The environmental roots of the relationship between glucocorticoids and body mass in the wild

Lucas D. Lalande[1], Emmanuelle Gilot-Fromont[1,2], Jeffrey Carbillet[1,3], François Débias[1], Jeanne Duhayer[1,4], Jean-Michel Gaillard[1], Jean-François Lemaître[1], Rupert Palme[5], Sylvia Pardonnet[1,6], Maryline Pellerin[7], Benjamin Rey[1], Pauline Vuarin[1]

[1] Université de Lyon, Université Lyon 1, CNRS, Laboratoire de Biométrie et Biologie Evolutive UMR 5558, F-69622 Villeurbanne, France

[2] Université de Lyon, VetAgro Sup, Marcy l'Etoile, France

[3] Current institution: Institute of Ecology and Earth Sciences, University of Tartu, Tartu, 51014, Estonia

[4] Current institution: Office Français de la Biodiversité, Direction de la Recherche et de l'Appui Scientifique, Service Départemental de la Haute-Garonne, Villeneuve-de-Rivière, 31800, France

[5] Unit of Physiology, Pathophysiology and Experimental Endocrinology, Department of Biomedical Sciences, University of Veterinary Medicine, Veterinärplatz 1, 1210 Vienna, Austria

[6] Current institution: Université de Strasbourg, CNRS, IPHC UMR 7178, Strasbourg, France

[7] Office Français de la Biodiversité, Direction de la Recherche et de l'Appui Scientifique, Service Conservation et Gestion Durable des Espèces Exploités, Châteauvillain, 52210, France

Abstract

Environmental fluctuations force animals to adjust glucocorticoids (GCs) secretion and release to current conditions. GCs are a widely used proxy of an individual stress level. While short-term elevation in GCs is arguably beneficial for fitness components, previous studies have documented that the relationship between long-term baseline GCs elevation and fitness components is largely inconsistent. Using longitudinal data on roe deer (*Capreolus capreolus*) from two populations with markedly different environmental contexts, we tested whether baseline GC levels negatively correlate with body mass – a trait positively associated with demographic individual performance – on the short- to long-term. In support, higher baseline GC concentrations were associated to lighter body mass, both measured during the same capture event, in juvenile and adult males of both populations. We also found evidence of a stronger association between higher GC levels and lower body mass for males born in poor years. GCs were not related to body mass neither on the long-term, nor in females of neither population. We propose that the sex-specific association between GCs and body mass are consistent between populations and regulated by environmental conditions at a finer-scale, and are driven by sex-specific life histories. The sex- and context-dependent responses of stress highlight the complexity of studying stress in the wild.

Keywords: stress response, ungulates, body condition, Faecal Cortisol Metabolites, individual performance

Introduction

Throughout their life, individuals must adjust their morphology, physiology and/or behaviour to cope with environmental variation. Part of this variation is predictable as individuals can rely on environmental cues (*e.g.* such as photoperiod or temperature at the daily or seasonal scales) to anticipate future conditions (Wingfield 2003, 2008). Whereas predictable variation is not considered as stressful *per se* (*i.e.* eliciting a stress response), an unpredictable perturbation can disrupt life cycles and trigger a stress response through the activation of the hypothalamic-pituitary-adrenal (HPA) axis and the release of glucocorticoids (GCs), departing them from the baseline level (Reeder and Kramer 2005). The primary role of these hormones (namely cortisol and corticosterone) is to maintain an organism's energy balance (*i.e.* energy homeostasis) according to its requirements in its current environment (Wingfield 2013, Hau et al. 2016). On the short-term, an elevation of GC concentration in an individual facing a challenging situation is beneficial because it promotes processes enhancing survival through reallocation of stored energy from non-immediately essential functions (e.g. growth, reproduction) towards cardiovascular functions or locomotor and foraging activities (Sapolsky et al. 2000). After a temporary perturbation, the GC concentration often quickly returns to the baseline level (Reeder and Kramer 2005). However, GC concentration may remain elevated above the baseline level on the long-term (*i.e.* days to weeks) as a result from exposure to repeated or long-lasting perturbations such as prolonged inclement weather or food shortage (McEwen and Wingfield 2010, Monaghan 2014, Hau et al. 2016). Such elevated GC concentration in the long-term can have adverse consequences on individual performance through disruption of the immune function (Dhabhar 2014), inhibition of growth, or decreased body condition (Reeder and Kramer 2005) with an intensity depending on the species (Boonstra 2013). GC concentration measurements are a widely used proxy of an individual

stress level (Palme 2019), although GC concentration may not always give the full picture of the stress response (MacDougall-Shackleton et al. 2019).

While many studies analysed the effect of an increase of GC beyond the baseline level (i.e. acute stress-induced GC concentration) on individual performance, fewer have considered how GCs at baseline concentration affect the performance of animals in the wild. Results from these rare studies remain equivocal (Dantzer et al. 2014), which could be explained by the complex influence of environmental conditions (Henderson et al. 2017). When resources are limited, high levels of GCs can be detrimental because they increase energy, but this detrimental effect may not be observed when resources are abundant. Food availability (*i.e.* energy availability) or behavioural flexibility stimulating foraging activity can thus compensate for the energy requirements induced by high GC levels (Henderson et al. 2017). Animals inhabiting suboptimal habitats (*e.g.* exposed to human disturbance, predation, intra- or interspecific competition or pathogens) experience continuous stressful conditions and generally show a higher GC concentration compared to conspecifics inhabiting optimal areas (Dantzer et al. 2013, 2014, Formenti et al. 2018, Boudreau et al. 2019, Dulude-de Broin et al. 2020, Carbillet et al. 2020).

Additionally, there is evidence that the direction of the GC-performance relationship can also depend on individual attributes, such as body condition, sex or age (Bonier et al. 2009, Dantzer et al. 2014). Under high GC concentration requiring high energy demands, high quality individuals may perform better than poor quality ones. In African striped mice (*Rhabdomys pumilio*), elevated baseline GC concentration was related to the selective disappearance of light individuals (Vuarin et al. 2019). Since the relationship between stress and performance is complex and involves individual attributes and environmental context, both sources of variation have to be investigated to disentangle their respective roles (Crespi et al. 2013, Dantzer et al. 2014).

Focusing on body mass provides a relevant approach to investigate the detrimental effects of prolonged exposure to a high GC concentration. Indeed, body mass is a trait easily measured in the field that constitutes a reliable proxy of body condition in many species, especially income breeders (Hewison et al. 1996, Andersen et al. 1998). Moreover, body mass is representative of the amount of energy available for an individual, and high levels of GCs are known to have a crucial role on body mass by increasing protein and amino-acid catabolism and mobilising lipids (promoting gluconeogenesis), consequently decreasing body mass (Sapolsky et al. 2000, Landys et al. 2006, Rabasa and Dickson 2016). Also, and importantly, body mass is often positively linked to fitness components (*e.g.* Gaillard et al., 2000; Ronget et al., 2018).

However, the relationship between baseline GC concentration and body mass is complex. Indeed, within seasonal baseline levels, GCs actually result in increased feeding behaviours potentially promoting fat storing and body mass gain, as opposed to the previously-mentioned GC actions on protein and amino-acid catabolism and lipid mobilisation (Landys et al. 2006). Case studies of the relationship between baseline GCs and body mass/condition have produced contradictory results (George et al. 2014, Hennin et al. 2016, Grace et al. 2017, Vágási et al. 2018). For instance, high GC levels, within baseline range, such as when preparing for migration, promoted higher foraging rates and thus entailed fat storing and increased body mass in the dark-eyed junco (*Junco hyemalis*, Holberton et al., 2007). Conversely, low body mass and poor body condition were associated with higher baseline cortisol concentrations in Eurasian badgers (*Meles meles*, George et al., 2014). Finally, experimental increase in glucocorticoid concentration through predation risk manipulation resulted in no changes in body condition in snowshoe hares (*Lepus americanus*, Boudreau et al., 2019).

We aimed to contribute at better understanding how high baseline GC concentration relates to body mass of roe deer (*Capreolus capreolus*), an income breeder species for which body mass is a good proxy for body condition (Hewison et al. 1996, Andersen et al. 2000, Pettorelli et al. 2006). We took advantage of the detailed and intensive monitoring data collected through capture-marking-recapture for more than a decade at the individual level in two populations subject to markedly different ecological contexts (*i.e.* one inhabiting a good quality habitat and one population being strongly food-limited; Pettorelli et al., 2006). To avoid measuring the capture stress response (Romero & Reed, 2005), longer-term, indirect measures of GC concentration can be obtained from biological matrices other than blood (Sheriff et al. 2011). Indeed, blood GC concentration is highly variable and a point in time measure and, for example, circulating GCs concentration increases drastically within 3 minutes following an individual's capture (Sapolsky et al. 2000, Romero and Reed 2005). In this context, levels of faecal glucocorticoid metabolites (FGMs) are particularly relevant as they represent an integrative measure of GC concentration several hours before the capture event (*i.e.* baseline stress; Palme, 2019). Thus, we here measured FGMs, as arguably representative of baseline adrenocortical activity. In roe deer, FGMs reflect adrenocortical activity over a few hours, but with a time delay of ~12h (Dehnhard et al. 2001).

As chronic stress can have both immediate and long-term consequences on fitness components (Monaghan and Haussmann 2015), we tested the immediate relationship between concomitant body mass and FGMs (*i.e.* short-term relationship), the relationship between FGMs in a given year and the change of body mass between two consecutive years (*i.e.* medium-term relationship) and the relationship between FGM measured on juveniles (*i.e.* individuals in their first year of life) and body mass later-on in an individual life (*i.e.* long-term relationship). We first analysed the relationship between FGMs and body mass measured at the same capture event. We expected individuals with higher FGM concentration to be

lighter than individuals with low FGM concentration. As roe deer is an income breeder species that does not store fat (Hewison et al. 1996, Andersen et al. 1998), we expected the catabolic actions of GCs to directly impact body mass and condition and to overcome the effects of increased feeding behaviours promoted by GCs. Then, since chronically elevated FGMs are expected to be deleterious on the medium to long-term, we tested whether FGMs measured at a given capture influenced body mass changes across lifespan. Thus, we first assessed the relationship between FGMs measured in a given year and a given body mass change between two consecutive years, separately for growing individuals and prime age adults having reached their asymptotic mass (*i.e.* between 4 and 10 years old; Douhard et al., 2017). We expected that higher FGM concentration should result in a smaller mass gain for growing individuals, and result in a decrease in body mass between two consecutive years for prime age adults, between two consecutive years, as chronic stress can be linked to inhibited growth or decreased body condition (Reeder and Kramer 2005). Finally, we tested for the effect of the stress experienced during the first year of life on the individual body mass relative to the population and sex at a given age, from the second year of life onwards. We predicted that individuals with higher FGMs during the first year of life should be lighter in later in life, as roe deer performance later in life is affected by environmental factors during the first year of life (Gaillard et al., 2003). Lastly, in all analyses we expected negative relationships between FGMs and body mass to be steeper in the most food-limited population (Henderson et al. 2017).

Materials and Method

Study population and sample collection

We studied roe deer in two populations inhabiting closed forests at Trois-Fontaine (TF – 1360 ha) in north-eastern France (48°43’N, 4°55’E) and at Chizé (CH – 2614 ha) in western France

(46°05'N, 0°25'W). The TF population is characterised by a homogeneous habitat of good quality on a broad spatial scale, with high forest productivity due to rich soils. On the other hand, the CH population inhabits a less suitable heterogeneous habitat comprising three types of varying quality (Pettorelli et al. 2001) with low forest productivity due to poor soils and frequent summer droughts (Pettorelli et al. 2006). Since 1975 in TF and 1977 in CH, a Capture-Mark-Recapture program has taken place every winter, with 10-12 capture days per year (Gaillard et al. 1993). Roe deer were captured during this period by drive-netting and animal manipulations occurred between 1 and 4 hours after capture. Individuals of known age (i.e. captured within their first year of life) were weighed, and faecal matter and blood samples have been collected since 2010. During the capture period, diet is similar and mostly composed of brambles (*Rubus* sp.) and ivy (*Hedera helix*) in the two deciduous forests (Tixier and Duncan 1996), so FGM measurements between populations should not be biased according to diet composition. Body mass measured on juveniles (*i.e.* at about 8 months of age) depends on the date of capture. Juveniles gain on average 12 g/day and 24 g/day in CH and TF, respectively, during the capture period (Douhard et al. 2017). Therefore, we standardised juvenile body mass as the expected body mass on the 27th of January, the median date of captures at CH and TF (Douhard et al., 2017). In these two populations, the cohort quality is reliably measured by the cohort-specific average of juvenile mass corrected for the Julian date of capture (Gaillard et al. 1996). This proxy of environmental quality from the birth of an individual (typically in May) to its capture as juvenile in winter was obtained for all capture years, and is what we refer to when mentioning 'cohort quality' hereafter.

Faecal glucocorticoid metabolites (FGMs) assay

Baseline adrenocortical activity was estimated through FGMs (Palme 2019). We collected faecal matters rectally at capture from 2010 to 2021. Faeces were frozen at -20°C within 24 hours prior to 2013 in CH and 2017 in TF, and immediately frozen at -80°C after collection

since then. Extraction of FGM followed a methanol-based procedure and the analysis was performed using a group-specific 11-oxoaetiocholanolone enzyme immunoassay (EIA), a method previously described in details (Möstl et al. 2002) and validated for roe deer (Zbyryt et al. 2018). In brief, 0.5 g (± 0.005) of faeces were vortexed in 5 mL of 80% methanol before being centrifuged for 15 minutes at 2500 *g* (Palme et al. 2013). The amount of FGM was determined in an aliquot of the supernatant diluted 10 times in assay buffer. Measurements were done in duplicate with intra- and inter-assay coefficients lower than 10% and 15%, respectively. FGMs are expressed as nanograms per grams of wet faeces (ng/g). The data were then log-transformed for the statistical analyses (henceforth called FGMs).

Statistical analyses

All analyses were performed using R version 4.0.5 (R Core Team 2021). To test whether the two populations differed in their mean individual FGMs in support of our prediction, we compared mean population-specific FGMs, using Mann-Whitney U tests due to the non-normality of the FGMs distribution. Individual FGM repeatability was calculated for all individuals, and separately for each population, using the 'rptR' package (Stoffel et al. 2017). Repeatability analysis included individuals sampled only once as to improve estimates of the within-individual variance (Martin et al. 2011). Within-individual FGM repeatability was detectable but weak in both CH (r = 0.14, 95% CI = [0.03, 0.26]) and TF (r = 0.15 [0.01, 0.29]). The relationship between FGMs and body mass was tested using linear mixed effect models (LMMs) with a normal error distribution. Analyses were performed separately for sex and population, except for the second analysis testing for the relationship between FGMs and body mass change between two consecutive years, due to sample size (Table S2).

Short-term relationships between FGMs and body mass measured at the same capture event

We first assessed the relationship between FGMs and body mass measured the same year (*i.e.* at the same capture) to test the hypothesis that higher baseline FGMs result in short-term adverse consequences on body mass. Individuals in their first year of life (*i.e* juveniles) were analysed separately from individuals in their second year of life onwards, because the first year of life is the critical period of roe deer population dynamics (Hamel et al. 2009, Gaillard et al. 2013). However, body mass varies with age, and at a given age, varies between sexes and in relation to environmental conditions at birth (*i.e.* cohort effects, Hamel et al., 2016). We thus tested the relationship between FGMs measured in a given year and individual body mass relative to the average body mass of all individuals of the same age, population and sex, keeping ages with at least 3 individuals. Therefore, the average body mass was calculated up to 10 and 15 years old in males and females at CH, respectively, and up to 12 and 13 years old in males and females at TF, respectively, excluding older ages for which we did not have at least three individuals. For juveniles, the response variable was the mass corrected for the date of capture (see above) and fixed explanatory variables included the individual FGMs, cohort quality and their interaction. The year of birth of the individuals (*i.e.* cohort) was included as a random effect. For individuals aged 2 years or older, the response variable used to test for the FGMs-mass relationship was the individual body mass minus the average mass of roe deer from the same population, of the same sex and with the same age, regardless of their year of capture (hereafter 'relative body mass). Fixed effects included continuous variations in FGMs, cohort quality and their interaction. Random effects of the cohort were included on the intercepts, as well as the individual identity (ID) to account for repeated measurements of the same individual.

Medium-term relationships between FGMs and body mass change between two consecutive years

Baseline FGMs can reflect medium-term consequences of GCs on body mass. The relationship between FGMs and the change of body mass between two consecutive years was analysed separately for growing (*i.e.* between age 1 and 2) individuals, and for prime age adults which had reach their asymptotic body mass (from 4 to 10 years old, Hewison et al., 2011). The response variable was the change in relative body mass. Briefly, the change in relative mass expresses the change in body mass of a given individual between two ages in relation to the change in body mass of all individuals of the same sex and population between the same ages. The relative mass was calculated as the difference between the mass of an individual at age x, and the mean mass of all individuals of age x of the same sex and the same population. The change in relative body mass was calculated as the difference between the relative mass at age $x + 1$ and the relative mass at age x. For both growing and prime age individuals, two models were run to account for *i)* FGMs measured at age x and *ii)* the average of the FGMs measured at age x and age $x + 1$. Due to small sample size and to test for sex and population differences, the analysis was performed on data pooled from both sexes and both populations (Table S2). Fixed effects included body mass at age x (*i.e.* initial body mass), cohort quality, population and sex, and their interactions with FGMs (at age x or average of the FGM values measured at age x and age $x + 1$). Random effects of the cohort were included on the intercepts, and for prime age individuals, random effects of individual ID were also included on intercepts to account for repeated measurements of the same individual.

Long-term relationships between FGMs during early life and body mass later on

As elevated baseline FGMs are expected to have negative effects on body mass on the long-term, and as environmental conditions during the first year of life have carry-over effects on performance later in life in roe deer (Gaillard et al. 2003), we tested whether FGMs during development are associated with adult body mass. Only individuals for which we measured

FGMs as juvenile and body mass beyond the second year of life were analysed. The response variable was the relative individual body mass as defined above. Fixed effects included FGMs measured when juvenile, cohort quality and their two-way interaction. Random effects of the cohort were included on the intercept, as well as individual ID to account for repeated measurements of the same individual.

We also performed model selection for short and long-term analyses on populations and sexes pooled to test explicitly for population and sex differences in the way individuals cope with FGMs (Table S4, Table S7). cohort quality was expressed as a relative cohort quality (*i.e.* the difference between mean cohort quality in each population and an individual cohort quality), so there is no redundancy with the population variable. Fixed effects included relative cohort quality, population and sex and their two-way interactions with FGMs, and random effects of the cohort were included on the intercepts, as well as individual ID to account for repeated measurements of the same individual.

Model averaging

For all analyses, the final models were selected based on AICc (Akaike Information Criterion corrected for small sample sizes). Among competitive models (assessed as the set of models within 2 ΔAICc, Burnham et al., 2002) we performed conditional model averaging using the model with the lowest AICc value, the simpler nested models within it and the non-nested models, but without considering models with uninformative variables (*sensu* Arnold, 2010). The null model was selected as the most plausible model if it was present among the set of models within 2 ΔAICc. For each variable we estimated its effect size (β) with 85% confidence intervals (85% CI, following Arnold (2010)'s recommendations), and calculated marginal and conditional R^2. We provided full model selection tables in supplementary information (Table S3-8). All continuous covariates were mean-centered so that the intercept is the mass (for juveniles) or the relative individual body mass (for individuals older than one

year of age) for the mean cohort quality and/or mean FGMs. Visual inspection of model residuals confirmed that they fulfilled the assumptions of Gaussian distribution and homoscedasticity.

Results

Our sample size included 917 observations of body mass in CH (405 on males and 512 on females) and 964 in TF (456 on males and 508 on females). Among these observations, 529 (233 for males and 296 for females) were associated with FGM measurements in CH and 495 (240 for males and 255 for females) in TF. Two raw FGM measures were unusually high: 5192 and 6194 ng/g, for a female in CH aged 10, and a female in TF aged 1, respectively (see Figure S1). Below, results exclude these extreme values (analyses including them are reported in Table S8), but we specify when adding them yielded different conclusions.

FGM concentrations ranged from 8 to 3428 ng/g with a median value of 689 ng/g. The median FGMs was 674 ng/g (range: 34-3275 ng/g) in CH, and 715 ng/g (range: 8-3428 ng/g) in TF. FGMs were not detectably different between the two populations ($W = 138720$, $p = 0.1$). In each population, FGMs did not differ between males and females (CH: $W = 36041$, $p = 0.4$; TF: $W = 29828$, $p = 0.6$).

Short-term relationships between FGMs and body mass measured at the same capture event

Individuals in their first year of life

We analysed the relationship between FGMs and body mass measured the same year on 368 fawns (78 females and 96 males in CH, 91 females and 103 males in TF). Since the random effect ‘cohort’ created singularities for all subsets (except for females of CH), it was removed in all analyses and the models therefore consisted of linear models.

The selected model included a positive interaction between cohort quality and FGMs on body mass for male juveniles of CH ($\beta_{\text{Cohort quality}}$ = 0.91 [0.5, 1.4], β_{FGM} = -0.52 [-1.0, -0.04], $\beta_{\text{Cohort quality:FGM}}$ = 0.82 [0.1, 1.5], Figure 1A, Table 1, Table S3). As cohort quality increased, the negative relationship between FGM and juvenile mass vanished (Figure 1A). We also found evidence of a negative relationship between FGMs and body mass in male juveniles of TF, and evidence of a positive association between cohort quality and juveniles mass, but FGMs and cohort quality did not interact (β_{FGM} = -0.99 [-1.6, -0.4], $\beta_{\text{Cohort quality}}$ = 1.07 [0.8, 1.4], Figure 1A, Table 1, Table S3). For females, we only found a positive link between body mass and cohort quality (Figure 1B, Table 1, Table S3).

Individuals in their second year of life onwards

The dataset included 655 observations on 377 individuals: 104 females (218 observations) and 83 males (136 obs.) in CH, and 106 females (164 obs.) and 84 males (137 obs.) in TF. The random effect 'cohort' created singularities in some subsets. Hence, the models only included individual ID as random effect.

We found evidence of a negative relationship between individual relative body mass and FGMs in males of both populations ($\beta_{\text{FGM,CH}}$ = -0.52 [-0.8, -0.2], $\beta_{\text{FGM,TF}}$ = -0.92 [-1.2, -0.6], Figure 1C, Table 1, Table S3) that was buffered by an improvement of cohort quality at TF, as indicated by the statistically significant interaction between cohort quality and FGMs in males ($\beta_{\text{Cohort quality}}$ = 0.08 [-0.3, 0.5], β_{FGM} = -0.92 [-1.2, -0.6], $\beta_{\text{Cohort quality:FGM}}$ = 1.60 [1.1, 2.1], Figure 1C, Table 1, Table S3). For females of CH, relative body mass increased with cohort quality ($\beta_{\text{Cohort quality}}$ = 0.60 [0.3, 0.9], Table 1, Table S3) but did not vary in relation to FGMs (Table 1, Table S3). We found no evidence of any link among FGMs, cohort quality and relative body mass in females of TF (Table 1, Table S3).

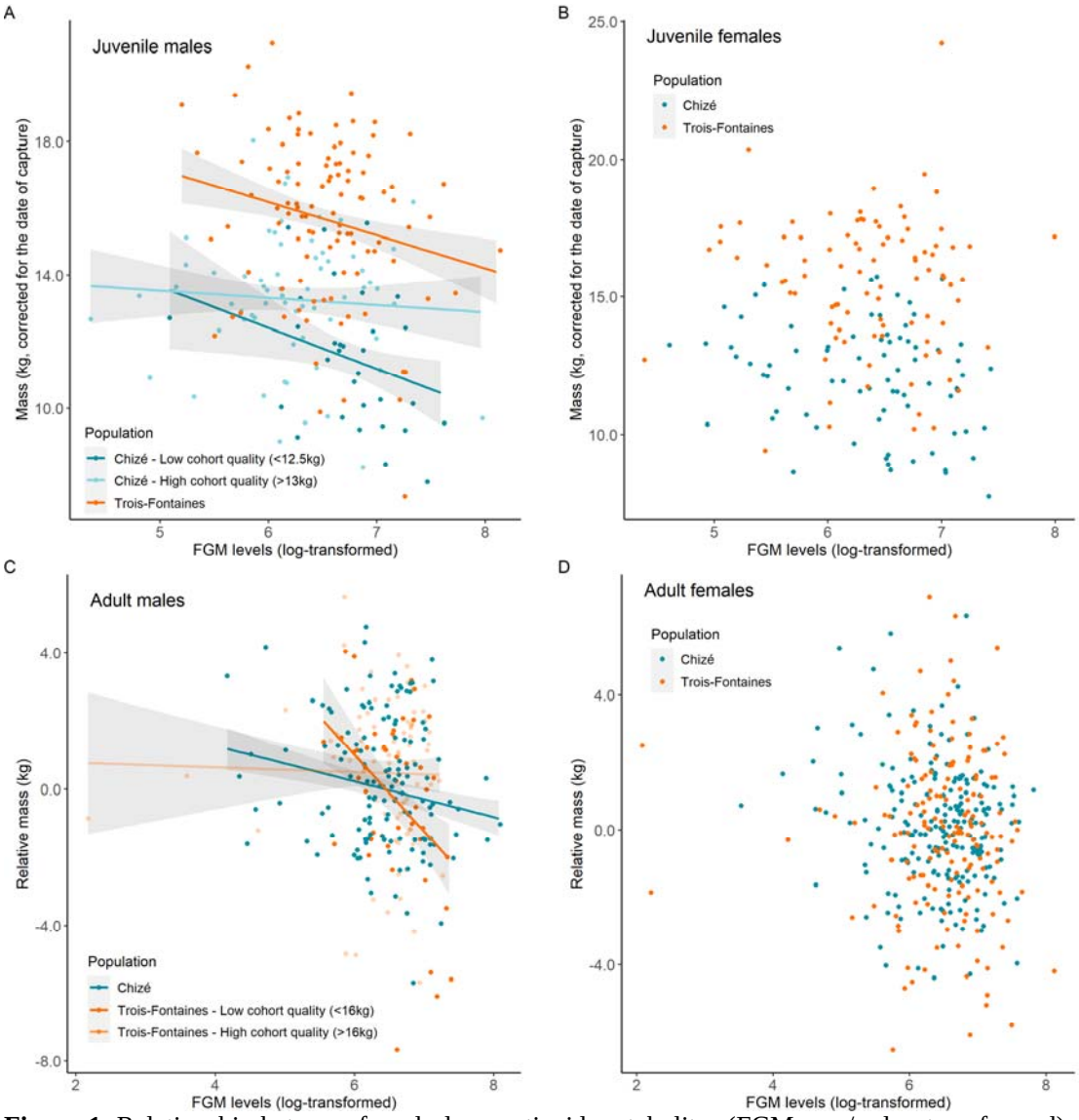

Figure 1. Relationship between faecal glucocorticoid metabolites (FGMs; ng/g, log-transformed) and body mass for (A) males captured as juveniles in the population of Chizé (CH, N = 96) according to cohort quality (dark blue: low cohort quality, light blue: high cohort quality), and in the population of Trois-Fontaines (TF, N = 103, orange line and points), and for (B) females captured as juveniles at CH (N = 78, blue points) and at TF (N = 98, orange points). Relationship between FGMs and individual body mass minus the average body mass of all individuals of the same age, population and sex for (C) males captured as adult at CH (N = 83 individuals, n = 136 observations, blue line and points) and at TF (N = 84 individuals, n = 137 observations) according to cohort quality (dark orange: low cohort quality, light orange: high cohort quality), and for (D) females captured as adults at CH (N = 104 individuals, n = 218 observations, blue points) and at TF (N = 106 individuals, n = 164 observations, orange points). Points are raw data and lines are predictions from the selected models with 85% confidence intervals.

Medium-term relationships between FGMs and change in body mass between two consecutive years

Growing individuals

The dataset included 99 individuals with FGMs measured as juveniles, and 67 individuals when including FGMs measured during the first and second years of life to calculate the mean value. Models included cohort as random effect.

Prime age adults

We obtained 131 observations on 90 individuals for which FGMs were measured during year t, and 91 observations on 71 individuals for which we had FGMs measured during years t and t+1 to calculate the mean value. However, we kept a single observation per individual since the inclusion of individual ID as a random effect created singularities. For individuals with several observations, we kept the one for which the individual's age was the closest to the mean age of all individuals with a unique observation according to sex and population. The final dataset comprised 72 individuals with FGMs measured in year t and 52 individuals for which we had measurements in years t and t+1.

In none cases (*i.e*. neither for growing nor adult individuals) was a relationship found between FGMs and change in relative body mass. Similarly, we found no evidence that mass measured during year t, cohort quality, population or sex were related to changes in relative body mass (Table 2, Table S5, Table S8).

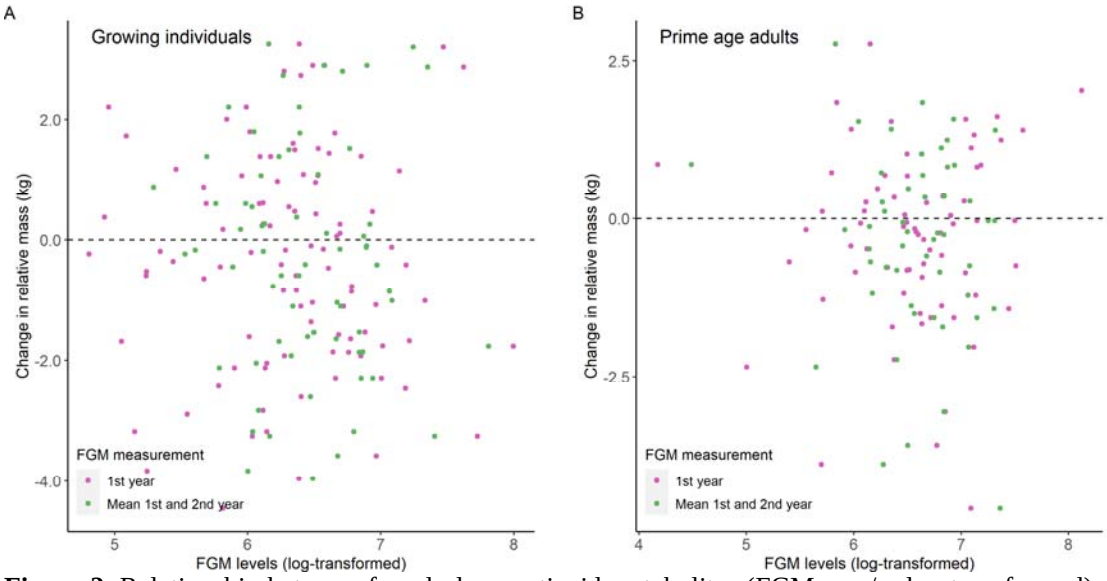

Figure 2. Relationship between faecal glucocorticoid metabolites (FGMs; ng/g, log-transformed) and change in relative body mass between two consecutive years for (A) growing individuals (between the first and second years of life), with FGMs either measured the first year of life (N = 99, pink points) or considered as the mean FGMs between the first and second years (N = 67, dot-green points), and (B) for prime age adults which had reach their asymptotic body mass (from 4 years old to 10 years old), with FGMs either measured in a given year *t* (N = 72, pink points) or considered as the mean FGM between year *t* and year *t+1* (N = 52, green points). Points are raw data.

Long-term relationships between FGMs during early-life and body mass later on

We used 345 observations on 159 individuals for which we measured FGMs as fawn and body mass as adult: 34 females (78 obs.) and 44 males (87 obs.) in CH, and 42 females (99 obs.) and 39 males (81 obs.) in TF. We only included individual ID as a random effect, as 'cohort' created singularities.

We found no evidence of a relationship between FGM and relative body mass in either subset. Only females of CH exhibited a positive association between cohort quality and relative body mass (β = 0.85 [0.4, 1.3], Table 3, Table S6, Table S8).

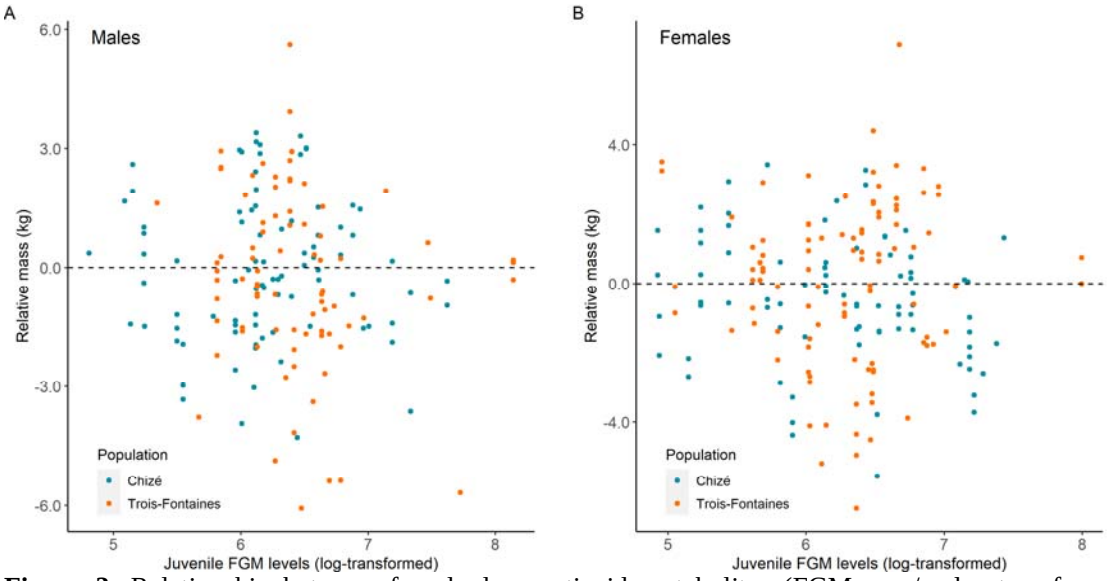

Figure 3. Relationship between faecal glucocorticoid metabolites (FGMs; ng/g, log-transformed) measured in juveniles and individual body mass minus the average body mass of all individuals of the same age, sex and population for (A) males from the population of Chizé (CH, N = 44 individuals, n = 87 observations, blue points) and of the population of Trois-Fontaines (TF, N = 39 individuals, n = 81 observations, orange points) captured at 2 years or older, and (B) females from CH (N = 34 individuals, n = 78 observations, blue points) and from TF (N = 42 individuals, n = 99 observations, orange points) captured at 2 years or older. Points are raw data.

Table 1. Linear and linear mixed effect models selected for the short-term relationship between body mass (or relative body mass for individuals aged 2 years or more) and concomitant faecal glucocorticoid metabolites (FGMs). Models were separated according to population (Chizé, CH *vs.* Trois-Fontaines, TF), sex, and age (individuals in their first year of life *vs.* individuals aged 2 years or more) and we accounted for cohort quality (Qcohort). Models were selected through model selection based on AICc and parameters estimated through model averaging. Parameter estimates are given with 85% confidence intervals (85%CI).

Response variable	Age	Subset	Model selected	Variables	Estimate [85%CI]	R^2 marginal	R^2 conditional
Body mass	**1st year of life**	**Males, CH**	Qcohort*log(FGM)	Intercept	12.76 [12.4, 13.1]	0.22	-
				Qcohort	0.91 [0.5, 1.4]		
				log(FGM)	-0.52 [-1.0, -0.04]		
				Qcohort:log(FGM)	0.82 [0.1, 1.5]		
		Females, CH	Qcohort	Intercept	12.13 [11.8, 12.4]	0.13	-
				Qcohort	0.83 [0.5, 1.2]		
		Males, TF	Qcohort + log(FGM)	Intercept	15.66 [15.4, 16.0]	0.25	-
				Qcohort	1.07 [0.8, 1.4]		
				log(FGM)	-0.99 [-1.6, -0.4]		
		Females, TF	Qcohort	Intercept	15.50 [15.2, 15.8]	0.17	-
				Qcohort	1.40 [0.9, 1.9]		
Relative body mass	**2nd year onwards**	**Males, CH**	log(FGM)	Intercept	0.02 [-0.3, 0.3]	0.03	0.75
				log(FGM)	-0.52 [-0.8, -0.3]		
		Females, CH	Qcohort	Intercept	0.11 [-0.1, 0.3]	0.05	0.61
				Qcohort	0.6 [0.3, 0.9]		
		Males, TF	Qcohort*log(FGM)	Intercept	0.01 [-0.4, 0.4]	0.11	0.85
				Qcohort	0.08 [-0.3, 0.5]		
				log(FGM)	-0.92 [-1.2, -0.6]		
				Qcohort:log(FGM)	1.60 [1.1, 2.1]		
		Females, TF	Constant	Intercept	-0.21 [-0.5, 0.1]	0.00	0.83

Table 2. Linear mixed effects models selected for the medium-term relationship between the change in relative body mass between two consecutive years and faecal glucocorticoid metabolites (FGMs) either measured in a given year or as the mean of FGMs measured in a given year and the following one. Models were separated according to age (growing individuals, *i.e.* between first and second years of life, *vs.* prime age adults having reached their asymptotic size, *i.e.* between 4 and 10 years old) and we accounted for cohort quality (Qcohort). Models were selected through model selection based on AICc and parameters estimated through model averaging. Parameter estimates are given with 85% confidence intervals (85%CI).

Response variable	Age	Subset	Model selected	Variables	Estimate [85%CI]	R^2 marginal	R^2 conditional
Change in relative body mass between two consecutive years	Growing individuals	FGM measured the 1st year	Constant	Intercept	-0.35 [-0.8, 0.1]	0.00	0.23
		Mean of FGMs measured the first and second year of life	Constant	Intercept	-0.37 [-0.9, 0.2]	0.00	0.29
	Prime age adults	FGM measured the year t	Constant	Intercept	-0.24 [-0.5, 0.04]	0.00	0.08
		Mean of FGMs measured the year t and year t+1	Constant	Intercept	-0.31 [-0.8, 0.1]	0.00	0.12

Table 3. Linear mixed effects models selected for the long-term relationship between adult relative body mass (from 2 years old onwards) and juvenile faecal glucocorticoid metabolites (FGMs). Models were separated according to population (Chizé, CH *vs.* Trois-Fontaines, TF) and sex and we accounted for cohort quality (Qcohort). Models were selected through model selection based on AICc and parameters estimated through model averaging. Parameter estimates are given with 85% confidence intervals (85%CI).

Response variable	Subset	Model selected	Variables	Estimate [85%CI]	R^2 marginal	R^2 conditional
Relative body mass	Males, CH	Constant	Intercept	-0.14 [-0.5, 0.2]	0.00	0.55
	Females, CH	Qcohort	Intercept Qcohort	-0.41 [-0.8, -0.01] 0.85 [0.4, 1.3]	0.11	0.72
	Males, TF	Constant	Intercept	-0.74 [-1.3, -0.2]	0.00	0.77
	Females, TF	Constant	Intercept	-0.15 [-0.7, 0.4]	0.00	0.76

Discussion

The relationship between GCs and fitness-related traits such as body mass is yet to be fully deciphered. Recent reviews indicate that studies in the wild have led to contrasting results by showing either negative, positive or no relationships between measures of stress and studied traits (Bonier et al. 2009, Crespi et al. 2013, Dantzer et al. 2014). A salient conclusion from these studies is that the relationship depends on an individual's ecological context and internal state. In the present study, the longitudinal monitoring of individual roe deer in two populations subjected to markedly different environmental contexts – one facing limiting resources and the other benefiting from higher availability and quality of resources – allowed us to analyse the relationship between baseline stress level and body mass, while accounting for ecological factors and internal factors such as sex and age. In the short-term analysis, we found clear evidence of a sex-specific negative relationship between baseline FGMs and body mass, an important driver of fitness in this species (Gaillard et al. 2000), in relation to population and environmental quality around birth.

In males of both populations, higher FGMs were related to lower body mass at all ages. However, this relationship was dampened, and even vanished when cohort quality increased for juveniles of the food-limited population (*i.e.* Chizé, CH) and adults of the less-food-limited one (*i.e.* Trois-Fontaines, TF). While we expected population differences in the relationship between FGMs and body mass (*i.e.* a stronger negative relationship in the more than in the less-food-limited population), relationships were rather modulated at a finer within-population scale according to yearly variations in cohort quality in two of the subsets. This is in line with the hypothesis that chronic stress levels may be harmful when resources are limited, due to the energy demand caused by stress, compared to when resources are abundant. Thus, higher food availability can offset the higher energy expenditure caused by an elevation of GC levels (Henderson et al., 2017). Also, a striking result of our analyses is

that FGMs are related to body mass in males but not in females. When investigating the consequences of high concentrations of GCs on a given trait, the question of whether or not the two sexes respond in the same way or not is rarely tackled. Most of the studies addressing this issue have focused on birds (*e.g.* Bonier et al., 2007; Schmidt et al., 2012; Spencer & Verhulst, 2008; Verhulst et al., 2006), and the few studies that considered mammals have been conducted on laboratory rodents. In these cases, the negative relationship between GCs and the trait of interest was found either in females (Schulz et al. 2011) or in males (Liu et al. 2006, Mueller and Bale 2007, Schulz et al. 2011, Dumeige et al. 2017). One plausible mechanism for such sex-specific differences in response to GCs could be that GCs bind to two types of receptors that lead to different physiological responses. At low to moderate circulating levels, GCs primarily bind to high-affinity mineralocorticoid receptors; but, as these become saturated, GCs then bind to low-affinity mineralocorticoid receptors, which explains the distinct GC effects at acute and baseline concentrations (Busch and Hayward 2009). Although we do not have information on sex-specific expression of high- *vs.* low-affinity mineralocorticoid receptors in the studied roe deer populations, this could potentially explain sex differences observed in the relation between FGMs and body mass (*e.g.* Dumeige et al., 2017 for an example of sex-specific effect of GCs due to difference in receptor expression in laboratory rats).

Although the roe deer is a weakly dimorphic and polygynous species (Andersen et al. 1998), differences in the relationships between FGMs and body mass between sexes is not surprising. In the two populations, similar high rates of early mortality produce divergent responses in both sexes (Garratt et al. 2015): females born in poor years display higher adult performance than those born in favourable years due to a strong viability selection that limits intra-clan competition, whereas males born in poor years live shorter than those born in good years, illustrating a silver spoon effect (*sensu* Grafen, 1988). This differential sex-specific

response to cohort quality could partly explain why we found evidence of relationships between FGMs and body mass only in males. Indeed, GCs mobilise stored energy to face adverse conditions (Sapolsky et al. 2000, Reeder and Kramer 2005). Thus, for individuals in poor body condition (here males), energy expenditure may exceed energy intake, with detrimental consequences on performance later in life (McEwen and Wingfield 2010) measured by body mass in the present study, unlike individuals in good condition (here females). Additionally, male and female roe deer display different life histories despite being weakly dimorphic in size (Andersen et al. 1998). While sexual size dimorphism is inexistent during early-life, males weigh on average 1 kg more than females at the onset of their first winter, meaning that the allocation of energy to growth is higher in males than in females (Hewison et al. 2011), leaving thereby less energy to be allocated to maintenance especially for individuals facing poor food conditions. Also, while female roe deer are income breeders relying on available resources concurrently to breeding without storing energy, males are partly capital breeders and store some fat (Hewison et al. 2011). By having a higher post-weaning growth rate and by relying more on a capital breeder tactic than females, and by having in addition to allocate to antler growth (only males possess antlers in roe deer), males with high FGM concentrations are unable to maintain their body mass, on the contrary to females or to males with lower FGM concentrations. Finally, it is possible to look at the difference between males and females for the relationships between FGMs and body mass the other way around: potentially, lighter males are more subject to environmental and intra-sexual pressures to access mating and defend good-quality territories. Thus, they may display higher levels of FGMs, compared to males of better condition, less impacted by (pre-) breeding. Indeed, it has been shown that body mass and antler length were under selection in males and predicted male breeding success (Vanpé et al., 2010; but note that female body mass is also under selective pressure, Gaillard et al., 2000).

FGMs have been previously used as proxies for the stress response in wild populations, but the results should be interpreted with caution. The reliability of FGM measurements can vary according to factors such as sex, reproductive status, season or diet (Palme 2019). As our captures all took place at the same period of the year, on identified and sexed roe deer, those sources of variations were mostly taken into account in our analyses. Nevertheless, FGMs do not fully reflect an individual's stress response because GCs only represent one part of the complex endocrine pathway involved in this response (MacDougall-Shackleton et al. 2019). Moreover, although GCs are often referred to as "stress hormones", at baseline levels, their primary role is to acquire, deposit and mobilise energy (Busch and Hayward 2009). Thus, unlike acute GC concentrations, baseline GCs do not only provide information on how an individual responds to stressors, but also on its physiology and activity (Reeder and Kramer 2005). Also, it has been largely demonstrated that the acute GC response tends to be attenuated in individuals repeatedly exposed to stressors (Goessling et al. 2015). However, baseline GC level can also, but not always, be lower in individuals chronically exposed to environmental stress, making difficult the interpretation of FGM levels in the wild, where we cannot be certain that low baseline GCs actually represent a non-stressed individual rather than an individual chronically exposed to stressors (Davis and Maney 2018).

In conclusion, we found that stress may have immediate adverse consequences on body mass. We also showed that males are more sensitive to variation in baseline FGMs than females. Finally, we highlighted that the extent to which stress levels correlated with body mass depends on the ecological context. Through this work, we therefore emphasise the need to account for both environmental and individual factors, including life-histories, to better capture the relationship between the stress response and fitness-related traits. To do so, it appears critical to have access to longitudinal data. Measuring proxies of stress together with

fitness-related traits throughout the life of individuals is likely to be the only way to properly refine our understanding of the implication of stress on fitness.

Conflict of interest

The authors declare having no conflict of interest.

Ethics

The research presented in this manuscript was done according to all institutional and/or national guidelines. For both populations (Trois-Fontaines and Chizé), 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).

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