



HAL
open science

Glucocorticoids negatively relate to body mass on the short-term in a free-ranging ungulate

Lucas D Lalande, Emmanuelle Gilot-Fromont, Jeffrey Carbillet, François Débias, Jeanne Duhayer, Jean-Michel Gaillard, Jean-françois Lemaître, Rupert Palme, Sylvia Pardonnet, Maryline Pellerin, et al.

► To cite this version:

Lucas D Lalande, Emmanuelle Gilot-Fromont, Jeffrey Carbillet, François Débias, Jeanne Duhayer, et al.. Glucocorticoids negatively relate to body mass on the short-term in a free-ranging ungulate. *Oikos*, 2023, 10.1111/oik.09769 . hal-04154267

HAL Id: hal-04154267

<https://cnrs.hal.science/hal-04154267>

Submitted on 7 Jul 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

Glucocorticoids negatively relate to body mass on the short-term in a free-ranging ungulate

Lucas D. Lalande¹, Emmanuelle Gilot-Fromont^{1,2}, Jeffrey Carbillet^{1,3}, François Débias¹, Jeanne Duhayer^{1,4}, Jean-Michel Gaillard¹, Jean-François Lemaître¹, Rupert Palme⁵, Sylvia Pardonnet^{1,6}, Maryline Pellerin⁷, Benjamin Rey¹, Pauline Vuarin¹

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 Exploitées, Châteauvillain, 52210, France

1 **Abstract**

2 Environmental fluctuations force animals to adjust glucocorticoids (GCs) secretion and
3 release to current conditions. GCs are a widely used proxy of an individual stress level. While
4 short-term elevation in GCs is arguably beneficial for fitness components, previous studies
5 have documented that the relationship between long-term baseline GCs elevation and fitness
6 components can vary according to ecological and individual factors and according to the life-
7 history of the species studied. Using longitudinal data on roe deer (*Capreolus capreolus*) from
8 two populations facing markedly different environmental contexts, we tested whether baseline
9 GC levels negatively correlate with body mass – a trait positively associated with
10 demographic individual performance – on the short- to long-term. In support, higher baseline
11 GC concentrations were associated to lighter body mass, both measured during the same
12 capture event, in adults of both populations. Overall, we showed that despite the marked
13 environmental and demographic differences between populations and despite the between-sex
14 differences in life history (*i.e.* reproductive tactics), the relationship between body mass and
15 GCs is consistent across environmental contexts, but might differ according to the life history
16 stage of an individual. This work opens promising perspectives to further explore the
17 relationship between GC and fitness-related traits according to life history stages in free-
18 ranging mammals across seasonal and environmental contexts. The timing and context-
19 dependence of GC levels highlight the complexity of studying stress responses in the wild.

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

22 **Introduction**

23 Throughout their life, individuals have to adjust their morphology, physiology and/or
24 behaviour to cope with environmental variation. Part of this variation is predictable as
25 individuals can rely on environmental cues (*e.g.* photoperiod or temperature at the daily or
26 seasonal scales) to anticipate future conditions (Wingfield 2003, 2008). Whereas predictable
27 variation is not considered as stressful *per se* (*i.e.* eliciting a stress response), an unpredictable
28 perturbation can disrupt life cycles and trigger a stress response through the activation of the
29 hypothalamic-pituitary-adrenal (HPA) axis and the release of glucocorticoids (GCs),
30 departing them from the baseline level (Reeder and Kramer 2005). The primary role of these
31 hormones (namely cortisol and corticosterone) is to maintain an organism's energy balance
32 according to its requirements in its current environment (Wingfield 2013, Hau et al. 2016),
33 meaning that GCs promote allostasis (*i.e.* achieving stability through change) by ensuring
34 energy homeostasis despite predictable and unpredictable environmental and life history
35 variation (McEwen and Wingfield 2003, 2010, Romero et al. 2009). On the short-term, an
36 elevation of GC concentration in an individual facing a challenging situation is beneficial
37 because it promotes processes enhancing survival through reallocation of stored energy from
38 non-immediately essential functions (*e.g.* growth, reproduction) towards cardiovascular
39 functions or locomotion and foraging activities (Sapolsky et al. 2000). After a temporary
40 perturbation, the GC concentration often quickly returns to the baseline level (Reeder and
41 Kramer 2005). However, baseline GC concentration may remain elevated on the long-term
42 (*i.e.* days to weeks) as a result from exposure to repeated or long-lasting perturbations such as
43 prolonged inclement weather or food shortage (McEwen and Wingfield 2010, Hau et al.
44 2016). Such elevated GC concentration in the long-term can have adverse consequences on
45 individual performance through disruption of the immune function (Dhabhar 2014), inhibition
46 of growth, or decreased body condition (Reeder and Kramer 2005), with an intensity

47 depending on the species (Boonstra 2013). Indeed, long-term GC elevation can cause
48 ‘allostatic overload’ (*i.e.* when the energy intake is lower than the energy required to support
49 daily and seasonal activities and to cope with unpredictable perturbations, McEwen and
50 Wingfield 2010). Although variations in GC concentration does not reflect only stress
51 (MacDougall-Shackleton et al. 2019), GC levels are a widely used proxy for evaluating an
52 individual physiological stress response (Palme 2019).

53 While many studies analysed the effect of an increase of GC beyond the baseline level (*i.e.*
54 acute stress-induced GC concentration) on individual performance, fewer have considered
55 how GCs at baseline concentration (*i.e.* homeostatic levels of hormones) affect the
56 performance of animals in the wild. Results from these rare studies remain equivocal
57 (Rogovin et al. 2003, 2008, Altmann et al. 2004, Ethan Pride 2005, Pauli and Buskirk 2007,
58 Cabezas et al. 2007, Pedersen and Greives 2008, Pinho et al. 2019), which could be explained
59 by the complex influence of environmental conditions (Henderson et al. 2017). When
60 resources are limited, increased energy demands can be detrimental by resulting in high levels
61 of GC and allostatic overload. Nevertheless, this detrimental effect may not be observed when
62 resources are abundant, as high energy input can contribute reducing allostatic load (McEwen
63 and Wingfield 2003, 2010, Romero et al. 2009). Food availability (*i.e.* energy availability) or
64 behavioural flexibility stimulating foraging activity can thus compensate for elevated GC
65 levels and associated higher energy requirements (Henderson et al. 2017). Animals inhabiting
66 suboptimal habitats (*e.g.* exposed to human disturbance, predation, intra- or interspecific
67 competition or pathogens) experience continuous stressful conditions and generally show a
68 higher GC concentration compared to conspecifics inhabiting optimal areas (Dantzer et al.
69 2013, 2014, Formenti et al. 2018, Boudreau et al. 2019, Dulude-de Broin et al. 2020, Carbillet
70 et al. 2020).

71 Additionally, there is evidence that the direction of the relationship between GCs and
72 performance can also depend on individual attributes, such as body condition, sex or
73 reproductive status and reproductive tactics (Tilbrook et al. 2000, Ricklefs and Wikelski 2002,
74 Wey et al. 2015, Blumstein et al. 2016, Vuarin et al. 2019). Under high energy demands
75 triggered by elevated GC concentration, high quality individuals are more likely to prevent
76 themselves from reaching allostatic overload and may perform better than poor quality ones.
77 In African striped mice (*Rhabdomys pumilio*), elevated baseline GC concentration was related
78 to the selective disappearance of light individuals (Vuarin et al. 2019). Since the relationship
79 between GCs and performance is complex and involves individual attributes and
80 environmental context, both sources of variation have to be investigated to disentangle their
81 respective roles (Crespi et al. 2013, Dantzer et al. 2014).

82 Focusing on body mass provides a relevant approach to investigate the detrimental effects of
83 prolonged exposure to a high GC concentration. Indeed, body mass is often positively linked
84 to fitness components (*e.g.* Gaillard et al., 2000; Ronget et al., 2018) and is a trait easily
85 measured in the field that constitutes a reliable proxy of body condition in many species,
86 especially income breeders (Hewison et al. 1996, Andersen et al. 1998). High levels of GCs
87 are known to have a crucial role on body mass by increasing protein and amino-acid
88 catabolism and mobilising lipids (promoting gluconeogenesis), consequently decreasing body
89 mass (Boonstra et al. 1998, Dallman et al. 1999, Hodges et al. 2006, Rabasa and Dickson
90 2016).

91 However, the relationship between baseline GC concentration and body mass is complex.
92 Indeed, within seasonal baseline levels, GCs actually result in increased feeding behaviours
93 potentially promoting fat storing and body mass gain, as opposed to the previously-mentioned
94 GC actions on protein and amino-acid catabolism and lipid mobilisation (Landys et al. 2006).
95 Case studies have shown that the relationship between baseline GCs and body mass or

96 condition can be positive, negative or null (*e.g.* George et al. 2014, Wey et al. 2015, Hennin et
97 al. 2016, Boudreau et al. 2019). For instance, low body mass and poor body condition were
98 associated with higher baseline cortisol concentrations in Eurasian badgers (*Meles meles*,
99 George et al., 2014). On the other hand, experimental increase in GC concentration through
100 predation risk manipulation resulted in no changes in body condition in snowshoe hares
101 (*Lepus americanus*, Boudreau et al., 2019). Thus, more exploratory research are needed in
102 natural settings to better understand which factors can modulate this relationship.

103 In this exploratory study, we aimed to contribute to a better understanding of how high
104 baseline GC concentration relates to body mass in roe deer (*Capreolus capreolus*), an income
105 breeder for which body mass is a good proxy for body condition (Hewison et al. 1996,
106 Andersen et al. 2000, Pettorelli et al. 2006). We took advantage of the detailed and intensive
107 monitoring data collected through capture-mark-recapture for more than a decade at the
108 individual level in two populations subject to markedly different ecological contexts (*i.e.* one
109 inhabiting a good quality habitat and one population being strongly food-limited; Pettorelli et
110 al., 2006). To avoid measuring the capture-induced GC response (Romero & Reed, 2005),
111 longer-term, indirect measures of GC concentration can be obtained from biological matrices
112 other than blood (Sheriff et al. 2011). Indeed, blood GC concentration is a point in time
113 measure and circulating GCs concentration typically increases drastically within 3 minutes
114 following an individual's capture (Sapolsky et al. 2000, Romero and Reed 2005), which
115 makes it difficult to obtain reliable measures of the HPA baseline activity in free-ranging
116 animals (but see Sheriff et al. 2011, Lavergne et al. 2021). In this context, levels of faecal
117 glucocorticoid metabolites (FGMs) are particularly relevant as they represent an integrative
118 measure of GC concentration several hours before the capture event (*i.e.* baseline stress;
119 Palme, 2019). Thus, we measured FGMs, as arguably representative of baseline

120 adrenocortical activity over a few hours, with a time delay of 12h on average in roe deer
121 (ranging from 6 to 23 hours, Dehnhard et al. 2001).

122 As chronic stress can have both immediate and long-term consequences on fitness
123 components (Monaghan and Hausmann 2015), we tested the immediate relationship between
124 concomitant body mass and FGMs (*i.e.* short-term relationship), the relationship between
125 FGMs in a given year and the change of body mass between two consecutive years (*i.e.*
126 medium-term relationship) and the relationship between FGM measured on juveniles (*i.e.*
127 individuals in their first year of life) and body mass during the prime-age and senescent life
128 stages (*i.e.* long-term relationship). We first analysed the relationship between FGMs and
129 body mass measured at the same capture event. We expected individuals with higher FGM
130 concentration to be lighter than individuals with low FGM concentration. As roe deer are
131 income breeders that do not store fat (Hewison et al. 1996, Andersen et al. 1998), we expected
132 the catabolic actions of GCs to directly impact body mass and condition and to overcome the
133 effects of increased feeding behaviours promoted by GCs. Then, since chronically elevated
134 FGMs are expected to be deleterious on the medium to long-term, we tested whether FGMs
135 measured at a given capture influenced body mass changes across lifespan. Thus, we first
136 assessed the relationship between FGMs measured in a given year and a given body mass
137 change between two consecutive years, separately for growing individuals and prime-aged
138 adults having reached their full mass (*i.e.* between 4 and 10 years old; Douhard et al., 2017).
139 We expected that higher FGM concentration should result in a smaller mass gain for growing
140 individuals, and in a decrease in body mass for prime-aged adults, between two consecutive
141 years, as chronic stress can be linked to inhibited growth or decreased body condition (Reeder
142 and Kramer 2005). Finally, we tested for the effect of the stress experienced during the first
143 year of life on the individual body mass relative to the population and sex at a given age, from
144 the second year of life onwards. We predicted that individuals with higher FGMs during the

145 first year of life should be lighter later in life, as late-life performance in roe deer is affected
146 by early-life environmental conditions (Gaillard et al., 2003). Lastly, in all analyses we
147 expected the negative relationship between FGMs and body mass to be steeper in the food-
148 limited population due to higher allostatic load (McEwen and Wingfield 2003, Henderson et
149 al. 2017), and we expected sexes to respond differently to higher FGMs levels due to the
150 different reproductive tactics of males and females (Ricklefs and Wikelski 2002).

151 **Materials and Method**

152 **Study population and sample collection**

153 We studied roe deer in two populations inhabiting closed forests at Trois-Fontaines (TF –
154 1360 ha) in north-eastern France (48°43'N, 4°55'E) and at Chizé (CH – 2614 ha) in western
155 France (46°05'N, 0°25'W). Roe deer are medium-sized ungulates, weighing around 25 kg and
156 common in lowland woodlands throughout most of Europe. Roe deer display weak sexual
157 selection, with adult males only 10% heavier than females and party size less than three
158 females per buck. They are income breeders (Andersen et al. 2000), and to meet the markedly
159 increased energy needs during the late gestation and early lactation periods, adult females rely
160 on food resources rather than body reserves. Both sexes allocate high energy expenditure to
161 reproduction. Females produce twins every year from 2 to 12 years old (Andersen et al.
162 1998), and males allocate heavily in territory defence for 5-6 months during the rut period
163 (Johansson 1996). The TF population is characterised by a homogeneous habitat of good
164 quality on a broad spatial scale, with high forest productivity due to rich soils. On the other
165 hand, the CH population inhabits a less suitable heterogeneous habitat comprising three types
166 of varying quality (Pettorelli et al. 2001), with low forest productivity due to poor soils and
167 frequent summer droughts (Pettorelli et al. 2006). In both study sites, large carnivores are
168 absent, but hunting occurs occasionally to control population growth. Since 1975 in TF and

169 1977 in CH, a Capture-Mark-Recapture (CMR) program has taken place every winter, and
170 CMR analyses show that both populations were quite below carrying capacity during the
171 present study period (2010-2021 in TF, 2013-2021 in CH, unpublished data). Captures take
172 place during 10-12 days each year, which are spread across December (at TF) or January (at
173 CH) and March (Gaillard et al. 1993) and consists of drive-netting captures with 30-100
174 beaters pushing individuals towards nets surrounding specific areas of the forests. Given that
175 captures took place each year over 3 months, we might expect endocrine activity to vary
176 throughout the capture season according to environmental conditions (*i.e.* populations) and
177 sex (Dantzer et al. 2010, Sheriff et al. 2012). Therefore, we tested whether FGM levels varied
178 as a function of the Julian date, population and sex and found that FGMs increased throughout
179 the season in a population-specific manner (Supporting Information SI). Thus, all FGM
180 measurements were standardised for the median Julian date of capture (9th of February)
181 specifically for each population. Successive capture events within a capture season may also
182 have consequences on FGM measurements during the following captures. However, most
183 capture days were more than 48 hours apart while in roe deer, FGMs peak from 6 to 23 hours
184 after an ATCH challenge and return to baseline levels between 28 and 31 hours after
185 treatment (Dehnhard et al. 2001). In some cases, captures took place during two consecutive
186 days, but were then conducted on opposite areas of the forest to minimise disturbances.
187 Likewise, morning and afternoon captures of a given day took place in different areas within
188 both forests. We thus considered that FGM levels were not influenced by previous captures.
189 Concerning the potential impact of the capture event itself, since roe deer were captured by
190 drive-netting and most animal manipulations occurred between 1 and 4 hours after capture,
191 we tested for a possible impact of this delay on FGM levels. We did not detect any increase or
192 decrease in FGMs (log-transformed) along with the time between capture and sampling
193 (linear regression accounting for repeated measurements of a given individual: $0.006 \text{ hour}^{-1} \pm$

194 0.01 SE, $t = 0.44$, $p = 0.7$), even when the delay was $> 6h$ (mean FGMs 6h onwards after
195 capture compared to mean FGMs measured within 6h following capture, accounting for
196 repeated measurement of a given individual, -0.06 ± 0.06 SE, $t = -1.05$, $p = 0.3$) (Dehnhard et
197 al. 2001). Individuals of known age (*i.e.* captured within their first year of life) were weighed,
198 and faecal matter has been collected since 2010. During the capture period, diet is similar and
199 mostly composed of brambles (*Rubus* sp.) and ivy (*Hedera helix*) in the two deciduous forests
200 (Tixier and Duncan 1996), so FGM measurements between populations should not be biased
201 according to diet composition. During this period, females can be gestating, and differences in
202 female reproductive status could result in FGM variability (Brunton et al. 2008, Dantzer et al.
203 2010). Nevertheless, we did not account for females' reproductive status in our models, since
204 i) we have information about reproductive status (*i.e.* pregnant or not and number of foetuses)
205 only at CH where ultrasounds are performed on captured females, ii) most of them (*i.e.* 92 %)
206 were gestating at that time and iii) due to the delayed embryonic implantation (Aitken 1974),
207 gestation is at a very early stage during the capture season. Body mass measured on juveniles
208 (*i.e.* at about 8 months of age) depends on the date of capture. Juveniles gained on average 12
209 g/day and 24 g/day in CH and TF, respectively, during the capture period (Douhard et al.
210 2017). Therefore, we standardised juvenile body mass with a linear regression, using the
211 above-mentioned Julian date-body mass relationship. Thus, we computed the individual body
212 mass expected on the 9th of February, the median date of captures at CH and TF. In these two
213 populations, cohort quality is reliably measured by the cohort-specific average juvenile mass
214 corrected for the Julian date of capture (Gaillard et al. 1996). This proxy of environmental
215 quality from the birth of an individual (typically in May) to its capture as juvenile in winter
216 was obtained for all years, and will be referred to as 'cohort quality' hereafter.

217 **Faecal glucocorticoid metabolites (FGMs)**

218 Baseline adrenocortical activity was estimated through FGMs (Palme 2019). We collected
219 faecal matter rectally at capture from 2010 to 2021. Faeces were frozen at -20 °C within 24
220 hours prior to 2013 in CH and 2017 in TF, and immediately frozen at -80 °C after collection
221 since then. The time between faecal sampling and freezing, as well as freezing temperature,
222 may impact FGM values, with longer delays and higher temperature likely to result in lower
223 FGM levels due to bacterial activity (Lexen et al. 2008, Hadinger et al. 2015, Carbillet et al.
224 2023b). In CH, the first FGM values available in our dataset are post-2013, so all samples
225 were immediately frozen at -80 °C. However, in TF, FGM values are effectively higher when
226 samples were immediately frozen (0.43 ± 0.06 SE, $t = 7.62$, $p < 0.0001$). This is accounted for
227 in our models by adding the year of capture as a random effect. Extraction of FGM followed a
228 methanol-based procedure and the analysis was performed using a group-specific 11-
229 oxoetiocholanolone enzyme immunoassay (EIA), a method previously described in details
230 (Möstl et al. 2002) and validated for roe deer (Zbyryt et al. 2018). In brief, 0.5 g (± 0.005) of
231 faeces were vortexed in 5 mL of 80% methanol before being centrifuged for 15 minutes at
232 2500 g (Palme et al. 2013). The amount of FGM was determined in an aliquot of the
233 supernatant diluted 10 times in assay buffer. Measurements were done in duplicate with intra-
234 and inter-assay coefficients lower than 10% and 15%, respectively. FGMs are expressed as
235 nanograms per grams of wet faeces (ng/g). The data were then log-transformed for the
236 statistical analyses (henceforth called FGMs).

237 **Statistical analyses**

238 All analyses were performed using R version 4.2.2 (R Core Team 2022). Two raw FGM
239 measures were unusually high: 5192 and 6194 ng/g, for a female in CH aged 10, and a female
240 in TF aged 1, respectively (see SI). Results exclude these extreme values (analyses including

241 them are reported in SI), but we specify whether adding them yielded different conclusions or
242 not.

243 *FGM repeatability*

244 Individual FGM repeatability was calculated for all individuals, and separately for each
245 population, using the ‘rptR’ package (Stoffel et al. 2017). Repeatability analysis included
246 individuals sampled only once to improve estimates of the within-individual variance (Martin
247 et al. 2011). Within-individual FGM repeatability was detectable but weak in both CH ($r =$
248 0.14 , 95% CI = $[0.03, 0.26]$) and TF ($r = 0.15$ $[0.01, 0.29]$).

249 *Model structure*

250 We tested the hypothesis that body mass is related to FGM levels, and that this relationship
251 may depend on individual (*i.e.* sex) and environmental (*i.e.* population and condition at birth)
252 characteristics, using linear mixed effect models (LMMs) with a normal error distribution. All
253 continuous covariates were mean-centred so that the intercept is the relative individual body
254 mass for the mean cohort quality and/or mean FGMs. Visual inspection of model residuals
255 confirmed that they fulfilled the assumptions of Gaussian distribution and homoscedasticity.

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

257 We first assessed the relationship between FGMs and body mass measured the same year (*i.e.*
258 at the same capture) to test the hypothesis that higher baseline FGMs result in short-term
259 adverse consequences on body mass. Individuals in their first year of life (*i.e.* juveniles) were
260 analysed separately from individuals in their second year of life onwards, because juveniles
261 have to allocate to growth and are much more susceptible to any environmental harshness
262 than adults, making the first year of life is the critical period of roe deer population dynamics
263 (Hamel et al. 2009, Gaillard et al. 2013). In addition, metabolic rate is generally higher in
264 juveniles than in adults due to the costs of growth (Glazier 2005) and metabolic rates can alter

265 hormones metabolization and excretion, making it difficult to compare juvenile and adult
266 FGM concentrations (Goymann 2012). Since juveniles are not yet reproductively active, they
267 also likely display different endocrine profiles than adults (Dantzer et al. 2010). Finally, adult
268 roe deer habituate faster than juveniles to stress, which can in turn affect the relationship
269 between FGM and fitness-related trait (Bonnot et al. 2018). Body mass varies with age, and at
270 a given age, varies between sexes and according to environmental conditions at birth (*i.e.*
271 cohort effects, Hamel et al. 2016). We thus tested the relationship between FGMs measured in
272 a given year and individual body mass relative to the average body mass of all individuals of
273 the same age, population and sex, considering only ages for which we had data from at least 3
274 individuals. Therefore, the average body mass was calculated up to 10 and 15 years old in
275 males and females at CH, respectively, and up to 12 and 13 years old in males and females at
276 TF, respectively. For juveniles, we analysed the relationship between FGMs and body mass
277 measured the same year on 368 juveniles (78 females and 96 males in CH, 91 females and
278 103 males in TF). The response variable was the mass corrected for the date of capture (see
279 above) and fixed explanatory variables included FGMs (corrected for the date of capture and
280 the population), cohort quality, population, sex and the two-way interactions between FGMs
281 and the other covariables. Cohort quality was expressed as a relative cohort quality (*i.e.* the
282 difference between mean cohort quality in each population and an individual cohort quality),
283 so there is no redundancy with the population variable. The year of birth of the individuals
284 (*i.e.* cohort) was included as a random effect. For individuals aged 2 years or older, the dataset
285 included 655 observations on 377 individuals: 104 females (218 observations) and 83 males
286 (136 obs.) in CH, and 106 females (164 obs.) and 84 males (137 obs.) in TF. The response
287 variable used to test for the FGMs-mass relationship was the individual body mass minus the
288 average mass of roe deer of the same population, same sex and same age, regardless of their
289 year of capture (hereafter 'relative body mass'). Fixed effects included continuous variation in

290 FGMs, relative cohort quality, population, sex and the two-way interactions between FGMs
291 and other covariables. Random effects of the cohort and of the year of capture were also
292 included. Random effect of the individual identity (ID) was also included to account for
293 repeated measurements on the same individuals.

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

296 Baseline FGMs can reflect medium-term consequences of GCs on body mass. The
297 relationship between FGMs and the change of body mass between two consecutive years was
298 analysed separately for early-growing individuals (*i.e.* between age 1 and 2), late-growing
299 individuals (*i.e.* between the second year of life and adulthood at 4 years old, Hewison et al.
300 2011) and for prime-aged adults which had reached their full body mass (*i.e.* from 4 to 10
301 years old, Hewison et al., 2011). The response variable was the change in relative body mass.
302 Briefly, the change in relative mass expresses the change in body mass of a given individual
303 between two ages in relation to the change in body mass of all individuals of the same sex and
304 population between the same ages. The relative mass was calculated as the difference between
305 the mass of an individual at age x , and the mean mass of all individuals of age t of the same
306 sex and the same population. The change in relative body mass was calculated as the
307 difference between the relative mass at age $t + 1$ and the relative mass at age t . Fixed effects
308 included relative cohort quality, population, sex, FGMs (either measured at age t or
309 considered as the average of the FGM values measured at age t and age $t + 1$), body mass at
310 age t (*i.e.* initial body mass) and all two-way interactions between FGMs and the other
311 covariables. Random effect of the cohort was included, and for late-growing and prime-aged
312 individuals, random effects of the year of capture and individual ID were also included. For
313 growing individuals, the dataset included 99 individuals with FGMs measured as juveniles,
314 and 67 individuals when including FGMs measured during the first and second years of life to

315 calculate the mean value. For both late-growing individuals and adults, we kept a single
316 observation per individual since the inclusion of individual ID as a random effect created
317 singularities. For individuals with several observations, we kept the one for which the
318 individual's age was the closest to the mean age of all individuals with a unique observation
319 according to sex and population, among observations with complete data. The final dataset
320 comprised 85 individuals in their late-growth period and 90 prime-aged adults with FGMs
321 measured at age t , and 63 late-growing individuals and 71 prime-aged adults for which we
322 had measurements at age t and $t+1$.

323 *Long-term relationships between FGMs during early life and body mass later in life*

324 As elevated baseline FGMs are expected to have negative effects on body mass on the long-
325 term, and as environmental conditions during the first year of life have carry-over effects on
326 performance later in life in roe deer (Gaillard et al. 2003), we tested whether FGMs during
327 development are associated with adult body mass. Only individuals for which we measured
328 FGMs as juvenile and body mass beyond the second year of life were analysed. We used 345
329 observations on 159 individuals for which we measured FGMs as juvenile and body mass as
330 adult: 34 females (78 obs.) and 44 males (87 obs.) in CH, and 42 females (99 obs.) and 39
331 males (81 obs.) in TF. The response variable was the relative individual body mass as defined
332 above. Fixed effects included FGMs measured when juvenile, relative cohort quality,
333 population, sex and the two-way interactions between FGMs and the other covariables.
334 Random effects of the cohort and the year of capture were included, as well as individual ID
335 to account for repeated measurements on the same individuals.

336 *Model selection*

337 Final models were selected based on the second order Akaike Information Criterion (AICc,
338 *i.e.* Akaike Information Criterion corrected for small sample sizes). We compared all sub-

339 models included in the full model described above and for each model AICc scores were
340 computed with the “*MuMIn*” package (v. 1.47.5, Bartoń 2023). We retained the best-fitting
341 model as the one with the lowest AICc score (Burnham and Anderson 2002), or the simplest
342 model (*i.e.* with the lowest number of parameters) within the set of models within 7 Δ AICc.
343 Indeed, models within 7 Δ AICc are plausible models, become increasingly equivocal up to 14
344 Δ AICc, and implausible afterwards (Burnham et al. 2011). For each variable we estimated its
345 effect size (β) with 95% confidence intervals (95% CI) and calculated marginal and
346 conditional R^2 . We provide full model selection tables in SI.

347 **Results**

348 FGM concentrations ranged from 8 to 3428 ng/g with a median value of 689 ng/g. The
349 median FGMs was 674 ng/g (range: 34-3275 ng/g) in CH, and 715 ng/g (range: 8-3428 ng/g)
350 in TF.

351

352 **Short-term relationships between FGMs and body mass measured at the same capture** 353 **event**

354 *Juveniles*

355 The retained model highlighted the expected positive relationship between cohort quality and
356 body mass ($\beta_{\text{Cohort quality}} = 1.08 [0.84, 1.32]$, Table 1, SI), but no relationship between FGMs
357 and body mass could be evidenced (Figure 1(a), Table 1, SI). Results were similar when
358 including female of TF with a high FGM value (SI). Note that since the random effect of the
359 cohort created singularities, it was removed and models therefore consisted of linear models.

360 *Adults*

361 We found support for a short-term negative relationship between individual relative body
362 mass and FGMs in adults ($\beta_{\text{FGM}} = -0.32 [-0.46, -0.18]$, Figure 1(b), Table 1, SI). Results were

363 similar when including the high FGM value measured on a female of CH (SI). Since the
364 random effect of the cohort created singularities, the models only included individual ID and
365 year of capture as random effects.

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

368 *Early-growing individuals*

369 We did not find any evidence for a relationship between FGMs, either measured in juveniles
370 or considered as the mean FGM value between the first and second years of life, and the
371 change in relative body mass for growing individuals (Figure 2(a), Table 1, SI). Results were
372 similar when including the female of CH with the highest FGM value (SI). All models
373 included cohort as random effect.

374 *Late-growing individuals*

375 We found a negative relationship between body mass gain and initial mass ($\beta_{\text{mass}} = -0.15$ [-
376 0.25, -0.05], Table 1, SI) for the dataset accounting for FGMs measured in juveniles. With the
377 dataset including the mean FGM value between FGMs measured at age t and age $t+1$, we also
378 found a negative relationship between late growth and body mass measured at age t ($\beta_{\text{mass}} = -$
379 0.17 [-0.27, -0.07], Table 1, SI). However, in both cases, we found no support for a
380 relationship between FGMs and change in relative body mass (Figure 2(b), Table 1, SI).
381 Models resulted in singularities when the random effect of the cohort was included so that
382 only the year of capture was included as a random effect in the models.

383 *Prime-aged adults*

384 In no cases (*i.e.* neither when accounting for FGM measured at age t or for the mean FGM
385 value between age t and age $t+1$) was a relationship found between FGMs and change in

386 relative body mass (Figure 2(c), Table 1, SI). Similarly, we found no evidence that mass
387 measured at age t , cohort quality, population or sex were related to changes in relative body
388 mass (Table 1, SI). Models resulted in singularities when the random effect of the cohort was
389 included, thus, only the random effect of the year of capture was included in the models.

390 **Long-term relationships between FGMs during early-life and body mass later in life**

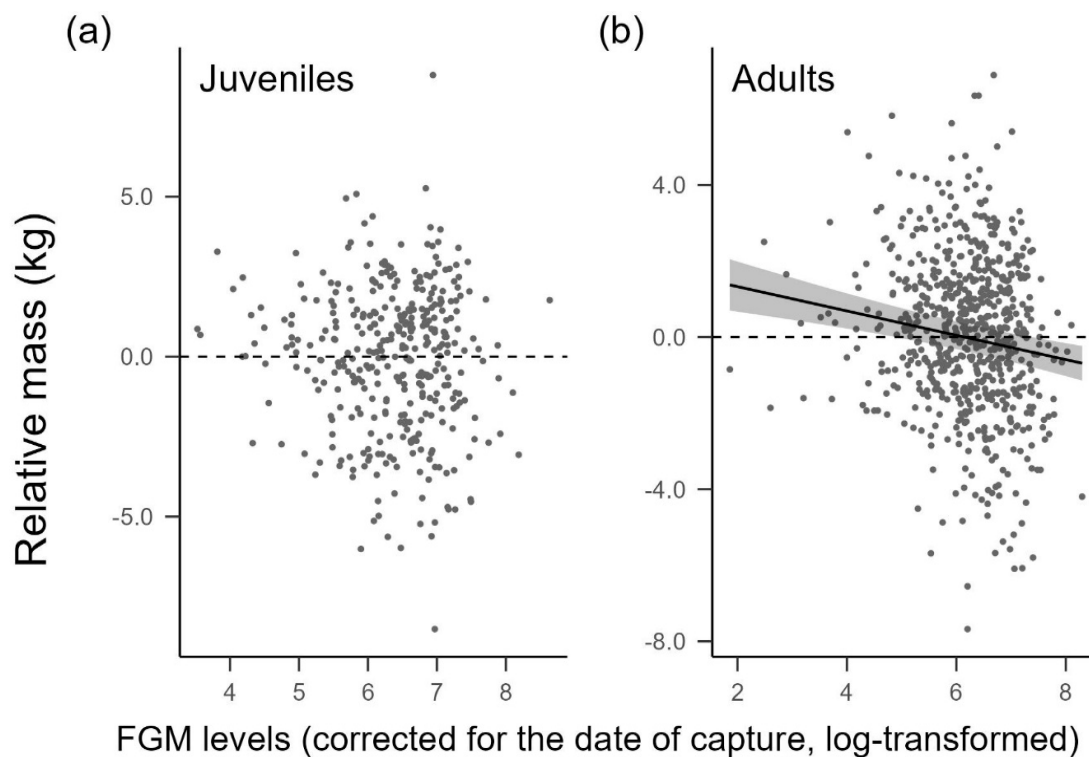
391 We found no evidence for a relationship between FGM measured in juveniles, cohort quality,
392 population or sex, and adult relative body mass (Figure 3, Table 1, SI). Results were similar
393 when including the three observations of the adult female of CH with the highest FGM value
394 measured as juvenile (SI). We only included individual ID and year of capture as random
395 effects, because including the cohort created singularities.

396 **Table 1.** Linear and linear mixed effect models selected for the short-, medium- and
 397 long-term relationships between relative body mass and faecal glucocorticoid
 398 metabolites (FGMs). Models accounted for sex, population and for relative cohort
 399 quality (Qcohort, the difference between the mean cohort quality in each population
 400 and an individual cohort quality). Models were selected through model selection
 401 based on AICc. 95%CI: 95% confidence intervals, V: variance, SD: standard-
 402 deviation.

SHORT-TERM								
Juveniles			Adults					
Random effects	V	SD	Random effects	V	SD			
			Individual ID	3.45	1.86			
			Year of capture	0.29	0.54			
Fixed effects	Estimate	95%CI	Fixed effects	Estimate	95%CI			
Intercept	-0.06	[-0.28, 0.16]	Intercept	-0.02	[-0.39, 0.35]			
Qcohort	1.08	[0.84, 1.32]	FGM	-0.32	[-0.46, -0.18]			
Marginal R ²	0.18		Marginal R ²	0.02				
Conditional R ²			Conditional R ²	0.81				
MEDIUM-TERM								
FGM measured at age <i>t</i>								
Early-growth			Late-growth			Prime-aged		
Random effects	V	SD	Random effects	V	SD	Random effects	V	SD
Cohort	0.65	0.81	Year of capture	0.41	0.64	Year of capture	0.24	0.49
Fixed effects	Estimate	95%CI	Fixed effects	Estimate	95%CI	Fixed effects	Estimate	95%CI
Intercept	-0.35	[-0.92, 0.22]	Intercept	-0.55	[-1.02, -0.08]	Intercept	-0.19	[-0.60, 0.22]
			Initial mass	-0.15	[-0.25, -0.05]			
Marginal R ²	-		Marginal R ²	0.09		Marginal R ²	-	
Conditional R ²	0.21		Conditional R ²	0.32		Conditional R ²	0.15	
Mean FGM (FGM _{<i>t</i>} and FGM _{<i>t+1</i>})								
Early-growth			Late-growth			Prime-aged		
Random effects	V	SD	Random effects	V	SD	Random effects	V	SD
Cohort	0.90	0.95	Year of capture	0.32	0.56	Year of capture	0.18	0.42
Fixed effects	Estimate	95%CI	Fixed effects	Estimate	95%CI	Fixed effects	Estimate	95%CI
Intercept	-0.37	[-1.11, 0.37]	Intercept	-0.47	[-0.94, -0.00]	Intercept	-0.28	[-0.71, 0.15]
			Initial mass	-0.17	[-0.27, -0.07]			
Marginal R ²	-		Marginal R ²	0.13		Marginal R ²	-	
Conditional R ²	0.26		Conditional R ²	0.32		Conditional R ²	0.10	
LONG-TERM								
Random effects	V			SD				
Individual ID	3.65			1.91				
Year of capture	0.63			0.79				

Fixed effects	Estimate	95%CI
Intercept	-0.06	[-0.63, 0.51]
Marginal R ²	-	
Conditional R ²	0.83	

403



404

405

406

407

408

409

410

411

Figure 1. Relationship between faecal glucocorticoid metabolites (log-transformed FGMs, corrected for the date of capture and population) and individual relative body mass (individual body mass (corrected for the date of capture for juveniles) minus the average body mass of all individuals of the same age, population and sex) for (a) juveniles (N = 368 individuals) and for (b) adults aged 2 years old onwards (N = 655 observations on 377 individuals). Points are raw data and line is the prediction from the retained model with 95% confidence intervals.

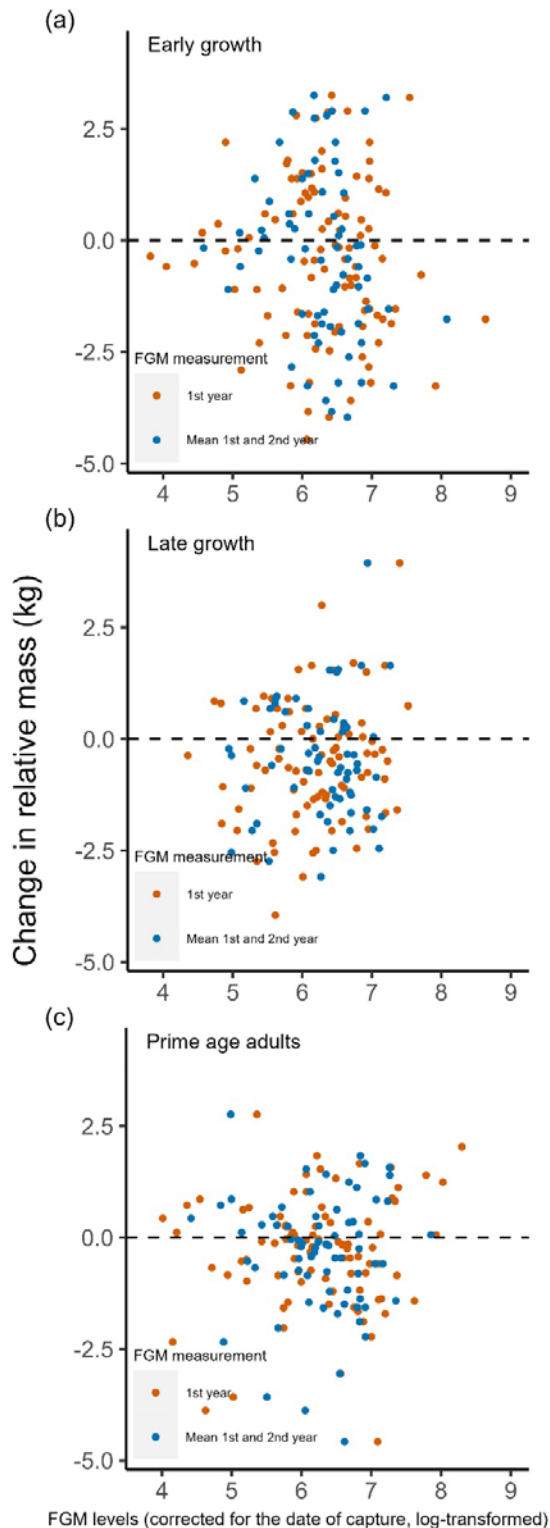
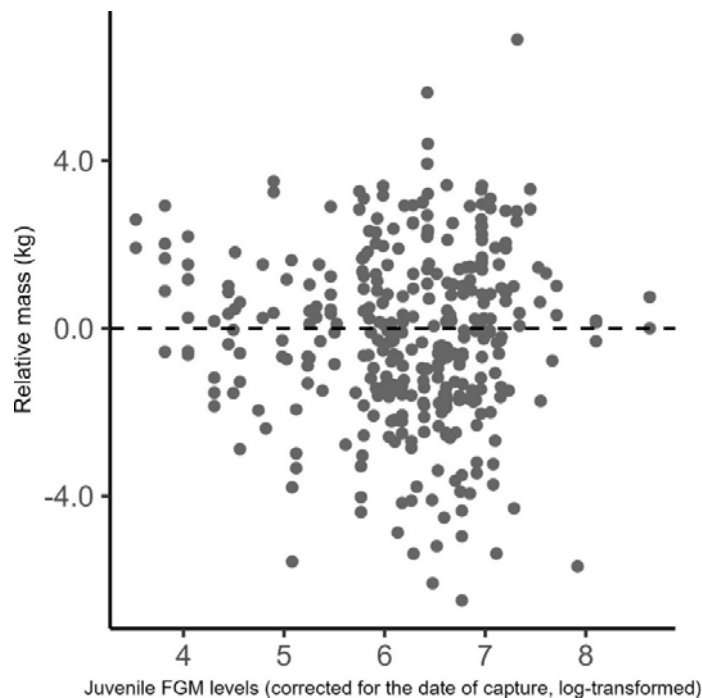


Figure 2. Relationship between faecal glucocorticoid metabolites (log-transformed FGMs, corrected for the date of capture and population) and change in relative body mass between two consecutive years for (a) early-growing individuals (between the first and second years of life), with FGMs either measured the first year of life (N = 99, orange points) or considered as the mean FGMs between the first and second years (N = 67, blue points); for (b) late-growing individuals (between 2 and 4 years old) with FGMs either measured at age t (N = 85, orange points) or considered as the mean FGMs between years t and $t+1$ (N = 63, blue points) and for (c) prime-aged adults which had reached their full body mass (from 4 years old to 10 years old), with FGMs either measured at a given age t (N = 90, orange points) or considered as the mean FGM between age t and age $t+1$ (N = 71, blue points). Points are raw data



435

436

437 **Figure 3.** Relationship between faecal glucocorticoid metabolites (log-transformed FGMs,
438 corrected for the date of capture and population) measured in juveniles and individual relative
439 body mass (*i.e.* individual body mass minus the average body mass of all individuals of the
440 same age, sex and population) (N = 345 observations on 159 individuals). Points are raw
441 data.

441

442 **Discussion**

443 The relationship between GCs and fitness-related traits such as body mass is yet to be fully

444 deciphered. Recent reviews indicate that studies in the wild have led to contrasting results by

445 showing either negative, positive or no relationships between measures of stress and studied

446 traits (Bonier et al. 2009, Crespi et al. 2013, Dantzer et al. 2014). A salient conclusion from

447 these studies is that the relationship depends on an individual's ecological context and internal

448 state. In the present study, the longitudinal monitoring of individual roe deer in two

449 populations exposed to markedly different environmental contexts – one facing limiting

450 resources and the other benefiting from a higher availability and quality of resources –

451 allowed us to analyse the relationship between FGMs and body mass, while accounting for

452 ecological factors and individual attributes such as sex and age. On the short-term, we found

453 clear evidence for a negative relationship between baseline adult FGMs and adult body mass,
454 an important driver of fitness in this species (Gaillard et al. 2000).

455 We could not detect any relationship between FGMs and the change in relative body mass
456 between two consecutive years, neither in growing or prime-aged individuals. In late-growing
457 individuals only, a negative relationship between initial body mass and relative body mass
458 gain appeared, so that lighter individuals of age t tended to gain more weight from one year to
459 the other, suggesting the existence of compensatory growth mechanisms in these populations
460 (Metcalf and Monaghan 2001). Likewise, we found no support for a relationship between
461 early-life FGM levels and adult body mass. Indeed, we found that FGMs and body mass were
462 negatively associated only on the short-term and in adult individuals only. This suggest that
463 FGMs relate to body mass, but without any carry-over effects, and that FGMs are related to
464 body mass differently according to life-history stages. High viability selection at the juvenile
465 stage in the two populations (Toigo et al. 2006, Douhard et al. 2014) could explain that we
466 could not observe any carry-over effects of FGMs on body mass, and an absence of evidence
467 for a short-term relationship between FGMs and body mass in juveniles.

468 Roe deer body mass correlated negatively with FGM levels on the short-term, in adults, with
469 no detectable population or sex differences. This result suggests that the relationship between
470 FGM and body mass is consistent across individuals and between environmental contexts in
471 this species. Roe deer are income breeders, relying mostly on acquired resources rather than
472 on stored energy (Andersen et al. 2000). As GCs stimulate activity through the mobilisation
473 of energy stored (Sapolsky et al. 2000, Reeder and Kramer 2005), the physiological costs of
474 elevated GC levels are expected to directly impair body condition as individuals do not have
475 body reserves to buffer elevated energy requirements (Henderson et al. 2017). However,
476 given marked between-population differences in environmental context we would have
477 expected individuals at TF to be able to mitigate the physiological costs of high GC levels by

478 reducing their allostatic load (McEwen and Wingfield 2010, Henderson et al. 2017),
479 compared to individuals at CH which were expected to enter allostatic overload, thus
480 expecting different allostatic load in the two populations (McEwen and Wingfield 2010). Both
481 populations differ in terms of overall habitat quality, with CH being characterised by a low
482 forest productivity due to poor soils, mild winters, but frequent droughts during summer, and
483 TF by a high forest productivity due to rich soils and relatively wet summers (Pettorelli et al.
484 2006). Accordingly, life history parameters differ between populations. This is especially the
485 case for juvenile survival (Gaillard et al. 1993), body condition (Gilot-Fromont et al. 2012),
486 senescence patterns (haematological parameters: Jégo et al. 2014, body mass: Douhard et al.
487 2017, immune system: Cheynel et al. 2017), and the relation between FGMs and immune
488 traits (Carbillet et al. 2023a). Thus, differences in the relationship between FGMs and body
489 mass was expected to occur between populations, with the strongest negative association in
490 CH, the poorer habitat in which individuals would be more at risk of allostatic overload
491 (McEwen and Wingfield 2010, Henderson et al. 2017). Red deer (*Cervus elaphus*) showed
492 different allostatic loads across populations with different densities and environmental
493 conditions, with individuals facing high density or poor-quality habitat having higher FGM
494 levels and lower body mass (Caslini et al. 2016). Our results rather suggest that both roe deer
495 populations are in a state of allostatic overload. During the winter season, roe deer face more
496 severe winters at TF than at CH, which can in turn mitigate, during this period, the overall
497 better resource quality in TF. This could partly explain why no population differences were
498 detected. It also suggests that allostatic load can change across seasons, as shown in wild grey
499 mouse lemurs (*Microcebus murinus*, Hämäläinen et al. 2015), and that this variation could
500 operate in a population-specific way. It is therefore of great interest to assess the GC-fitness
501 relationship across different environmental contexts, including different years or climatic
502 conditions, and through various life history stages. Finally, the absence of large predators and

503 the weak hunting pressure in both population might at least partly account for the absence of
504 support for a steeper relationship at CH. Studies of roe deer populations facing varying
505 conditions in terms of presence/absence of large predators and hunting pressure, in Poland,
506 showed that hunted populations without large predators had highest FGM levels with largest
507 variation (Zbyryt et al. 2018). In support, observed variation in FGM levels was high in both
508 populations (CV = 59.7 % and 55.3 % in CH and TF, respectively), which could mitigate the
509 relationship between body mass and FGMs and differences between populations.

510 Similarly, we could not detect any sex difference, despite the marked differences in the stress
511 response in males and females reported in mammals, due in part to the interaction between the
512 HPA and reproductive axes (Viau 2002, Wilson et al. 2005, and see Toufexis et al. 2014,
513 Novais et al. 2016 for reviews). This absence of sex-differences also suggests that during this
514 period of the year, female reproductive status does not influence the relationship between
515 FGMs and body mass. In reindeer (*Rangifer tarandus*), cortisol levels did not differ between
516 males, non-pregnant or pregnant females, but showed seasonal variation (Bubenik et al.
517 1998). Accordingly, red deer showed no sex-differences in their levels of FGMs but also
518 showed seasonal variation (Huber et al. 2003). Thus, it would be interesting to collect FGM
519 data of roe deer during different seasons as the stress response can vary accordingly (Bubenik
520 et al. 1998, Vera et al. 2011). It would also provide an opportunity to investigate whether the
521 different reproductive tactics of males and females can affect the relationship between GC and
522 fitness-related traits. Females of an iteroparous, long-lived species such as roe deer are
523 expected to trade reproduction for survival when environmental conditions are poor
524 (Hirshfield and Tinkle 1975). Thus, females are expected to be stress-responsive during their
525 reproductive period to be able to switch between alternative physiological states according to
526 whether they reproduce or not, due to their future opportunities of reproducing (Ricklefs and
527 Wikelski 2002). On the other hand, males allocate heavily to reproduction by defending

528 territories for half of the year (Johansson 1996). Territory defence results in elevated
529 physiological damages, whatever their reproductive success. Therefore, females could show a
530 larger variability in the way they respond to GC than males which are more constrained. This
531 provides promising perspectives to better understand the relationship between GC levels and
532 fitness-related traits according to sex-specific life history stages. It would also be interesting
533 to investigate whether offspring have different life-history trajectories according to their
534 mothers' baseline FGMs during gestation, as shown in North American red squirrels
535 (*Tamiasciurus hudsonicus*, Dantzer et al. 2013), or according to whether mother were
536 captured or not during gestation to further investigate the impact of capture on individuals.

537 FGMs have been previously used as proxies to evaluate the homeostatic level or allostatic
538 load in wild populations, but the results should be interpreted with caution. FGMs do not fully
539 reflect an individual's stress response because GCs only represent one part of the complex
540 endocrine pathway involved in this response (MacDougall-Shackleton et al. 2019). Moreover,
541 although GCs are often referred to as "stress hormones", at baseline levels, their primary role
542 is to acquire, deposit and mobilise energy (Busch and Hayward 2009). Thus, unlike acute GC
543 concentrations, baseline GCs do not only provide information on how an individual responds
544 to stressors, but also on its physiology and activity (Reeder and Kramer 2005). It has been
545 reported that the acute GC response tends to be attenuated in individuals repeatedly exposed
546 to stressors (*e.g.* Ader et al. 1968, Kant et al. 1983, Vera et al. 2011). However, baseline GC
547 levels can also, but not always, be lower in individuals chronically exposed to environmental
548 stressors, making it difficult to interpret FGM levels in the wild. Indeed, whether low baseline
549 GCs actually represent a non-stressed individual rather than an individual chronically exposed
550 to stressors is difficult to tell (Davis and Maney 2018).

551 In conclusion, we found that high baseline FGMs may have immediate adverse consequences
552 on body mass and that the relationship between body mass and FGM levels seems to depend

553 on an individual life-stage, rather than on the environmental context or sex. Through this
554 work, we therefore emphasise the need to account for both environmental and individual
555 factors, including life history traits, to better capture the relationship between the stress
556 response and fitness-related traits. We also put emphasis on the idea to collect FGM across
557 different temporal and environmental contexts to evaluate how the GC-fitness relationship can
558 be modulated according to the seasonal and environmental conditions. To do so, it appears
559 critical to have access to longitudinal data. Measuring proxies of stress together with fitness-
560 related traits throughout the life of individuals is likely to be the only way to properly refine
561 our understanding of the implications of stress for fitness.

562 **Conflict of interest**

563 The authors declare having no conflict of interest.

564 **Ethics**

565 The research presented in this manuscript was done according to all institutional and/or
566 national guidelines. For both populations (Trois-Fontaines and Chizé), the protocol of capture
567 of roe deer, under the authority of the Office Français de la Biodiversité (OFB), was approved
568 by the Director of Food, Agriculture and Forest (Prefectoral order 2009-14 from Paris). All
569 procedures were approved by the Ethical Committee of Lyon 1 University (project DR2014-
570 09, June 5, 2014).

571 **Funding**

572 This project was funded by the Université de Lyon, VetAgro Sup and the Office Français de
573 la Biodiversité (OFB, project CNV-REC-2019-08).

574 **Acknowledgements**

575 This work was conducted as part of a Ph.D. funded by the Université de Lyon and the Office
576 Français de la Biodiversité (OFB). We are grateful to all technicians, researchers and
577 volunteers participating in the collect of data on both sites (Trois-Fontaines and Chizé). We
578 particularly thank the editor and two anonymous reviewers for their insights and valuable
579 comments, and Philippe Veber and Marie-Laure Delignette-Muller for their precious help
580 considering the statistical analyses.

581 **References**

- 582 Ader, R., Friedman, S. B., Grotta, L. J. and Schaefer, A. 1968. Attenuation of the plasma
583 corticosterone response to handling and electric shock stimulation in the infant rat.
584 *Physiol. Behav.* **3**(2): 327–331. 10.1016/0031-9384(68)90109-1
- 585 Aitken, R. J. 1974. Delayed implantation in roe deer (*Capreolus capreolus*). *Reproduction*
586 **39**(1): 225–233. 10.1530/jrf.0.0390225
- 587 Altmann, J., Lynch, J. W., Nguyen, N., Alberts, S. C. and Gesquiere, L. R. 2004. Life-history
588 correlates of steroid concentrations in wild peripartum baboons. *Am. J. Primatol.*
589 **64**(1): 95–106. 10.1002/ajp.20064
- 590 Andersen, R., Duncan, P. and Linnell, J. D. C. 1998. *The European roe deer: The biology of*
591 *success*. Scandinavian University Press, Oslo.
- 592 Andersen, R., Gaillard, J.-M., Linnell, J. D. C. and Duncan, P. 2000. Factors affecting
593 maternal care in an income breeder, the European roe deer. *J. Anim. Ecol.* **69**(4): 672–
594 682. 10.1046/j.1365-2656.2000.00425.x
- 595 Bartoń, K. 2023. MuMIn: Multi-Model Inference. [https://CRAN.R-](https://CRAN.R-project.org/package=MuMIn)
596 [project.org/package=MuMIn](https://CRAN.R-project.org/package=MuMIn)
- 597 Blumstein, D. T., Keeley, K. N. and Smith, J. E. 2016. Fitness and hormonal correlates of
598 social and ecological stressors of female yellow-bellied marmots. *Anim. Behav.* **112**:
599 1–11. 10.1016/j.anbehav.2015.11.002
- 600 Bonier, F., Martin, P., Moore, I. and Wingfield, J. 2009. Do baseline glucocorticoids predict
601 fitness? *Trends Ecol. Evol.* **24**(11): 634–42. 10.1016/j.tree.2009.04.013
- 602 Bonnot, N. C., Bergvall, U. A., Jarnemo, A. and Kjellander, P. 2018. Who’s afraid of the big
603 bad wolf? Variation in the stress response among personalities and populations in a
604 large wild herbivore. *Oecologia* **188**(1): 85–95. 10.1007/s00442-018-4174-7
- 605 Boonstra, R., Hik, D., Singleton, G. R. and Tinnikov, A. 1998. The impact of predator-
606 induced stress on the snowshoe hare cycle. *Ecol. Monogr.* **68**(3): 371–394.
607 10.1890/0012-9615(1998)068[0371:TIOPIS]2.0.CO;2

- 608 Boonstra, R. 2013. Reality as the leading cause of stress: Rethinking the impact of chronic
609 stress in nature. *Funct. Ecol.* **27**: 11–23. 10.1111/1365-2435.12008
- 610 Boudreau, M. R., Seguin, J. L., Boonstra, R., Palme, R., Boutin, S., Krebs, C. J. and Murray,
611 D. L. 2019. Experimental increase in predation risk causes a cascading stress response
612 in free-ranging snowshoe hares. *Oecologia* **191**(2): 311–323. 10.1007/s00442-019-
613 04500-2
- 614 Brunton, P. J., Russell, J. A. and Douglas, A. J. 2008. Adaptive responses of the maternal
615 hypothalamic-pituitary-adrenal axis during pregnancy and lactation. *J.*
616 *Neuroendocrinol.* **20**(6): 764–776. 10.1111/j.1365-2826.2008.01735.x
- 617 Bubenik, G. A., Schams, D., White, R. G., Rowell, J., Blake, J. and Bartos, L. 1998. Seasonal
618 levels of metabolic hormones and substrates in male and female reindeer (*Rangifer*
619 *tarandus*). *Comp. Biochem. Phys. C* **120**(2): 307–315. 10.1016/S0742-8413(98)10010-
620 5
- 621 Burnham, K. P., Anderson, D. R. and Huyvaert, K. P. 2011. AIC model selection and
622 multimodel inference in behavioral ecology: Some background, observations, and
623 comparisons. *Behav. Ecol. Sociobiol.* **65**(1): 23–35. 10.1007/s00265-010-1029-6
- 624 Burnham, K. P. and Anderson, D. R. 2002. *Model selection and multimodel inference: A*
625 *practical information-theoretic approach*. Springer, New York.
- 626 Busch, D. S. and Hayward, L. S. 2009. Stress in a conservation context: A discussion of
627 glucocorticoid actions and how levels change with conservation-relevant variables.
628 *Biol. Conserv.* **142**(12): 2844–2853. 10.1016/j.biocon.2009.08.013
- 629 Cabezas, S., Blas, J., Marchant, T. A. and Moreno, S. 2007. Physiological stress levels predict
630 survival probabilities in wild rabbits. *Horm. Behav.* **51**(3): 313–320.
631 10.1016/j.yhbeh.2006.11.004
- 632 Carbillet, J., Rey, B., Palme, R., Morellet, N., Bonnot, N., Chaval, Y., Cargnelutti, B.,
633 Hewison, A. J. M., Gilot-Fromont, E. and Verheyden, H. 2020. Under cover of the
634 night: Context-dependency of anthropogenic disturbance on stress levels of wild roe
635 deer *Capreolus capreolus*. *Conserv. Physiol.* **8**(1): coaa086. 10.1093/conphys/coaa086
- 636 Carbillet, J., Hollain, M., Rey, B., Palme, R., Pellerin, M., Regis, C., Geffré, A., Duhayer, J.,
637 Pardonnet, S., Debias, F., Merlet, J., Lemaître, J.-F., Verheyden, H. and Gilot-
638 Fromont, E. 2023a. Age and spatio-temporal variations in food resources modulate
639 stress-immunity relationships in three populations of wild roe deer. *Gen. Comp.*
640 *Endocrinol.* **330**: 114141. 10.1016/j.ygcen.2022.114141
- 641 Carbillet, J., Palme, R., Maublanc, M.-L., Cebe, N., Gilot-Fromont, E., Verheyden, H. and
642 Rey, B. 2023b. Instability of fecal glucocorticoid metabolites at 4°C: Time to freeze
643 matters. *J. Exp. Zool. Part A. Ecol. Integr. Physiol.* in press. 10.1002/jez.2704
- 644 Caslini, C., Comin, A., Peric, T., Prandi, A., Pedrotti, L. and Mattiello, S. 2016. Use of hair
645 cortisol analysis for comparing population status in wild red deer (*Cervus elaphus*)
646 living in areas with different characteristics. *Eur. J. Wildlife Res.* **62**(6): 713–723.
647 10.1007/s10344-016-1049-2

- 648 Cheynel, L., Lemaître, J.-F., Gaillard, J.-M., Rey, B., Bourgoïn, G., Ferté, H., Jégo, M.,
649 Débias, F., Pellerin, M., Jacob, L. and Gilot-Fromont, E. 2017. Immunosenescence
650 patterns differ between populations but not between sexes in a long-lived mammal.
651 *Sci. Rep.* **7**(1): 1–11. 10.1038/s41598-017-13686-5
- 652 Crespi, E. J., Williams, T. D., Jessop, T. S. and Delehanty, B. 2013. Life history and the
653 ecology of stress: how do glucocorticoid hormones influence life-history variation in
654 animals? *Funct. Ecol.* **27**(1): 93–106. 10.1111/1365-2435.12009
- 655 Dallman, M. F., Akana, S. F., Bhatnagar, S., Bell, M. E., Choi, S., Chu, A., Horsley, C.,
656 Levin, N., Meijer, O., Soriano, L. R., Strack, A. M. and Viau, V. 1999. Starvation:
657 early signals, sensors, and sequelae. *Endocrinology* **140**(9): 4015–4023.
658 10.1210/endo.140.9.7001
- 659 Dantzer, B., McAdam, A. G., Palme, R., Fletcher, Q. E., Boutin, S., Humphries, M. M. and
660 Boonstra, R. 2010. Fecal cortisol metabolite levels in free-ranging North American red
661 squirrels: Assay validation and the effects of reproductive condition. *Gen. Comp.*
662 *Endocrinol.* **167**(2): 279–286. 10.1016/j.ygcen.2010.03.024
- 663 Dantzer, B., Newman, A. E. M., Boonstra, R., Palme, R., Boutin, S., Humphries, M. M. and
664 McAdam, A. G. 2013. Density triggers maternal hormones that increase adaptive
665 offspring growth in a wild mammal. *Science* **340**(6137): 1215–1217.
666 10.1126/science.1235765
- 667 Dantzer, B., Fletcher, Q. E., Boonstra, R. and Sheriff, M. J. 2014. Measures of physiological
668 stress: A transparent or opaque window into the status, management and conservation
669 of species? *Conserv. Physiol.* **2**(1): cou023. 10.1093/conphys/cou023
- 670 Davis, A. K. and Maney, D. L. 2018. The use of glucocorticoid hormones or leucocyte
671 profiles to measure stress in vertebrates: What’s the difference? *Methods Ecol. Evol.*
672 **9**(6): 1556–1568. 10.1111/2041-210X.13020
- 673 Dehnhard, M., Clauss, M., Lechner-Doll, M., Meyer, H. H. D. and Palme, R. 2001.
674 Noninvasive monitoring of adrenocortical activity in roe deer (*Capreolus capreolus*)
675 by measurement of fecal cortisol metabolites. *Gen. Comp. Endocrinol.* **123**(1): 111–
676 120. 10.1006/gcen.2001.7656
- 677 Dhabhar, F. S. 2014. Effects of stress on immune function: The good, the bad, and the
678 beautiful. *Immunol. Res.* **58**(2): 193–210. 10.1007/s12026-014-8517-0
- 679 Douhard, M., Plard, F., Gaillard, J.-M., Capron, G., Delorme, D., Klein, F., Duncan, P., Loe,
680 L. E. and Bonenfant, C. 2014. Fitness consequences of environmental conditions at
681 different life stages in a long-lived vertebrate. *Proceedings of the Royal Society B:*
682 *Biological Sciences* **281**(1785): 20140276. 10.1098/rspb.2014.0276
- 683 Douhard, F., Gaillard, J.-M., Pellerin, M., Jacob, L. and Lemaître, J.-F. 2017. The cost of
684 growing large: Costs of post-weaning growth on body mass senescence in a wild
685 mammal. *Oikos* **126**(9): 1329–1338. 10.1111/oik.04421
- 686 Dulude-de Broin, F., Hamel, S., Mastromonaco, G. F. and Côté, S. D. 2020. Predation risk
687 and mountain goat reproduction: Evidence for stress-induced breeding suppression in
688 a wild ungulate. *Funct. Ecol.* **34**(5): 1003–1014. 10.1111/1365-2435.13514

- 689 Ethan Pride, R. 2005. High faecal glucocorticoid levels predict mortality in ring-tailed lemurs
690 (*Lemur catta*). *Biol. Lett.* **1**(1): 60–63. 10.1098/rsbl.2004.0245
- 691 Formenti, N., Viganó, R., Fraquelli, C., Trogu, T., Bonfanti, M., Lanfranchi, P., Palme, R. and
692 Ferrari, N. 2018. Increased hormonal stress response of Apennine chamois induced by
693 interspecific interactions and anthropogenic disturbance. *Eur. J. Wildlife Res.* **64**(6):
694 68. 10.1007/s10344-018-1228-4
- 695 Gaillard, J.-M., Delorme, D., Boutin, J.-M., Van Laere, G., Boisaubert, B. and Pradel, R.
696 1993. Roe deer survival patterns: A comparative analysis of contrasting populations. *J.*
697 *Anim. Ecol.* **62**(4): 778–791. 10.2307/5396
- 698 Gaillard, J.-M., Delorme, D., Boutin, J.-M., Van Laere, G. and Boisaubert, B. 1996. Body
699 mass of roe deer fawns during winter in 2 contrasting populations. *J. Wildlife Manage.*
700 **60**(1): 29–36. 10.2307/3802036
- 701 Gaillard, J.-M., Festa-Bianchet, M., Delorme, D. and Jorgenson, J. 2000. Body mass and
702 individual fitness in female ungulates: Bigger is not always better. *P. Roy. Soc. Lond.*
703 *B Biol.* **267**(1442): 471–477. 10.1098/rspb.2000.1024
- 704 Gaillard, J.-M., Loison, A., Toïgo, C., Delorme, D. and Van Laere, G. 2003. Cohort effects
705 and deer population dynamics. *Écoscience* **10**(4): 412–420.
706 10.1080/11956860.2003.11682789
- 707 Gaillard, J.-M., Mark Hewison, A. J., Klein, F., Plard, F., Douhard, M., Davison, R. and
708 Bonenfant, C. 2013. How does climate change influence demographic processes of
709 widespread species? Lessons from the comparative analysis of contrasted populations
710 of roe deer. *Ecol. Lett.* **16**(s1): 48–57. 10.1111/ele.12059
- 711 George, S. C., Smith, T. E., Mac Cana, P. S. S., Coleman, R. and Montgomery, W. I. 2014.
712 Physiological stress in the Eurasian badger (*Meles meles*): Effects of host, disease and
713 environment. *Gen. Comp. Endocrinol.* **200**: 54–60. 10.1016/j.ygcen.2014.02.017
- 714 Gilot-Fromont, E., Jégo, M., Bonenfant, C., Gibert, P., Rannou, B., Klein, F. and Gaillard, J.-
715 M. 2012. Immune phenotype and body condition in roe deer: Individuals with high
716 body condition have different, not stronger immunity. *PLoS ONE* **7**(9): e45576.
717 10.1371/journal.pone.0045576
- 718 Glazier, D. S. 2005. Beyond the ‘3/4-power law’: Variation in the intra- and interspecific
719 scaling of metabolic rate in animals. *Biol. Rev.* **80**(4): 611–662.
720 10.1017/S1464793105006834
- 721 Goymann, W. 2012. On the use of non-invasive hormone research in uncontrolled, natural
722 environments: the problem with sex, diet, metabolic rate and the individual. *Methods*
723 *in Ecology and Evolution* **3**(4): 757–765. 10.1111/j.2041-210X.2012.00203.x
- 724 Hadinger, U., Haymerle, A., Knauer, F., Schwarzenberger, F. and Walzer, C. 2015. Faecal
725 cortisol metabolites to assess stress in wildlife: evaluation of a field method in free-
726 ranging chamois. *Methods in Ecology and Evolution* **6**(11): 1349–1357.
727 10.1111/2041-210X.12422

- 728 Hämäläinen, A., Heistermann, M. and Kraus, C. 2015. The stress of growing old: Sex- and
729 season-specific effects of age on allostatic load in wild grey mouse lemurs. *Oecologia*
730 **178**(4): 1063–1075. 10.1007/s00442-015-3297-3
- 731 Hamel, S., Gaillard, J.-M., Festa-Bianchet, M. and Côté, S. D. 2009. Individual quality, early-
732 life conditions, and reproductive success in contrasted populations of large herbivores.
733 *Ecology* **90**(7): 1981–1995. 10.1890/08-0596.1
- 734 Hamel, S., Gaillard, J.-M., Yoccoz, N. G., Albon, S., Côté, S. D., Craine, J. M., Festa-
735 Bianchet, M., Garel, M., Lee, P., Moss, C., Nussey, D. H., Pelletier, F., Stien, A. and
736 Tveraa, T. 2016. Cohort variation in individual body mass dissipates with age in large
737 herbivores. *Ecol. Monogr.* **86**(4): 517–543. 10.1002/ecm.1232
- 738 Hau, M., Casagrande, S., Ouyang, J. and Baugh, A. 2016. Glucocorticoid-mediated
739 phenotypes in vertebrates: Multilevel variation and evolution. *Adv. Stud. Behav.* **48**:
740 41–115. 10.1016/bs.asb.2016.01.002
- 741 Henderson, L. J., Evans, N. P., Heidinger, B. J., Herborn, K. A. and Arnold, K. E. 2017. Do
742 glucocorticoids predict fitness? Linking environmental conditions, corticosterone and
743 reproductive success in the blue tit, *Cyanistes caeruleus*. *Roy. Soc. Open Sci.* **4**(10):
744 170875. 10.1098/rsos.170875
- 745 Hennin, H., Wells-Berlin, A. and Love, O. 2016. Baseline glucocorticoids are drivers of body
746 mass gain in a diving seabird. *Ecol. Evol.* **6**(6): 1702–1711. 10.1002/ece3.1999
- 747 Hewison, A. J. M., Angibault, J. M., Bideau, E., Vincent, J. P., Boutin, J. and Sempéré, A.
748 1996. Annual variation in body composition of roe deer (*Capreolus capreolus*) in
749 moderate environmental conditions. *Can. J. Zool.* **74**(2): 245–253. 10.1139/z96-031
- 750 Hewison, A. J. M., Gaillard, J.-M., Delorme, D., Van Laere, G., Amblard, T. and Klein, F.
751 2011. Reproductive constraints, not environmental conditions, shape the ontogeny of
752 sex-specific mass-size allometry in roe deer. *Oikos* **120**(8): 1217–1226.
753 10.1111/j.1600-0706.2011.19316.x
- 754 Hirshfield, M. F. and Tinkle, D. W. 1975. Natural selection and the evolution of reproductive
755 effort. *P. Natl. Acad. Sci. U.S.A.* **72**(6): 2227–2231. 10.1073/pnas.72.6.2227
- 756 Hodges, K. E., Boonstra, R. and Krebs, C. J. 2006. Overwinter mass loss of snowshoe hares
757 in the Yukon: Starvation, stress, adaptation or artefact? *J. Anim. Ecol.* **75**(1): 1–13.
758 10.1111/j.1365-2656.2005.01018.x
- 759 Huber, S., Palme, R. and Arnold, W. 2003. Effects of season, sex, and sample collection on
760 concentrations of fecal cortisol metabolites in red deer (*Cervus elaphus*). *Gen. Comp.*
761 *Endocrinol.* **130**(1): 48–54. 10.1016/s0016-6480(02)00535-x
- 762 Jégo, M., Lemaître, J.-F., Bourgoïn, G., Capron, G., Warnant, C., Klein, F., Gilot-Fromont,
763 E. and Gaillard, J.-M. 2014. Haematological parameters do senesce in the wild:
764 Evidence from different populations of a long-lived mammal. *J. Evolution. Biol.*
765 **27**(12): 2745–2752. 10.1111/jeb.12535
- 766 Johansson, A. 1996. Territory establishment and antler cycle in male roe deer. *Ethology*
767 **102**(4): 549–559. 10.1111/j.1439-0310.1996.tb01147.x

- 768 Kant, G. J., Bunnell, B. N., Mougey, E. H., Pennington, L. L. and Meyerhoff, J. L. 1983.
769 Effects of repeated stress on pituitary cyclic AMP, and plasma prolactin,
770 corticosterone and growth hormone in male rats. *Pharmacol. Biochem. Behav.* **18**(6):
771 967–971. 10.1016/s0091-3057(83)80022-7
- 772 Landys, M. M., Ramenofsky, M. and Wingfield, J. C. 2006. Actions of glucocorticoids at a
773 seasonal baseline as compared to stress-related levels in the regulation of periodic life
774 processes. *Gen. Comp. Endocrinol.* **148**(2): 132–149. 10.1016/j.ygcen.2006.02.013
- 775 Lavergne, S. G., Krebs, C. J., Kenney, A. J., Boutin, S., Murray, D., Palme, R. and Boonstra,
776 R. 2021. The impact of variable predation risk on stress in snowshoe hares over the
777 cycle in North America’s boreal forest: Adjusting to change. *Oecologia* **197**(1): 71–
778 88. 10.1007/s00442-021-05019-1
- 779 Lexen, E., El-Bahr, S., Sommerfeld-Stur, I., Palme, R. and Möstl, E. 2008. Monitoring the
780 adrenocortical response to disturbances in sheep by measuring glucocorticoid
781 metabolites in the faeces. *Wiener tierärztliche Monatsschrift* **95**: 64–71.
- 782 MacDougall-Shackleton, S. A., Bonier, F., Romero, L. M. and Moore, I. T. 2019.
783 Glucocorticoids and “stress” are not synonymous. *Integr. Org. Biol.* **1**(1): obz017.
784 10.1093/iob/obz017
- 785 Martin, J. G. A., Nussey, D. H., Wilson, A. J. and Réale, D. 2011. Measuring individual
786 differences in reaction norms in field and experimental studies: A power analysis of
787 random regression models. *Methods Ecol. Evol.* **2**(4): 362–374. 10.1111/j.2041-
788 210X.2010.00084.x
- 789 McEwen, B. S. and Wingfield, J. C. 2003. The concept of allostasis in biology and
790 biomedicine. *Horm. Behav.* **43**(1): 2–15. 10.1016/S0018-506X(02)00024-7
- 791 McEwen, B. S. and Wingfield, J. C. 2010. What is in a name? Integrating homeostasis,
792 allostasis and stress. *Horm. Behav.* **57**(2): 105–111. 10.1016/j.yhbeh.2009.09.011
- 793 Metcalfe, N. B. and Monaghan, P. 2001. Compensation for a bad start: Grow now, pay later?
794 *Trends Ecol. Evol.* **16**(5): 254–260. 10.1016/s0169-5347(01)02124-3
- 795 Monaghan, P. and Haussmann, M. F. 2015. The positive and negative consequences of
796 stressors during early life. *Early Hum. Dev.* **91**(11): 643–647.
797 10.1016/j.earlhumdev.2015.08.008
- 798 Möstl, E., Maggs, J. L., Schrötter, G., Besenfelder, U. and Palme, R. 2002. Measurement of
799 cortisol metabolites in faeces of ruminants. *Vet. Res. Commun.* **26**(2): 127–139.
800 10.1023/A:1014095618125
- 801 Novais, A., Monteiro, S., Roque, S., Correia-Neves, M. and Sousa, N. 2016. How age, sex
802 and genotype shape the stress response. *Neurobiol. Stress* **6**: 44–56.
803 10.1016/j.ynstr.2016.11.004
- 804 Palme, R., Touma, C., Arias, N., Dominchin, M. F. and Lepschy, M. 2013. Steroid extraction:
805 Get the best out of faecal samples. *Wien. Tierarztl. Monat.* **100**(9/10): 238–246.

- 806 Palme, R. 2019. Non-invasive measurement of glucocorticoids: Advances and problems.
807 *Physiol. Behav.* **199**: 229–243. 10.1016/j.physbeh.2018.11.021
- 808 Pauli, J. N. and Buskirk, S. W. 2007. Risk-disturbance overrides density dependence in a
809 hunted colonial rodent, the black-tailed prairie dog *Cynomys ludovicianus*. *J. Appl.*
810 *Ecol.* **44**(6): 1219–1230. 10.1111/j.1365-2664.2007.01337.x
- 811 Pedersen, A. B. and Greives, T. J. 2008. The interaction of parasites and resources cause
812 crashes in a wild mouse population. *J. Anim. Ecol.* **77**(2): 370–377. 10.1111/j.1365-
813 2656.2007.01321.x
- 814 Pettorelli, N., Gaillard, J.-M., Duncan, P., Ouellet, J.-P. and Van Laere, G. 2001. Population
815 density and small-scale variation in habitat quality affect phenotypic quality in roe
816 deer. *Oecologia* **128**(3): 400–405. 10.1007/s004420100682
- 817 Pettorelli, N., Gaillard, J.-M., Mysterud, A., Duncan, P., Stenseth, N. C., Delorme, D., Laere,
818 G. V., Toïgo, C. and Klein, F. 2006. Using a proxy of plant productivity (NDVI) to
819 find key periods for animal performance: The case of roe deer. *Oikos* **112**(3): 565–
820 572. <https://doi.org/10.1111/j.0030-1299.2006.14447.x>
- 821 Pinho, G. M., Ortiz-Ross, X., Reese, A. N. and Blumstein, D. T. 2019. Correlates of maternal
822 glucocorticoid levels in a socially flexible rodent. *Horm. Behav.* **116**: 104577.
823 10.1016/j.yhbeh.2019.104577
- 824 R Core Team 2022. R: A language and environment for statistical computing. [https://www.R-](https://www.R-project.org)
825 [project.org](https://www.R-project.org)
- 826 Rabasa, C. and Dickson, S. L. 2016. Impact of stress on metabolism and energy balance.
827 *Curr. Opin. Behav. Sci.* **9**: 71–77. 10.1016/j.cobeha.2016.01.011
- 828 Reeder, D. M. and Kramer, K. M. 2005. Stress in free-ranging mammals: Integrating
829 physiology, ecology, and natural history. *J. Mammal.* **86**(2): 225–235. 10.1644/BHE-
830 003.1
- 831 Ricklefs, R. E. and Wikelski, M. 2002. The physiology/life-history nexus. *Trends Ecol. Evol.*
832 **17**(10): 462–468. 10.1016/S0169-5347(02)02578-8
- 833 Rogovin, K. A., Randall, J. A., Kolosova, I. E. and Moshkin, M. P. 2003. Social correlates of
834 stress in adult males of the great gerbil, *Rhombomys opimus*, in years of high and low
835 population densities. *Horm. Behav.* **43**(1): 132–139. 10.1016/s0018-506x(02)00028-4
- 836 Rogovin, K. A., Randall, J. A., Kolosova, I. E. and Moshkin, M. P. 2008. Long-term
837 dynamics of fecal corticosterone in male great gerbils (*Rhombomys opimus* Licht.):
838 Effects of environment and social demography. *Physiol. Biochem. Zool.* **81**(5): 612–
839 626. 10.1086/588757
- 840 Romero, L. M., Dickens, M. J. and Cyr, N. E. 2009. The Reactive Scope Model - A new
841 model integrating homeostasis, allostasis, and stress. *Horm. Behav.* **55**(3): 375–389.
842 10.1016/j.yhbeh.2008.12.009

- 843 Romero, L. M. and Reed, J. M. 2005. Collecting baseline corticosterone samples in the field:
844 Is under 3 min good enough? *Comp. Biochem. Phys. A* **140**(1): 73–79.
845 10.1016/j.cbpb.2004.11.004
- 846 Ronget, V., Gaillard, J.-M., Coulson, T., Garratt, M., Gueyffier, F., Lega, J.-C. and Lemaître,
847 J.-F. 2018. Causes and consequences of variation in offspring body mass: Meta-
848 analyses in birds and mammals. *Biol. Rev.* **93**(1): 1–27. 10.1111/brv.12329
- 849 Sapolsky, R. M., Romero, L. M. and Munck, A. U. 2000. How do glucocorticoids influence
850 stress responses? Integrating permissive, suppressive, stimulatory, and preparative
851 actions. *Endocr. Rev.* **21**(1): 55–89. 10.1210/edrv.21.1.0389
- 852 Sheriff, M. J., Dantzer, B., Delehanty, B., Palme, R. and Boonstra, R. 2011. Measuring stress
853 in wildlife: Techniques for quantifying glucocorticoids. *Oecologia* **166**(4): 869–887.
854 10.1007/s00442-011-1943-y
- 855 Sheriff, M. J., Wheeler, H., Donker, S. A., Krebs, C. J., Palme, R., Hik, D. S. and Boonstra,
856 R. 2012. Mountain-top and valley-bottom experiences: the stress axis as an integrator
857 of environmental variability in arctic ground squirrel populations. *J. Zool.* **287**(1): 65–
858 75. 10.1111/j.1469-7998.2011.00888.x
- 859 Stoffel, M. A., Nakagawa, S. and Schielzeth, H. 2017. rptR: repeatability estimation and
860 variance decomposition by generalized linear mixed-effects models. *Methods Ecol.*
861 *Evol.* **8**(11): 1639–1644. 10.1111/2041-210X.12797
- 862 Tilbrook, A. J., Turner, A. I. and Clarke, I. J. 2000. Effects of stress on reproduction in non-
863 rodent mammals: The role of glucocorticoids and sex differences. *Rev. Reprod.* **5**(2):
864 105–113. 10.1530/ror.0.0050105
- 865 Tixier, H. and Duncan, P. 1996. Are European roe deer browsers? A review of variations in
866 the composition of their diets. *Rev. Ecol. - Terre Vie* **51**(1): 3–17.
867 10.3406/revec.1996.2189
- 868 Toigo, C., Gaillard, J.-M., Laere, G. V., Hewison, M. and Morellet, N. 2006. How does
869 environmental variation influence body mass, body size, and body condition? Roe
870 deer as a case study. *Ecography* **29**(3): 301–308. <https://doi.org/10.1111/j.2006.0906-7590.04394.x>
- 872 Toufexis, D., Rivarola, M. A., Lara, H. and Viau, V. 2014. Stress and the reproductive axis. *J.*
873 *Neuroendocrinol.* **26**(9): 573–586. 10.1111/jne.12179
- 874 Vera, F., Antenucci, C. D. and Zenuto, R. R. 2011. Cortisol and corticosterone exhibit
875 different seasonal variation and responses to acute stress and captivity in tuco-tucos
876 (*Ctenomys talarum*). *Gen. Comp. Endocrinol.* **170**(3): 550–557.
877 10.1016/j.ygcen.2010.11.012
- 878 Viau, V. 2002. Functional cross-talk between the hypothalamic-pituitary-gonadal and -adrenal
879 axes. *J. Neuroendocrinol.* **14**(6): 506–513. 10.1046/j.1365-2826.2002.00798.x
- 880 Vuarin, P., Pillay, N. and Schradin, C. 2019. Elevated basal corticosterone levels increase
881 disappearance risk of light but not heavy individuals in a long-term monitored rodent
882 population. *Horm. Behav.* **113**: 95–102. 10.1016/j.yhbeh.2019.05.001

- 883 Wey, T. W., Lin, L., Patton, M. L. and Blumstein, D. T. 2015. Stress hormone metabolites
884 predict overwinter survival in yellow-bellied marmots. *Acta Ethol.* **18**(2): 181–185.
885 10.1007/s10211-014-0204-6
- 886 Wilson, M. E., Legendre, A., Pazol, K., Fisher, J. and Chikazawa, K. 2005. Gonadal steroid
887 modulation of the limbic-hypothalamic- pituitary-adrenal (LHPA) axis is influenced
888 by social status in female rhesus monkeys. *Endocrine* **26**(2): 89–97.
889 10.1385/ENDO:26:2:089
- 890 Wingfield, J. C. 2003. Control of behavioural strategies for capricious environments. *Anim.*
891 *Behav.* **66**(5): 807–816. 10.1006/anbe.2003.2298
- 892 Wingfield, J. C. 2008. Comparative endocrinology, environment and global change. *Gen.*
893 *Comp. Endocrinol.* **157**(3): 207–216. 10.1016/j.ygcn.2008.04.017
- 894 Wingfield, J. C. 2013. Ecological processes and the ecology of stress: The impacts of abiotic
895 environmental factors. *Funct. Ecol.* **27**(1): 37–44. 10.1111/1365-2435.12039
- 896 Zbyryt, A., Bubnicki, J. W., Kuijper, D. P. J., Dehnhard, M., Churski, M., Schmidt, K. and
897 Editor, B. W. 2018. Do wild ungulates experience higher stress with humans than with
898 large carnivores? *Behav. Ecol.* **29**(1): 19–30. 10.1093/beheco/axx142
- 899