

# Risk-taking neonates do not pay a survival cost in a free-ranging large mammal

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## Abstract

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

## Introduction

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

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

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

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

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

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

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

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

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

## Methods

### *Study site and population*

We conducted this study in Phoenix Park, a 7.07 km<sup>2</sup> urban park (~80%: open grassland, ~20% mixed woodland) located in Dublin, Ireland. Within this park, there is a resident population of free-ranging fallow deer, consisting of approximately 600 individuals in autumn, after the birth of fawns. There is a natural segregation between adult sexes, causing adult bucks and does to spend most of the year spatially separated (Ciuti et al., 2004). Neonates are captured and ear-tagged with colour coded tags annually in June, when most births occur. As a result of this marking procedure, an estimated 80% of the population is individually recognizable. Fallow deer are a hider species and fawns remain hidden, usually in tall grass or understory vegetation, away from the main doe herd during the first two-three weeks of life after which they are brought into the doe herd by their mothers (Chapman & Chapman, 1997; Ciuti et al., 2006). Fawns are occasionally predated upon by red foxes (*Vulpes vulpes*), the only natural predator in the park, and domestic dogs who are brought into the park by visitors. Deer are culled annually by professional stalkers over the winter period as part of the population management led by the Office of Public Works.

### *Neonate personality at capture*

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



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

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

#### *Survival data*

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

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

#### *Ethical note*

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

#### *Statistical analysis*

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

### *Predicting birthweights*

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

### *Neonate personality*

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

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

#### *Survival model*

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

## **Results**

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

## Discussion

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

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

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

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

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

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

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



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

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

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502

## Tables

**Table 1:** Overview of the individually recognizable fallow deer fawns that were monitored for survival over the period of June 2018-May 2021. “Still alive” and “dead” refer to the survival status of the 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	-



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

Explanatory variables	AHR	[95% CI]	z-value
<b>Birthweight</b>	<b>0.73</b>	<b>[0.55, 0.97]</b>	<b>-2.14</b>
<b>Heartrate</b>	<b>1.40</b>	<b>[1.00, 1.94]</b>	<b>1.98</b>
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

## Figure legends

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

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

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