

1 **Risk-taking neonates do not pay a survival cost in a free-ranging**
2 **large mammal**

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29

30 **Data accessibility statement**

31 We fully support open and transparent science. Therefore, data files and R-markdown files of the
32 analysis will be uploaded on Dryad, OSF or Zenodo after acceptance. We will then also include the
33 data DOI at the end of the article. During review, these files are already made available to the editor
34 and reviewers.

35 **Abstract**

36 Recent debate has focused on whether variation in personality primarily reflects variation in
37 resource allocation or resource acquisition of individuals. These two mechanisms differ in their
38 expected patterns between personality and survival. If personality mainly reflects variation in
39 resource allocation, then bold (i.e. risk-taking) individuals are expected to live shorter, whereas the
40 opposite pattern is expected with resource acquisition. Here we studied the relationship between
41 neonate personality and early-life survival in 269 juveniles of a population of fallow deer (*Dama*
42 *dama*). We found that bolder individuals were more likely to survive, and therefore, paid no
43 apparent survival cost. Interestingly, the physiological but not the behavioural dimension of neonate
44 boldness was directly linked to survival, suggesting that these individuals may be of higher state than
45 their shyer counterparts. As the first study linking neonate personality to survival in a free-ranging
46 mammal, we provide novel insights into drivers behind early-life individual variation.

47 **Introduction**

48 Individuals within a population tend to differ consistently among each other in their average
49 behaviour, and these among-individual differences (i.e. animal personality) have been shown to play
50 a major role in ecology and evolution (Wolf & Weissing, 2012). How these differences arise and are
51 maintained in evolution, however, remains an unsolved question. One of the most prominent
52 hypotheses, the *extended* pace-of-life syndrome hypothesis (POLS; see Réale et al., 2010), theorizes
53 that life-history trade-offs maintain the variation in personality. Within this framework, individuals
54 are expected to covary in their behavioural, physiological, and life-history traits (Réale et al., 2010;
55 Dammhahn et al., 2018). The trade-off in resources allocated to current versus future reproduction
56 has been suggested as an underlying driver of these covariations, where individuals exhibit their own
57 pace-of-life (POL), along the slow-fast continuum, depending on how much of their resources they
58 allocate to either (Dammhahn et al., 2018). Within the extended POLS, individuals with a fast POL
59 are expected to show risk-taking behaviour, which in turn leads to faster growth, at the cost of
60 mortality (Réale et al., 2010; Fig. 1A). These fast POL individuals are thought to allocate most of their
61 resources towards current reproduction, whereas individuals with a slow POL are expected to show
62 the opposite patterns by allocating most of their resources to future reproduction, i.e. risk-averse
63 behaviour, slow growth rates, but higher survival (Réale et al., 2010; Dammhahn et al., 2018).

64 The empirical support for patterns predicted under the extended POLS, however, have so far
65 been ambivalent at best (Royauté et al., 2018; Moiron et al., 2020, Haave-Audet et al., 2021).
66 Especially when it comes to survival, there has been no support for the POLS prediction that bolder
67 (i.e. more risk-taking) animals have shorter lifespans in recent meta-analyses (Moiron et al., 2020;
68 Haave-Audet et al., 2021). Haave-Audet et al. (2021) found no relationship between personality and
69 survival, whereas Moiron et al. (2020) reported weak evidence that bolder animals actually survive
70 longer, but this was only the case in wild populations, highlighting the importance of ecology for
71 these patterns. This suggests that bold individuals may be of higher quality in general (Moiron et al.,
72 2020), due to their ability to systematically gain more resources than shy individuals (Laskowski et

73 al., 2021). This would enable them to consistently allocate more resources to both current and
74 future reproduction, which could lead to higher survival *and* reproduction overall (Laskowski et al.,
75 2021; Fig. 1B). There is indeed accumulating evidence that the relationship between personality and
76 survival is mediated by variation in resource acquisition, and not so much by resource allocation
77 (Moiron et al., 2020; Laskowski et al., 2021; Haave-Audet et al., 2021).

78 This relationship between personality and resource acquisition is not new and has been
79 previously suggested as a driver of both short- and long-term behavioural consistency under state-
80 dependent models (Luttbeg & Sih, 2010). Under this framework, individuals are expected to express
81 the optimal behaviour based on their underlying state (e.g. body condition, size, energy reserves).
82 Behavioural consistency on the long-term is then maintained by positive feedback loops between
83 state and behaviour (Luttbeg & Sih, 2010; Sih et al., 2015) and thus, these models theorize that
84 variation in animal personality is a consequence of variation in initial state (Luttbeg & Sih, 2010).
85 Under neutral ecological conditions, individuals that are in a high state are expected to behave
86 boldly, and this risk-taking behaviour then maintains their high state due to higher resource
87 acquisition (Luttbeg & Sih, 2010). Low-state individuals, on the other hand, will not be able to
88 behave boldly and therefore make the ‘best out of a bad situation’ by being shy, i.e. risk-averse
89 (Luttbeg & Sih, 2010).

90 Models revolving around among-individual differences in resource allocation (such as POLS),
91 and models revolving around among-individual differences in resource acquisition (such as state-
92 dependent personality models), are not mutually exclusive and even overlap. Both frameworks, for
93 instance, predict a positive relationship between boldness and growth – a prediction which is
94 supported by empirical data (Royauté et al., 2018; Niemelä & Dingemanse, 2018). Where the two
95 types of models differ, however, is in the relationship between personality and survival (Laskowski et
96 al., 2021). If resource allocation is the driver of among-individual patterns, then bold individuals will
97 have shorter lifespans, either due to higher predation or injury risk as a consequence of their risk-

98 taking behaviour, or due to the higher metabolic costs of faster growth rates (Réale et al., 2010;
99 Dammhahn et al., 2018). If, however, resource acquisition is the primary driver of the relationship
100 between personality and survival, then bolder animals are expected to have a similar or even longer
101 lifespan than shy individuals (Laskowski et al., 2021; Haave-Audet et al., 2021). Therefore, we can
102 distinguish between resource allocation and resource acquisition as main drivers of variation in
103 personality, by studying the relationship between behaviour and survival. Although an increasing
104 number of studies have already investigated this relationship, the majority focuses on (sub)adults,
105 with a lack of data on juveniles, especially in free-living mammals. For example, in a recent extensive
106 meta-analysis including 82 studies examining the relationship between behaviour and survival, only
107 3 included juvenile free-living mammals either partly or as the main subject of the study (Haave-
108 Audet et al., 2021). None of these, however, have focused on neonates that were within their first
109 weeks of life.

110 Here we aimed to provide insights into the drivers of personality in juveniles of a free-
111 ranging mammal, of which there is a paucity of data, by investigating the relationship between initial
112 state, neonate personality, and early-life survival of fallow deer (*Dama dama*) fawns. Fallow deer are
113 an excellent fit-for-purpose study species, since neonates display repeatable among-individual
114 differences within days of being born (Amin et al., 2021). Amin et al. (2021) have shown how
115 neonates of this population vary in their coping with human captures in both their physiological (i.e.
116 heart rates at the end of capture) and behavioural (i.e. latency to leave upon release) response.
117 Furthermore, these responses are correlated, with bold (i.e. risk-taking) individuals having lower
118 heart rates and higher latencies than shy individuals (Amin et al., 2021). There is also evidence that
119 neonate personality is related with resource acquisition months later, with individuals that displayed
120 bold behaviour at capture having the opportunity to collect more resources (Amin et al., 2022).

121 Here we specifically tested the relationship between i) initial state (taking birthweights as
122 proxy) and early-life survival and ii) neonate personality and early-life survival. Even though the

123 physiological and behavioural neonate responses are correlated (Amin et al., 2021), we decided to
124 include both metrics in our analysis since a previous study suggests that they can be measuring
125 different traits (Amin et al., 2022). For our first objective, we predicted that neonates with a higher
126 birthweight would be in better condition and, therefore, that they would have a higher chance of
127 survival. For our second objective, we had two separate hypotheses. If among-individual variation in
128 *resource allocation* is the main driver of personality (as predicted under the extended POLS), then
129 we would expect bold individuals to have lower survival than shy individuals (Laskowski et al.,
130 2021; Haave-Audet et al., 2021; Fig. 1A). If, however, patterns between behaviour and survival are
131 driven by among-individual differences in *resource acquisition*, as state-dependent models predict,
132 then we would expect that bold individuals will not have any survival costs and survive just as well or
133 even better than shy individuals (Laskowski et al., 2021; Haave-Audet et al., 2021; Fig. 1).

134 **Methods**

135

136 *Study site and population*

137 We conducted this study in Phoenix Park, a 7.07 km² urban park (~80%: open grassland, ~20% mixed
138 woodland) located in Dublin, Ireland. Within this park, there is a resident population of free-ranging
139 fallow deer, consisting of approximately 600 individuals in autumn, after the birth of fawns. There is
140 a natural segregation between adult sexes, causing adult bucks and does to spend most of the year
141 spatially separated (Ciuti et al., 2004). Neonates are captured and ear-tagged with colour coded tags
142 annually in June, when most births occur. As a result of this marking procedure, an estimated 80% of
143 the population is individually recognizable. Fallow deer are a hider species and fawns remain hidden,
144 usually in tall grass or understory vegetation, away from the main doe herd during the first two-
145 three weeks of life after which they are brought into the doe herd by their mothers (Chapman &
146 Chapman, 1997; Ciuti et al., 2006). Fawns are occasionally predated upon by red foxes (*Vulpes*
147 *vulpes*), the only natural predator in the park, and domestic dogs who are brought into the park by
148 visitors. Deer are culled annually by professional stalkers over the winter period as part of the
149 population management led by the Office of Public Works.

150

151 *Neonate personality at capture*

152 As a part of monitoring and management of the deer in the park, neonate fawns have been routinely
153 captured and ear-tagged with plastic tags (Allflex medium, Mullinahone Co-op, Ireland) on an annual
154 basis in June since the 1970's (Hayden et al., 1992). Fawns were located by patrolling geographical
155 areas typically used by does as fawning sites. After location, fawns were captured and immobilized
156 using fishing nets (1-1.5m diameter; various brands). We tagged a total of 285 fawns over three
157 consecutive years (n = 102 in 2018, n = 83 in 2019, n = 100 in 2020), of which 137 individuals were
158 recaptured at least once. We recorded the following covariates which have been shown to affect
159 neonatal response to handling (Amin et al. 2021): weight (in kg) was measured using a digital scale

160 by laying the fawn in a 100-litre bag (resolution: 0.01 kg – Dario Markenartikelvertrieb, Hamburg,
161 Germany); air temperature was measured at the bed-site location using a digital thermometer
162 (Grandbeing, China). Prior behaviour of the fawn, i.e. its alertness, was scored (*sensu* Amin et al.,
163 2021) on a scale from 0 (inactive) to 1 (active).

164 As measures of neonate personality, we selected a physiological trait (heart rates prior to
165 release, i.e. the physiological response of fawns to human handling) and a behavioural trait (latency
166 to leave upon release), both shown to be repeatable at the among-individual level (Amin et al.,
167 2021). Heart rates were taken directly before the weighting of the fawns and quantified by counting
168 the number of beats per 20 seconds using a Lightweight Dual Head Stethoscope (MDF®, California,
169 USA). The latency to leave (in seconds) on release was defined as the time it took the fawn to stand
170 up after opening the weighing bag. We took 10 seconds as the maximum value and assigned that to
171 individuals that had not moved before then (Amin et al., 2021). For further details of neonate
172 captures, see Amin et al. (2021).

173

174 *Survival data*

175 We acquired survival data by analysing every individual sighting from data collected between the
176 June 2018 and the start of May 2021. The fallow deer population in Phoenix Park was monitored by
177 members of the UCD Laboratory of Wildlife Ecology and Behaviour on a weekly basis by surveying all
178 sectors of the park systematically, following the protocol defined by Griffin et al (*under review*) in
179 addition to concurrent core data collections aimed at monitoring the entire population during key
180 periods of the annual biological cycle (e.g. weaning, rut, antler growth and shed). In total, we
181 collected 19,048 observations of the 285 fawns over the 3 years of study. Due to the large extent of
182 our sample size, we inferred mortality when an individual was not sighted for at least 6 months
183 without being seen at least twice afterwards to account for human error sightings. In those cases, an
184 individuals' last sighting was taken as their potential date of death. Since certain individuals had
185 missing values for some of the variables we used in our models (see statistical analysis), we had to

186 omit them from our analysis. Therefore, the final sample size consisted of 269 individuals, of which
187 176 were alive and 93 dead (Table 1). Out of these 269 fawns, 63 individuals were found dead over
188 the course of this study: in these cases, we used the date on which their carcass was found as the
189 death date.

190

191 *Ethical note*

192 We gave the highest priority to animal welfare during neonate captures. Fawns that were evidently
193 newborn, i.e. with a fully wet coat, were not captured and in such instances, we abandoned searches
194 in that area to avoid disturbing the fawn. Individuals of the capture team always wore gloves during
195 handling to prevent the transfer of human odours to the fawn (Galli et al, 2008). We operated in
196 utmost silence during animal handling and left the bed-site immediately after the release of the
197 fawn. Fawns were released in a location adjacent to the capture site and facing in a direction away
198 from the capture team. The survival data collection was entirely observational, where observers
199 kept a minimum distance of 50m from the deer to limit disturbance. The study protocol and all
200 research procedures were approved by the Animal Research Ethics Committee (University College
201 Dublin) under permit number AREC-E-18-28. All methods were in accordance with the Guidelines for
202 the treatment of animals in behavioural research and teaching (Animal Behaviour, 2020).

203

204 *Statistical analysis*

205 To study the relationship between survival, initial state (birthweight) and neonate personality, we
206 ran a cox proportional hazards model. We report below a step by step explanation on how we
207 estimated birthweights for each individual (section 'predicting birthweights'), how we computed
208 neonate response at the among-individual level (section 'neonate personality'), and how we built
209 and ran the survival model (section 'survival model'). All analyses were performed in RStudio
210 (Version 1.3.1093) using R version 4.0.2 (R Core Team, 2021).

211

212 *Predicting birthweights*

213 Fawns were captured once or multiple times during their first 2 weeks of life. In order to calibrate
214 the capture weights of the fawns to a comparable birthweight (i.e. day 1 estimate), we ran a linear
215 mixed-effects model (lme4-package; Bates et al., 2015), which was then subsequently used to
216 predict birthweights for each individual fawn. We used the weights as the response variable, the
217 estimated age in days at capture (both linear and quadratic term) as a fixed factor, and included
218 fawn ID as a random intercept. We ran this model on data collected over three subsequent years,
219 which consisted of a total of 459 captures on 275 individuals. Our model explained most of the
220 variation in weight ($R^2_{\text{marginal}} = 0.56$; $R^2_{\text{conditional}} = 0.93$; Table S1), with weight at capture being mostly
221 explained by our estimate of age and individual variation (i.e. the random intercept). We therefore
222 used this model to predict the birthweight of the fawns that we have included in our survival
223 analysis.

224

225 *Neonate personality*

226 Because of the inability to incorporate repeated measures into covariates of a cox proportional
227 hazards model, we opted to use the best linear unbiased predictors (BLUPs) extracted from
228 univariate models for both the heartrates as well as the latency to leave at capture. In both cases,
229 we used the same model structure as in our previous study (Amin et al., 2021). For the heartrates,
230 the model included prior behaviour (both linear and quadratic term), time of the day (in hours),
231 weight, and air temperature as explanatory variables. For latency to leave, the model included the
232 capture number, prior behaviour, and weight (both linear and quadratic term) as explanatory
233 variables. Fawn ID was used as a random intercept for both models. To improve model convergence,
234 all numerical explanatory variables were scaled prior to analysis, such that each variable was centred
235 at their mean value and standardised to units of 1 phenotypic standard deviation. Full details of the
236 univariate models are given in the supplementary material (Supplementary S1).

237 The use of BLUPs in behavioural ecology has been criticized before, due to uncertainty around the
238 mean not being taken into account (Hadfield et al., 2010; Houslay & Wilson, 2017). As a solution, it
239 has been proposed to take forward the uncertainty, by using a posterior distribution instead of just
240 the BLUP (Hadfield et al., 2010). A recent study using simulations has indeed shown that such a
241 solution reduces uncertainty, but in the process introduces a negative bias (Dingemanse et al.,
242 2020). We therefore have decided to use the BLUPs as a measure of among-individual responses,
243 which have increased uncertainty but do not suffer from this systematic bias.

244

245 *Survival model*

246 We modelled mortality risk by running a cox proportional hazards model using the *survival* package
247 (Therneau & Grambsch, 2000). The model included predicted birthweight (full details above),
248 heartrate and latency to leave at capture (both as BLUPs, see above) as main predictors. In addition,
249 we included birthyear (categorical, 3 levels), sex (categorical, 2 levels) and birthdate (categorical, 3-
250 levels i.e. early, mid, and late fawning season) as fixed factors due to their potential as confounding
251 variables. Individuals that were still alive by the end of the data collection were right-censored (Klein
252 et al., 2003), but this was at a different moment in the lifetime for each cohort due to the nature of
253 our study (Table 1). The proportional hazards assumption was checked and the Schoenfeld residuals
254 were plotted. Additionally, the linearity of the variables and the presence of outliers in the data were
255 checked using the *survminer* package (Kassamara et al., 2021). In all cases, model assumptions were
256 successfully met. Survival plots were also made using the *survminer* package (Kassamara et al.,
257 2021), which were used for visualisation purposes only. We considered an effect statistically clear
258 when the 95% Confidence Interval of the Adjusted Hazard Ratio (AHR) did not overlap with 1.

259

260 **Results**

261 We found that birthweight had a statistically clear positive effect on survival (Table 2; Fig 2A).

262 Individuals that were heavier at birth had a lower risk of early-life mortality (AHR= 0.73, 95% CI

263 [0.55, 0.97], $p = 0.032$, $n = 269$). In terms of neonate personality traits, we found that heartrates
264 were positively associated with mortality (Table 2; Fig 2B). Individuals with higher heartrates at
265 capture had an increased risk of early-life mortality (AHR= 1.40, 95% CI [1.00, 1.94], $p = 0.048$, $n =$
266 269). There was, however, no statistically clear effect of the behavioural response, i.e. latency to
267 leave, with early-life survival (Table 2; Fig 2C). We also found no statistically clear effect of our other
268 explanatory variables, i.e. birthyear, sex, and birthdate, on early-life mortality risk (Table 2).

269 **Discussion**

270

271 Although animal personality is a widespread phenomenon that plays a key role ecology and
272 evolution (Wolf & Weissing, 2012), the underlying drivers of this variation are still subject to debate.
273 This is mainly centred on whether resource allocation or acquisition is the main driver of among-
274 individual differences in behaviour (Laskowski et al., 2021). Differentiation between these two can
275 be made by relating personality to survival (Laskowski et al., 2021; Haave-Audet et al., 2021; Fig 1).
276 Models assuming differences in resource allocation to be underlying behavioural differences expect
277 trade-offs between behavioural types (Réale et al., 2010), whereas models assuming resource
278 acquisition as underlying driver expect bold individuals to be better off, due to differences in initial
279 state (Luttbeg & Sih, 2010). Here we present empirical data on this matter, in a population of free-
280 ranging fallow deer. We found that individuals with i) a higher birth weight – our proxy for initial
281 state – and ii) a bold physiological response had a higher probability of early-life survival, whereas
282 there was no clear effect of the behavioural response of neonates on survival. Altogether, our results
283 suggest that among-individual differences in resource acquisition, and not allocation, play a major
284 role in maintaining variation in early-life personality.

285

286 Birth weights have been shown to be positively associated with early survival in many different
287 species in a broad range of taxa (e.g. Clutton-Brock et al., 1987; Cabrera et al., 2012; Maniscalco,
288 2014), making it a suitable proxy for initial state. Our results support these previous findings; with
289 every kg increase in birth weights, fawns had a 27% increase in survival. Although birth weights can
290 be related to abiotic factors (Albion et al., 1983), there is a robust body of evidence that connects
291 offspring birth weight to maternal condition or traits (Carrión et al., 2008, Kertz et al., 1997,
292 Paputungan & Makarechian, 2000; Griffin et al., *under review*). In this population specifically, Griffin
293 et al. (*under review*) have previously shown how among-individual differences in maternal behaviour
294 are associated with fawn birth weights. Mothers that have increased interactions with park visitors,

295 i.e. beg for food more, tend to deliver fawns with higher birth weights (Griffin et al., *under review*).
296 Griffin et al. (*under review*) suggested that this effect on fawn birth weight could imply artificial
297 selection through human wildlife interactions, if birth weights are associated with survival, an effect
298 that we provide support for here.

299

300 During stressful situations, individuals tend to have an increase in the activity of the hypothalamic–
301 pituitary–adrenal (HPA) axis. The HPA-axis causes an increase in circulating glucocorticoid (GC)
302 levels, which in turn also leads to higher cardiac activity (Sapolsky et al., 2000). Individuals typically
303 differ in the strength of this response, which is usually related to their behavioural response
304 (Koolhaas et al., 1999). Here we investigated whether among-individual differences in heart rates
305 during capture were related to early-life survival. High heart rates were previously shown to be
306 associated with high chronic hair cortisol levels and a shy behavioural response, i.e. low latency to
307 leave (Amin et al., 2021). Individuals with a strong physiological response are therefore more stress-
308 sensitive, since they adopt a more active coping response during capture and handling by humans, a
309 potential predator. We show that neonates with high heart rates during capture had a lower
310 probability of survival. This indicates that individuals that are more stress-sensitive, i.e. have a
311 stronger physiological response during capture, are less likely to survive. Previous studies have
312 shown a similar pattern in juveniles of other species, where high levels of GC were also negatively
313 associated with survival. In white-tailed deer (*Odocoileus virginianus*) for instance, higher baseline
314 salivary cortisol was associated with lower survival at 12 weeks, although sample sizes were very low
315 (Gingery et al., 2021). Similarly, juvenile European white storks (*Ciconia ciconia*) that had higher
316 levels of blood GCs also had lower survival rates (Blas et al., 2007). Here we have shown that these
317 effects are also present at the among-individual level in neonates.

318

319 Boldness has been suggested to be associated with increased mortality (Bremner-Harrison et al.,
320 2006; Smith & Blumstein, 2008; Greenberg & Holekamp, 2017); by being bold, individuals are more

321 exposed to risks of injury or predation. Recent meta-analyses have, however, failed to confirm that
322 boldness is associated with lower levels of survival (Moiron et al., 2020; Haave-Audet et al., 2021)
323 and there is even ample evidence that it can be associated with higher levels of survival (Réale &
324 Festa-Bianchet, 2003; Réale et al., 2009; Sinn et al., 2014; Haage et al., 2017). Still, very little is
325 known about how these patterns apply to neonates of free-living mammals, a study group that has
326 rarely been focused upon. In the context of this study, we found no clear effect of among-individual
327 differences in the behavioural response of neonates on survival. Individuals that behaved boldly did
328 not suffer from any survival costs. This is contrary to what is predicted under models where resource
329 allocation is the main driver of behavioural differences (Laskowski et al., 2021). It is possible that the
330 lack of a clear negative pattern is due to the low predation risk in this population, since predation
331 has been shown to be an important factor in relationships between behaviour and survival (Réale &
332 Festa-Bianchet, 2003; Dhellemmes et al., 2021). It is, however, important to note that under the
333 resource allocation models, boldness should still be expected to be negatively related to survival
334 even with low predation, since bold individuals are supposed to allocate less resources to survival in
335 general (Réale et al., 2010). Therefore, we found no support for resource allocation as the main
336 driver of among-individual variation in neonate fallow deer.

337

338 Previous studies have shown how certain personality types can be more vulnerable to predation
339 (e.g. Réale & Festa-Bianchet, 2003; Ciuti et al., 2012; Brodin et al., 2019), which has been suggested
340 as a key mechanism in maintaining variation. We found here that bold individuals had a higher
341 chance of survival, although the relationship with survival was only present in the physiological
342 response (i.e. heart rates) and not with the behavioural response (i.e. latency to leave). This is
343 surprising since previous research has shown that these physiological and behavioural responses are
344 related to each other during capture (Amin et al., 2021). Furthermore, the behavioural response of
345 these neonates has been previously shown to be related to among-individual differences in time
346 spent scanning months later, allowing bolder individuals to spend more time on resource acquisition

347 (Amin et al., 2022). The lack of a pattern in the behavioural response suggests that the survival
348 patterns reported here are not due to differences in predator exposure or predator interactions.
349 Rather, since survival was related to the physiological response, our findings imply that this response
350 may be linked to the internal state of individuals. In this case, a bolder physiological response (i.e.
351 lower heart rate) was related to higher survival, suggesting that boldness is positively associated
352 with state, as predicted by state-dependent theory (Luttbeg & Sih, 2010). The findings presented
353 here, in combination with previous work on neonates in this population (Amin et al., 2021; 2022),
354 provide a mechanistic overview of how personality can affect life-history, through resource
355 acquisition (Fig. 3).

356

357 In conclusion, we have studied the relationship between neonate personality and survival for the
358 first time in a free-ranging mammal population, aiming to provide novel insights into the drivers of
359 variation at the individual level. We found a positive relationship between boldness in neonates and
360 their survival during the first years of life. However, survival was only related to their physiological
361 and not their behavioural response at capture. These patterns suggest that, in this context, bold
362 neonates may have higher state, and therefore be of higher quality than their shy conspecifics. Our
363 results provide no support for resource allocation as the main driver behind among-individual
364 differences, as boldness did not have a survival cost. Rather, the patterns we report here are
365 coherent with models that have resource acquisition as the main driver of individual variation
366 (Laskowski et al., 2021).

367

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- 502

503 **Tables**

504

505 **Table 1:** *Overview of the individually recognizable fallow deer fawns that were monitored for survival*
506 *over the period of June 2018-May 2021. “Still alive” and “dead” refer to the survival status of the*
507 *fawns by May 2021, ergo a different monitoring period for fawns belonging to different cohorts.*

Cohort	Individuals	Still alive	Dead	Time observed
2018	93	45	48	31 months
2019	80	50	30	21 months
2020	96	81	15	9 months
Total	269	176	93	-

508

509 **Table 2:** Summary table of the cox proportional hazard model. We have given the Adjusted Hazard
510 Ratio (AHR) \pm 95% CI for each explanatory variable in our model. AHR values below 1 indicate a
511 decreased risk of mortality, whereas AHR values below 1 indicate an increased risk of mortality for
512 each increasing unit of the responding explanatory variable. Additionally, we have also provided the
513 z-value for each variable. The model was run on a sample size of 269 individuals of which 176 were
514 still alive by the end of the sampling period. Statistically clear effects are displayed in bold.

Explanatory variables	AHR	[95% CI]	z-value
Birthweight	0.73	[0.55, 0.97]	-2.14
Heartrate	1.40	[1.00, 1.94]	1.98
Latency to leave	1.21	[0.66, 2.22]	0.62
Birthyear (2019)	0.86	[0.52, 1.44]	-0.56
Birthyear (2020)	0.74	[0.38, 1.44]	-0.89
Sex (m)	1.16	[0.76, 1.78]	0.68
Birthdate (mid)	1.24	[0.75, 2.07]	0.83
Birthdate (late)	1.49	[0.89, 2.50]	1.50

515

516 **Figure legends**

517 **Figure 1:** Alternative scenarios of the relationship between risk-taking behaviour and resource
518 allocation versus acquisition and the patterns they generate between behaviour and growth (top
519 row), and between behaviour and survival (bottom row). Under every scenario, risk-taking behaviour
520 is associated with increased growth (top row). However, each scenario generates a different pattern
521 between behaviour and survival. In A), among-individual differences in behaviour relate mostly to
522 differences in resource allocation. Individuals that display more risk-taking behaviour allocate more
523 towards current reproduction and therefore have increased growth, but reduced survival. In B),
524 among-individual differences in behaviour relate mostly to differences in resource acquisition.
525 Individuals that display more risk-taking behaviour acquire more resources and are therefore able to
526 maintain high state, leading to higher growth and survival. In C) among-individual differences in
527 behaviour relate to differences in resource allocation and acquisition. In this case, risk-taking
528 individuals will also have increased growth, but without the cost of survival. A trade-off between
529 behavioural types, where both extremes (bold vs shy) have equal reproductive output overall is only
530 present under scenario A, whereas under scenarios B and C risk-taking individuals acquire or
531 maintain higher overall quality without paying any survival costs. Figure is largely inspired by
532 Laskowski et al. (2021).

533 **Figure 2:** Survival plots visualising the effects of A) birthweight, B) heartrates at capture, and C)
534 latency to leave at capture on the early-life survival of fallow deer fawns. Lines are given with 95%
535 confidence intervals to indicate uncertainty. Marks on the lines indicate right-censored individuals,
536 with clusters around day 320 and 690 indicating the end of observation time for cohort 2020 and
537 2019 respectively (Table 1). Statistical inferences cannot be made based on this figure. Categorical
538 distinction into high and low, with the median value as divider, has been made for visualisation
539 purposes only. All inferences have been made on the model output (Table 2), which modelled the
540 effect of these three variables on early-life survival on a continuous scale.

541 **Figure 3:** An overview of the complex relationships between neonate personality, resource
542 acquisition and survival. Neonate physiological (i.e. heart rates) and behavioural (i.e. latency to
543 leave) responses to human capture are repeatable and negatively correlated to each other (see
544 Amin et al., 2021). Despite their correlation, both are related to different aspects of later behaviour
545 or life-history. The behavioural response is related to behaviour later in life, where bold neonates
546 spend less time scanning and have thus more time for resource acquisition (Amin et al., 2022),
547 whereas the physiological response is related to survival, where a bolder physiological response is
548 positively associated with survival (this study). Altogether, this overview shows how personality can
549 affect resource acquisition, with underlying physiological patterns suggesting that personality is also
550 related to state. Here, boldness is positively associated with both resource acquisition and state.