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Maternal effects shape offspring physiological condition but do not senesce in a wild mammal

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Abstract

In vertebrates, offspring survival often decreases with increasing maternal age. While many studies have reported a decline in fitness-related traits of offspring with increasing maternal age, the study of senescence in maternal effect through age-specific changes in offspring physiological condition is still at its infancy. We assessed the influence of maternal age and body mass on offspring physiological condition in two populations of roe deer (*Capreolus capreolus*) subjected to markedly different environmental conditions. We measured seven markers to index body condition and characterize the immune profile in 86 fawns which became recently independent of their known-aged mothers. We did not find striking effects of maternal age on offspring physiological condition measured at 8 months of age. This absence of evidence for senescence in maternal effects is likely due to the strong viability selection observed in the very first months of life in this species. Offspring physiological condition was, on the other hand, positively influenced by maternal body mass. Between-population differences in environmental conditions experienced by fawns also influenced their average body condition and immune phenotype. Fawns facing food limitation displayed lower values in some markers of body condition (body mass and haemoglobin levels) than those living in good quality habitat. They also allocated preferentially to humoral immunity, contrary to those living in good conditions, which allocated more to cellular response. These results shed a new light on the eco-physiological pathways mediating the relationship between mother's mass and offspring condition.

KEYWORDS
ageing, body condition, eco-immunology, life history, roe deer

1 | INTRODUCTION

With increasing age, most vertebrates show a decline in reproductive traits, which is ultimately responsible for a decrease in reproductive success (Lemaître & Gaillard, 2017; Nussey et al., 2013). In females, this age-related decline in reproductive success, known as reproductive senescence, is particularly visible through a decline in the birth rate, clutch/litter size or survival of offspring born to old mothers. Empirical evidence from wild populations shows that senescent females are less efficient at raising offspring (i.e. less offspring weaned or offspring with low viability, e.g. in American red squirrels, *Tamiasciurus hudsonicus*, in Descamps et al., 2008; in meerkats, *Suricata suricatta*, in Sharp & Clutton-Brock, 2010; in bottlenose dolphins, *Tursiops aduncus*, Karniski et al., 2018; Ivimey-Cook & Moorad, 2020 for a review—but see also Ivimey-Cook & Moorad, 2020 for some exceptions, e.g. collared flycatcher, *Ficedula albicollis*). A delayed date of birth/laying or a lower body mass of offspring with increasing mother age often accounts for the observed decrease in offspring survival born to old females (Lemaître & Gaillard, 2017).

The proximate causes of reproductive senescence are still poorly understood, but a physiological deterioration of the female's reproductive system over time leading to changes in age-specific maternal effects may be involved (maternal effect senescence), independently of any age-specific changes in fertility (Karniski et al., 2018; Lemaître & Gaillard, 2017; Moorad & Nussey, 2016). Maternal effects comprise a wide range of phenotypic influences of the mother on offspring phenotype, which are not related to maternal and offspring's own genotype (Bernardo, 1996; Wolf & Wade, 2009). They can be direct—through post-natal maternal care—such as feeding or licking/grooming behaviour (Cameron, Fish & Meaney, 2008; Cameron, Shahrokh, et al., 2008; Gouldsborough et al., 1998; Mousseau & Fox, 1998), but also indirect. In the latter case, mothers can influence the immune development of their offspring during the pre- and post-natal stages, in particular through the transmission of antibodies providing direct protection during ontogenesis of the offspring's immune system (Grindstaff et al., 2003). Generally, maternal traits influence offspring size and growth (e.g. influence of maternal body mass in collared lemming, *Dicrostonyx groenlandicus*, Boonstra & Hochachka, 1997 or in Harbour seal, *Phoca vitulina*, Ellis et al., 2000), and thereby offspring survival. These maternal effects on offspring traits are expected to be particularly strong in mammals compared to other taxa because of both the extended period of maternal care and the close association between mother and offspring during gestation and lactation (Reinhold, 2002). However, these maternal effects may be prone to senescence and thus decline with increasing mother age. For instance, diminished ability to forage (Catry et al., 2006) or to store body reserves in old females leads to decrease the amount of resources transferred to offspring (Lecomte et al., 2010), especially during the offspring rearing period, when energy and nutrient demands peak (Clutton-Brock et al., 1989; Sadleir, 1984). Age-related decline in resource acquisition is likely to affect both the quality and the quantity of milk produced by old females and could explain why old females often produce lighter offspring (e.g. in northern fur seals, *Callorhinus ursinus*, Boltnev & York, 2001). Milk mostly contains water, lipids, proteins, sugars and minerals such as calcium (Oftedal, 1984), and its composition varies with maternal body mass and condition in many species (reviewed in Skibiel & Hood, 2015). The variation in milk composition, especially of fat and protein content, influences mass, growth rate (Mellish et al., 1999) and survival (Skibiel & Hood, 2015) of offspring in mammals.

Age-related changes of the immune profile in females (e.g. Palacios et al., 2007; Ujvari & Madsen, 2011) may be another mechanism by which maternal effects vary during ageing. Mother-to-offspring transmission of immunity is a major determinant of immune capacities in young vertebrates (Grindstaff et al., 2003). This transmission includes the transfer of IgG (or IgY in birds) immunoglobulins, but also has persistent effects on the offspring immune response that may far outreach the presence of maternally derived antibodies (Lemke et al., 2003; Reid et al., 2006). The ability to transmit immune competence should also depend on females' own immune status and history of antigen stimulation, which are both changing with age. A decline in the transmission of immune defences with increasing maternal age could thus not only influence the development of immunity in offspring but also their survival prospects, as recently documented in Soay sheep, *Ovis aries* (Sparks et al., 2020).

Although several studies reported a decline in offspring condition with increasing maternal age—through fitness-related traits such as offspring body mass (Descamps et al., 2008; Nussey et al., 2006; Sharp & Clutton-Brock, 2010), the effect of maternal age on offspring physiological condition (set of physiological traits describing the health status of the individuals at a finer scale) has remained poorly investigated (but see Froy et al., 2017; Saino et al., 2002). A study on the blue-footed booby (*Sula nebouxii*) has provided experimental evidence of a decreased quality of eggs produced by older mothers, coupled with a decline in offspring rearing capacities, growth (e.g. ulna length, $\beta = -0.20$ [−0.39: −0.02] and T-lymphocyte response (second chick, $\beta = -0.16$ [−0.31; −0.02]) (Beamonte-Barrientos et al., 2010). To the best of our knowledge, such studies are lacking in wild mammals, and the effect of increasing maternal age at conception on physiological traits such as immunity remains to be explored. Here, we assessed the effect of maternal age and body mass on offspring physiological condition in a wild mammal, the roe deer (*Capreolus capreolus*). In this weakly polygynous ungulate, females show senescence in many traits including body mass (Douhard et al., 2017), haematological traits related to body condition (Jégo, Lemaître, et al., 2014) and immune competence (Cheynel et al., 2017), all traits that are supposed to be linked to offspring condition. We analysed seven markers to measure both physiological body condition and immunity in 86 roe deer fawns which became recently independent of their known-age mothers. In particular, we measured circulating concentrations of albumin, fructosamine and haemoglobin as physiological markers of individual condition (Gilot-Fromont et al., 2012; Jégo, Lemaître, et al., 2014). To assess immune functions, we measured neutrophil and lymphocyte counts, and gamma-globulin and haptoglobin levels, as markers of cellular and

humoral effectors of both innate and adaptive components (Gilot-Fromont et al., 2012). Based on our current knowledge, we expected lower levels of physiological markers in fawns born to older females compared to prime-aged ones. In addition, as adult body mass is a reliable proxy of individual performance in female roe deer (Plard et al., 2015), we also expected that the deleterious effect of mother age on offspring condition should be more pronounced for fawns born to the lightest females since these latter likely have lower capacities to transfer resources to their offspring.

2 | MATERIALS AND METHODS

2.1 | Ethics

All applicable institutional and/or national guidelines for the care and use of animals were followed. The protocol of capture and blood sampling of roe deer under the authority of the Office Français de la Biodiversité (OFB) was approved by the Director of Food, Agriculture and Forest (Prefectoral order 2009-14 from Paris). All procedures were approved by the Ethical Committee of Lyon 1 University (project DR2014-09, June 5, 2014).

2.2 | Study population

Roe deer data were collected in two populations living in enclosed forests, at Trois Fontaines located in north-eastern France (1,360 ha, 48°43′N, 4°55′E) and at Chizé located in western France (2,614 ha, 46°50N, 0°25′W). The Trois Fontaines forest offers habitats of high quality to roe deer, due to rich soils and a continental climate characterized by cold winters and warm rainy summers. In contrast, the Chizé forest offers a relatively poor habitat to roe deer because of the low productivity of the soils and a temperate oceanic climate with Mediterranean influences characterized by frequent summer droughts (Pettorelli et al., 2006). The contrasting environmental conditions encountered by roe deer in the studied populations are associated with marked differences in adult body mass (Gaillard et al., 2013), offspring survival (Gaillard et al., 1997) and immune profile (Cheynel et al., 2017). Roe deer populations were monitored as part of a long-term Capture–Mark–Recapture program. As roe deer females give birth in spring, systematic searches for newborn fawns were conducted between April and June. Upon capture, fawns were individually marked (but no blood samples were collected at this stage), and the filiation with the mother was assessed from either field observations or from a pedigree built in these populations and encompassing roe deer born from 1996 onwards (see Quéméré et al., 2018 for further details). Roe deer captures are also organized every winter between December and March (see Gaillard et al., 1993 for details on capture sessions). At the time of capture, roe deer offspring are approximately 8-months of age. Lactation can last until September or October (Sempéré et al., 1988), but offspring orphaned in early August are able to survive (D. Delorme, *pers. comm.*). Roe deer offspring captured in winter were thus fully independent from their mother. During captures, sex and body mass (to the nearest 50g) were recorded and a basic clinical examination was performed. We also collected blood samples from the jugular vein (up to 20 ml for a 20 kg roe deer). Whole blood was EDTA-preserved for cell count, and serum was extracted for other measures. Samples were received at the laboratory within 48 hr after sampling and analysed within 4 hr.

2.3 | Characterization of body condition and immunity

We assessed body condition of fawns through four haematological traits that reflect energetic and protein reserves. Albumin is the most abundant plasma protein, and its measure reflects the level of protein resources, independently of the immune status (Sams et al., 1998; Stockham & Scott, 2008). It is thus considered as a relevant indicator of physiological status in ruminant species (Milner et al., 2003; Pérez et al., 2006) and strongly correlates to other indices of body condition in roe deer (Gilot-Fromont et al., 2012). Albumin was separated from other proteins and quantified by refractometry followed by electrophoresis, using an automatic agarose gel (HYDRASYS; Sebia) and expressed as mg/ml of serum. Fructosamine levels represent glycated proteins and indicate glycaemia during the 2–3 weeks preceding sampling. This marker gives information on the level of carbohydrate reserves (Stockham & Scott, 2008). Fructosamine concentration was measured using Thermo scientific reagents and ABX Pentrafructosamine reagents on a Konelab 30i automaton (Fisher Thermo Scientific) and expressed as µmol/L of serum. Total blood haemoglobin concentration (in g/dl) reflects blood oxygen-carrying capacity. As high haemoglobin concentration improves overall aerobic capacity (Minias, 2015), it is considered as a robust indicator of physiological condition and nutritional status of individuals (Minias, 2015). In roe deer, haemoglobin concentration was related to body mass and other body condition metrics (e.g. albumin concentration, Gilot-Fromont et al., 2012). Haemoglobin concentrations were issued from a complete blood count performed using an ABC Vet automaton (Horiba Medical) and measured following cyan methaemoglobin conversion at 550 nm, the most commonly used method in mammals (Stockham & Scott, 2008).

We assessed the immune phenotype of fawns by counting neutrophils and lymphocytes and by measuring gamma-globulin and haptoglobin levels (see also Cheynel et al., 2017). Neutrophils and lymphocytes represent between 70%–80% and 20%–30% of the total white blood cells, respectively. Neutrophil count is representative of the cellular innate immunity. As lymphocytes include both T and B cells, with B cells being particularly involved in the production of antibodies, we used them to represent the cellular adaptive immunity. We determined neutrophil and lymphocyte composition based on the identification of the first hundred white blood cells in Wright-Giemsa-stained blood smears (Gilot-Fromont et al., 2012; Houwen, 2001). With this proportion of neutrophils and

lymphocytes (in %) and the total white blood cell count measured by impedance technology, we calculated the concentration of neutrophils and lymphocytes (10^3 cells/ml). Gamma-globulins represent the majority of circulating antibodies and reflect the humoral adaptive immunity. Gamma-globulins (mg/ml) were separated from other proteins and quantified by refractometry, followed by electrophoresis, using an automatic agarose gel (HYDRASYS; Sebia). Finally, we measured the specific level of haptoglobin, a protein belonging to the alpha2-globulin fraction synthesized in case of chronic infection or inflammation, representing humoral innate immunity. Haptoglobin analyses were performed on a Konelab 30i automaton (Fisher Thermo Scientific) using phase Haptoglobin assay (Tridelta Development LTD) chromogenic kit. A correlation matrix among all the physiological traits measured in this study (Table S1, Supporting Information) showed that the haematological and immunological traits considered here are not strongly correlated between each other's and thus provide independent information.

2.4 | Statistical analysis

We performed statistical analyses on 86 fawns born between 2009 and 2017 and sampled at 8 months of age. All fawns were born to identified mothers of known-aged. The age of mothers at parturition ranged between 3 and 12 years, which encompasses the entire reproductive life of most roe deer females (Gaillard et al., 1992). The detailed distribution of individuals by sex, study site and maternal age is given in Appendix S2. Representations of each offspring trait as a function of maternal age are provided in Appendix S3.

2.5 | Linear mixed models

We tested the effect of maternal age on body condition (body mass and haematological traits) and immunological traits of offspring using linear mixed-effect models (LMMs). Each offspring trait was analysed as a response variable. For each offspring trait, we first built a base model to investigate the effect of all possible confounding factors (maternal body mass entered as a covariate, offspring sex entered as a fixed-factor, offspring body mass entered as a covariate and population entered as a fixed-factor, and maternal age at last measurement to account for selective disappearance, see below). Maternal body mass was the mean adult body mass of females between 4 and 10 years of age and was entered in the models as a two-class factor: 'heavy' (i.e. mother with a higher body mass than the median mass of its corresponding population, threshold at 23.8 kg at Trois Fontaines and 20.7 kg at Chizé) and 'light' (i.e. mother with a body mass lower than the median mass of its corresponding population). A two-class factor was chosen to facilitate the interpretation of the interaction between maternal body mass and maternal age (entered as a continuous variable, see below). Offspring body mass was adjusted to the median date of capture (i.e. January 27th). This adjustment is required because fawns grow throughout their first winter (Hewison et al., 2002). The average daily mass gain throughout the winter was 12 ± 0.005 (*SE*) g/day at Chizé and 24 ± 0.008 g/day at Trois Fontaines (linear regression with date of capture as the sole covariate; no sex differences was detected; see Douhard et al., 2017 for further details). The birth cohort was included as a random effect to control for the marked differences in environmental conditions faced by roe deer during early life (Douhard et al., 2014), which could ultimately influence physiological traits. Individual identity of the mother was also included as a random effect to account for confounding effects of pseudo-replication (sensu Hurlbert 1984). To control for the possible effect of selective disappearance of mothers (Van de Pol & Verhulst, 2006), we included the maternal age at last observation as a covariate in all our models (since longevity was unknown for most of the females analysed here). Indeed, a possible positive association between female's longevity and physiological condition in their offspring could further mask senescence (see Nussey et al., 2008).

Then, in a second step, we tested the effect of maternal age by adding different age functions to the base models selected for each trait. Four different types of age functions were tested: linear, quadratic, two classes ('prime-aged', i.e. females aged between 3 and 7 years and 'old', i.e. females aged 8 years or more, Gaillard et al., 1993) and linear with a threshold. For threshold models, the threshold was determined by maximum likelihood estimation among values ranging between 3 and 11 years of age (see Ulm & Cox, 1989). Depending of the variables retained in the basal model, two-way interactions between maternal age and maternal body mass, offspring sex and population were also included.

For the two steps described above, we used a model selection procedure based on the Akaike Information Criterion (AIC, Burnham & Anderson, 2002). We retained the model with the lowest AIC, and when the difference of AICs between competing models was less than 2, we retained the model with least parameters to satisfy parsimony rules (Burnham & Anderson, 2002; see Appendix S4 for the comparison of the most competitive models and Appendix S5 for the AIC values of all the models tested). Finally, the goodness of fit of the selected models was assessed through calculating conditional (i.e. total variance explained by the best supported model) and marginal (i.e. variance explained by fixed effects alone) R^2 formulations (Nakagawa & Schielzeth, 2013).

2.6 | Effect sizes

We calculated the effect size of maternal age on each offspring physiological trait even when it was not included in the selected model. Effect sizes were calculated as partial correlation coefficients, which measure the standardized effect of maternal age on an offspring trait, while controlling for the potential effects of other traits. To obtain the different effect sizes, for each physiological trait we first fitted

TABLE 1 Parameter estimates of the selected linear mixed-effect model for body condition (i.e. body mass and haematological traits) and immune traits in offspring (roe deer fawns at 8 months of age)

	Best model selected	Estimate ± *SE*	*t*-value	*p*	R^2m	R^2c
Body condition						
Body mass	Population					
	Intercept	14.89 ± 0.83	17.80	***	0.39	0.61
	Population (Chizé)	−3.57 ± 0.54	−6.58	***		
	Maternal age at last observation	0.14 ± 0.09	1.53	–		
Albumin	Offspring body mass					
	Intercept	23.51 ± 3.05	7.72	***	0.09	0.86
	Offspring body mass	0.65 ± 0.15	4.38	***		
	Maternal age at last observation	0.28 ± 0.15	1.85	–		
Fructosamine	Maternal body mass + Offspring body mass					
	Intercept	168.43 ± 20.98	8.03	***	0.18	0.59
	Maternal body mass (heavy)	14.41 ± 5.87	2.46	*		
	Offspring body mass	5.51 ± 1.16	4.77	***		
	Maternal age at last observation	−1.54 ± 1.28	−1.20	–		
Haemoglobin	Population					
	Intercept	17.45 ± 0.56	30.90	***	0.33	0.44
	Population (Chizé)	−2.24 ± 0.37	−6.06	***		
	Maternal age at last observation	0.01 ± 0.06	0.08	–		
Immune traits						
Neutrophil count	Maternal body mass + Population					
	Intercept	5.46 ± 0.70	7.77	***	0.16	0.49
	Maternal body mass (heavy)	0.91 ± 0.41	2.22	*		
	Population (Chizé)	−1.37 ± 0.46	−2.98	**		
	Maternal age at last observation	−0.03 ± 0.08	−0.39	–		
Lymphocyte count	Offspring body mass + Population					
	Intercept	5.65 ± 1.12	5.06	***	0.14	0.51
	Offspring body mass	−0.15 ± 0.07	−2.28	*		
	Population (Chizé)	−1.40 ± 0.43	−3.29	**		
	Maternal age at last observation	−0.03 ± 0.06	−0.60	–		
Gamma-globulin	Maternal age × Population					
	Intercept	13.89 ± 0.81	17.12	***	0.44	0.59
	Population (Chizé)	6.72 ± 0.91	7.37	***		
	Maternal age (linear)	−0.01 ± 0.21	−0.07	–		
	Maternal age × population (Chizé)	−1.22 ± 0.43	−2.85	**		
	Maternal age at last observation	0.08 ± 0.19	0.41	–		
Haptoglobin	Null					
	Intercept	−0.90 ± 0.15	−5.89	***	0.00	0.56
	Maternal age at last observation	−0.004 ± 0.01	−0.38	–		

Note: Estimates are reported (±one standard error (*SE*)). Statistical significance is represented by $^*p < .05$, $^{**}p < .01$ and $^{***}p < .001$. R^2m and R^2c correspond to the marginal and conditional variance of the model, respectively (see text for further detail).

the mixed-effect model including maternal age (linear), maternal age at last observation and body mass as fixed factors, and cohort and maternal identity as a random effect on the intercept (i.e. additive model). We then used the equation provided by Nakagawa and Cuthill (2007, p. 82) for mixed-effect models to calculate effect size. We calculated confidence intervals of effect sizes following Nakagawa and

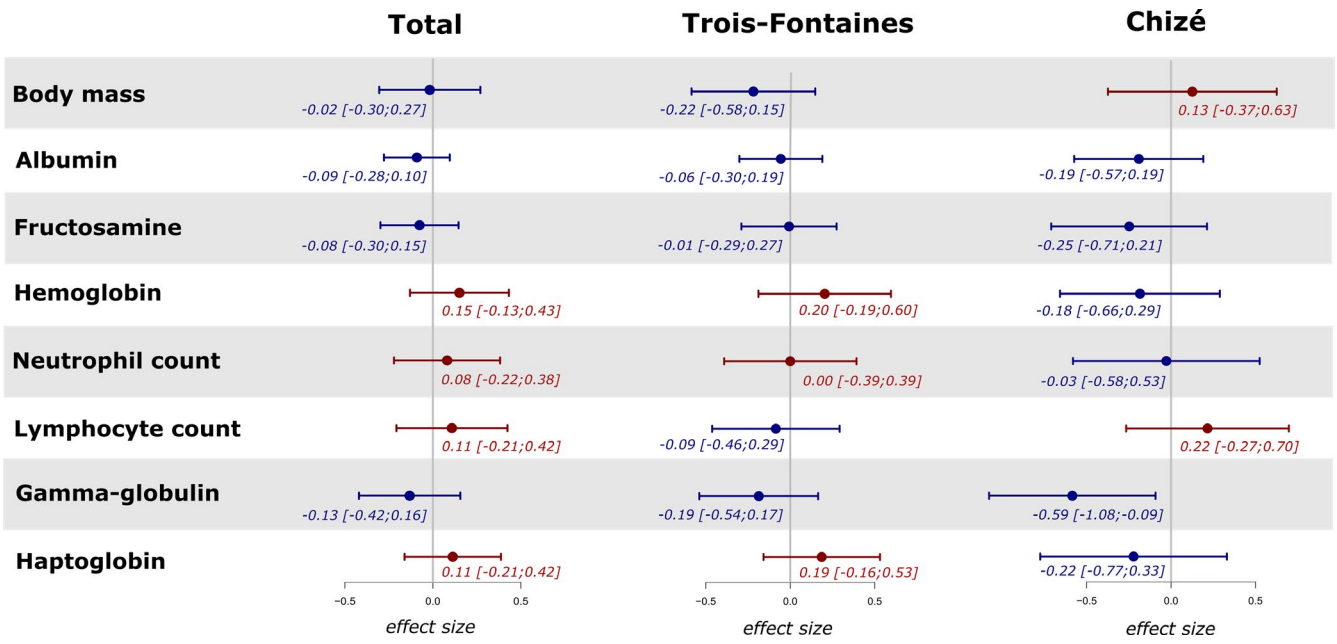

FIGURE 1 Effect size of maternal age on offspring body condition and immunological traits, with Trois Fontaines and Chizé combined and separated. Effect sizes are reported together with associated 95%-confidence interval. Blue colour represents a negative effect size and red colour a positive effect sizes

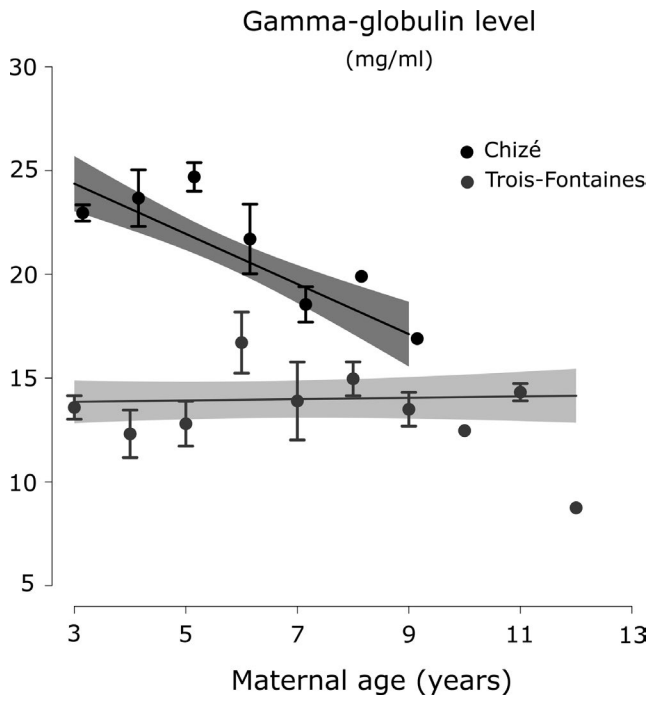

FIGURE 2 Predicted effect of maternal age on offspring gamma-globulin levels in two populations of roe deer (Trois Fontaines and Chizé). Plots are based on predicted effects from the selected model (see Table 1). The lines represent model predictions and the shaded areas the 95% CIs. The points correspond to the average value per age, and the bars correspond to ± Standard Error

Cuthill (2007)'s recommendations. We calculated effect sizes on the whole data set and in the two populations separately to compare the direction of the effect between populations. All analyses were carried out in R version 3.2.3 (R Core Development Team, 2015) and using the function lmer from package lme4 (Bates et al., 2015).

3 | RESULTS

We did not find striking effects of maternal age on markers of body condition or immune traits in roe deer offspring, neither in the combined data set (see best models selected in Table 1 and effect sizes in Figure 1) nor within each of the two populations (see Figure 1). We only found a negative effect of maternal age on the offspring level of gamma-globulins at Chizé (see parameter estimates in Table 1, effect size in Figure 1 and the model prediction in Figure 2). Maternal age at last observation, added in our analyses to control for the possible selective disappearance of poor-quality mothers, did not show detectable effects on offspring traits (see effects reported in Table 1). Finally, we found a positive association between maternal body mass and two traits of offspring condition. Fawns born to heavier mothers had higher fructosamine (+9%, Figure 3a and Table 1) and neutrophil levels (+15%, Figure 3b and Table 1) than those born to lighter mothers.

We also found marked differences in the offspring physiological traits between the two populations. Thus, two markers of body condition and three markers of immunity of fawns strongly differed between the two populations. Fawns at Chizé were lighter (−24%, Table 1), had lower levels of haemoglobin (−13%, Table 1), neutrophil (−25%, Table 1) and lymphocyte counts (−25%, Table 1), and much higher levels of gamma-globulins (+48%, Table 1) than those at Trois Fontaines. Finally, albumin and fructosamine levels were positively associated with offspring body mass, contrary to

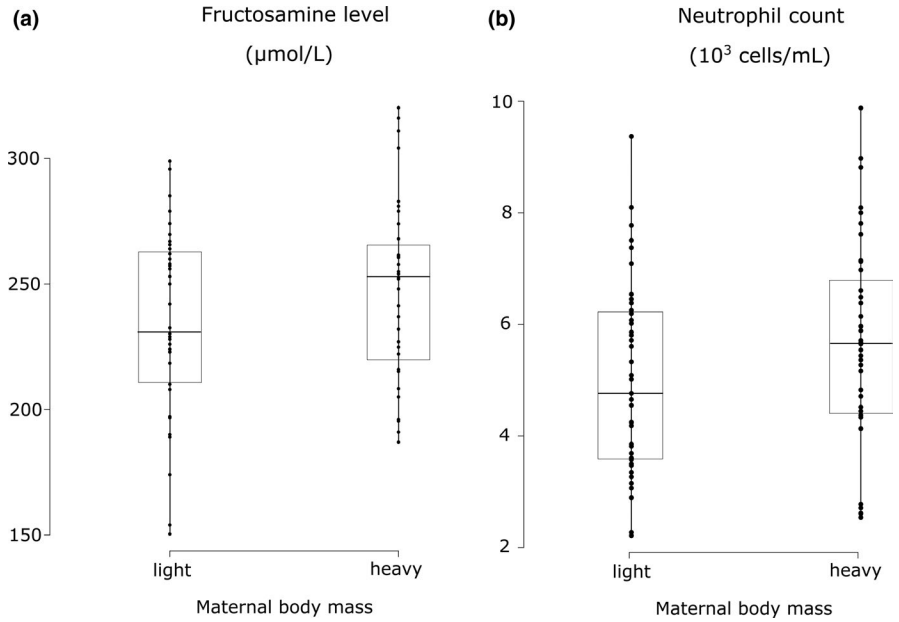

FIGURE 3 Effect of maternal body mass ('heavy' vs. 'light' mothers, a threshold at 23.8 kg at Trois Fontaines and 20.7 kg at Chizé) on (a) offspring fructosamine levels and (b) neutrophil count

lymphocyte count, which was negatively associated with offspring body mass (Table 1).

4 | DISCUSSION

Our results provide a thorough assessment of the effect of both maternal age and body mass on the physiology of recently emancipated offspring. We found that in roe deer, maternal body mass but not maternal age influences offspring physiological condition and immunity. We also highlight that environmental conditions experienced by roe deer fawns throughout their first months of life, likely through resource quality, play a key role in their physiology.

Although maternal age is an important determinant of early survival across multiple animal taxa (see Ivimey-Cook & Moorad, 2020 for a recent review), which suggests that fawns born to old mothers suffer from lower body condition and impaired health and physiological performance, we did not detect here an effect of maternal age on offspring body mass and only a limited influence on immune profile. Only gamma-globulin concentration appeared to be down-regulated in fawns born to old mothers from Chizé, in accordance to what was reported in some published case studies (e.g. reduced T-lymphocyte response in chicks born to old mothers, Beamonte-Barrientos et al., 2010). In our study, this lack of effect of maternal age on offspring condition does not seem to be due to selective disappearance of poor-quality mothers with increasing age (Hayward et al., 2013; Nussey et al., 2011). However, a detrimental effect of maternal age on offspring condition cannot be excluded and might have occurred earlier in life. As juvenile survival between birth and 8 months of age is the critical stage of roe deer population (Gaillard et al. 2013), a strong viability selection (sensu Fisher, 1930) in offspring might account the lack of effect of maternal age in the present analysis. In roe deer, viability selection is particularly pronounced in early life, before weaning (Garratt et al., 2015). If fawns born from old females show poor physiological condition, they might die in the first weeks of their life (i.e. well before their first winter). Thus, the 8-month old fawns captured in our study may only include individuals of quite high body condition. Quantification of physiological markers in newborn fawns would thus be necessary to assess maternal age influences offspring condition and immunity during the neonatal stage. Finally, we also cannot exclude the fact that the statistical power remains limited in our study due to the size of the data set ($N = 86$ mother-fawn pairs).

On the other hand, the physiological condition of roe deer fawns is mainly influenced by both maternal body mass and environmental conditions. For many years, studies have reported a positive influence of maternal body size on offspring size and development in vertebrates (see Ronget et al., 2018 for a review). More specifically in roe deer, maternal body mass is positively associated with reproductive success (Gaillard, Festa-Bianchet, Delorme, et al., 2000; Gaillard, Festa-Bianchet, Yoccoz, et al., 2000) and with both offspring birth mass and early survival (Plard et al., 2015). The positive influence of maternal body mass on offspring body condition was revealed here at the physiological level. A positive association occurred between maternal body mass and offspring fructosamine levels. This reflects higher levels of carbohydrate reserves of fawns born to heavy mothers and suggests thereby a potential for higher physiological performance of these fawns. In addition, maternal body mass was positively associated with an offspring cellular immune trait (i.e. neutrophil count), but not associated with offspring humoral traits (i.e. gamma-globulin and haptoglobin). Neutrophils represent the majority of white blood cells and constitute an important part of the innate cellular immune response. The immune function is known to be energy demanding and strongly dependent of the quality and quantity of nutritional resources. The cellular part of the immune function entails particularly high costs of production compared to the humoral component (Klasing, 2004). This positive effect of maternal body mass on the offspring condition, particularly on the most

energy-demanding traits such as neutrophils, may be the result of a higher allocation of maternal resources to offspring. Such effect may involve a higher milk production and/or an increased protein content in milk of heavy mothers (Landete-Castillejos et al., 2003). High maternal milk production enhances offspring mass gain and immunity (Landete-Castillejos et al., 2002, 2003). Therefore, even if 8 months old roe deer are not yet fully emancipated, the quantity and quality of milk provided by their mother likely has long-lasting effects on their physiological condition. Finally, as body mass of roe deer females is influenced by the quality of their own early-life environmental conditions (Quéméré et al., 2018), a long-term effect of early-life environmental conditions on the quality of maternal effects and on the physiology of the offspring could take place.

Finally, we found that environmental conditions influenced physiological traits, especially the immune phenotype, of roe deer fawns. Two markers of fawn body condition (body mass and haemoglobin) and two cellular immune traits (neutrophil and lymphocyte counts) were lower at Chizé where roe deer experience poor living conditions compared to their conspecifics at Trois Fontaines. Fawns at Chizé also showed higher allocation to humoral immunity (i.e. higher levels of gamma-globulins), which is less costly to maintain and use (compared to nonspecific immunity, Klasing, 2004), than fawns at Trois Fontaines. These results are expected because roe deer at Chizé experience habitats of overall low productivity due to poor soils and frequent summer droughts (Pettorelli et al., 2006) and have thereby access to fewer/less quality resources to allocate to the different physiological functions including immunity. Previous studies have shown that fawn survival, female fecundity, adult body mass (Gaillard et al., 2013), age-specific telomere length (Wilbourn et al., 2017) and many markers of adult immune performance (Cheynel et al., 2017) are consistently lower at Chizé than at Trois Fontaines. A large proportion of females at Chizé experience nutrient limitation and consequently display low body mass (Gaillard et al., 2013). Nutrient limitation should affect their milk production and quality, as milk is very dependent on both diet quality (Sutton, 1989) and food availability (Landete-Castillejos et al., 2003; Oldham & Friggens, 1989). In addition, the lactation period in roe deer takes place during summer, which is often particularly dry in the Chizé forest (Pettorelli et al., 2006). Thus, the ability of mothers to transfer resources to their offspring during their first months of life would be limited at Chizé, explaining the level of cellular immunity of fawns being lower at Chizé than at Trois Fontaines. Variation in annual environmental conditions is also likely to exacerbate the nutrient limitation at Chizé (Quéméré et al., 2018). Finally, at Chizé, roe deer face high parasite burden (e.g. *Trichuris sp.* Cheynel et al., 2017) that may both impair their body condition (Jégo, Ferté, et al., 2014) and trigger specific immunity, contributing to the high level of antibodies. However, it is important to bear in mind that this interpretation relies on the comparison of only two populations and could thus be refined by information collected in additional populations.

Overall, our study reveals that increased maternal age does not lead to impaired physiological condition of weaned roe deer fawns at the onset of the winter, but that maternal body mass does influence positively offspring physiological performance. Our findings thus shed a new light on the physiological factors that link mother's mass and offspring performance.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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SUPPORTING INFORMATION

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