How do conditions at birth influence early-life growth rates in wild boar?

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Abstract. Weather conditions and population density individuals experience at birth influence their life-history traits and thereby population dynamics. Early-life individual growth is a key fitness-related trait; however, how it is affected by such conditions at birth remains to be explored. Taking advantage of long-term monitoring of three wild boar (*Sus scrofa*) populations living in contrasting ecological contexts, we assess how weather conditions (temperature and precipitation) and the number of removed individuals at birth influence early-life growth rates. We found that the number of individuals removed before the early-growth period had a positive effect on early-life growth rate across sites. This might be interpreted as a density-dependent response involving an increase in food availability per capita that favors faster growth. Alternatively, if the number of removed individuals increases with population density, this result might be attributable to decreasing litter sizes at high density, leading mothers to allocate more resources to individual offspring, which favors higher juvenile growth rates. Early-life growth rates also increased with spring-time temperature and decreasing precipitation. Thus, early-life growth is expected to increase in response to warmer and drier springs, which should become more frequent in the future under current climate change. We found that conditions at birth explained very little among-year variation in early-life growth rates (i.e., weak cohort effects) and that within-year variation in early-life growth rates was more likely caused by strong individual differences.

Key words: cohort effects; conditions at birth; individual growth; repeatability analysis; *Sus scrofa*.

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INTRODUCTION

Life-history traits are shaped by the environmental conditions (e.g., population density, weather conditions) individuals experience at birth (Lindström 1999, Gaillard et al. 2000, Monaghan 2008). These conditions at birth do not affect natural populations independently of each other, as weather conditions generally interact with density-dependent effects. Indeed, the negative effect of bad weather conditions is expected to be more evident near the carrying capacity (e.g., *Ovis aries* Coulson 2001 and *Halobaena caerulea* Barbraud and Weimerskirch 2003). For example, bad weather conditions (rain-on-snow events) reduce food availability for Svalbard reindeer (*Rangifer tarandus*), which leads to decreased fecundity and survival. The negative effect of bad weather conditions on vital rates is stronger at high population densities, leading to

population crashes (Hansen et al. 2019). While there are an increasing number of studies focused on the combined effects of weather and density on vital rates (survival, fecundity; see Portier et al. 1998, Gamelon et al. 2017*b*, Layton-Matthews et al. 2020 for case studies), how early-life growth is influenced by the interplay between weather conditions and density has yet to be explored.

The rate of body size growth early in life is a key life-history trait that influences asymptotic size, reproductive success, and longevity (Metcalfe and Monaghan 2001, Hamel et al. 2016). Early-life growth rates (hereafter called ELGR) are known to be plastic (Dmitriew 2011) and to vary across latitudinal clines (e.g., Conover and Present 1990 for countergradient variation) as well as among cohorts. Juveniles born in a year with low population density and good weather conditions may have faster growth rates (potentially with fitness advantage throughout life, see "silver spoon effects") over those born in a year characterized by high density and poor weather conditions. The strength of these cohort effects can be more pronounced in poor environments, as observed in roe deer *Capreolus capreolus* (Pettorelli et al. 2006). Differences in individual ability to acquire (van Noordwijk and de Jong 1986) and allocate (Cody 1966, Descamps et al. 2016) resources may also account for individual-level variance in ELGR. The susceptibility of ELGR to environmental conditions at birth is thus expected to vary both within and across populations.

Taking advantage of long-term individual monitoring of three wild boar (*Sus scrofa*) populations in contrasting ecological contexts, we assessed how the interplay between the number of removed individuals and weather conditions at birth shapes ELGR. We expected the lowest ELGRs to occur under poor weather conditions in resource-poor sites. We also decomposed the variation in ELGR to assess the relative role of cohort effects and among-individual differences.

Materials and Methods

Data collection

The study was conducted in three sites where the size of wild boar populations is mostly controlled by harvesting (i.e., hunting and/or removal of individuals). The first site is the 11,000 ha forest of Châteauvillain in northeastern France (48.02° N, 4.56° E), characterized by a climate intermediate between continental and oceanic. Châteauvillain is considered resource rich as the study area is dominated by oak *Quercus* spp. (41%) and beech *Fagus sylvatica* (30%) (Servanty et al. 2009) that produce acorns and beechnuts, respectively, which offers a regular high-quality forage availability to wild boar (Servanty et al. 2011, Gamelon et al. 2017*a*). The second site is the 2614 ha Réserve Biologique Intégrale at Chizé in southwestern France (46.05° N, 0.25° W), characterized by mild winters and often warm and dry summers. Productivity of the forest is low as the soil in this site is shallow and calciferous and summer droughts are frequent (Gaillard et al. 2003*b*). Chizé is considered as a resource-poor habitat for ungulates (Gaillard et al. 2003*a*, Douhard et al. 2013), with the richest habitat for wild boar (oak *Quercus* spp. and hornbeam *Carpinus betulus*) covering approximately 40% of the reserve (Toïgo et al. 2006). The third site is the 2674 ha national reserve at La Petite Pierre located in the Vosges mountains (48.50° N, 7.00° E) and is characterized by a mixture of continental and oceanic climates, with cool summers and mild winters. The forest is evenly composed by beech, *F. sylvatica*, and coniferous species (mainly silver fir *Abies alba*, Norway spruce *Picea abies*, and Scots pine *Pinus sylvestris*, Hamann et al. 1997). La Petite Pierre is also considered as a resource-poor forest because the soil is acidic and therefore not highly fertile, which leads to poorly diversified vegetation of low nutritive quality for ungulates (Storms et al. 2008, Pellerin et al. 2010).

In all three sites, a capture–mark–recapture–recovery program has allowed capturing, marking using traps, and then releasing a large number of wild boars each year between March and September (Fig. 1). Sex, date, and body mass to the nearest 0.1 kg are recorded for each individual caught, and multiple captures (alive and dead when shot by hunters) are available. This allowed estimating ELGR (in g/d) for individuals with repeated measurements by assuming linear growth until a body mass of 20 kg (about 6 months of age) was reached (as supported by previous analyses, see Gaillard et al. 1992, Veylit et al. 2020). We retained measurements taken

more than seven days apart for each individual. Analyses were conducted on 991 individuals (516 males, 475 females) at Châteauvillain between 1983 and 2016, 742 individuals (365 males, 377 females) at Chizé between 2003 and 2016, and 523 individuals (238 males, 285 females) at La Petite Pierre between 2008 and 2017.

As weather conditions at birth may influence ELGR, we considered cumulative precipitation (in mm) and mean temperature (in °C) in April when the birth peak occurs (Appendix S1: Fig S1). Weather data were obtained from Météo France (Beauvoir sur Niort weather station for Chizé; stations in Villiers le sec, Chaumont-ville, and Chaumont-Semoutiers for Châteauvillain; Phalsbourg for La Petite Pierre). The number of removed individuals (i.e., the annual number of individuals killed or translocated) during the hunting season (October–February) may also influence ELGR in spring (from April). Both weather conditions and the number of removed individuals differed among study sites (Appendix S1: Fig. S2, Table S1).

Statistical analysis

Early-life growth rate was entered as the response variable in linear mixed models with year of birth as a random intercept to account for repeated measurements of ELGR within a year. Temperature and precipitation in April and the number of removed individuals were included as continuous covariates, in interaction with the study site, which was included as a categorical

factor. As the correlations between weather conditions and the number of removed individuals were consistently below 0.7 (Appendix S1: Table S2), no collinearity problems occurred and we included these covariates in the same model (following Dormann et al. 2013's recommendations). To test for the interactive effect of weather and the number of removed individuals, precipitation and temperature were included as covariates in interaction with the number of removed individuals and study site. We also tested for a different effect of temperature on ELGR at different precipitation levels. Sex was included as a categorical factor. Year of birth was included as a continuous variable to test for a possible linear temporal trend in ELGR. We tested all derived models.

We then partitioned the variance in ELGR into within-year (i.e., differences among individuals) and between-year variances and estimated the repeatability (R) of ELGR in a given year as:

$$R = \frac{V_{BY}}{(V_{BY} + V_{WY})}$$

where V_{BY} is the between-year variance in ELGR, and V_{WY} the within-year variance (Nakagawa and Schielzeth 2010). First, we estimated R from a model including only year as a random factor to calculate the ratio of within- and between-year variances in ELGR. Then, from the model retained based on Akaike's information criterion, corrected for sample sizes (AIC$_c$; Anderson and Burnham 2002), we included the fixed effects to calculate the repeatability in ELGR after
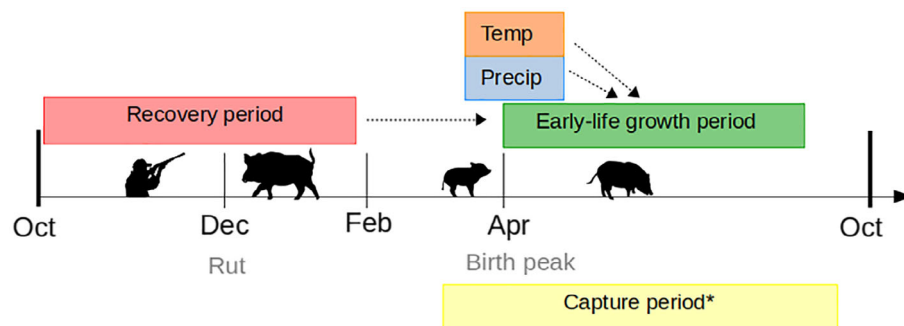

Fig. 1. Wild boar life cycle. Data on the number of removed individuals are collected during the hunting season (October–February) coinciding with the rut and gestation periods. Weather variables (temperature and precipitation) that influence early-life growth rates were collected during the birth peak, in April, and the period of early-life growth coincides with the capture period (which may vary slightly between sites).

controlling for fixed effects. When AIC_c values of two competing models were within two units, we retained the simplest model (i.e., the model with the fewest parameters) to satisfy parsimony rules.

Analyses were conducted in R v. 3.6.0 using the nlme package (v. 3.1-140, Anderson and Burnham 2002, Pinheiro et al. 2019). Associated 95% confidence intervals for model estimates were calculated using the delta method (Powell 2007). Repeatability and associated standard errors (SE) were estimated from 1000 bootstrap iterations using rptR (v. 0.9.22, Stoffel et al. 2017).

Results

Early-life growth rates fluctuated over the study period in all sites (Appendix S1: Fig. S3). Average ELGR were estimated to be 79.62 ± 49.84 g/d in Châteauvillain, 27.62 ± 49.09 g/d in Chizé, and 57.01 ± 39.90 g/d in La Petite Pierre. ELGR was affected by sex, weather conditions at birth, number of removed individuals the winter before the early-life growth period, and interactions between these effects and study site. The same analysis conducted on each site separately allowed for a simpler interpretation of complex interactive effects.

In Châteauvillain, following the rules of parsimony, the model (Table 1) included a weak sex effect with males growing slightly faster than females (by 8.10 ± 2.94 g/d, Table 2). This model also included an interaction between temperature and the number of removed individuals, such that ELGR increased with temperature at a greater rate when the number of removed individuals was higher (Fig. 2A). Growth rate repeatability from the model including the random effect of year was 0.23 (SE: 0.05). After controlling for fixed effects, R was 0.14 (SE: 0.04) and the fixed effects in the model (i.e., sex, number of removed individuals, and temperature) explained 9.30% (SE: 0.04) of the phenotypic variance in early-life growth rates. The selected model performed much better than the constant model ($\Delta AIC_c = 16.04$).

In Chizé, the selected model included a weak positive effect of the number of removed individuals on ELGR (0.21 ± 0.11 Table 2, Fig. 2B). Growth rate repeatability within a year was 0.28 (SE: 0.10). When controlling for fixed effects, it

was 0.21 (SE: 0.08) and the number of removed individuals explained only 3.30% (SE: 0.03) of the observed phenotypic variance in early-life growth rates. Indeed, the selected model only slightly outperformed the constant model ($\Delta AIC_c = 1.73$), indicating weak support for an influence of conditions at birth on early-life growth rates at Chizé.

In La Petite Pierre, the selected model included an interaction between temperature and precipitation (Table 2, Fig. 2C). At high precipitation levels, temperature had virtually no effect on ELGR, whereas at low precipitation levels, ELGR increased with April temperature. Temperature also had a positive effect on ELGR (0.28 ± 0.05, Table 2). Growth rate repeatability within a year was 0.16 (SE: 0.07). After controlling for fixed effects, it was close to 0 (SE: 0.01). The fixed effects in the model (i.e., the number of removed individuals, precipitation, and temperature) explained 15.10% (SE: 0.03) of the phenotypic variance in ELGR, indicating a very low repeatability in ELGR after controlling for fixed effects. The best model substantially outperformed the constant model ($\Delta AIC_c = 15.09$).

Discussion

Using three populations of wild boar exposed to contrasting ecological contexts, we examined the interactive effects of environmental conditions at birth on juvenile growth. More specifically, we assessed the effects of temperature and precipitation in April. These weather conditions at birth may directly affect ELGR by inducing thermoregulation costs (Vetter et al. 2015). As piglets are born without extensive energy stores, they are expected to be vulnerable to weight loss during cold weather (see Le Dividich and Noblet 1983 in domestic pigs). Temperature and precipitation in April may also indirectly affect ELGR through resource availability. Thus, evidence is accumulating that spring conditions may influence fruit production such as oak seeds (acorns; Caignard et al. 2017, Schermer et al. 2019), a major food resource for wild boar. Therefore, warm springs are expected to be associated with higher seed production and higher food availability for the wild boar, allowing a higher allocation to body mass (Gamelon et al. 2017a) and growth. Here,

Table 1. Model selection based on AIC$_c$ showing the 10 best models for each site and the constant model.

Site	NR	T	P	Sex	Year	NR × T	NR × P	T × P	df	AIC$_c$
Châteauvillain	X	X	X	X			X			8	10,439.45
	X	X		X			X			7	**10,439.47**
	X	X	X	X			X	X		9	10,440.99
	X	X	X	X			X		X	9	10,441.16
	X	X		X	X		X			8	10,441.37
	X	X	X	X	X		X			9	10,441.41
	X	X	X	X			X	X	X	10	10,442.76
	X	X	X	X	X		X	X		10	10,442.77
	X	X	X	X	X		X		X	10	10,443.15
	X	X	X	X	X		X	X	X	11	10,444.62
										3	10,455.51
Chizé	X	X	X				X		X	8	7789.81
	X	X					X			6	7789.87
	X	X	X				X			7	7790.12
	X									4	**7790.58**
	X	X	X				X	X	X	9	7790.94
	X	X	X			X	X			8	7791.02
	X	X	X				X	X		8	7791.12
	X	X	X			X	X	X		9	7791.15
	X	X								5	7791.38
	X	X	X			X	X		X	9	7791.48
										3	7792.31
La Petite Pierre	X	X	X						X	7	**5267.17**
	X	X	X					X	X	8	5267.67
	X	X	X				X		X	8	5268.28
	X	X	X			X			X	8	5269.21
	X	X	X	X					X	8	5269.23
	X	X	X				X	X	X	9	5269.61
	X	X	X	X				X	X	9	5269.71
	X	X	X			X		X	X	9	5269.73
	X	X	X			X	X		X	9	5270.11
	X	X	X	X			X		X	9	5270.32
										3	5282.26

Note: Effects of sex (*Sex*), annual trend (*Year*), mean temperature (*T*), and cumulative precipitation (*P*) in April, and number of removed individuals (*NR*) on wild boar ELGR, at Châteauvillain, Chizé, and La Petite Pierre, France. Selected models are indicated in bold. AIC$_c$, Akaike's information criterion, corrected for sample sizes.

we found that April temperature had a positive effect on ELGR in Châteauvillain and La Petite Pierre. Moreover, the average ELGR was higher in Châteauvillain, where wild boar have access to abundant food resources (Servanty et al. 2011, Gamelon et al. 2017*a*), than in Chizé and La Petite Pierre where fruit production was lower as the soil quality in these sites is poor. In addition to seeds, earthworms constitute an important food resource for wild boar (Baubet et al. 2003, 2004). Interestingly, we did not find evidence for higher ELGR under cold and wet conditions when earthworm emergence is higher. Rather, ELGR increased with warm and dry conditions in La Petite Pierre (Fig. 2C).

While most size dimorphic ungulates exhibit sex-specific maternal allocation (Byers and Moodie 1990), which leads to sex-specific ELGR, wild boar is a rare example of an ungulate species with similar early-life growth rates for both sexes. Indeed, in accordance with previous work (Gaillard et al. 1992, Veylit et al. 2020), we found no support for ELGR being sex-specific for the populations at Chizé and La Petite Pierre. In Châteauvillain, a sex-specific ELGR was detected but the effect size was very weak.

For the three sites, we consistently found low-to-moderate (as defined by Nakagawa and Schielzeth 2010) within-year repeatability of ELGR (ranging from 0.16 to 0.28), which

Table 2. Effects of mean temperature (*T*), cumulative precipitation in April (*P*), number of removed individuals (*NR*) as well as sex (*Sex*, with "M" referring to males) on early-life growth rate at Châteauvillain, Chizé, and La Petite Pierre, France.

Site	Parameter	Slope ± SE	Standardized slope ± SE
Châteauvillain	*Sex* (M)	8.10 ± 2.94	8.10 ± 2.94
	NR	−0.33 ± 0.10	−3.69 ± 4.06
	T	−20.10 ± 9.06	7.01 ± 3.81
	T × NR	0.03 ± 0.01	10.86 ± 3.48
Chizé	NR	0.21 ± 0.11	9.46 ± 4.82
La Petite Pierre	P	4.95 ± 0.93	−18.29 ± 4.03
	T	26.79 ± 4.35	4.23 ± 2.00
	NR	0.28 ± 0.05	9.83 ± 1.86
	P × T	−0.55 ± 0.10	−18.25 ± 3.41

Note: Coefficients are shown for unstandardized and standardized covariates (i.e., normalized). SE, standard error.

indicates high among-individual variation. The proportion of variance in ELGR explained by the environmental covariates was generally low, ranging from 3.30% for Chizé to 15.10% for La Petite Pierre. Environmental conditions thus explain a small proportion of the variance in ELGR and it is likely that strong individual differences account for such a high within-year variation in ELGR (Niemelä and Dingemanse 2017, Renaud et al. 2019). As wild boar are closer to income breeders along the capital-income breeder continuum (Servanty et al. 2009, Gamelon et al. 2017a), current conditions are expected to influence maternal body condition and offspring ELGR. Differences in milk quality provisioned to offspring for ELGR are thus dependent on what resources mothers are able to acquire (Gamelon et al. 2017a) and provision to offspring. Therefore, differences in ELGR among individuals within a year likely originated from contrasting maternal attributes (e.g., mass, age, litter size) to acquire and allocate resources.

In all three sites, there was a positive relationship between the number of removed individuals and ELGR. The number of removed individuals may be interpreted biologically in two ways. A high number of individuals removed during winter (October–February) may reduce the number of individuals in the population in the following spring (from April onwards; Fig. 1). In this case, the observed positive relationship between ELGR and number of removed

individuals may be interpreted as a density-dependent response that involved an increase in food availability per capita favoring a faster growth. Alternatively, under specific management strategies (e.g., if the removal rate is constant over years), the number of removed individuals may be interpreted as a proxy for the population density (Cattadori et al. 2003, Flanders-Wanner et al. 2004). In that case, the positive relationship between ELGR and the number of removed individuals may be related to a confounding effect of density-dependent response of litter size. At high densities, mothers usually produce smaller litters because of stronger competition for resources to allocate to reproduction (Stefan and Krebs 2001 in snowshoe hares *Lepus americanus*, Both et al. 2000 in great tits *Parus major*, and Sidorovich et al. 2007 in gray wolves *Canis lupus*). In many species, smaller litters have both higher survival (Lack 1947) and juvenile growth (Rödel et al. 2008 in rabbits and rats). Indeed, in domesticated pigs, mass gain between birth and weaning was negatively related to litter size (Andersen et al. 2011). At high densities, females may thus produce fewer higher quality offspring (Sinervo et al. 2000). We expected these density-dependent responses to be stronger in the resource-poor sites than in Châteauvillain, which is characterized by high resource availability. Additional data will be needed to reliably estimate population density in each of the three sites (St. Clair 2012) and to discriminate between the two biological interpretations.

We detected an effect of interacting conditions at birth on ELGR in two populations. In Châteauvillain, the positive effect of temperature on ELGR was stronger at higher numbers of removed individuals. In La Petite Pierre, ELGR increased with temperature, but only at low precipitation levels. This positive association between April temperature and growth may also be linked to decreased litter size at high temperatures, as observed in a German wild boar population (Frauendorf et al. 2016) and to increased maternal provisioning to individual offspring. However, in all sites the effects of conditions at birth are largely overshadowed by individual-level variation in ELGR. Therefore, strong phenotypic plasticity rather than environmental conditions at birth appears to drive variation in wild boar ELGR.
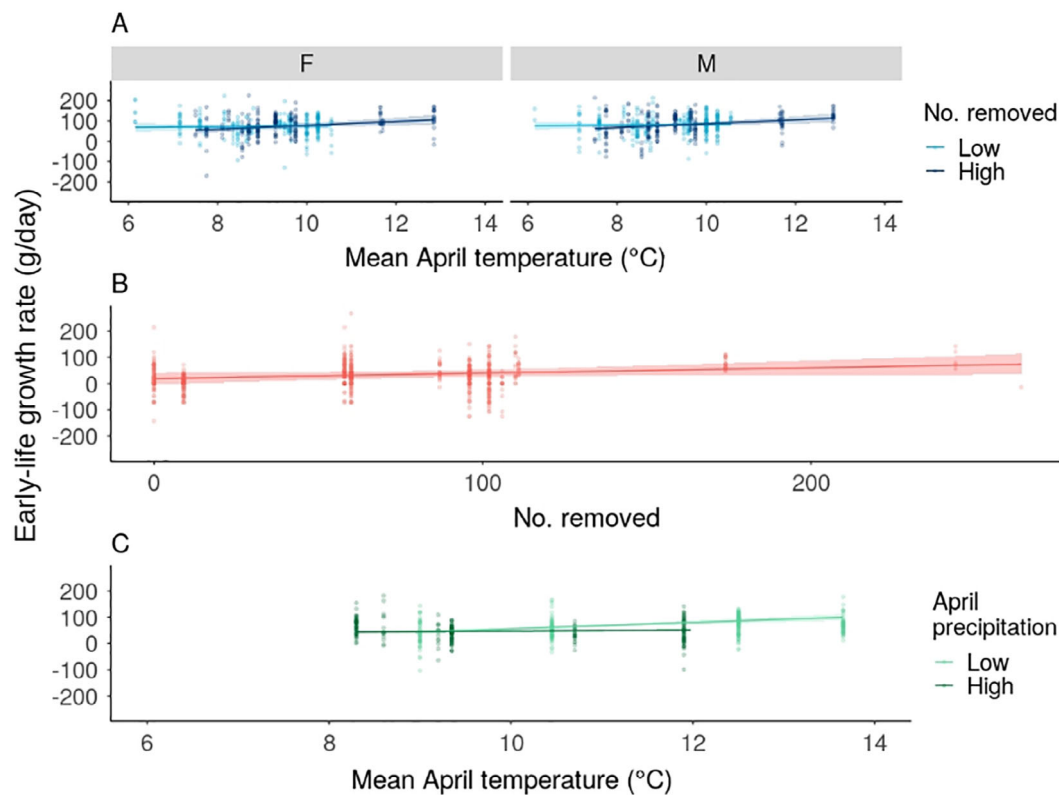
Fig. 2. Early-life growth rate vs. environmental variables for three populations of wild boar. At Châteauvillain (A), early-life growth rates are shown as a function of April temperature for females (F) and males (M), at the 25% ("Low", light blue) and 75% quantiles ("High", dark blue) for the number of removed individuals. At Chizé (B), early-life growth rates are shown as a function of the number of removed individuals, and at La Petite Pierre (C), early-life growth rates are shown as a function of April temperatures at the 25% ("low", light green) and 75% quantiles ("high", dark green) April precipitation levels. Regression lines are reported with associated 95% confidence intervals from the selected models (Tables 1, 2).

Here, we found that various environmental conditions at birth (e.g., temperature, number of individuals removed) may explain a small part of the observed phenotypic variance in ELGR in wild boar. Thus, individuals are able to respond plastically to different environmental conditions to a small extent. In particular, wild boar born in conditions that are expected to increase in frequency with global climatic change (e.g., warmer and drier springs) grow more quickly in early life. Increasing ELGR may shorten the time to reach the threshold size for reproduction and lead to reproduction at earlier ages, at least for females (Servanty et al. 2009). This shortening in generation time may ultimately accelerate the population turnover, with potential important implications throughout Europe as wild boar populations are already increasing in size and distribution (Massei et al. 2015). Importantly, environmental conditions at birth explained only very little among-year variation in ELGR and strong individual differences likely induced high within-year variation in ELGR.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3167/full