence, the degree of sexual size  
73 dimorphism. We used body mass data derived from the intensive (> 7000 individuals), long-term (> 20 years)  
74 capture-mark-recapture monitoring of five roe deer populations living under markedly different ecological  
75 conditions to investigate the following predictions. First, because males must allocate to antler growth during  
76 the winter months, loss of body mass should be greater (or mass gain should be lower) in males than females so  
77 that sexual mass dimorphism is lowest at the onset of spring. Second, roe deer in the two Swedish populations  
78 should lose more body mass than those in the three French populations because of the much harsher winter in  
79 the north of the species' range, although this may vary among years in relation to specific annual conditions.

## 81 **Materials & Methods**

### 82 *Study sites*

83 We focused on five intensively monitored populations of roe deer, three in France and two in Sweden, living on  
84 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, see Table S10 for sample sizes per year). Julian date indicates when body mass was measured where 1 = Jan 1<sup>st</sup> (see Bonnot et al. 2024 for data and code).

	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	2001-2023	1978-2015	1976-2015
<b>Sample size:</b> observations (individuals)	2432 (493)	1516 (540)	503 (361)	5571 (3297)	3887 (2564)
<b>Julian date:</b> (start, end)	2-92	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, see Kjellander et al. 2006 for more details) or drive nets (France, see Lemaître et al. 2018 and Hewison et al. 2009 for more details). 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.

104 *Ethical statement*

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

114 *Data analysis*

115 We analysed individual body mass of adult animals only in relation to sex and capture date defined as the  
116 number of days after 1<sup>st</sup> January (hereafter, Julian date 1, see Bonnot et al. 2024). Although captures  
117 occasionally took place during October, November or December, we excluded these few data so as to consider a  
118 common winter start date across all five populations. However, because a given Julian date cannot be  
119 considered strictly equivalent between France and Sweden from a phenological point of view (e.g. different  
120 dates for spring vegetation green-up), we performed the analysis separately for each population. Hence, while  
121 the analysed range for Julian date started from 1 (i.e. January 1<sup>st</sup>), the end date differed somewhat among  
122 populations (see Table 1). Note that, as a consequence of this choice, it was not possible to formally test our  
123 second hypothesis with just five independent data points (populations).

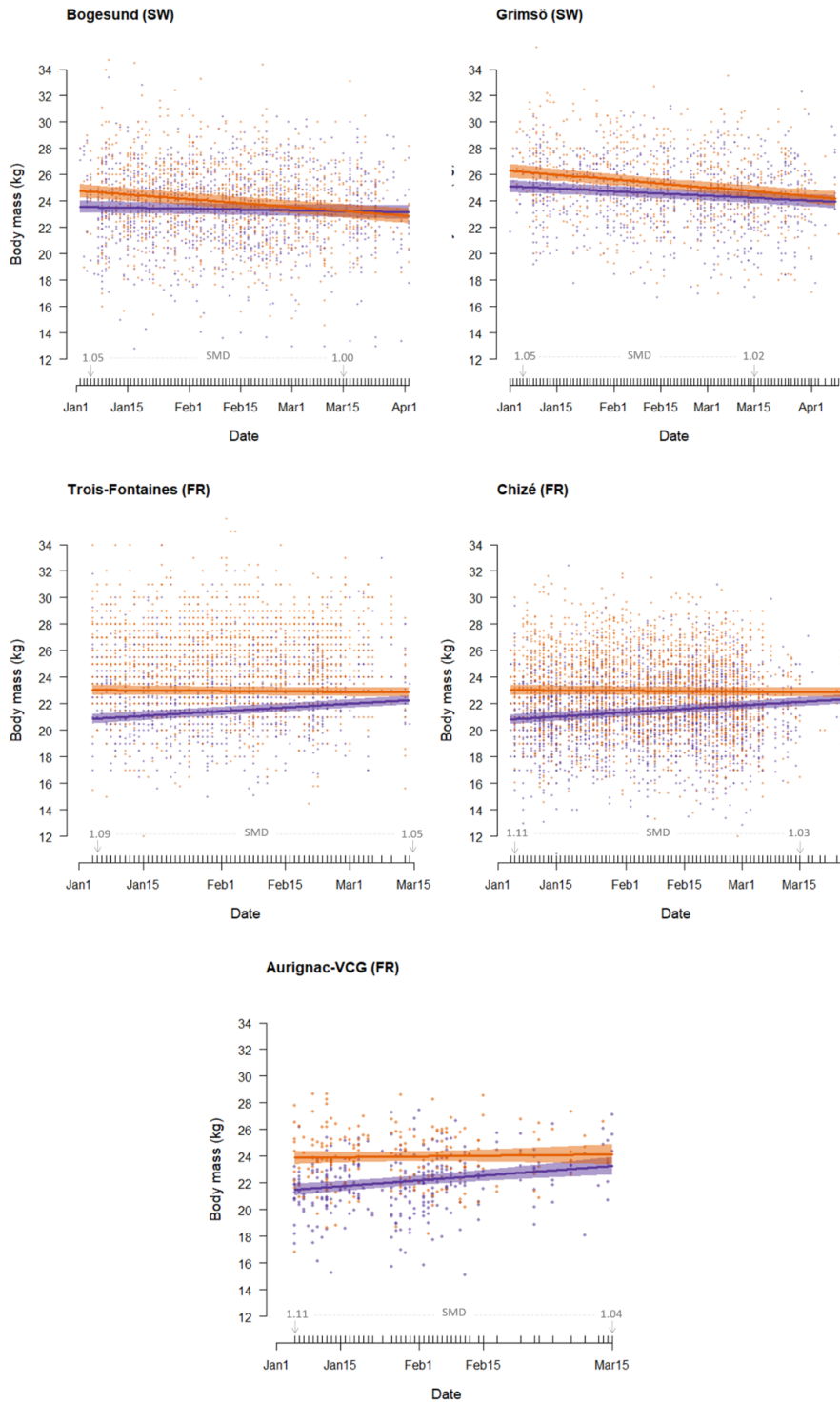
124 Preliminary analysis indicated that body mass change over winter was adequately modelled as a linear function  
125 of date in all populations (little or no improvement in model fit when looking for non-linearity using quadratic,  
126 cubic or smoothing functions, see Table S6 in Appendix), and that including exact age did not influence the  
127 outcome (analyses restricted to known aged individuals, results not presented). Therefore, to evaluate sex-  
128 specific body mass trajectories over winter, we built linear mixed models with the lme4 (Bates et al. 2015)  
129 package in R where the full model contained sex, Julian date and their two-way interaction. We first scaled  
130 Julian date for each population by centering (i.e. subtracting each value from the mean Julian date) and then  
131 dividing it by its standard deviation. For the Aurignac-VCG population only, we also included the spatial sector  
132 of capture as a two-modality fixed factor (mixed vs. open habitat) to control for body mass differences in  
133 relation to landscape structure at this study site (i.e. roe deer heaviest in open areas, Hewison et al. 2009); note,  
134 we did not include animals caught in the strict forest sector because of systematic differences in capture date  
135 among sectors). Finally, we initially included individual identity (to control for repeated measures) and year (to  
136 control for annual variation in conditions) as random effects on both the intercept and the slope. While these

137 models successfully converged in two out of five cases, the low number of repeated measures of individuals  
138 (Table 1) precluded convergence for the three French populations. Therefore, to investigate whether issues of  
139 pseudo-replication might affect model selection for these populations, we re-ran the analysis on a reduced data  
140 set that included a single observation per individual (with year as a random effect on both the intercept and  
141 slope). As we obtained equivalent results with this approach (same model selected, essentially identical  
142 parameter estimates), below we present the analysis based on the full data set in the main text, with the  
143 equivalent analysis on the reduced data set provided in the Appendix (Tables S7-9, Fig. S1). We performed  
144 model selection in relation to AIC values and weights for the candidate model set. For each population, we  
145 retained the model with the lowest AIC value as long as it differed by at least 2 points from any simpler  
146 competing model (see Arnold 2010).

## 147

## 148 **Results**

149 In all five populations, the best supported model describing over-winter variation in body mass consistently  
150 included the sex by date interaction (for all five populations,  $\Delta\text{AIC} > 3.5$  compared to the second-best model),  
151 showing that average change in body mass over winter differed between males and females (see Tables S1-S5  
152 for scaled parameter estimates). More specifically, in the two Swedish populations, body mass (mean  $\pm$  sd) of  
153 males decreased by  $-21.1$  g ( $\pm 3.1$ , Bogesund, and  $-21.5$  g ( $\pm 3.7$ , Grimsö) per day between 1<sup>st</sup> January and the  
154 end of the winter, while this decrease was much less marked for females ( $-4.5 \pm 2.8$  g and  $-12.0 \pm 3.7$  g /day,  
155 respectively). In contrast, in the three French populations, female body mass increased by between  $14.2$  g ( $\pm$   
156  $3.1$ , Trois-Fontaines) and  $25.8$  g ( $\pm 6.1$ , Aurignac-VCG) per day over winter, while that of males remained more  
157 or less constant (from  $-2.3 \pm 3.0$  g/day at Chizé to  $3.9 \pm 4.3$  g/day at Trois-Fontaines). As a result, while males  
158 were clearly heavier, on average, than females at the onset of winter in all five populations, albeit more  
159 pronouncedly in France (mean  $\pm$  se: Chizé:  $23.0 \pm 0.2$  kg for males vs.  $20.7 \pm 0.2$  kg for females; Trois-  
160 Fontaines:  $25.0 \pm 0.2$  kg for males vs.  $22.8 \pm 0.2$  kg for females; Aurignac-VCG:  $23.9 \pm 0.3$  kg for males vs.  
161  $21.4 \pm 0.2$  kg for females, i.e. a sexual mass dimorphism of about 10%) than in Sweden (Bogesund:  $24.8 \pm 0.2$   
162 kg for males vs.  $23.5 \pm 0.2$  kg for females; Grimsö:  $26.3 \pm 0.2$  kg for males vs.  $25.1 \pm 0.2$  kg for females, i.e. a  
163 sexual mass dimorphism of about 5%), by mid-March (Julian date = 74), males did not weigh substantially  
164 more than females in all populations (Fig. 1). Finally, at Aurignac-VCG only, the best supported model  
165 included an additive effect of sector, indicating that deer weighed, on average,  $0.81$  kg ( $\pm 0.2$ ) more in the open  
166 sector than those in the partially wooded sector.



167

168 **Fig. 1:** Body mass (kg) of male (orange) and female (purple) adults (>1.5 years old) in five intensively  
 169 monitored populations of roe deer situated in Sweden (Bogesund, Grimsö) and France (Chizé, Trois-Fontaines,  
 170 Aurignac-VCG) in relation to date over winter. Sexual mass dimorphism (SMD) calculated as the ratio of  
 171 predicted male mass to female mass at the start (1<sup>st</sup> January) and end (15<sup>th</sup> March) of the winter period is  
 172 indicated for each population.

173 Lastly, there was some evidence that over-winter body mass change varied among years to a greater extent in  
 174 the Swedish populations compared to the French populations: the proportion of the variance attributable to the  
 175 random effect of year on the slope of the body-mass-date relationship was 2.5-9.0 times higher in Bogesund and  
 176 Grimsö than in the three French populations (Table 2).

177  
 178 **Table 2:** Variance attributed to the residual, fixed and random components of the model describing sex-specific  
 179 over-winter variation in body mass across five populations of roe deer. To facilitate reliable comparison, we  
 180 derived these variance components using an identical model structure for each population, with individual  
 181 identity as a random effect on the intercept, and year as a random effect on both the intercept and the slope. The  
 182 proportion of the total variance explained by the random effect of year on the slope is provided as a percentage.

	Residual	Fixed effects	Random effects			
			ID intercept	Year intercept	Year slope	% variance slope(Year)
Bogesund (SW)	1.67	0.18	5.97	0.63	0.05	0.53%
Grimsö (SW)	1.83	0.30	4.92	0.60	0.06	0.72%
Trois-Fontaines (FR)	2.52	0.88	4.20	1.05	0.01	0.09%
Chizé (FR)	1.87	0.64	4.00	0.88	0.01	0.08%
Aurignac-VCG (FR)	0.94	1.16	3.49	0.06	0.01	0.21%

## 186 Discussion

187 From the analysis of the body mass of over 7000 individual roe deer living along a gradient of ecological  
 188 conditions in terms of winter harshness, from near the northern-most extreme to the southern part of their core  
 189 geographical range, we found strong support for both our predictions, i/ that over-winter body mass change was  
 190 sex-specific whereby males lost more (or gained less) than females, so that sexual dimorphism in mass was  
 191 virtually absent by the end of the winter; ii/ but that this pattern was strongly modulated by winter severity such  
 192 that while roe deer in Sweden lost mass, on average, those in France gained mass. There was also some  
 193 indication that over-winter body mass change was more variable among years in the Swedish populations  
 194 compared to the French populations, providing additional support for the latter hypothesis. The costs of  
 195 allocation to sex-specific reproductive schedules likely drive seasonal variations in the degree of sexual mass  
 196 dimorphism in this weakly polygynous ungulate.



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

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

215  
216 *On the impact of winter severity for body mass change*

217 While roe deer are consistently heavier in Sweden than France at winter onset (Fig. 1), the severity of  
218 conditions during the Scandinavian winter caused an average body mass loss of between 0.4 kg (females at  
219 Bogesund) and 2.1 kg (males at Grimsö). Note that these figures are likely conservative, as resource scarcity  
220 during winter may begin well before the New Year in northern environments depending on the annual timing of  
221 first snowfall. For an animal of around 20-25 kg this loss is clearly considerable and indicates that the capacity  
222 to store fat reserves and, therefore, seasonal fluctuations in body mass, are much greater in the north of its range  
223 than previously documented for this medium-sized income breeder (Kjellander et al. 2006). **Indeed, there was**  
224 **also some indication in our data that over-winter body mass change varied from year to year somewhat more**  
225 **markedly in Sweden compared to France (see Table 2), presumably in response to the harshness of winter**  
226 **conditions in a given year.** This is likely an adaptation to buffer against severe winters, as further south, in the  
227 heart of its range, over-winter body mass is generally stable and may even increase slightly (Hewison et al.  
228 1996, 2002). Larger body size (Linstedt & Boyce 1985) and the capacity to store fat (Trondrud et al. 2021,  
229 Denryter et al. 2022) have been widely interpreted as adaptations which increase fasting endurance in response  
230 to the dramatic fluctuations of resource availability in highly seasonal environments. Although differences in  
231 the operational sex ratio across populations could theoretically influence relative priority of allocation to sexual

232 secondary characters, such as antlers, in polygynous systems driven by variation in the intensity of male-male  
233 competition (Weir et al. 2011), this is highly unlikely in our specific case. Indeed, the roe deer is only weakly  
234 polygynous (Vanpé et al. 2008) and the adult sex ratio (number of males/total number of males and females) is  
235 ostensibly the same across the five populations (Chizé: 0.44; Trois-Fontaines: 0.47; Aurignac-VCG: 0.41;  
236 Bogesund: 0.43; Grimsö: 0.41). Larger body size has often been reported at higher latitudes within species of  
237 mammals (Ashton et al. 2000), in line with Bergmann's rule, and is thought to reflect natural selection for  
238 greater thermoregulatory buffering in endotherms (He et al. 2023). Our data are also in line with this general  
239 pattern, but indicate that sexual selection is the ultimate driver of between-sex differences in over-winter body  
240 mass change, suggesting similar priority of energy allocation to this secondary sexual trait across hugely  
241 contrasted environments.

#### 242 243 *On the life history implications of annual body mass loss during winter*

244 The repeated annual cycles of fat accumulation and depletion that underpin a capital breeding tactic are  
245 predicted to carry life history costs (Houston et al. 2006). While there is clear evidence to indicate that roe deer  
246 females adopt an income breeder tactic relative to other large herbivores (Andersen et al. 2000), our results  
247 imply that males must accumulate body condition prior to winter to offset the energetic costs of antler growth  
248 and subsequent territory establishment and, in this sense, can be considered capital breeders relative to females  
249 (Apollonio et al. 2020). In polygynous mammals, allocation to traits that confer an advantage in contest  
250 competition for females are predicted to impose costs in terms of survival (Clinton & Leboeuf 1993). Previous  
251 work has established that, despite the low level of polygyny in roe deer (Vanpé et al. 2008), the sex difference  
252 in annual survival of adults is equivalent to that of more polygynous and size dimorphic ungulates (Gaillard et  
253 al. 1993). We suggest that the repeated energetic cost of allocating to secondary sexual traits every winter is a  
254 proximal driver that, together with the direct costs of territorial defense and male-male competition for mates,  
255 contributes to the survival deficit for males in this weakly dimorphic ungulate. Most deer species cast and re-  
256 grow antlers during spring, when resources are plentiful (Mysterud et al. 2005b). However, because of their  
257 unusual schedule of allocation to reproduction, roe deer males are repeatedly faced with a trade-off between  
258 maintaining accumulated mass to offset the costs of establishing and defending a mating territory in spring, a  
259 full four months prior to the rut, and growing antlers during the winter season of food scarcity. The relative  
260 importance of antler size, body mass and territory quality for determining male reproductive success has yet to  
261 be established. **Despite the huge among individual variation in body mass at the onset of winter within all five  
262 populations (Fig. 1, Table 2), there was little evidence for individual variation in over-winter body mass change,  
263 although we could not formally evaluate this due to the very low number of repeat measures.** Future  
264 investigations of inter-individual variation in over-winter body mass change in relation to environmental  
265 severity would be highly informative for understanding individual tactics of energy allocation to secondary  
266 sexual traits and their life history consequences.

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273 methodology; all authors collected the data and discussed the analytical approach; N.C.B. analysed the data.;  
274 A.J.M.H. wrote the first draft of the manuscript and all authors contributed critically to revision.

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## 281 **Conflict of interest disclosure:**

282 The authors declare they have no conflict of interest relating to the content of this article. A.J.M.H. and N.C.B.  
283 are recommenders for PCIEcology.

## 285 **Data, scripts, code and supplementary information availability:**

286 Data and code can be found at Bonnot et al. (2024), while supplementary information is given in an Appendix at  
287 the end of this article.

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## Appendix

### 1.1 Model selection:

Table S1a: 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 selected model is shaded grey.

Fixed effects	Random intercept	Random slope	$\Delta$ AIC	weight
Sex + Julian date + Sex:Julian date	ID & Year	ID & Year	0.0	1.00
Sex + Julian date	ID & Year	ID & Year	26.2	0
Julian date	ID & Year	ID & Year	27.2	0
Sex	ID & Year	ID & Year	37.7	0
null	ID & Year	ID & Year	38.4	0

Table S1b: Model summary for the selected model: parameter coefficients for the fixed effects (mean and standard error, s.e.) and variance components for the fixed, random and residual effects, describing sex-specific over-winter variation in body mass in the **Bogesund** population. Note that Julian date was centered and scaled (see text). The reference category is female.

Parameter	Coefficient	s.e.	Variance
<b>Fixed effects</b>			<b>0.17</b>
Intercept	23.38	0.22	
Sex (male)	0.55	0.24	
Julian date	-0.10	0.06	
Sex (male):Julian date	-0.37	0.07	
<b>Random effects</b>			<b>6.65</b>
Individual identity (intercept)			5.92
Individual identity (slope)			0.05
Year (intercept)			0.63
Year (slope)			0.04
<b>Residual</b>			<b>1.63</b>

401 Table S2a: Model fit and selection (fixed and random effects, difference in AIC score compared to the best  
 402 model, AIC weight) describing sex-specific over-winter variation in body mass in the **Grimsö** population. The  
 403 selected model is shaded grey.  
 404

<b>Fixed effects</b>	<b>Random intercept</b>	<b>Random slope</b>	<b>ΔAIC</b>	<b>weight</b>
Sex + Julian date + Sex:Julian date	ID & Year	ID & Year	0.0	0.90
Sex + Julian date	ID & Year	ID & Year	4.4	0.01
Julian date	ID & Year	ID & Year	15.1	0.00
Sex	ID & Year	ID & Year	27.4	0.00
null	ID & Year	ID & Year	37.3	0.00

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407 Table S2b: Model summary for the selected model: parameter coefficients for the fixed effects (mean and  
 408 standard error, s.e.) and variance components for the fixed, random and residual effects, describing sex-specific  
 409 over-winter variation in body mass in the **Grimsö** population. Note that Julian date was centered and scaled (see  
 410 text). The reference category is female.  
 411

<b>Parameter</b>	<b>Coefficient</b>	<b>s.e.</b>	<b>Variance</b>
<b>Fixed effects</b>			<b>0.30</b>
Intercept	24.56	0.19	
Sex (male)	0.74	0.22	
Julian date	-0.30	0.08	
Sex (male):Julian date	-0.24	0.09	
<b>Random effects</b>			<b>5.65</b>
Individual identity (intercept)			4.92
Individual identity (slope)			0.06
Year (intercept)			0.60
Year (slope)			0.06
<b>Residual</b>			<b>1.76</b>

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413 Table S3a: Model fit and selection (fixed and random effects, difference in AIC score compared to the best  
 414 model, AIC weight,) describing sex-specific over-winter variation in body mass in the **Aurignac-VCG**  
 415 population. The selected model is shaded grey.  
 416

<b>Fixed effects</b>	<b>Random intercept</b>	<b>Random slope</b>	<b>ΔAIC</b>	<b>weight</b>
Sex + Julian date + Sex:Julian date + Sector	ID & Year	Year	0.0	0.87
Sex + Julian date + Sector	ID & Year	Year	4.0	0.12
Sex + Sector	ID & Year	Year	9.9	0.01
Sex + Julian date + Sex:Julian date	ID & Year	Year	12.0	0.00
Sex + Julian date	ID & Year	Year	15.3	0.00
Sex	ID & Year	Year	22.4	0.00
Julian date + Sector	ID & Year	Year	67.1	0.00
Sector	ID & Year	Year	73.8	0.00
Julian date	ID & Year	Year	82.2	0.00
null	ID & Year	Year	88.7	0.00

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Table S3b: Model summary for the selected model: parameter coefficients for the fixed effects (mean and standard error, s.e.) and variance components for the fixed, random and residual effects, describing sex-specific over-winter variation in body mass in the **Aurignac-VCG** population. Note that Julian date was centered and scaled (see text). The reference category is female and the mixed sector.

<b>Parameter</b>	<b>Coefficient</b>	<b>s.e.</b>	<b>Variance</b>
<b>Fixed effects</b>			<b>1.16</b>
Intercept	21.30	0.20	
Sex (male)	1.87	0.22	
Julian date	0.43	0.10	
Sector (open)	0.81	0.21	
Sex (male):Julian date	-0.37	0.15	
<b>Random effects</b>			<b>3.56</b>
Individual identity (intercept)			3.49
Year (intercept)			0.06
Year (slope)			0.01
<b>Residual</b>			<b>0.94</b>

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426 Table S4a: Model fit and selection (fixed and random effects, difference in AIC score compared to the best  
 427 model, AIC weight,) describing sex-specific over-winter variation in body mass in the **Chizé** population. The  
 428 selected model is shaded grey.

<b>Fixed effects</b>	<b>Random intercept</b>	<b>Random slope</b>	<b>ΔAIC</b>	<b>weight</b>
Sex + Julian date + Sex:Julian date	ID & Year	Year	0.0	1.0
Sex + Julian date	ID & Year	Year	47.2	0.0
Sex	ID & Year	Year	66.2	0.0
Julian date	ID & Year	Year	375.9	0.0
null	ID & Year	Year	396.3	0.0

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433 Table S4b: Model summary for the selected model: parameter coefficients for the fixed effects (mean and  
 434 standard error, s.e.) and variance components for the fixed, random and residual effects, describing sex-specific  
 435 over-winter variation in body mass in the **Chizé** population. Note that Julian date was centered and scaled (see  
 436 text). The reference category is female.

437

<b>Parameter</b>	<b>Coefficient</b>	<b>s.e.</b>	<b>Variance</b>
<b>Fixed effects</b>			<b>0.64</b>
Intercept	21.44	0.16	
Sex (male)	1.52	0.08	
Julian date	0.33	0.04	
Sex (male):Julian date	-0.37	0.05	
<b>Random effects</b>			<b>4.88</b>
Individual identity (intercept)			4.00
Year (intercept)			0.88
Year (slope)			0.01
<b>Residual</b>			<b>1.87</b>

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439 Table S5a: Model fit and selection (fixed and random effects, difference in AIC score compared to the best  
 440 model, AIC weight,) describing sex-specific over-winter variation in body mass in the **Trois-Fontaines**  
 441 population. The selected model is shaded grey.

<b>Fixed effects</b>	<b>Random intercept</b>	<b>Random slope</b>	<b>ΔAIC</b>	<b>weight</b>
Sex + Julian date + Sex:Julian date	ID & Year	Year	0.0	0.86
Sex + Julian date	ID & Year	Year	3.7	0.14
Sex	ID & Year	Year	14.1	0.00
Julian date	ID & Year	Year	322.1	0.00
null	ID & Year	Year	333.0	0.00

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Table S5b: Model summary for the selected model: parameter coefficients for the fixed effects (mean and standard error, s.e.) and variance components for the fixed, random and residual effects, describing sex-specific over-winter variation in body mass in the **Trois-Fontaines** population. Note that Julian date was centered and scaled (see text). The reference category is female.

<b>Parameter</b>	<b>Coefficient</b>	<b>s.e.</b>	<b>Variance</b>
<b>Fixed effects</b>			<b>0.88</b>
Intercept	23.28	0.18	
Sex (male)	1.83	0.10	
Julian date	0.23	0.05	
Sex (male):Julian date	-0.17	0.07	
<b>Random effects</b>			<b>5.25</b>
Individual identity (intercept)			4.20
Year (intercept)			1.05
Year (slope)			0.01
<b>Residual</b>			<b>2.52</b>

451

452 *1.2 Test for non-linear variation in over-winter body mass*

453 In preliminary analysis, in addition to a linear function, we modelled body mass change over winter with  
 454 quadratic, cubic or smoothing functions of date using the ‘lme4’ and ‘gamm4’ packages (Bates et al. 2015; Wood  
 455 & Scheipl 2020) in R. All models included sex, Julian date and their two-way interaction, as well as individual  
 456 identity (to control for repeated measures on individuals) and year (to control for annual variation in conditions)  
 457 as random factors. In three out of five cases, the linear function provided the best fit (Table S6), whereas the cubic  
 458 model provided a somewhat better fit in the Grimsö population, while the quadratic model performed slightly  
 459 better in the Aurignac-VCG population. Because this improvement was marginal from a biological point of view,  
 460 and to facilitate comparison among populations, we present results from linear models in the main text, i.e.  
 461 assuming that the rate of change in body mass during winter is constant over the entire study window.

462 Wood, S. & Scheipl, F. (2020) gamm4: Generalized Additive Mixed Models using ‘mgcv’ and ‘lme4’. R  
 463 package version 0.2-6.

464 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4.  
 465 *Journal of Statistical Software*, 67, 1-48.

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

473

Population	linear	quadratic	cubic	GAMM
<b>Bogesund</b>	<b>9526.9</b>	9553.2	9530.4	9543.0
<b>Grimsö</b>	6348.3	6348.6	<b>6342.7</b>	6364.8
<b>Aurignac-VCG</b>	2057.3	<b>2056.3</b>	2058.6	2130.5
<b>Chizé</b>	<b>24095.6</b>	24146.1	24102.4	24439.6
<b>Trois-Fontaines</b>	<b>17777.2</b>	17782.8	17783.7	18109.9

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476 2.1 Model selection on a reduced data set, featuring a single observation per individual (with year as a random  
 477 effect on both the intercept and slope) for the three populations where the full model (which also included a  
 478 random effect of individual identity on both the intercept and slope) did not converge

479 Table S7: Model fit and selection (fixed and random effects, difference in AIC score compared to the best  
 480 model, AIC weight) on the reduced data set, describing sex-specific over-winter variation in body mass in the  
 481 **Aurignac-VCG population**. The selected model is shaded grey.  
 482

Fixed effects	Random intercept & slope	$\Delta$ AIC	weight
Sex + Julian date + Sex:Julian date + Sector	Year	0.0	0.63
Sex + Julian date + Sector	Year	2.0	0.23
Sex + Sector	Year	3.1	0.13
Sex + Julian date + Sex:Julian date	Year	9.6	0.01
Sex + Julian date	Year	11.1	0.00
Sex	Year	14.7	0.00
Julian date + Sector	Year	64.8	0.00
Sector	Year	65.5	0.00
Julian date	Year	79.0	0.00
null	Year	82.3	0.00

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485 Table S8: Model fit and selection (fixed and random effects, difference in AIC score compared to the best  
 486 model, AIC weight) on the reduced data set, describing sex-specific over-winter variation in body mass in the  
 487 **Chizé population**. The selected model is shaded grey.  
 488

Fixed effects	Random intercept & slope	$\Delta$ AIC	weight
Sex + Julian date + Sex:Julian date	Year	0.0	1.0
Sex + Julian date	Year	26.7	0.0
Sex	Year	31.2	0.0
Julian date	Year	329.9	0.0
null	Year	335.9	0.0

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491 Table S9: Model fit and selection (fixed and random effects, difference in AIC score compared to the best  
 492 model, AIC weight) on the reduced data set, describing sex-specific over-winter variation in body mass in the  
 493 **Trois-Fontaines population**. The selected model is shaded grey.  
 494

Fixed effects	Random intercept & slope	$\Delta$ AIC	weight
Sex + Julian date + Sex:Julian date	Year	0.0	0.50
Sex + Julian date	Year	0.3	0.42
Sex	Year	3.7	0.08
Julian date	Year	291.9	0.00
null	Year	298.3	0.00

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497 2.2 Estimated over-winter changes in body mass in the three French populations (Chizé, Trois-Fontaines,  
498 Aurignac-VCG) based on a reduced data set, featuring a single observation per individual

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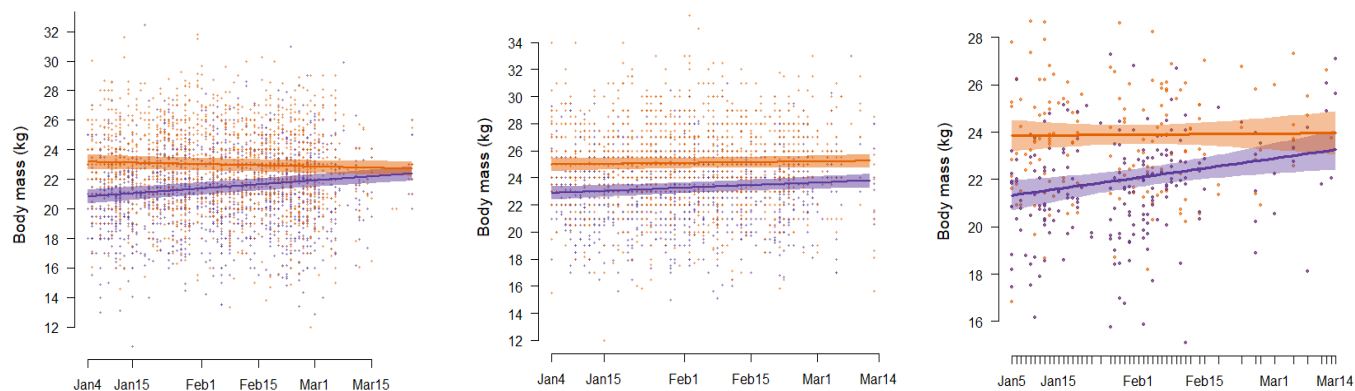
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506 **Fig. S1:** Body mass (kg) of male (purple) and female (orange) adults (>1.5 years old) in three intensively  
507 monitored populations of roe deer situated in France (Chizé, Trois-Fontaines, Aurignac-VCG) in relation to date  
508 over winter (based on the model selection presented in Tables S7-S9).

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511 Table S10: Sample size per year and sex for the five populations of roe deer situated in Sweden (Bogesund,  
512 Grimsö) and France (Aurignac-VCG , Chizé, Trois-Fontaines), with the number of unique individuals measured  
513 that year in brackets.

Year	Grimsö		Bogesund		Aurignac-VCG		Chizé		Trois-Fontaines	
	F	M	F	M	F	M	F	M	F	M
1974	3 (2)	3 (3)	/	/	/	/	/	/	/	/
1975	4 (4)	1 (1)	/	/	/	/	/	/	/	/
1976	2 (2)	3 (3)	/	/	/	/	/	/	23 (23)	23 (23)
1977	11 (11)	6 (6)	/	/	/	/	/	/	53 (53)	55 (55)
1978	2 (2)	4 (4)	/	/	/	/	41 (41)	24 (24)	39 (39)	41 (41)
1979	6 (6)	1 (1)	/	/	/	/	53 (53)	32 (32)	57 (57)	59 (59)
1980	2 (2)	3 (3)	/	/	/	/	56 (56)	49 (49)	60 (60)	44 (44)
1981	/	/	/	/	/	/	66 (66)	56 (56)	39 (39)	45 (45)
1982	/	/	/	/	/	/	68 (68)	55 (55)	66 (66)	41 (40)
1983	/	/	/	/	/	/	87 (87)	68 (67)	75 (75)	56 (56)
1984	/	1 (1)	/	/	/	/	117 (117)	76 (76)	72 (72)	58 (58)
1985	8 (8)	/	/	/	/	/	79 (79)	65 (65)	80 (78)	62 (62)
1986	3 (3)	1 (1)	/	/	/	/	127 (127)	70 (70)	79 (79)	63 (63)
1987	41 (20)	16 (9)	/	/	/	/	97 (97)	68 (68)	54 (54)	46 (46)
1988	16 (10)	10 (8)	/	/	/	/	73 (73)	54 (54)	37 (37)	42 (42)
1989	12 (9)	3 (3)	6 (4)	1 (1)	/	/	74 (74)	58 (58)	38 (38)	33 (33)
1990	28 (19)	28 (11)	18 (11)	21 (11)	/	/	66 (66)	52 (52)	53 (53)	44 (44)
1991	36 (24)	24 (16)	18 (13)	12 (11)	/	/	64 (64)	54 (54)	58 (58)	43 (43)
1992	33 (16)	30 (15)	43 (36)	26 (20)	/	/	72 (72)	55 (55)	55 (55)	38 (38)
1993	36 (19)	32 (19)	21 (13)	12 (9)	/	/	58 (58)	39 (39)	42 (42)	39 (39)
1994	58 (31)	43 (20)	8 (8)	12 (12)	/	/	49 (49)	40 (40)	52 (52)	45 (45)
1995	43 (25)	30 (13)	32 (25)	19 (12)	/	/	55 (55)	39 (39)	45 (45)	49 (49)
1996	37 (22)	21 (12)	49 (33)	26 (15)	/	/	55 (55)	41 (41)	39 (39)	41 (41)
1997	40 (17)	10 (6)	87 (41)	34 (19)	/	/	67 (67)	63 (63)	37 (37)	40 (40)
1998	17 (17)	6 (6)	7 (7)	16 (10)	/	/	81 (81)	89 (89)	34 (34)	29 (29)
1999	25 (20)	7 (6)	36 (24)	31 (16)	/	/	62 (62)	74 (74)	40 (40)	26 (26)
2000	9 (9)	5 (4)	34 (23)	19 (11)	/	/	48 (48)	46 (46)	8 (8)	10 (10)
2001	26 (21)	13 (10)	61 (36)	59 (34)	/	2 (2)	85 (84)	77 (77)	47 (47)	37 (37)
2002	8 (8)	8 (7)	46 (29)	57 (34)	5 (5)	5 (5)	83 (83)	65 (65)	44 (44)	59 (59)
2003	14 (14)	3 (3)	37 (26)	44 (29)	8 (8)	5 (5)	91 (90)	77 (77)	63 (63)	69 (69)
2004	23 (17)	8 (6)	62 (42)	66 (37)	/	/	136 (136)	99 (99)	64 (64)	75 (75)
2005	15 (14)	12 (10)	95 (31)	92 (34)	12 (12)	8 (8)	126 (126)	93 (93)	85 (85)	75 (75)
2006	36 (29)	29 (19)	62 (28)	64 (19)	14 (14)	12 (12)	127 (127)	111 (111)	57 (57)	51 (51)
2007	31 (28)	19 (14)	22 (12)	19 (9)	13 (13)	5 (5)	79 (79)	69 (69)	33 (33)	38 (38)
2008	16 (14)	8 (7)	16 (11)	11 (7)	15 (15)	5 (5)	85 (85)	51 (51)	36 (36)	25 (25)
2009	40 (29)	23 (17)	30 (14)	15 (12)	12 (12)	8 (8)	79 (79)	73 (73)	37 (37)	30 (30)
2010	58 (29)	37 (22)	97 (43)	73 (21)	15 (14)	10 (10)	108 (108)	73 (73)	45 (45)	36 (36)
2011	39 (22)	28 (14)	93 (36)	51 (26)	16 (16)	11 (11)	111 (110)	91 (91)	62 (62)	41 (41)
2012	16 (13)	14 (13)	64 (27)	44 (18)	19 (19)	8 (8)	90 (90)	61 (61)	42 (42)	37 (37)
2013	21 (16)	24 (19)	110 (37)	75 (25)	13 (13)	10 (10)	110 (110)	82 (82)	59 (59)	55 (55)
2014	21 (14)	20 (14)	46 (20)	48 (12)	17 (17)	8 (8)	94 (94)	77 (77)	58 (58)	52 (52)
2015	19 (15)	26 (17)	80 (22)	43 (12)	18 (17)	11 (11)	108 (108)	78 (78)	42 (42)	38 (38)
2016	18 (10)	35 (24)	96 (18)	66 (12)	15 (15)	12 (12)	/	/	49 (49)	39 (39)
2017	23 (16)	25 (17)	/	/	19 (19)	7 (7)	/	/	/	/
2018	/	/	/	/	14 (14)	15 (14)	/	/	/	/
2019	/	/	/	/	12 (12)	12 (12)	/	/	/	/
2020	/	/	/	/	16 (16)	15 (15)	/	/	/	/
2021	/	/	/	/	13 (13)	9 (9)	/	/	/	/
2022	/	/	/	/	16 (16)	13 (13)	/	/	/	/
2023	/	/	/	/	16 (16)	14 (14)	/	/	/	/