

## Eruption patterns of permanent front teeth as an indicator of performance in roe deer



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### ABSTRACT

In most species of vertebrates, teeth play a central role in the long-term performance of individuals. However, patterns of tooth development have been little investigated as an indicator of animal performance. We filled this gap using data collected during long-term capture-mark-recapture monitoring of 1152 roe deer fawns at Chizé, western France. This population fluctuated greatly in size during the 27 years of monitoring, offering a unique opportunity to assess how the eruption patterns of front teeth perform as indicator of animal performance. We used three indices of the eruption of permanent front teeth, the simplest being whether or not incisor  $I_2$  has erupted, and the most complex being a 12-level factor distinguishing the different stages of tooth eruption. We also assessed the relevance of these indices as compared to fawn body mass, a widely used indicator of animal performance of deer populations. Dental indices and body mass were positively correlated (all  $r > 0.62$ ). Similarly to body mass, all indices based on tooth eruption patterns responded to changes of population size and can be reliably used to assess the relationship between roe deer and their environment. We found a linear decrease in body mass with increasing population size ( $r^2 = 0.54$ ) and a simultaneous delay in tooth development ( $r^2 = 0.48$ – $0.55$  from the least to the most accurate indicator). However, tooth development would be not further delayed in years with the highest densities ( $>15$  adult roe deer/100 ha). A path analysis supported the population density effect on tooth eruption patterns being mainly determined by the effect of population size on body mass. Our study provides managers with simple indices (e.g., presence-absence of  $I_2$ ) that provide a technically more easy way to standardize measurements of deer density-dependent responses over large geographical and temporal scales than would be possible with body mass.

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### 1. Introduction

Populations of large herbivores are commonly (e.g., in North America, Western Eurasia) controlled through hunting using yearly quotas (Gordon et al., 2004). Quotas are often determined using estimates, or indices, of population density as a proxy for demographic status (Williams et al., 2002). Management decisions are then based on the observed population changes between

consecutive years. This approach has recently been challenged because counting large herbivores is an especially difficult task (Caughley, 1977) and includes problems of both limited accuracy and poor precision (Morellet et al., 2007). Furthermore, monitoring only population abundance does not provide any information on the relationship between the focal population and its habitat. Morellet et al. (2007) have therefore proposed that managers should consider changes in both population parameters and habitat characteristics, as well as their interaction, for successful management of ungulate populations. These changes can be monitored through indicators of ecological change (*sensu* Cederlund et al., 1998) including indicators of animal performance (e.g., Bonenfant et al., 2002; Gaillard et al., 1996; Garel et al., 2011b; Strickland et al., 2008), relative measure of animal abundance (e.g., Garel et al., 2010; Loison et al., 2006; Vincent et al., 1991), assessment of habitat quality and/or evaluation of the impact of large herbivores on

*Abbreviations:* BM, body mass; DFI, dental formula index; PFTI, permanent front tooth index.

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habitat structure and composition (Chevrier et al., 2012; Morellet et al., 2001). Simultaneously monitoring temporal changes in these ecological indicators provides an adaptive way for setting hunting quotas and for achieving specific management objectives.

Using indicators of ecological changes to monitor populations of large herbivores typically rely on interpreting the functional relationship between a biological parameter and the changes in population size. Thus, monitoring density-dependence provides a way to measure population-habitat relationships and all parameters that respond to changes in relative density (i.e., changes in population size for a given habitat quality) can be viewed as candidate ecological indicators. So far, juvenile and yearling body mass correspond to the ecological indicators of animal performance that are most often used to monitor the status of ungulate populations in relation to habitat quality (e.g., Bonenfant et al., 2002; Gaillard et al., 1996; Garel et al., 2011b; Strickland et al., 2008). Body size has also been found to be a reliable indicator of animal performance in roe deer (*Capreolus capreolus*; Hewison et al., 1996; Zannè et al., 2006). Recently, it has been shown that body mass and hind foot length display different density-dependent responses: hind foot length is less sensitive to density than body mass and decreases with increasing density only when environmental conditions become very harsh (Toïgo et al., 2006). Monitoring indicators based on body development could improve the reliability of assessments of the relationship between a population and its habitat along the colonization-saturation continuum by describing the full range of variation in density for a given population.

Developing alternative indicators to body mass presents other advantages. First, body mass is prone to sampling variation caused by varying degrees of fullness of the digestive tract or loss of body fluids, and large seasonal variation (e.g., caused by rutting activities in males, see Garel et al., 2011a; Leader-Williams and Ricketts, 1982). Precision of measurements has implications in terms of monitoring because imprecise measurements should require an increased sample size to detect biological signals. Second, monitoring growth patterns of a part of the animal body (e.g., hind foot length) is an interesting alternative for collecting data (see Zannè et al., 2006 for an example of hind feet collected over large spatio-temporal scales by hunters) and for standardizing measurements (with the simultaneous increase of precision). Focusing on such biological indicators enables data to be collected from part rather than the whole animal; sampling the whole animal can be difficult if the animal is large or if hunters take only part of the animal (e.g., head).

In this context, monitoring tooth eruption patterns could be a biological and technical relevant alternative for monitoring populations of large herbivores, although it has been poorly investigated up to now despite the central role of teeth in the life history of large herbivores. Previous studies in deer species have shown that eruption of permanent teeth is delayed in young animals under food restriction (Robinette et al., 1957) and increasing local density (Loe et al., 2004); and similar patterns have been reported in human populations (Garn et al., 1965). These results suggest that tooth eruption patterns could be used as an indicator of animal performance (*sensu* Morellet et al., 2007). Two density-dependent responses in tooth eruption could be expected. First, like body mass growth (e.g., Garel et al., 2011b; Toïgo et al., 2006), tooth eruption can be delayed at high density (H1). Second, because of their functional role in acquiring and chewing food as a preparation for digestion, teeth may have different growth priority as compared to body mass, and we may therefore expect different responses of teeth to food restriction compared to body mass response (H2). Tooth eruption should have a higher priority than growth of muscle or fat tissue and should therefore be less affected by nutritional deficiencies in the diet than total body mass (H2a), i.e., body mass is expected to decrease first, whereas tooth eruption pattern should be quite stable and would start to be delayed only under very harsh

environmental conditions (Klein, 1964; Toïgo et al., 2006). Alternatively, tooth eruption may start to be delayed simultaneously with body mass because both are interrelated (Kaur and Singh, 1992) but may cease to be delayed under very harsh environmental conditions because of their functional role in food intake (H2b). In both cases, monitoring of tooth eruption patterns and body mass concurrently should thus provide a meaningful signal of populations facing with changing environmental conditions.

The roe deer is a widespread and abundant ungulate species in Eurasia and is a highly-valued game species for which monitoring tools are required by managers (Cederlund et al., 1998). We studied a population of roe deer intensively monitored by capture-mark-recapture for 27 years, which experienced large variation in population size (Fig. 1 and Table 4). This long-term monitoring offers a unique opportunity to assess both the relevance of tooth eruption patterns to identify the relationships between roe deer and their environment (H1), and the existence of a different growth priority of tooth eruption compared to growth in body mass (H2a,b). We focused on the eruption patterns of permanent front teeth because ungulate population dynamics has been reported to be mostly sensitive to early performance (Gaillard et al., 2000). In addition, annual changes in animal performance of younger-aged individuals are the best indicator of changes of animal density along the colonization-saturation continuum (Bonenfant et al., 2009). We analyzed 3 indices of eruption patterns of permanent front teeth, with the simple one being whether or not incisor  $I_2$  has erupted and for the most complex one a 12 level factor distinguishing the different stages of tooth eruption. Indeed, we aimed at providing managers with tooth indices that can be easily standardized and measured over large geographical and temporal scales at which management operates. Lastly, we used a path analysis (Shipley, 2002) to quantify to what extent density effects on tooth eruption pattern operate through body mass or might also result from direct effects of density on tooth development (Loe et al., 2004).

## 2. Materials and methods

### 2.1. Study area

We studied the roe deer population in the Chizé wildlife reserve (2614 ha), western France (46°05'N, 0°25'W). The climate is oceanic with Mediterranean influences, mild winters, and warm and often dry summers. This fenced reserve managed by the Office National des Forêts (ONF) consists of a forest dominated by oak (*Quercus* sp.) and beech (*Fagus sylvatica*) with low productivity because of infertile soils and frequent summer droughts. High variation in population size (controlled by yearly removals; Fig. 1, Table 4; from 165 to 512 roe deer, mean = 315, standard deviation = 100) offers highly contrasted conditions to test our biological hypotheses (H1–H2a,b).

### 2.2. Data

The Chizé population has been intensively monitored using capture-mark-recapture methods since 1977. Roe deer are caught annually between October and March (mostly in January–February) using drive netting (i.e., about 5 km of vertical nets per capture day, 10–12 capture days per year), a method approved by the French Environment Ministry (articles L.424–1, R.411–14 and R.422–87 of the French code of environment). In addition, newborns are ear-tagged during the fawning period (May–June, Gaillard et al., 1993). A high proportion of the population (~70%) was individually marked during most years and allowed obtaining reliable estimates of yearly adult population size (> 1 year of age in March) using a generalization of the Cormack–Jolly–Seber model (Gaillard et al., 1986). During the study period, the population fluctuated markedly due to variation in both yearly removals and density-dependent responses

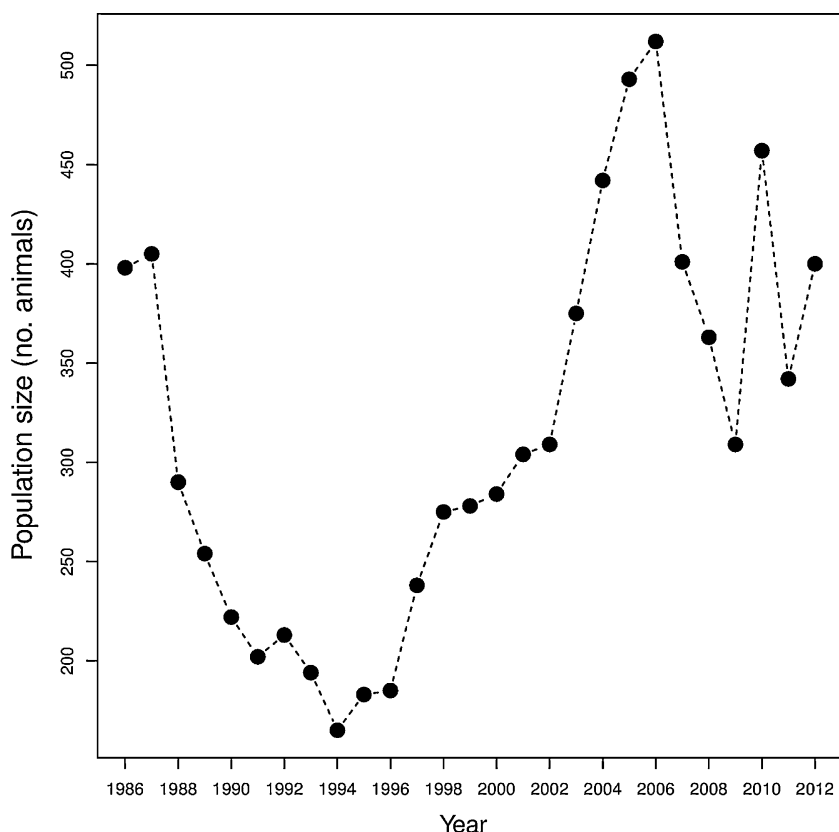


Fig. 1. Between-year variation in the number of adult roe deer (> 1 year of age in March) at Chizé, western France, during 1986–2012.

Table 1

Dental formula corresponding to the respective eruption stages of permanent front teeth. Dental formula is coded using lower case for milk front tooth, “-” for absence of the front tooth (*i.e.*, milk front tooth fallen), *upper case in italics* for front tooth in growing phase and upper case for permanent front tooth. The number (1–3) refers to the incisor number. Two categorical variables were computed from the dental formulae: dental formula index (12 levels) and permanent front tooth index (five levels); see text for details.

Dental formulae	Description	Dental formula index	Permanent front tooth index
i1i2i3c1	All milk front teeth	1	1
-1i2i3c1	First incisor fallen out	2	1
<i>I</i> 1i2i3c1	First incisor growing	3	2
<i>I</i> 1i2i3c1	First incisor permanent	4	2
I1-2i3c1	Second incisor fallen out	5	2
<i>I</i> 1i2i3c1	Second incisor growing	6	3
<i>I</i> 1i2i3c1	Second incisor permanent	7	3
I1i2-3c1	Third incisor fallen out	8	3
<i>I</i> 1i2i3c1	Third incisor growing	9	4
<i>I</i> 1i2i3c1	Third incisor permanent	10	4
<i>I</i> 1i2I3-1	Canine fallen out	11	4
<i>I</i> 1i2I3C1	Canine growing	12	5

of demographic parameters (Fig. 1). Body mass (nearest 50 g) and the dental formula (Table 1) of captured animals less than 1 year of age have been measured each autumn–winter between 1987 and 2013 (cohorts 1986–2012). In the following, we restricted our study to data collected (Table 2) during January–February period (*i.e.*, when 98% of 8 months-old fawns have been captured).

### 2.3. Definition of variables

We calculated two indices from the dental formulae (Table 1): one based on the dental formula (dental formula index, DFI – 12 modalities) and one based on pooling dental formulae according

Table 2

Number of roe deer fawns (< 1 year of age) captured at Chizé, western France, during winter 1987–2013. Sample sizes are given according to their dental formula index (Table 1).

Dental formula index	n
1	13
2	2
3	0
4	158
5	50
6	102
7	390
8	40
9	119
10	163
11	26
12	89
Total	1152

to the presence of 0, 1, 2, 3 or 4 permanent front teeth (permanent front tooth index, PFTI – 5 modalities). We also used the proportion of fawns with an erupted second incisor  $I_2$  (binomial variable scored 1 if  $I_2$  was visible and 0 if  $I_2$  was not visible or if the jaw still had a deciduous tooth). Eruption of  $I_2$  was the most variable among the different permanent front teeth (with  $I_3$ ), being erupted in 80.6% of the fawns (34.5% for  $I_3$ ; the maximum variance for a binomial distribution being at  $p = 50\%$ ). We used the second incisor because logistic regression analyses perform best when failure and success rates are approximately even (Agresti, 2002 and see Loe et al., 2004 for a similar approach) and a preliminary analysis showed that  $I_2$  performed better than the others front teeth. PFTI and  $I_2$  were computed to provide managers with performance indices that could be more easily used at large temporal and spatial scales than DFI and that should be less prone to measurement errors due to the involvement of many observers. We also removed from the

computation of indices fawns with four permanent front teeth and with canine having reached its final size ( $n = 111$ ) because this dental formula also corresponds to the adult dentition and may be confusing in a management context (however, including these animals led qualitatively to the same results). Finally, we used fawn body mass (BM) to assess comparatively how dental indices perform as indicators of animal performance. Fawn body mass has been shown to be a reliable indicator of density dependence in roe deer (Gaillard et al., 1996; Toigo et al., 2006).

#### 2.4. Statistical analysis

We performed a two-step analysis. First, we computed annual adjusted estimates of DFI, PFTI,  $I_2$  and BM representing predicted values corrected for capture date and sex, *i.e.*, accounting for body and skeletal growth and sex-specific differences in body development (predictions were made at the median capture date and we used “male” as the reference level for the variable sex). We used linear models (DFI, PFTI and BM) and generalized linear models with logit link and binomial distribution ( $I_2$ ) including additive effects of capture date (as a covariate), and sex and year as factor, as well as all two-way interactions and the three-way interaction among all predictors. We used generalized additive models with smoothing splines to explore possible non-linear relationships with date. Finally, we used year-specific predictions of the best model as yearly averages of DFI, PFTI,  $I_2$  and BM, *i.e.*, corrected values of annual indices (DFI<sub>c</sub>, PFTI<sub>c</sub>,  $I_{2c}$  and BM<sub>c</sub>; see Garel et al., 2010 for a similar approach).

In a second step, we used linear, quadratic and threshold models to assess the relationship between the corrected values of annual indices and annual estimates of population size in the year of birth. Quadratic and threshold models were used to test two hypotheses: (H2a) indices should decrease with increasing population size only when environmental conditions are very harsh or (H2b) indices should decrease with increasing population size up to a given threshold above which they are not related at all to variation in population size. Specifically, two threshold models were built in a way that (H2a) indices remain constant below a given population size threshold and show a linear variation above it; or (H2b) indices show a linear variation below a given population size threshold and remain constant above it. Thresholds were evaluated using an iterative procedure: models including different threshold values of population size (measured by population size with an iteration step of 1 animal) were successively fitted. The population size threshold of the model with the lowest deviance was then retained. Model selection was performed using the Akaike Information Criterion (AIC) with second order adjustment of the AIC (AIC<sub>c</sub>) to correct for small sample bias (Burnham and Anderson, 2002). The most parsimonious models (*i.e.*, lowest AIC<sub>c</sub>) were selected as the best models. For models including a population size threshold, we corrected the AIC<sub>c</sub> by including in the penalization term the estimation of this extra-parameter. We computed the coefficients of determination for linear and generalized models as the squared correlation coefficient between predictions and observations ( $R^2$  in Liao and McGee, 2003).

We also used a path analysis to decompose direct from indirect (through BM) effects of population size on DFI (Shipley, 2002). We fitted two separate linear regressions for each dependent variable (BM and DFI). The first regression included the effects of population size, capture date, and sex on BM. The second regression included the effects of BM, population size, capture date, and sex on DFI. The indirect effect of, *e.g.*, population size on DFI through BM, was computed as the product of direct effect of population size on BM and the direct effect of BM on DFI. All variables were standardized (mean=0, SD=1) to make comparable (same unit) their relative contribution to the model. Models were fitted in a Bayesian

**Table 3**

Effects of year (27 modalities), sex (2 modalities), and capture date (covariate) on body mass (BM), on dental formula index (DFI), on permanent front tooth index (PFTI) and on proportion of second incisor erupted ( $I_2$ ) of fawns captured at Chizé (France) in winter between 1987 and 2013. Additive effects are denoted by +, and an interaction between predictors is denoted by ×. The table reports  $\Delta AIC_c$  (*i.e.*, the difference in AIC<sub>c</sub> between the best model (lowest AIC<sub>c</sub> and  $\Delta AIC_c = 0$ ) and candidate models). The selected models are in bold type.

Models	BM	DFI	PFTI	$I_2$
Null	510.54	409.41	370.52	182.28
Year	34.30	385.08	348.07	171.46
Year + sex	5.15	387.16	350.15	173.07
Year + date	29.08	15.92	20.45	<b>0.00</b>
Year × sex	29.80	415.18	377.20	210.84
Year × date	40.44	<b>0.00</b>	<b>0.00</b>	21.79
Year + sex + date	<b>0.00</b>	18.03	22.43	1.39
Year + sex × date	1.76	20.12	24.50	2.06
Year × sex + date	26.33	33.01	39.56	33.30
Year × date + sex	10.49	2.20	2.14	23.26
Year × sex × date	74.62	58.44	63.04	81.97

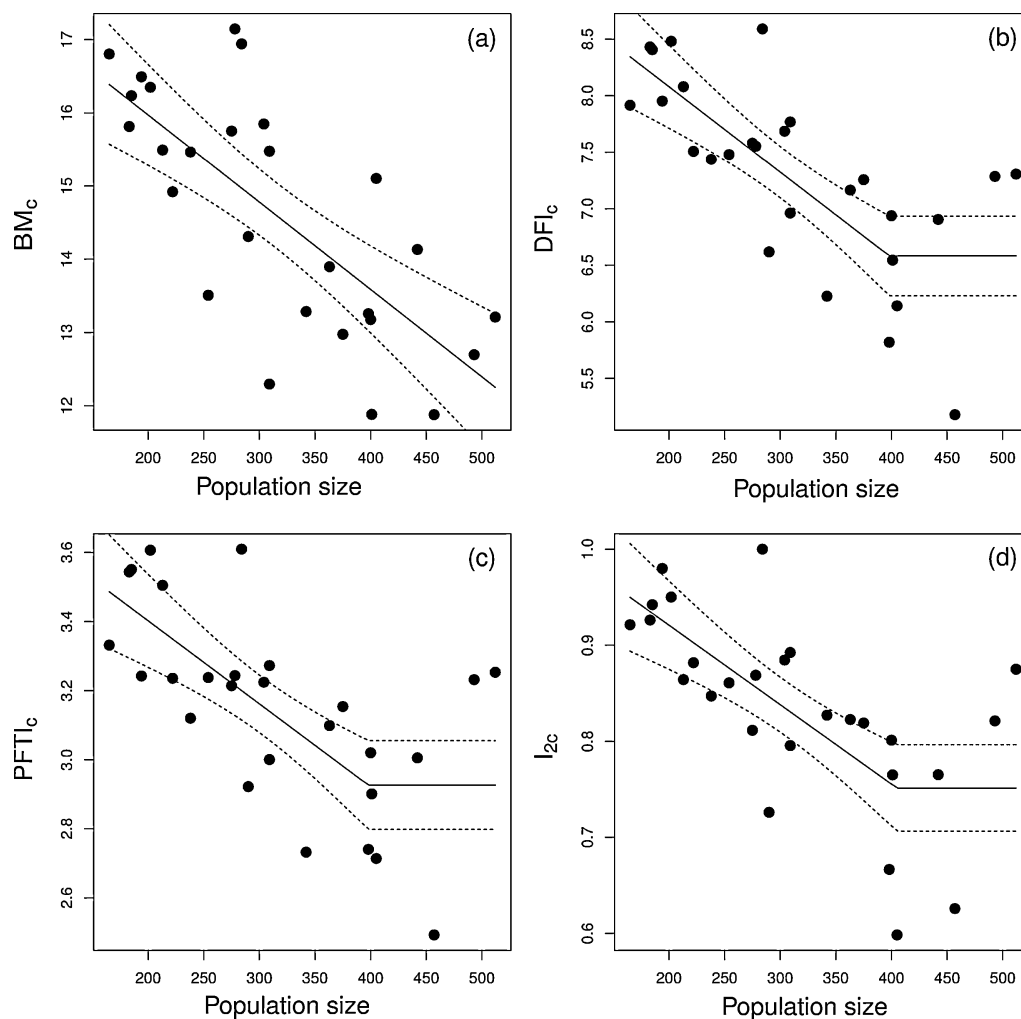
framework. This approach allowed us to account for uncertainty in parameters such as the product of direct effects (*i.e.*, the indirect effects). Bayesian methods assume prior distributions for model parameters (regression coefficients and residual variances) and use Bayes' theorem to derive the posterior distributions of parameters. Numerical methods based on Markov chain Monte Carlo simulations were used to derive posterior distributions. The following uninformative prior distributions were used: normal for regression intercepts and slopes with a mean of 0 and a variance of 1000, and uniform for the residual variances with values ranging between 0 and 100. An initial burn-in of 10,000 iterations was used, and posterior distributions of parameters were based on 20,000 more iterations. We used three chains to check for the stability of posterior distribution estimates. We reported the median of posterior distribution and 95% credible intervals to assess effect sizes and their associated uncertainty. Statistical significance was based on whether these CIs included 0 or not. Bayesian model fitting and model diagnostics such as the convergence of numerical simulations (Gelman and Hill, 2007) were done using the libraries rBugs and coda (Plummer et al., 2010; Yan and Prates, 2010) along with OpenBUGS 3.1.2 (Lunn et al., 2009). We performed all analyses using R 2.15.3 (R Development Core Team, 2011).

### 3. Results

A minimum of 14 fawns were captured each year, for which we had measurements of body mass and dental formula (average number of fawns per year  $\pm$  SD:  $43 \pm 17$ ; total number of fawns over the study period: 1152). We found a large variation in the eruption status for all types of permanent front teeth. Some fawns had completed eruption of their permanent front teeth by 5 January, whereas others had not yet initiated eruption of any permanent front teeth by 11 February (Table 2).

For BM, the selected model ( $r^2=0.39$ ; Table 3) included additive effects of year, sex and capture date. BM increased with increasing date of capture (slope of  $9.5 \pm 3.6$  g/d,  $F_{1,1123} = 7.10$ ,  $P = 0.008$ ) and, for a given date, male fawns were heavier than female fawns (by  $632 \pm 114$  g,  $F_{1,1123} = 30.82$ ,  $P < 0.001$ ). For both DFI ( $r^2 = 0.36$ ) and PFTI ( $r^2 = 0.34$ ), the selected model included an interaction between year and date of capture (Table 3) but no sex effect (DFI:  $F_{1,1097} = 0.007$ ,  $P = 0.934$ ; PFTI:  $F_{1,1097} = 0.063$ ,  $P = 0.802$ ). For  $I_2$ , only the additive effect of year and date of capture was selected (Table 3;  $r^2 = 0.21$ ; sex effect:  $\chi^2 = 0.716$ ,  $df = 1$ ,  $P = 0.397$ ).

Corrected values of annual BM<sub>c</sub> and DFI<sub>c</sub>, PFTI<sub>c</sub> and  $I_{2c}$  obtained from the selected models (Table 3) were highly and positively correlated (Table 4 and Fig. A1;  $r_{BM_c, DFI_c} = 0.73$  [0.49; 0.87]<sub>95%</sub>,



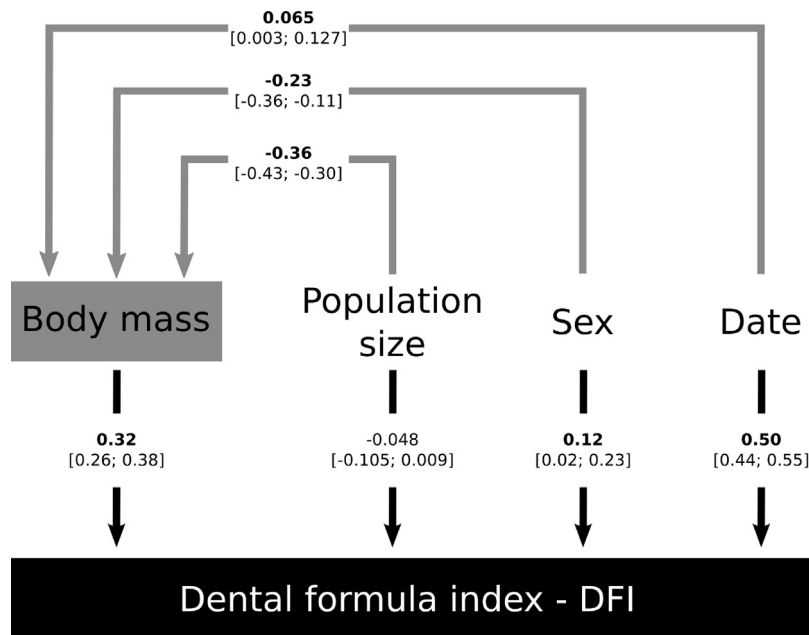
**Fig. 2.** Relationships (linear regressions, or threshold models, and 95% confidence intervals) between adjusted performance indices (Table 4) and population size in the year of birth of roe deer captured at Chizé, western France, during winter 1987–2013. (A) adjusted body mass index ( $BM_c$ , kg), (B) adjusted dental formula index ( $DFI_c$ ; threshold estimated at 398 roe deer), (C) adjusted permanent front tooth index ( $PFTI_c$ ; threshold estimated at 398 roe deer) and (D) adjusted proportion of fawns with an erupted second incisor ( $I_{2c}$ ; threshold estimated at 405 roe deer).

$P < 0.001$ ;  $r_{BM_c.PFTI_c} = 0.67$  [0.39; 0.84] $_{95\%}$ ,  $P < 0.001$ ;  $r_{BM_c.I_{2c}} = 0.62$  [0.32; 0.81] $_{95\%}$ ,  $P < 0.001$ ).  $BM_c$  was negatively and linearly correlated with population size in the year of birth ( $r^2 = 0.54$ ,  $\beta = -0.012$ ,  $SE = 0.002$ ,  $P < 0.001$ ; Fig. 2a, support to H1). All dental indices showed a similar relationship, except for some of the years with the highest population size at which dental development would be no longer sacrificed (Table 5 and Fig. 2b–d; support to H2b). For  $DFI_c$ ,  $PFTI_c$  and  $I_{2c}$ , the best model thus accounted for a linear decrease up to a population size of ca. 400 roe deer (i.e., 15 adult roe deer/100ha;  $DFI_c$ :  $r^2 = 0.55$ ,  $\beta = -0.008$ ,  $SE = 0.001$ ,  $P < 0.001$ ;  $PFTI_c$ :  $r^2 = 0.48$ ,  $\beta = -0.002$ ,  $SE = 0.0005$ ,  $P < 0.001$ ;  $I_{2c}$ :  $r^2 = 0.49$ ,  $\beta = -0.0008$ ,  $SE = 0.0002$ ,  $P < 0.001$ ) and a constant value above this threshold (Fig. 2b–d).

We performed the path analysis for cohorts born when population size estimates linearly influenced both  $BM_c$  and  $DFI_c$  (i.e., when population size the year of birth was  $< 398$  roe deer; see Fig. 2a and b and Table 4). The path analysis provided evidence for indirect effects of population size ( $-0.12$  [ $-0.15$ ;  $-0.09$ ] $_{CI95\%}$ ), date ( $0.021$  [ $0.001$ ;  $0.041$ ] $_{CI95\%}$ ) and sex ( $-0.07$  [ $-0.12$ ;  $-0.03$ ] $_{CI95\%}$ ) on  $DFI_c$  through their co-variation with  $BM_c$  as well as direct effects of body mass, sex and capture date (Fig. 3). Population size had less marked (statistically insignificant) direct effect on  $DFI_c$ . Total effect of sex, i.e., sum of direct (positive) and indirect (negative) effects of sex on  $DFI_c$ , was not significant ( $0.047$  [ $-0.068$ ;  $0.161$ ] $_{CI95\%}$ ).

#### 4. Discussion

In mammals, the relationships between the timing of eruption of permanent front teeth and variation in environmental conditions have been little investigated. This is surprising because mammals use their teeth to acquire and chew food as a preparation for digestion (Pérez-Barbería and Gordon, 1998), so that teeth play a central role in life-history (e.g., Veiberg et al., 2007 in Svalbard reindeer [*Rangifer tarandus platyrhynchus*], Loe et al., 2006 in red deer [*Cervus elaphus*], Ericsson and Wallin, 2001 in moose [*Alces alces*]). Here, we found non-linear density-dependent relationships in the timing of eruption of permanent front teeth using an intensively monitored population of roe deer subject to large variation in population size (Fig. 1). This population experienced poor resources in some years, an environmental context mostly lacking in similar studies (e.g., of humans, Garn et al., 1965; Kaur and Singh, 1992). While body mass decreased linearly with increasing population size, as previously reported in this population (Gaillard et al., 1996; Toïgo et al., 2006), our results support a concomitant delay in tooth development, as body mass decreases, up to a given threshold at which tooth development would be no longer sacrificed (H2b). Although previous studies have suggested that a lowered nutritional plane, through its well-known effects on body mass (Bonenfant et al., 2009), may delay tooth eruption in ungulates (Loe et al., 2004; Lutz,



**Fig. 3.** Path analysis of direct and indirect (through BM) effects of population size, sex and capture date on DFI of fawns captured at Chizé, western France, during winter 1987–2013 (excluding cohorts when population size was  $\geq 398$  roe deer; see text for details and Table 4). All variables were standardized (mean = 0, SD = 1). Standardized regression coefficient estimates are given with their associated 95% credible intervals. DFI and BM are the dependent variables. Black arrows correspond to direct effects of covariates on DFI. Grey arrows correspond to direct effects of covariates on BM. Coefficients statistically different from 0 are in bold (i.e., when credible intervals at 95% do not include 0). The parameter estimate for the factor “sex” corresponds to females.

**Table 4**

Adjusted body mass ( $BM_c$ ) and dental indices ( $DFI_c$ : dental formula index;  $PFTI_c$ : permanent front tooth index;  $I_{2c}$ : proportion of fawns with an erupted second incisor; Table 1) obtained from fawns captured each year at Chizé, western France, during winter 1987–2013. Population size was estimated from a generalization of the Cormack-Jolly-Seber model (Gaillard et al., 1986; Fig. 1). Indices were adjusted for median capture date (1st February) and for sex (“male” as reference; see text for more details).

Cohort	$BM_c$	$DFI_c$	$PFTI_c$	$I_{2c}$	Population size
1986	13.26	5.82	2.74	0.67	398
1987	15.10	6.14	2.71	0.60	405
1988	14.31	6.62	2.92	0.73	290
1989	13.51	7.48	3.24	0.86	254
1990	14.92	7.51	3.24	0.88	222
1991	16.35	8.48	3.61	0.95	202
1992	15.49	8.08	3.50	0.86	213
1993	16.49	7.95	3.24	0.98	194
1994	16.81	7.92	3.33	0.92	165
1995	15.82	8.43	3.54	0.93	183
1996	16.24	8.41	3.55	0.94	185
1997	15.47	7.44	3.12	0.85	238
1998	15.75	7.58	3.21	0.81	275
1999	17.15	7.55	3.24	0.87	278
2000	16.94	8.59	3.61	1.00	284
2001	15.85	7.69	3.22	0.88	304
2002	15.48	7.77	3.27	0.89	309
2003	12.97	7.26	3.15	0.82	375
2004	14.13	6.90	3.01	0.77	442
2005	12.70	7.28	3.23	0.82	493
2006	13.21	7.30	3.25	0.88	512
2007	11.88	6.55	2.90	0.77	401
2008	13.90	7.16	3.10	0.82	363
2009	12.30	6.96	3.00	0.80	309
2010	11.88	5.18	2.49	0.63	457
2011	13.29	6.23	2.73	0.83	342
2012	13.18	6.94	3.02	0.80	400

1993; Robinette et al., 1957), none has reported that this relationship might be hampered by harsh environmental conditions. This finding is mainly based on two years with extremely high population density (2005 and 2006) and more years of high population

**Table 5**

Relationships between population size the year of birth and adjusted body mass ( $BM_c$ ) and dental indices (Table 4) of fawns captured at Chizé, western France, during winter 1987–2013. Threshold models contrast two phases (“cst.” = no change with population size and “decrease” = linear decrease with increasing population size). Superscript “2” corresponds to a quadratic effect. In some cases (denoted “-”) the threshold value cannot be estimated (no reduction in deviance as compared to a linear model; see text for details). The table reports  $\Delta AIC_c$  (i.e., the difference in  $AIC_c$  between the best model (lowest  $AIC_c$  and  $\Delta AIC_c = 0$ ) and candidate models). The selected models are in bold type.

Models	$BM_c$	$DFI_c$	$PFTI_c$	$I_{2c}$
Null	18.24	16.24	12.30	12.93
Density	<b>0.00</b>	2.06	2.27	1.96
Density <sup>2</sup>	2.33	1.47	0.19	1.57
Threshold <sub>decrease&gt;cst.</sub>	1.85	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
Threshold <sub>cst.&gt;decrease</sub>	-	4.72	4.96	4.73

density are needed to confirm this result. However, this finding is consistent with the fact that the masticatory system processes the food that fuels the system in general and that dentition should therefore remain relatively resistant to limitation of food resources, even in presence of marked impact on body growth (Smith, 1989). This could be used by wildlife managers to detect the occurrence of harsh environmental conditions for their populations. Finally, our study demonstrates that a simple, easy-to-measure index of tooth development as  $I_{2c}$  can be at least as useful as body mass for monitoring density-dependent changes in roe deer body condition. We found that  $I_{2c}$  performed as well as  $PFTI_c$  (i.e., one front teeth performed as well as the information provided by the 4 front teeth), suggesting that some front teeth provided little information. We recommend that the choice of a given front tooth should be done carefully depending on the sampling period (involving either capturing or hunting animals) so that a substantial proportion of animals have erupted the target front teeth to improve statistical power (Agresti, 2002). Monitoring the pair of the two most variable front teeth could then be an intermediate, relevant, alternative between  $I_{2c}$  and  $PFTI_c$ .

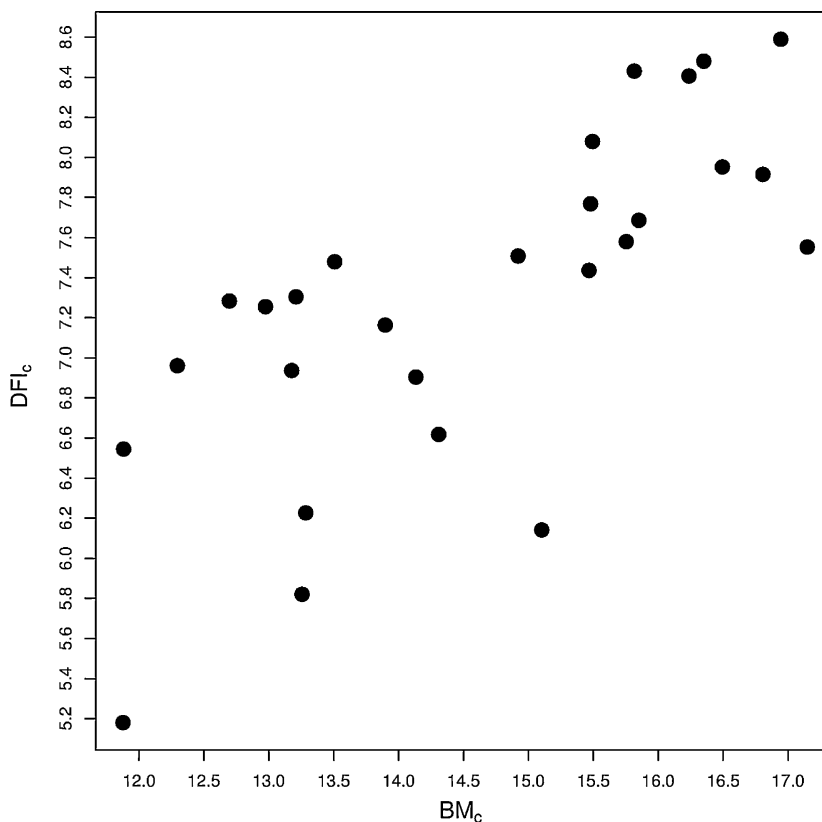


Fig. A1. Relationship between adjusted body mass index (BM<sub>c</sub>, kg) and adjusted dental formula index (DFI<sub>c</sub>). See Table 4 for raw values.

There are contrasting results for the existence of sex-specific patterns of front teeth eruption. In species with high sexual size dimorphism, such as red deer, teeth erupt earlier in females than in males (Loe et al., 2004). Conversely, in less dimorphic species like roe deer (this study; Table 3 and path analysis) and mule deer (Rees et al., 1966; Robinette et al., 1957), males and females display similar timing of tooth eruption. These results support the theory of sexual selection that predicts that males of species more dimorphic in size should reach size maturity later than females (Jarman, 1983). Indeed, in social systems promoting inter-male competition for mates, sexual selection is expected to favor larger males through rapid early growth and delayed maturation, whereas females are selected to mature early at the expense of structural size (Andersson, 1994). The intensity of intra-sexual competition increases with sexual size dimorphism in ungulates (e.g., Garel et al., 2011a) and hence divergence in growth tactics among sexes are expected to be exacerbated in highly dimorphic species.

As expected body mass, a proxy of body development, was positively and directly linked to tooth eruption patterns (Garn et al., 1965; Loe et al., 2004; Robinette et al., 1957; Table 4 and Fig. A1). We also found that most of the effect of population size on tooth eruption patterns was mediated through effect of population size on body mass (Fig. 3). Beyond population size, genotypic variation has also been reported to be a major determinant of tooth eruption in humans (Garn et al., 1965; Kaur and Singh, 1992) and has been proposed to account for observed differences in the timing of eruption of permanent teeth among populations of red deer (Loe et al., 2004). As for any indicator of ecological change (Morellet et al., 2007), such genetically-based differences among populations indicate that absolute between-population comparisons should not be performed. Only the monitoring of temporal changes of the indicator within a given population can be safely used for setting management quotas.

In a management context where collecting long-term data over large areas requires a large number of people to be involved (Bildstein, 1998), using the eruption pattern of front teeth offers a reliable alternative to measuring body mass or skeletal measurements as commonly done (Hewison et al., 1996; Toigo et al., 2006). Indeed, determining dental formula does not require a specific tool, which should help standardizing data collection and limiting sampling variance. By increasing the precision of measurements, managers would require a lower sample size to detect a given biological signal, thus reducing monitoring costs. In addition, increasing the precision of measurements should help managers to detect variation in life history traits that would have been overlooked by using unreliable measurements.

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#### Appendix A.

See Fig. A1.

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