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## Original Article

# Is a proactive mum a good mum? A mother's coping style influences early fawn survival in roe deer

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Individual differences in behavior may strongly shape life-history trajectories. However, few empirical studies to date have investigated the link between behavioral traits and fitness, especially in wild populations. We measured the impact of coping style in female roe deer (*Capreolus capreolus*) on early survival of their offspring. Specifically, we expected offspring of proactive mothers, which should be more mobile and aggressive, to survive better than those of reactive females, which should be more passive and react less in stressful contexts. To test this prediction, we accounted for confounding effects of variation in early survival linked to habitat heterogeneity, as we also expected bed-site selection to impact fawn survival. Fawn survival was highly dependent on the interaction between habitat use and the coping style of the mother. As expected, fawns of proactive mothers survived better in open habitats. However, unexpectedly, fawns of reactive mothers had the highest survival in closed habitats. Our findings provide clear evidence that interindividual differences in the coping style of the mother can markedly impact early offspring survival and, thereby, female fitness, in wild populations of mammals. Moreover, we provide evidence that fitness consequences of coping styles are habitat-dependent, providing a possible mechanism for the maintenance of within-population variation in behavior.

**Key Words:** body temperature, habitat use, individual differences, juvenile survival, maternal care.

## INTRODUCTION

It is increasingly recognized that, within populations, individuals exhibit consistent behavioral differences over their lifetime, and that these differences may have important ecological and evolutionary implications (Wilson et al. 1994; Réale et al. 2007). When these behavioral differences are manifested in stressful situations characterized by risky or challenging environments, they are generally interpreted within the “coping style” framework (Koolhaas et al. 1999). Koolhaas et al. (1999) defined a coping style as “a coherent set of behavioral and physiological stress responses which is consistent over time and which is characteristic to a certain group of individuals.” Two distinct coping styles are generally identified, although these stress responses are more likely best described by a continuum. Proactive individuals are fast explorers, highly aggressive, impulsive in decision-making, novelty seekers and take risks

in the face of potential dangers (Koolhaas et al. 1999, 2010). They are thus assumed to cope actively with the source of stress through a “flight-or-fight” response. In contrast, reactive individuals show the opposite physiological patterns and tend to react to challenges by freezing. From a physiological viewpoint, proactive individuals show a high sympathetic reactivity and a low hypothalamus-pituitary-adrenal (HPA) axis responsiveness compared with reactive individuals (Koolhaas et al. 1999). However, the associations between physiological traits and behavioral traits are still poorly documented. Fast explorers may have a lower HPA (Montiglio et al. 2012), which is associated with increased frequency and variation in heart rate (Visser et al. 2002). Similarly, Groenink et al. (1994) showed that a high rectal temperature reliably indicates stress-induced hyperthermia (SIH), which has been repeatedly associated with personality. For instance, in great tits (*Parus major*), bold individuals (assumed to be proactive, Schjolden et al. 2005) had lower body temperature and respiration rate during handling than shy individuals (Carere and van Oers 2004). It

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is widely recognized that coping styles relate the level of boldness and aggression to the magnitude of the physiological response to stress (Koolhaas et al. 1999; Frost et al. 2013). Consequently, proactive individuals are also assumed to be bold and aggressive, whereas reactive individuals should be shy and less aggressive.

Most work on characterizing coping styles has been carried out under controlled laboratory conditions (Koolhaas et al. 1999; Øverli et al. 2007), whereas evidence from field tests are much scarcer and have so far been conducted on semicaptive populations (e.g., Rödel et al. 2006; Hoffman et al. 2011). Furthermore, there is a crucial lack of empirical studies on the effect of coping styles on individual performance and, hence, on their consequences for population dynamics. From a meta-analysis of studies performed on domestic, captive and wild animals, Smith and Blumstein (2008) concluded that bolder and more aggressive individuals generally have higher reproductive success than shy or less aggressive individuals. For example, in bighorn sheep (*Ovis canadensis*), boldness is positively related to both weaning rate (Réale et al. 2000) and survival (Réale and Festa-Bianchet 2003). Hence, coping styles are likely to be associated with interindividual differences in reproductive success, as reported in the Ural owl (*Strix uralensis*) in which proactive and aggressive females produced more recruits (Kontiainen et al. 2009).

Large herbivores are widespread in most temperate ecosystems and are the subject of a number of detailed long-term monitoring studies of behavior and population dynamics (e.g., Gaillard et al. 2013 on roe deer; Hallett et al. 2004 on Soay sheep *Ovis aries*, Coulson et al. 2004 on red deer *Cervus elaphus*, Garel et al. 2007 on mouflon *Ovis gmelini*, Toïgo et al. 2007 on ibex *Capra ibex*, Servanty et al. 2011 on wild boar *Sus scrofa*). These studies have shown that spatial and temporal variation in juvenile survival is a key component of the population demography of large herbivores in the wild (see Gaillard et al. 2000 for a review). Environmental factors such as predation and population density during the preweaning stage are critical for shaping variation in juvenile survival. Likewise, climatic conditions during late gestation and early lactation also influence juvenile survival through their effects on plant biomass and quality and, thereby, the availability of food for the mother (Gaillard et al. 2000). In addition, maternal physiological and morphological traits such as size, age, and previous reproductive success strongly impact juvenile survival, generating marked individual differences in female reproductive success (Gaillard et al. 2000). However, whether a mother's coping style influences juvenile survival in wild large herbivores remains virtually unknown (Smith and Blumstein 2008).

We aim here to fill this gap in our knowledge of the link between the coping style of the mother and her reproductive success by investigating the impact of individual differences in coping styles of female roe deer on the early survival of their fawns in an intensively studied roe deer population. Roe deer females are income breeders (sensu Jönsson 1997) such that females do not store fat reserves, relying instead on current energy intake to offset the costs of reproduction (Andersen et al. 2000). For income breeders, the trade-off between foraging and risk of predation should be particularly acute (Bongi et al. 2008) because females have to forage intensively while simultaneously minimizing the risk of predation of their offspring (Linnell et al. 1995). Hence, females with newborns generally isolate themselves from conspecifics. This behavior is associated with lower disturbance by conspecifics and reduced risk of predation (Schwede et al. 1993). Females also often range less widely during the first months after parturition (Saïd et al. 2009). Moreover, roe

deer are hidiers (sensu Lent 1974) where, apart from short visits for suckling (3–7 times/day), the fawns lie hidden, secluded from the mother for most of the time up to the age of 6–8 weeks (Espmark 1969). Thus, high female aggressiveness and short mother-fawn distance are associated with increased offspring survival during the hiding phase in open habitats (Panzacchi et al. 2010). Bongi et al. (2008) found that females tend to select denser habitats with high cover and concealment, which may contribute to increase offspring survival. However, the extremely high energetic needs of roe deer females during lactation are expected to constrain them to use habitats where predation risk for fawns is high (Panzacchi et al. 2010). Hence, during the hider phase, a fawn's survival mostly depends on its mother's ranging behavior (van Moorter et al. 2009) and care (Andersen et al. 2000; Gaillard et al. 2000). Maternal care behavior is likely highly variable among individuals (Nowak et al. 2000) but, to our knowledge, although some information is available for birds (Kontiainen et al. 2009; Ringsby et al. 2009; Westneat et al. 2011; Betini and Norris 2012), no study has yet investigated how variation in coping styles among mothers impacts the survival of their offspring in any large mammal in the wild.

When faced with a challenge, proactive individuals are risk-takers that respond with high levels of general activity and aggression and low attack latency, whereas reactive individuals show high attack latency and a lack of initiative (Koolhaas et al. 1999, 2010). Ungulate females aggressively defend and protect their fawns (Truett 1979; Ozoga and Verme 1986; Lingle et al. 2005), and this is also the case in roe deer during attack by foxes (Jarnemo 2004). Consequently, we first hypothesized that the coping style of the mother should influence the survival of her fawns. In the absence of direct observations of maternal roe deer behavior in response to predation in our study area, we assumed that reactive mothers would not defend their fawns as strongly as proactive mothers against predators. Second, we hypothesized that the spatial behavior of the mother should impact the choice of bed-site by the fawn and thus affect its early survival, which is highly dependent on bed-site characteristics (van Moorter et al. 2009). Hence, fawns of females that mostly used habitats with protective cover should have access to the most secure bed-sites and should thereby have higher early survival. Finally, Boon et al. (2007) showed that the aggressiveness of the mother impacted the survival of her offspring in red squirrel (*Tamiasciurus hudsonicus* Erxleben), but that these effects varied across life-history stages and over time (i.e., temporal heterogeneity in the influence of behavior on individual performance). Furthermore, there is also some evidence that specific behavioral profiles occur more frequently in some environments than in others (Dingemanse et al. 2003; Stamps and Groothuis 2010; Pearish et al. 2013). Consequently, we hypothesized that fawn survival should be impacted by the coping style of the mother in a context-specific manner (i.e., spatial heterogeneity in the influence of behavior on individual performance), although we had no clear prediction as to the form of this relationship.

## MATERIAL AND METHODS

### Study site

The study was carried out at Aurignac (7500 ha) in the southwest of France (43°13'N, 0°52'E). The climate is oceanic with Mediterranean tendencies, with an average annual temperature of 11–12 °C and total precipitation of 800 mm. This hilly region is a mixed landscape mostly covered by open habitats interspersed with small woodland patches (mean ± SD: 2.9 ± 7.6 ha) and 2 main

forests (672 ha and 515 ha). Meadows and cultivated fields occupy 31.9% and 36.2%, respectively, of the total surface area of the study site. Woodland covers 19.3 % of the total study site and is dominated by oak (*Quercus spp.*) (see Hewison et al. 2009 for further details).

### Data collection for roe deer mothers

Each winter between 2003 and 2013, roe deer were caught from November to March (i.e., at least 6 weeks before parturition, Gaillard et al. 1993) using drive netting. Roe deer capture and marking procedures were performed according to French laws for animal welfare and approved by the French administration. Once the deer was caught in the net, it was tranquilized with an intramuscular injection of acepromazine (Calmivet 3cc). Then, we transferred the animal to a small wooden retaining box designed to minimize risk of injury and to limit stress. At the end of the capture event, each individual was weighed with an electronic balance, sexed, aged according to tooth eruption, marked with 2 plastic ear tags and equipped with a GPS collar (Lotek 3300 GPS).

Between 2009 and 2013, we recorded the behavior at capture, during handling and at release for 121 females. Of these, 86 were adults (i.e., older than 1 year at first winter capture), which generally give birth every year (Hewison 1996; Andersen et al. 1998). We attributed a score of 1 (occurrence) or 0 (absence) for each of the following behaviors: 1) the individual struggled in the net (see also Réale et al. 2000), 2) it turned upside down in the box, 3) it attempted to remove its collar at release, and 4) it fell (i.e., stumbled and fell to the ground) at release. In addition, we attributed a score of 1 if 5) the individual struggled and panted on the table during marking, or a score of 0.5 if it struggled only (otherwise 0), and a score of 1 (high speed running), 0.5 (moderate running), or 0 (trotting) in relation to 6) its flight behavior at release. Indeed, flight speed at release is commonly used for the assessment of temperament in cattle (Müller and von Keyserlingk 2006). An index of proactivity was then calculated as the sum of the scores for these 6 behavioral items describing a stress profile gradient ranging from 0 to 6, potentially taking 13 different values (9 over the recorded range), with 6 indicating a priori highly proactive individuals. We also measured the rectal temperature for each female (using a Digitemp Color thermometer with a precision of 0.1 °C, potentially taking 36 different values, over the recorded range). Following Montané et al. (2003)'s study showing that body temperature of roe deer decreases over time from capture to 45 min after capture before stabilizing, we recorded temperature more than 1 h after the capture event in all cases. We recorded the temperature of each individual at the beginning and at the end of the marking procedure, and used the mean of these 2 values (difference: range = [-0.4–0.7], mean = 0.1, and median = 0.0) to index the female's stress response based on the existence of a positive correlation between the HPA axis and SIH (Moe and Bakken 1997; Korhonen et al. 2000). Thus, we assumed that a high index of proactivity and a low rectal temperature indicated more proactive individuals, whereas a low index of proactivity and a high rectal temperature typified more reactive individuals.

### Data collection for roe deer fawns

Between 2004 and 2013, newborn fawns (97% less than 20 days old, average age at capture = 6.3 days) were caught by hand each year between the end of April and the middle of June, but more intensively since 2009 (30 fawns caught between 2004 and 2008, with

none in 2005 and 2006, and then 114 fawns caught since 2009), mostly by observing the behavior of the mother. We marked fawns only once the mother had fed it and moved away. We first weighed (with a precision of 50 g), sexed and aged fawns using 3 age-classes (<3, 3–5, and ≥6 days old) and then marked them with 2 metallic ear tags and an expandable very high frequency (VHF) radio collar (Biotrack). The age of fawns was established in relation to daily monitoring of the mother's appearance (size of her belly, presence/absence of udders) and behavior (reaction to a whistle mimicking the call of a fawn), which provided information on the approximate date of birth, and in relation to the fawn's behavior (Jullien et al. 1992). Roe deer females generally give birth to 2 fawns per litter (Hewison and Gaillard 2001), but even when we located both fawns of a single litter, we manipulated and marked only one of the siblings as the fate of litter mates is highly interdependent, especially in poor cohorts (Gaillard et al. 1998). We also recorded the characteristics of the site where fawns were found in terms of habitat type (woodland, crops, natural meadows, or artificial meadows such as ray grass, *Lolium perenne*). Subsequently, fawns were located each day from marking to the end of the summer (1.5 locations per day per individual on average) by radio-telemetry and triangulation. The radio-collars were equipped with a mortality sensor, providing us with information about the current fate of each fawn. When a mortality signal was detected, we immediately recovered the dead animal and, where possible, ascertained the cause of its death.

### Statistical analyses

#### *Proactivity index and rectal temperature of the mother: repeatability and intercorrelation*

Of the 39 mothers, we assessed the within-individual consistency of the proactivity index and of rectal temperature based on a subsample including only the 18 mothers that were caught at least twice between 2009 and 2013 (10 caught twice, 7 caught 3 times, and 1 caught 4 times) by calculating their repeatability with mixed models (Nakagawa and Schielzeth 2010). Bell et al. (2009) reported in a meta-analysis that repeatability of behavioral traits (excluding physiological traits such as body temperature) has an average value of 0.37. Repeatability coefficients, that is, intraclass correlation coefficients, were calculated using the "rpt.remlMM" function of the "rptR" package (Schielzeth and Nakagawa 2011) in R version 2.15.1 software (R Development Core Team 2013), which estimates repeatability as the ratio of between-individual variance to total variance with linear mixed-effects models (with individual identity as a random factor) using the restricted maximum likelihood (REML) method. Because it is widely employed in behavioral ecology, for comparative purposes we also used the Lessells and Boag (1987)'s method to estimate repeatability. Finally, because we had no a priori idea of the expected relationship between temperature and coping style, except for small mammals (Moe and Bakken 1997; Korhonen et al. 2000), we also tested this correlation in our sample of female roe deer.

#### *Early survival of fawns*

To assess the influence of the mother's coping style on early fawn survival, we excluded fawns with unknown mothers and fawns of mothers with missing data for either rectal temperature or the proactivity index. Analyses were thus based on 57 fawns that were monitored over their first spring–summer during 8 different years, belonging to 39 different females. To investigate the relationship between early fawn survival and habitat use, we used the broad scale habitat type in which the fawn was found. We checked that

the habitat type where fawns were found reliably described the habitat used during their first month of life using the VHF locations (between 7 and 37) of fawns collected during that period. On average, 75% of these locations fell within the habitat recorded at marking. In addition, we accounted for possible confounding effects of age, body development at capture, cohort effects, and spring weather conditions, all of which have been reported to influence markedly early survival of roe deer fawns (Gaillard et al. 1997; da Silva et al. 2009). Body development was calculated from the residuals of the simple linear regression between age and body mass at capture (see Gaillard et al. 1993 for further details). We tested for cohort effects by including the year of birth of the 57 fawns. To assess annual spring weather conditions, we used the number of degree-days higher than 7 °C from February to April as a proxy of the precocity of spring which has recently been shown to affect strongly roe deer population dynamics (Gaillard et al. 2013), and especially early fawn survival (Plard et al. 2014).

We estimated early fawn survival by fitting Cox proportional hazard models, which are the most widely used in multivariate analyses of survival (Cox 1972; Therneau and Grambsch 2000). The model was written as:

$$h(t) = \exp(\beta_1 X_1 + \dots + \beta_p X_p) h_0(t) \quad (1)$$

where  $h(t)$  is the hazard function at time  $t$  and measures the risk that a fawn dies at a given time,  $X_p$  are the covariates influencing early fawn survival (i.e., age, early body development and number of degree-days in the baseline model, plus rectal temperature and proactivity index of the mother, plus certain 2-way interactions in the most complex model),  $\beta_p$  are the regression coefficients of these respective covariates, and  $h_0(t)$  is the baseline hazard function. We carried out the analyses on the first 105 days of the fawns' life, which roughly corresponds to the period from the median date of parturition to weaning. We added the age at capture of each fawn to the total number of days of monitoring, allowing us to start the analyses from the birth date of each fawn.

The baseline model included the fawn's age at capture (discrete variable, 3 modalities), its index of body development (continuous variable, range = [-718.0–490.1], mean = 0.00, and median = 6.097) and the number of degree-days higher than 7 °C in the spring of capture (continuous variable, range = [55–64], mean and median = 59.5). Then, we investigated the potential effect of the mother's coping style on the survival of her offspring by adding the mother's proactivity index (continuous variable, range = [0.0–4.0], mean = 2.07, and median = 2.00) and the mother's rectal temperature (continuous variable, range = [37.0–40.5 °C], mean = 38.75 °C, and median = 38.80 °C) to the baseline model. In addition, we tested for the potential effect of habitat use on early survival by adding the habitat type recorded at fawn capture to the baseline model (discrete variable, 4 modalities: woodland, crops, natural meadows, and artificial meadows). Finally, because early fawn survival may be impacted by the coping style of the mother in a context-specific manner, either across space or through time (Smith and Blumstein 2008), we also tested for the effects of the four 2-way interactions between the mother's proactivity index with both habitat type and cohort, and between the mother's rectal temperature with both habitat type and cohort on early fawn survival. In all cases, models that included an interaction also included the main effects of the variables involved in that interaction.

We checked the assumption of proportional hazards that is critical to Cox proportional models through an analysis of residuals (Grambsch and Therneau 1994). We used model diagnostics based

on scaled Schoenfeld residuals and checked the hypothesis of log-linearity and identified the most influential observations. Model selection was based on the second order Akaike's Information Criterion (AICc, Burnham and Anderson 2002) and Akaike weights to identify the model that best described the data. All analyses were performed in R version 2.15.1 (R Development Core Team 2013) using the survival package (Therneau 2014).

## RESULTS

### Proactivity index and rectal temperature of the mother: repeatability and intercorrelation

The proactivity index did not deviate from a Gaussian distribution on a statistical basis ( $W = 0.960$ ,  $P$  value = 0.086), ranging between 0.0 and 4.0, with a median value of 2.0 and a mean of 2.1. The rectal temperature was also normally distributed ( $W = 0.980$ ,  $P$  value = 0.474), ranging between 37.0 and 40.5 °C, with both a median and a mean of 38.8 °C. There was suggestive evidence for consistent individual differences in the proactivity index (rpt. remLMM method:  $r = 0.201$ , 95% confidence interval = [0, 0.592]; Lessells and Boag method:  $r = 0.193$ , 95% confidence interval = [0.027, 0.636]). In contrast, rectal temperature was highly repeatable (rpt. remLMM method:  $r = 0.704$ , 95% confidence intervals = [0.185, 0.909]). Rectal temperature and the proactivity index were weakly, but significantly from a statistical viewpoint, positively correlated across mothers ( $P$  value = 0.037,  $r = 0.26$ , Appendix 1).

### Early fawn survival

Overall, 25 out of 57 (43.9%) fawns survived to 105 days. Of the 32 fawns which died, 10 died from predation, 4 died due to poor maternal care (abandonment, malnutrition), 7 died from human activity causes (5 from mowing and 2 from vehicle collisions), 3 died due to health problems (disease, cachexia), 2 died from accidents (falling into a ditch), and 6 died from unknown causes. There was no statistically significant variation in the proactivity index of the mother among these 6 categories of mortality causes ( $F_{5,26} = 2.05$ ,  $P$  value = 0.10). However, mothers whose fawns were predated tended to have a lower proactivity index than those whose fawns died of other causes ( $F_{1,30} = 2.93$ ,  $P$  value = 0.10). There was also no statistically significant relationship between the proactivity index of the mother and the age of the fawn at capture ( $F_{2,54} = 0.87$ ,  $P$  value = 0.43), indicating that there was no age-related sampling bias with respect to maternal coping style that might explain any link between fawn survival and the proactivity index. Similarly, there was no evidence of any habitat-related sampling bias because fawns were distributed more or less randomly across habitat types with respect to the proactivity index of their mother (see Appendix 2).

In addition to the baseline factors (number of degree-days > 7 °C, age at capture, early body development) that all influenced early fawn survival, the Cox proportional hazard model of early fawn survival with the highest support included the 2-way interaction between habitat type and proactivity index of the mother, plus an additive effect of mother's rectal temperature (AICc = 217.10,  $\Delta$ AICc = 2.16, AICc weight = 0.55, Table 1).

As expected, early survival decreased with time, with the sharpest decrease in survival occurring during the first 20 days of the fawns' life (Appendices 3, 4, 5). All things being equal, fawns that were older ( $\geq 6$  days old) at capture survived better than younger (<6 days old) fawns (93% of fawns vs. 53% of fawns reached

105 days of life, Appendix 3). As expected, fawns with a fast body development survived better than fawns with slow body development (68% of fawns for the heaviest fawns vs. 1% of fawns for the

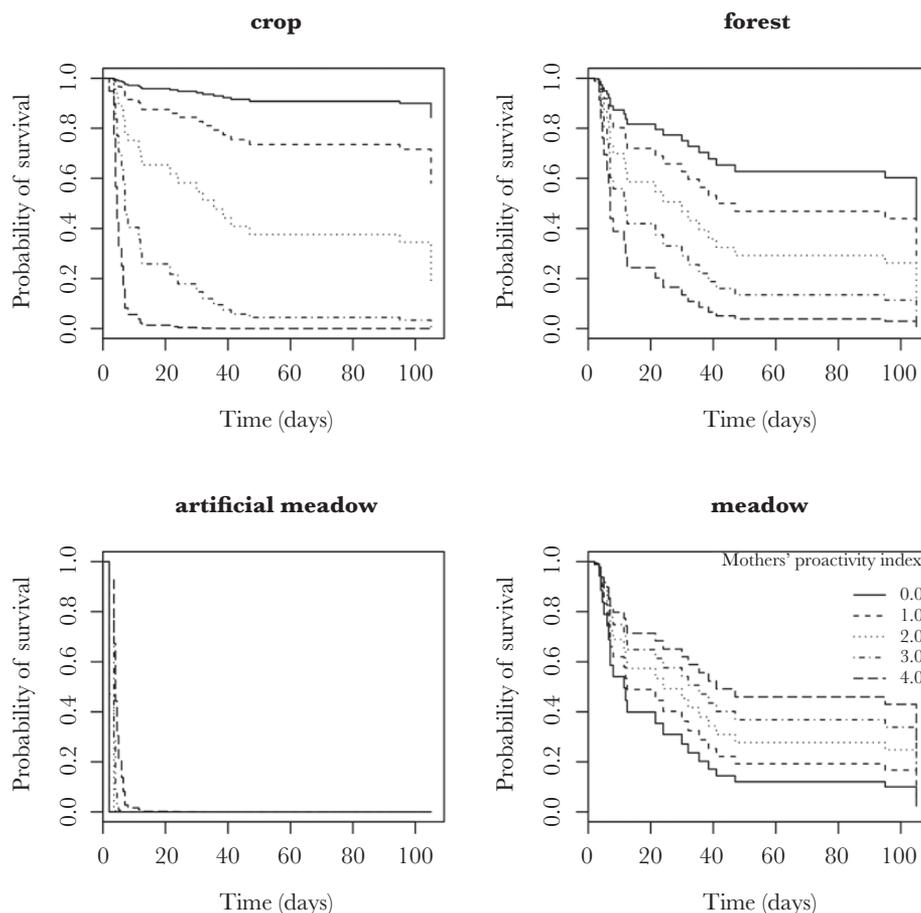
lightest fawns reached 105 days of life, Appendix 4). Likewise, as expected, early survival of fawns decreased with increasing number of degree-days (7% of fawns at 64 degree-days vs. 94% of fawns at 47 degree-days reached 105 days of life, Appendix 5).

**Table 1**  
**Candidate Cox proportional hazard models fitted to investigate variation in the probability of fawns surviving to 105 days of age**

Models	<i>K</i>	AICc	ΔAICc	AICcWt
Baseline model + habitat × PI + <i>T</i>	12	217.10	0.00	0.55
Baseline model + habitat + PI + <i>T</i>	9	219.26	2.16	0.32
Baseline model + cohort + habitat × PI + <i>T</i>	16	220.29	3.20	0.09
Baseline model + cohort	8	223.93	6.83	0.01
Baseline model + habitat × PI + habitat × <i>T</i>	15	224.64	7.54	0.01
Baseline model + PI + habitat × <i>T</i>	12	224.82	7.73	0.01
Baseline model + cohort + habitat + PI + <i>T</i>	13	226.81	9.71	0.01
Baseline model	4	228.70	11.60	0

The baseline model includes the number of degree-days, early body development, and the fawn's age at capture. To this baseline model, we then added the cohort effect (cohort), the proactivity index of the mother (PI), and the rectal temperature (*T*) of the mother, as well as the habitat type where the fawn was caught (habitat). AICc is the value of the corrected Akaike's Information Criterion and *K* is the number of estimated parameters for each model. The ranking of the models is based on the differences in the values for ΔAICc and on the Akaike weights. Only models with an AICc lower than that of the baseline model are presented.

In addition to this support for the variables in our baseline model, we found that habitat type and proactivity index of the mother both shaped early fawn survival. Fawns born to mothers with a high proactivity index survived much better than fawns born to mothers with a low proactivity index when they principally used natural meadows (44% of fawns for mothers with a proactivity index of 4.0 vs. 10% of fawns for mothers with a proactivity index of 0.0 reached 105 days of age, Figure 1). In contrast, early survival was lower for fawns born to mothers with a high proactivity index than for fawns born to mothers with a low proactivity index when they principally used either forest (4 % of fawns for mothers with a proactivity index of 4.0 vs. 61 % of fawns for mothers with a proactivity index of 0.0 reached 105 days of age) or crops (0 % of fawns for mothers with a proactivity index of 4.0 vs. 90 % of fawns for mothers with a proactivity index of 0.0 reached 105 days of age). No fawns born to mothers that principally used artificial meadows survived beyond 12 days of age (*N* = 6), irrespective of the proactivity index of their mother. In addition, fawns born to mothers with a low rectal temperature survived slightly less well (33% of fawns for mothers with a rectal temperature of 37.0 reached 105 days of age) than fawns born to mothers with a high



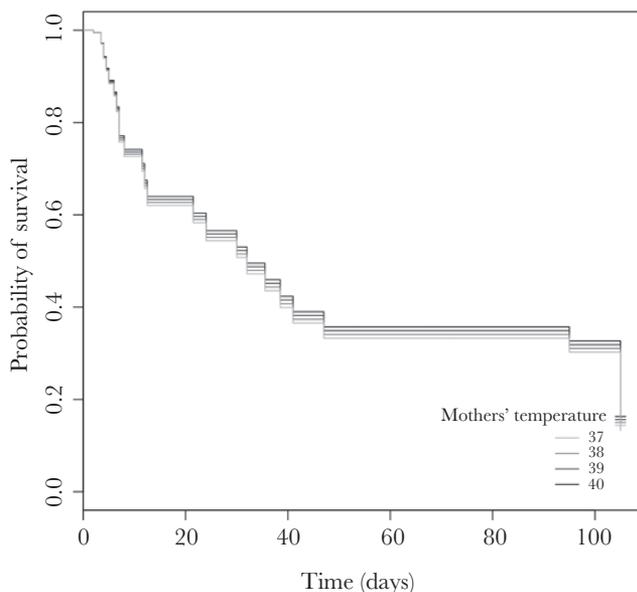
**Figure 1**  
 Probability of a roe deer fawn surviving to 105 days of life in relation to the proactivity index of its mother and to the habitat type (4 modalities: crops, forest, artificial meadows, natural meadows) in which the fawn was found. The proactivity index potentially varies between 0 and 6, but the highest observed value was 4. This representation was obtained from the best model that included the baseline factors (number of degree-days, early body development, fawn age at capture), the interaction between habitat type and the proactivity index of the mother, plus an additive effect of the mother's rectal temperature.

rectal temperature (37 % of fawns for mothers with a rectal temperature of 40.0 reached 105 days of age, [Figure 2](#)). Finally, contrary to our expectation, we found no evidence for a cohort effect on early survival, and no temporal variation in the influence of the mother's proactivity index or rectal temperature on early survival.

## DISCUSSION

### Overview

The central aim of our study was to investigate how variation in the mother's coping style and space use impact the early survival of her offspring. We detected consistent individual differences in both behavioral and physiological components of coping style, with roe deer mothers ranking along a continuum of the proactive-reactive response to stress. As expected, we found that the coping style of the mother affected early survival of her fawns. However, the pattern of variation in early fawn survival in relation to the coping style of their mother was context-specific. Compared with more reactive mothers, mothers with a more proactive coping style were more likely to wean a fawn in open meadows, but less likely to do so in forest or crops. Our findings therefore demonstrate that inter-individual differences in the coping style of mothers have a habitat-specific influence on offspring survival, and hence on female fitness, in wild populations of mammals. [Boon et al. \(2007\)](#) found that maternal personality impacted both survival and growth rate of offspring in red squirrels, but that these effects varied across life-history stages and among years, that is, temporal heterogeneity in the influence of personality on individual performance. Here, we detected spatial heterogeneity in the influence of the coping style of mothers on an important fitness component, early offspring survival, in roe deer. We suggest that both these forms of heterogeneity



**Figure 2**

Probability of a roe deer fawn surviving to 105 days of life in relation to the rectal temperature of its mother. We used a Cox proportional hazard model with temperature as an explanatory variable with values ranging between 37 and 40 °C. This representation was obtained from the best model that included the baseline factors (number of degree-days, early body development, and fawn age at capture), the interaction between habitat type and the proactivity index, plus an additive effect of the mother's rectal temperature.

may potentially contribute to the maintenance of behavioral variation in wild populations.

### Proactivity index and rectal temperature of the mother: repeatability and intercorrelation

In a meta-analysis, [Bell et al. \(2009\)](#) reported that behavioral traits are generally repeatable with an average value of 0.37. In comparison, relative to this average value for repeatability, we found that the level of proactivity was only a moderately repeatable trait ( $r = 0.201$ ,  $CI = [0, 0.592]$ ), whereas rectal temperature was highly repeatable ( $r = 0.70704$ ,  $CI = [0.185, 0.909]$ ). In addition, in our study, these 2 maternal traits covaried positively, although the relationship was weak. The fact that the correlation between rectal temperature and the proactivity index was positive was unexpected based on previous studies on small mammals ([Moe and Bakken 1997](#), [Korhonen et al. 2000](#)), but there has been no equivalent study to date on ungulates. This unexpected result could be due to the fact that body temperature at capture reflects the combination of 2 physiological components: in a nonstressed situation, body temperature is a proxy of individual metabolic rate ([Biro and Stamps 2008](#)), whereas in a situation of stress, body temperature rises and indicates "SIH" ([Bakken et al. 1999](#); [Korhonen et al. 2000](#)). Hence, temperature at capture might reflect the effects of among-individual differences in metabolic rate modulated by the stress response (see [Debeffe et al. 2014](#)).

Phenotypic correlations among such traits are typical of the proactive-reactive syndrome ([Koolhaas et al. 1999](#); [Sih et al. 2004](#)). We thus identified a gradient of coping style, varying from mothers with a marked behavioral (i.e., a high proactivity index) and physiological (i.e., a high rectal temperature) response to capture (i.e., the most proactive) to those with a low level of response (i.e., the most reactive). We have recently shown elsewhere that both this proactivity index and rectal temperature contribute to shape a dispersal syndrome among juvenile roe deer ([Debeffe et al. 2014](#)) and a risk management syndrome among adults ([Bonnot et al. 2015](#)), suggesting that they reliably index consistent interindividual variation in behavior. However, further work on a larger sample size will be necessary to obtain reliable estimates of repeatability for these traits so as to better apprehend how well they index a behavioral syndrome in roe deer more generally.

### Early fawn survival in relation to age, body development, and spring conditions

The results from our baseline model support previous studies that reported effects of age, body development and spring conditions on early survival in populations of large herbivores (see [Gaillard et al. 2000](#) for a review). Older fawns at capture survived better than younger ones. In large herbivores, most mortality occurs within the first few weeks of life (e.g., [Guinness et al. 1978](#)). Within this critical period, the mortality risk is especially high during the first few days of life, when newborns are subject to thermoregulation problems, abandonment by the mother, disease, and, in some hider species, predation because newborns are immobile and isolated from the mother for most of the time. High quality and quantity of food resources are key for early survival in most large herbivores ([Gaillard et al. 2000](#)), which grow very fast from birth to weaning ([Pontier et al. 1989](#)). Using the number of degree-days as a proxy of plant phenology ([Plard et al. 2014](#)), we found that fawn survival decreased with increasing number of degree-days. Energetic needs of mammalian mothers peak during late pregnancy and early

lactation (Clutton-Brock et al. 1989) so that the match between maternal energy requirements and the peak of resource availability is crucial to offspring survival. As roe deer birth timing is highly repeatable (Plard et al. 2013) and quite constrained (Gaillard et al. 2013), early vegetation flush leads to an increase in early fawn mortality (Plard et al. 2014) and, thereby, to lower population growth rate (Gaillard et al. 2013). These negative effects of early springs were reported for forest roe deer, but our study indicates that this relationship holds even for populations living in more open landscapes. Likewise, our results also support previous observations of a positive influence of fast early body development on early survival of roe deer fawns in forest populations (da Silva et al. 2009).

### Early fawn survival in relation to the mother's coping style and habitat type

The neonatal period is a critical phase for juvenile survival in most mammals and depends heavily on the nature and quality of the interactions between the mother and her offspring (Nowak 1996). In some species, mothers or other members of the group may actively defend the young (Leuthold 1977), sometimes directly attacking a predator and/or attempting to disrupt its chase (Jarnemo 2004; Lingle et al. 2005). These antipredator behaviors vary in relation to the hunting tactic of the predator (ambush vs. coursing), predator abundance and diversity, and habitat type. For example, Panzacchi et al. (2010) concluded that meadows are an especially risky habitat for roe deer fawns because the density of small rodents is generally high. Because of this, meadows are hunting hot spots for red foxes (*Vulpes vulpes*), so that predation risk of fawns is likely to be higher in this habitat. Our findings support this hypothesis, as fawns born to more proactive mothers survived better than those born to more reactive mothers when in open meadow habitat (natural meadows). We suggest that this is because, when attacked by fox, proactive mothers are more mobile and aggressive, and so successfully defend their fawn, compared with reactive mothers who are more passive and display a high attack latency. However, none of the 6 fawns monitored in artificial meadows survived beyond 12 days of age, irrespective of the mother's coping style. This presumably occurred because fawns in this habitat type were killed by mowing, the second most important mortality factor for roe deer fawns in agricultural landscapes (Jarnemo 2002). In contrast, in closed habitats (i.e., forest and crops), fawns born to more proactive mothers survived less well than those born to more reactive mothers.

The marked influence of habitat type on the success of a given mother's coping style that we describe above is likely related to habitat-specific differences in the trade-off between resource acquisition and predation risk (Bongi et al. 2008; Boon et al. 2008). The requirement for high quality forage is particularly acute for income breeders like roe deer (Bongi et al. 2008), so that risky tactics (e.g., in terms of exposure to fawn predation risk) may potentially be the most rewarding in terms of fitness. The quality of food resources for roe deer is far better in open habitats (Hewison et al. 2009; Abbas et al. 2011), so that females should preferentially select meadows. However, the risk of predation is also highest in open habitats (Panzacchi et al. 2010). As a result, females raising their fawns in meadows play a high risk-high benefit tactic, where the pay-off is greater if females actively defend their fawns. Our results indicate that this is the case for more proactive mothers who are better able to raise their fawns successfully in high risk open meadows, presumably because they respond more actively to the attack of a predator by actively defending their fawns (Jarnemo 2004), but also possibly because they are more attentive in general, thus also

minimizing mortality due to other causes. In forest habitats, food resources are less plentiful and predation risk is much lower than in open habitats because alternative prey such as rodents are less abundant. Furthermore, closed habitats provide visual obstruction so that antipredator behaviors such as vigilance may be less efficient and active defence of the fawn may be more difficult and/or inefficient. In this context, the best antipredator tactic for the mother may be to range further away from the fawn's bed site during feeding, so as not to provide cues of the fawn's location to predators (Fitzgibbon 1993). Because food resources are of lower quality in closed habitats (Hewison et al. 2009), females have to spend more time on food acquisition, especially during the energetically demanding early lactation period. In this case, the pay-off associated with the low risk-low benefit tactic adopted by the more reactive mothers is maximized in closed habitat. Although the above interpretation of our results is coherent with expectations, we did not have any direct observations of maternal behavior during attempted predation to confirm that this was the behavioral mechanism underlying the observed relationship between coping style and fawn survival. Future work should focus on how maternal care tactics, and specifically antipredation behaviors, vary between habitats and among individuals in relation to variation in coping styles.

### Coping styles, fitness, and the maintenance of behavioral variation

Only a few studies to date have provided empirical evidence of an influence of interindividual variation in behavior on fitness in the wild (Smith and Blumstein 2008), and only one has reported that a given behavioral phenotype is favored in some ecological conditions, but not in others, governed by life-history trade-offs (Boon et al. 2007). These authors found that both the direction and magnitude of the influence of maternal aggressiveness on offspring survival differed among years in North American red squirrel, likely in response to marked yearly variation in food availability. Our findings that the direction and magnitude of the influence of the mother's coping style on offspring survival differ across the landscape provide clear evidence of spatially dynamic associations between behavioral phenotype and fitness components. These combined results imply that both temporal and spatial variation in resource acquisition and allocation contribute to ensure that no given behavioral phenotype is consistently associated with the highest fitness. The exact mechanisms by which variation among individuals in behavioral traits is maintained in the wild are largely unknown. A potential explanation for differences in fawn survival that we reported in relation to their mother's behavior could involve genetic factors. Indeed, the aggressiveness of mothers toward their offspring, the responsiveness of mothers toward signals from their offspring or the nursing behavior of mothers can be under genetic control (Grandinson 2005). However, our findings directly suggest that spatial habitat heterogeneity could be involved. Indeed, recent theoretical models have demonstrated that, under variable food conditions, the involvement of behavioral traits in life-history trade-offs may lead to the maintenance of individual differences in behavioral phenotype (Stamps 2007; Wolf et al. 2007).

Depending on the strength of spatial variation in the fitness advantages associated with a given level of proactivity, one may hypothesize that certain behavioral phenotypes should predominate in a given habitat (see Dingemanse et al. 2004; Bergmüller and Taborsky 2010). For example, in chipmunks (*Tamias striatus*), the most exploratory and docile individuals established their home ranges in those areas that were most frequented by humans (Martin and Réale 2008). Further studies investigating correlations between behavior

and environment are needed so as to better understand their ecological and evolutionary implications in terms of the maintenance of interindividual behavioral variation (Ravigné et al. 2003). In particular, we lack empirical case studies that directly link interindividual variation in behavioral phenotype with fitness components across variable environments. Our work provides evidence that spatial heterogeneity in fitness pay-offs for different coping styles may promote the maintenance of behavioral variation in wild populations.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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