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# Trophy hunting mediates sex-specific associations between early-life environmental conditions and adult mortality in bighorn sheep

Mathieu Douhard 🆔   |   Marco Festa-Bianchet   |   Julie Landes 🆔   |   Fanie Pelletier

Département de Biologie, Université de Sherbrooke, Sherbrooke, Quebec, Canada

**Correspondence**
Mathieu Douhard
Email: mathieu.douhard@gmail.com

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## Abstract

1. Environmental conditions during early development, from conception to sexual maturity, can have lasting consequences on fitness components. Although adult life span often accounts for much of the variation in fitness in long-lived animals, we know little about how early environment affects adult life span in the wild, and even less about whether these effects differ between the sexes.

2. Using data collected over 45 years from wild bighorn sheep (*Ovis canadensis*), we investigated the effects of early environment on adult mortality in both sexes, distinguishing between natural and anthropogenic sources of mortality.

3. We used the average body mass of yearlings (at about 15 months of age) as a yearly index of environmental quality. We first examined sex differences in natural mortality responses to early environment by censoring harvested males in the year they were shot. We then investigated sex differences in the effects of early environment on overall mortality (natural and hunting mortality combined). Finally, we used path analysis to separate the direct influence of early environment from indirect influences, mediated by age at first reproduction, adult mass and horn length.

4. As early environmental conditions improved, natural adult mortality decreased in both sexes, although for males the effect was not statistically supported. Sex differences in the effects of early environment on adult mortality were detected only when natural and hunting mortality were pooled. Males that experienced favourable early environment had longer horns as adults and died earlier because of trophy hunting, which does not mimic natural mortality. Females that experienced favourable early environment started to reproduce earlier and early primiparity was associated with reduced mortality, suggesting a silver-spoon effect.

5. Our results show that early conditions affect males and females differently because of trophy hunting. These findings highlight the importance of considering natural and anthropogenic environmental factors across different life stages to understand sex differences in mortality.

**KEYWORDS**
cox models, early life, life history, predictive adaptive response, sex differences, survival, trophy hunting

# 1 | INTRODUCTION

Sensitivity to environmental conditions may vary with life stage (Fawcett & Frankenhuis, 2015). Early development, the period between conception and sexual maturity (Lindström, 1999), is a sensitive window in various species (English, Fawcett, Higginson, Trimmer, & Uller, 2016; Lucas, 1998). Environmental conditions during early development ("early environment" henceforth) can have delayed, long-term effects on individual life-history traits (Lindström, 1999) and even affect future generations (Burton & Metcalfe, 2014). Unlike genetic and parental effects, environmental factors measured at the population level, such as density and weather, influence all young born within the same birth pulse (Lindström, 1999). These cohort effects can have a strong influence on population dynamics (Albon, Clutton-Brock, & Langvatn, 1992; Le Galliard, Marquis, & Massot, 2010; Lindström & Kokko, 2002).

A recent meta-analysis of laboratory studies found no effect of early diet on life span (English & Uller, 2016), but the simplified environments of laboratory or captive studies may produce results different from those observed in the wild (Briga & Verhulst, 2015; Kawasaki, Brassil, Brooks, & Bonduriansky, 2008; Tidière et al., 2016). In addition, not all species are suitable for laboratory study. Life span studies in long-lived, wild, species offer important insights into evolutionary ecology, because life span is a major source of variation in lifetime reproductive success and fitness among these organisms (Clutton-Brock, 1988).

In long-lived vertebrates, males often have shorter adult life span than females (Clutton-Brock & Isvaran, 2007). Sex differences in life span for a given species, however, are not fixed. For example, human life expectancy increased since the mid-19th century in Western societies, but more slowly for men than for women (Oeppen & Vaupel, 2002). To date, only a handful of studies have investigated whether early environment can influence sex differences in adult life span or survival in human or wild vertebrate populations (Table 1). Although most studies show sex-specific effects of early environment, the sexual difference varied among species (Table 1). Several mechanisms for these sex differences have been proposed, but not tested.

Here, we address possible pathways by which early environment may influence adult mortality of each sex. First, individuals born in favourable environments may have a fitness advantage over those born in poor environments ("silver-spoon" effect, Grafen, 1988). Silver-spoon effects often involve variation in body growth (Madsen & Shine, 2000; van de Pol, Bruinzeel, Heg, van Der Jeugd, & Verhulst, 2006): a poor early environment is associated with reduced growth and age-specific mass, which in turn leads to increased adult mortality (Figure 1a). Alternatively, poor early environments that generate high juvenile mortality may remove weaker individuals (e.g. selective disappearance of lighter individuals, Rebke, Coulson, Becker, & Vaupel, 2010), leaving a cohort composed of a few robust adults that live longer ("filtering effect" sensu Douhard et al., 2014, Figure 1b). These two hypotheses highlight the role of developmental constraints, as in both cases the *average* fitness drops dramatically when individuals experience poor early environment. Monaghan (2008) referred to these situations as forming a "pathology zone."

An alternative view is that environmentally induced changes in phenotype are adaptive, so that the average fitness of individuals born under poor conditions is comparable to that of individuals born under good conditions (tolerance zone sensu Monaghan, 2008). Predictive adaptive response (PAR) is a form of adaptive developmental plasticity where the fitness benefits of responses to early environment are only revealed in the adult stage (Gluckman, Hanson, & Spencer, 2005). PAR models hypothesize that individuals adjust their phenotype during early development in anticipation of future conditions. The exact nature of the expectation distinguishes between the external and internal PAR hypotheses (Nettle, Frankenhuis, & Rickard, 2013). In external PAR, the juvenile prepares for a particular environment. If future environment is similar to early environment, then its phenotype will be well adapted to future environment (Figure 1c). However, individuals that experience a mismatch between early and adult environments should experience a fitness cost in terms of both survival and reproduction (Figure 1c). The internal PAR proposes that developmental plasticity did not evolve in response to predicted future environmental conditions, but rather in response to future somatic state (Nettle et al., 2013). It predicts that individuals experiencing poor early environment have a higher risk of premature death and should respond by reproducing earlier (Figure 1d). The internal PAR seems more appropriate than external PAR in long-lived species in variable environments, because it does not make assumptions about environmental stability. However, there are as yet no empirical tests of the internal PAR hypothesis in wild populations.

Between the zones of tolerance and pathology is an area where early environmental deterioration leads to a small average fitness decline because individuals partially compensate for a poor start in life (mitigation zone sensu Monaghan, 2008). Within this zone, trade-offs between traits or across life-history stages may occur. Individuals born under poor conditions can later show accelerated growth if resources subsequently improve, but a growth acceleration can increase adult mortality (Hector & Nakagawa, 2012; Metcalfe & Monaghan, 2001; Figure 1e). Individuals may also mitigate the effects of poor early environment by reproducing earlier, and more generally increasing the energy allocation to early reproduction, at the cost of reduced future survival (Cartwright, Nicoll, Jones, Tatayahn, & Norris, 2014; Hammers, Richardson, Burke, & Komdeur, 2013). In this scenario, contrary to the internal PAR, poor early environments increase adult mortality indirectly through greater allocation to reproduction (Figure 1f). A fitness disadvantage of being born in a poor environment may also be reduced because individuals born in good environments also face trade-offs. In particular, male body mass and development of secondary sexual characters may increase with the quality of early environment (Gustafsson, Qvarnström, & Sheldon, 1995; Jensen, Svorkmo-Lundberg, Ringsby, & Sæther, 2006; Schmidt, Stien, Albon, & Guinness, 2001) and such traits may be associated with increased mortality (Robinson, Pilkington, Clutton-Brock, Pemberton, & Kruuk, 2006). Therefore, under a "grow slow, die old" scenario, males born in poor environments would survive

**TABLE 1** Studies testing for sex-specific effects of early environment on adult life span or survival in wild vertebrate and human populations. Symbols indicate whether the effect was positive (+), negative (−) or non-statistically significant (0) as the quality of early environment improved. When the sign of non-statistically significant relationships was provided, we added it in brackets. We also report whether the interaction between sex and early environment was statistically significant (Yes/No) or not tested (NA)

| Species | Early environmental quality metric | Effect in ♂ | Effect in ♀ | Sex × early environment | Reference |
|---|---|---|---|---|---|
| Great tits (*Parus major*) | Mean population fledging success in year of birth | − | 0 | NA | Wilkin and Sheldon (2009) |
| Red-billed choughs (*Pyrrhocorax phrrhorcorax*) | Mean population fledging success in year of birth | + | + | NA | Reid, Bignal, Bignal, McCracken, and Monaghan (2003) |
| Blue-footed boobies (*Sula nexbouxii*) | Sea surface temperature in year of birth | − | 0 (−) | No | Ancona and Drummond (2013) |
| Roe deer (*Capreolus capreolus*) | Proportion of fawns that survived to 8 months of life | + | − | Yes | Garratt et al. (2015) |
| Banded mongooses (*Mungos mungo*) | Mean monthly rainfall in first year of life | −[a] | 0 (−) | NA | Marshall et al. (2017) |
| Red deer (*Cervus elaphus*) | Spring temperature in year of birth | 0 (+) | + | NA | Kruuk et al. (1999) |
| Human (pre-industrial Finns) | Mean rye yields over the first 10 years of life | 0 (−) | + | Yes | Griffin et al. (2018) |

[a]Only for males that successfully reproduced in their lifetime.

longer (Figure 1g). Although survival costs of large size or secondary sexual characters are rare under natural selective pressures (Jennions, Møller, & Petrie, 2001; Kotiaho, 2001), human harvest can selectively remove individuals with large mass or elaborate sexual characters (Allendorf & Hard, 2009).

We take advantage of a detailed long-term monitoring of wild bighorn sheep (*Ovis canadensis*) to evaluate whether and how early environment influences adult mortality in females and males. In this population, the effects of population density in the year of birth on life span of females have been described (Pigeon, Festa-Bianchet, & Pelletier, 2017; Pigeon & Pelletier, 2018). However, a comparison of the effects of early environment (sensu Lindström, 1999) on adult mortality in either sex has not been made. Our analysis involves several steps. First, we test the sex-specific effects of early environment on natural adult mortality and sex differences in such effects. Because males with large horns were subject to intense trophy hunting over much of the study (Pigeon, Festa-Bianchet, Coltman, & Pelletier, 2016), we then investigate how hunting influences sex differences in the effects of early environment on adult mortality. Finally, we use path analysis to separate the direct and indirect effects of early environment. We explored the indirect effects of early environment by measuring how it affected adult mass in both sexes, adult horn length in males and age at first reproduction in females. Path analysis allows us to assess which hypothesis in Figure 1 best represents the effects of early environment on adult mortality. Because viability selection appears to be stronger in male than in female lambs (Feder, Martin, Festa-Bianchet, Bérubé, & Jorgenson, 2008), we predict a weaker filtering effect or stronger silver-spoon effect in females than in males, excluding hunting mortality. When combining

natural and hunting mortality, we predict that males experiencing poor early environment should have larger body mass and horns as adults but a shorter life (a combination of "filtering effect" and "grow slow, die old" strategy).

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and population

Ram Mountain holds an isolated population of bighorn sheep, about 30 km east of the Rockies in Alberta, Canada (52°N, 115°W, elevation 1,700–2,200 m), with about 38 km² of alpine and subalpine habitats (Jorgenson, Festa-Bianchet, & Wishart, 1993). This population has been monitored intensively since 1973. Population density, measured as the number of females aged 2 years and older in June, varied from 16 to 103 over time through changes in environmental conditions and management. Between 1972 and 1981, density was limited by annual removals of 12%–24% of adult females (Jorgenson, Festa-Bianchet, & Wishart, 1993). Because the population was very small after 2000 and showed evidence of inbreeding (Rioux-Paquette, Festa-Bianchet, & Coltman, 2011), several individuals from another population were introduced in 2005, 2007 and 2015 to attempt a genetic rescue (Poirier & Festa-Bianchet, 2018). Predation on adult was rare except from 1997 to 2001 and from 2011 to 2013. In both cases, predation was likely due to specialist individual cougars (*Puma concolor*) and ended suddenly (Festa-Bianchet, Coulson, Gaillard, Hogg, & Pelletier, 2006). Predation risk was included in our analyses as a two-level factor, indicating annual presence or absence of cougar predation.
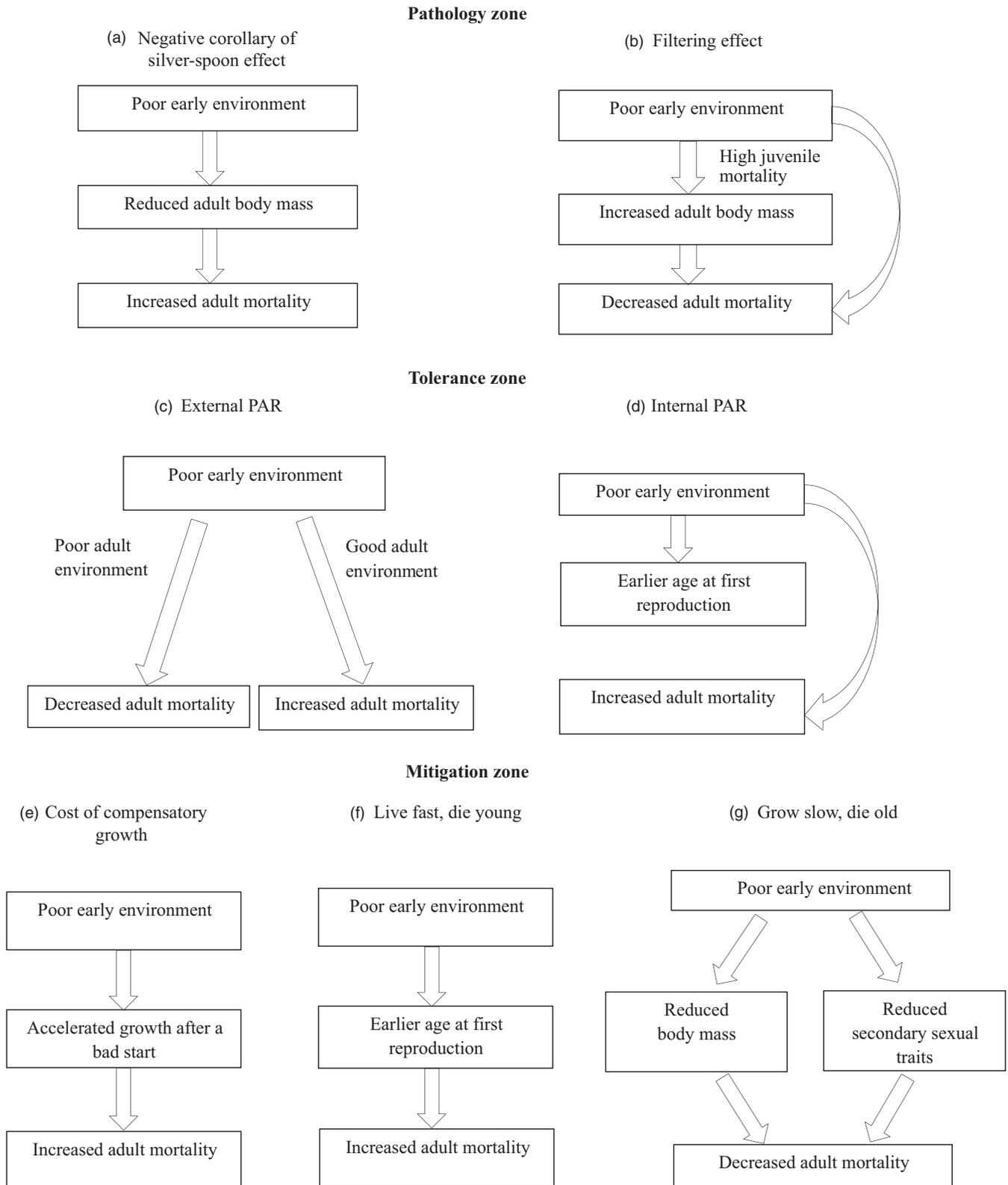
**Pathology zone**

(a) Negative corollary of
silver-spoon effect

```
Poor early environment
        ↓
Reduced adult body mass
        ↓
Increased adult mortality
```

(b) Filtering effect

```
Poor early environment
        ↓  High juvenile
           mortality
Increased adult body mass
        ↓
Decreased adult mortality
```

**Tolerance zone**

(c) External PAR

```
Poor early environment
   ↙ Poor adult      ↘ Good adult
     environment        environment
Decreased adult      Increased adult
mortality            mortality
```

(d) Internal PAR

```
Poor early environment
        ↓
Earlier age at first
reproduction
        ↓
Increased adult mortality
```

**Mitigation zone**

(e) Cost of compensatory
growth

```
Poor early environment
        ↓
Accelerated growth after a
bad start
        ↓
Increased adult mortality
```

(f) Live fast, die young

```
Poor early environment
        ↓
Earlier age at first
reproduction
        ↓
Increased adult mortality
```

(g) Grow slow, die old

```
Poor early environment
   ↙              ↘
Reduced          Reduced
body mass        secondary sexual
                 traits
   ↘              ↙
Decreased adult mortality
```

**FIGURE 1** Seven possible causal mechanisms linking early environment and adult mortality. The average fitness of individuals born under poor conditions can be much lower (pathology zone; a,b), similar (tolerance zone; c,d) or slightly lower (mitigation zone; e,f) than that of individuals born under good conditions. PAR = predictive adaptive response

Males with large horns were subjected to trophy hunting from late August to October until 2011 when hunting was closed. Age 4 is the youngest age at which males were harvested. Hunters were required to register shot rams, and an unlimited number of licences were available to Alberta residents (Festa-Bianchet, Pelletier, Jorgenson, Feder, & Hubbs, 2014).

## 2.2 | Bighorn sheep data

Each year, between May and September, sheep were repeatedly captured in a corral trap baited with salt, and observed in the field. Individuals were marked using visual collars and plastic ear tags. Almost all were first captured and marked as lambs or yearlings, so that their exact age was known. Females can produce one offspring per year in May–June from 2 years of age onwards. Given the very high resighting rate (96% and 99% for males and females respectively, Jorgenson, Festa-Bianchet, Gaillard, & Wishart, 1997), the age at last observation was used to estimate age at death. As we are interested in long-lasting effects of early environment, we considered individuals that lived at least 4 years and restricted our analyses to individuals born at Ram Mountain before 2011, yielding a total of 38 cohorts born from 1973 to 2010. Our last year of data was 2017 and the dataset included 202 females and 163 males.

At each capture, we classified adult females as lactating or non-lactating based on udder examination. We have precise data on age of primiparity because we can identify neonatal deaths when milk or colostrum is expressed at capture but no lamb is seen. Age at first reproduction of males was unknown. Since 1988, we genotyped tissue samples to identify fathers, but paternities of lambs that died before capture were unknown.

We measured mass to 0.25 kg with a spring scale at each capture unless the individual had been weighed <3 weeks earlier. Horn length (mm) was measured along the outside curvature using a flexible tape. Capture success varied with sex-age class, but each summer approximately 85% of sheep were captured at least once and >75% between two and nine times (Martin & Pelletier, 2011). All sex-age classes gained mass over the trapping season. Horns grow mainly from April to September. To account for differences in capture date, we adjusted morphological traits to 5 June and 15 September using linear mixed models (LMMs). More details about mass and horn adjustments procedures are reported elsewhere (Martin & Pelletier, 2011; Pigeon et al., 2016).

## 2.3 | Environmental conditions

The average mass of 15-month-old yearlings in September ($Y_{mass}$, Supporting Information Figure S1) is an index of annual resource availability in this population (Festa-Bianchet, Coltman, Turelli, & Jorgenson, 2004; Hamel, Côté, Gaillard, & Festa-Bianchet, 2009). $Y_{mass}$ decreased both with increasing population density and summer temperature (Supporting Information Figure S2). We measured early environment as the 3-year running average of annual $Y_{mass}$ centred on the year of birth (e.g. for the 2000 cohort, early environment was calculated using $Y_{mass}$ from 1999, 2000 and 2001, Supporting Information Figure S1). This proxy captures overall variation in food availability during gestation and postnatal development, following the definition of "early life" proposed by Lindström (1999). At age 2, females can be primiparous (Festa-Bianchet, Jorgenson, Lucherini, & Wishart, 1995) and males can obtain paternities in rare cases

(Coltman, Festa-Bianchet, Jorgenson, & Strobeck, 2002). The rut is between mid-November and early December. The 3-year period for quantifying early environment is a good compromise of the relative benefits of long and short periods. Although environmental effects on later life traits may be due to exposure at a specific point in development (Lucas, 1998), a longer period of time allows more lasting effects to accumulate (Griffin, Hayward, Bolund, Maklakov, & Lummaa, 2018). To characterize the adult environment, we included $Y_{mass}$ in a given survival year ("current environment" henceforth) in our models.

## 2.4 | Statistical analyses

We performed all analyses in R version 3.3.2 (R Development Core Team, 2015). We fitted Cox proportional hazards (CPH) models to analyse variation in adult mortality, using the "coxph" function in the package "survival" (Therneau, 2018). The CPH model assesses simultaneously the influence of multiple continuous or categorical predictor variables upon the time a specified event (e.g. death) takes to happen. The CPH model is a semi-parametric survival analysis because it makes no assumptions about the shape of the hazard function, that is the function of instantaneous risk of death. Regression coefficients ($\beta$) in our CPH models represent the log change in the hazard function per unit increase of the covariate, holding other covariates constant. A positive $\beta$ indicates a higher risk of death at every adult age with increasing value of the covariate. The exponentiated coefficients ($\exp(\beta)$), also known as hazard ratios, give effect sizes. CPH models allowed us to include censored data and to consider time-independent (e.g. sex) and time-dependent covariates (e.g. current environmental conditions). We included individual identity as a cluster variable to account for repetition of "alive" events within an individual (Therneau, Crowson, & Atkinson, 2018). One hundred seventy-four of the 202 females were followed from birth to death. Life histories for the remaining 28 were right-censored (9 were alive in 2017 and 19 were experimentally removed). Among 163 males, 108 died from natural causes, 52 were shot and 3 were alive in 2017. The assumption that the relative effect on mortality of any covariate is constant over age (no age-specific effects) was tested using the "cox.zph" function, and all models satisfied this assumption (Supporting Information Table S1).

### 2.4.1 | Natural mortality

We first analysed natural adult mortality by censoring males in the year they were shot (Bonenfant, Pelletier, Garel, & Bergeron, 2009). The starting model included sex, early environment, current environment, current predation risk and the following interactions: sex × early environment, sex × current environment, early environment × current environment, early environment × current environment × sex. The two latter interactions test for the external PAR hypothesis and its possible sex-specific occurrence. We tested successively interaction terms and, if these were not statistically significant, the main effects of variables, except for sex × early environment. We kept this latter interaction independent of its

significance to quantify both sex-specific responses to early environment and sex differences in these responses (for a similar procedure, see Griffin et al., 2018).

## 2.4.2 | Overall mortality

To assess the relationships between early environment and overall adult mortality, we reran the selected CPH model, determined following the model simplification described above, including hunting mortality by not censoring harvested males.

## 2.4.3 | Path analysis

We analysed direct and indirect effects (acting via other variables) of early environment on adult mortality for each sex separately using path analyses (Shipley, 2009). Path analysis involves the construction of a path diagram showing independent and dependent variables connected by arrows (the paths) according to a "causal order." Path analysis remains, however, a correlative approach (Holland, 1988). Each path coefficient (regression coefficient) estimates the link between two variables when all other variables are held constant. We examined indirect effects of early environment through age at first reproduction and adult mass in females, and through horn length and body mass in males. Mass and horn length were fitted with a normal distribution and age at first reproduction with a Conway–Maxwell–Poisson distribution because there were signs of under-dispersion in the Poisson model (Lynch, Thorson, & Shelton, 2014). Adult mass of females was mass at age 4 adjusted to 15 September. By age 4, females have reached about 95% of asymptotic mass (Nussey et al., 2011). In addition, adult females are highly consistent in the mass they attain by mid-September (Pelletier, Réale, Garant, Coltman, & Festa-Bianchet, 2007). In males, we considered mass and horn length at age 4 adjusted to 5 June because many were only caught in May–June. Measures of mass and horn length at age 4 were missing for 45 (27%) males. Instead of deleting individuals with missing values (see Nakagawa & Freckleton, 2008 about the dangers of this procedure), we used individual growth trajectories to predict missing values at age 4 (see Bonenfant et al., 2009 for a similar approach). Specifically, we fitted a linear mixed model where the response variable was log-transformed body mass or horn length adjusted to 5 June for all males aged ≤4 years. Linear and polynomial (up to third order) effects of age were entered as fixed variables, and ram identity was included as a random effect on both intercept and slope. Age at first reproduction and adult mass were known for nearly all females. We excluded from path analysis 8 females that died before they reproduced.

# 3 | RESULTS

## 3.1 | Natural mortality

Cohorts exposed to better environmental conditions during early life, measured by average mass of yearlings in the 3 years centred on the year of birth, had lower risk of adult mortality in

females ($\beta_F = -0.050 \pm 0.026$, $p = 0.05$, Figure 2a) but not males ($\beta_M = -0.007 \pm 0.035$, $p = 0.85$, Figure 2a). A 1-kg increase in the index of early environmental quality led to a 5% decrease in the risk of death at every age of adult females, whereas for males, the effect size was <1%. Statistically, however, the slopes of early environment–mortality risk relationships did not differ between the sexes ($\beta_M - \beta_F = 0.043 \pm 0.042$, $p = 0.30$). Contrary to the external PAR
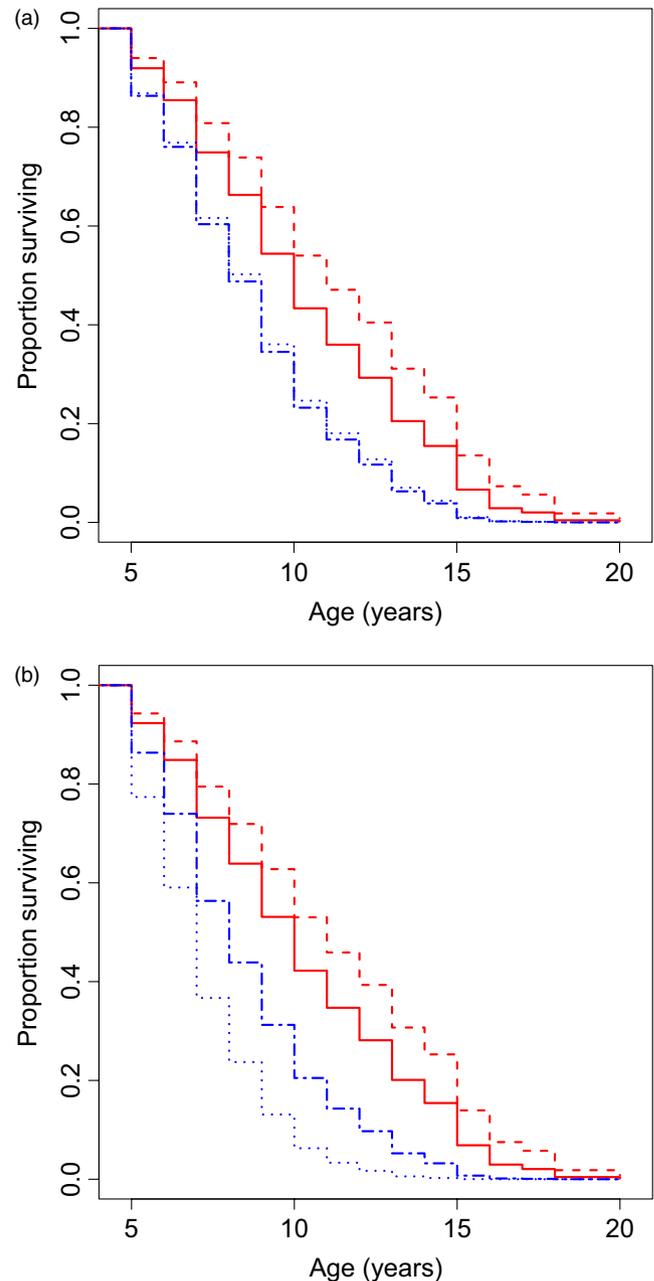


**FIGURE 2** Influence of early environmental conditions on (a) natural and (b) overall adult mortality of male and female bighorn sheep born at Ram Mountain, Alberta, Canada, between 1973 and 2010. Lines represent predicted relationships for the first and the third quartile of the early environmental quality index. Solid red line = lower quartile (poor environment) for females, dashed red line = upper quartile (good environment) for females, dot-dash blue line = lower quartile for males, dotted blue line = upper quartile for males.

hypothesis, there was no interaction between early and current environmental conditions on natural mortality risk in either sex (early environment × current environment: $\beta$ = −0.005 ± 0.006, $p$ = 0.46; early environment × current environment × sex: $\beta$ = 0.015 ± 0.012, $p$ = 0.22). The final model and variables not retained are summarized in Supporting Information Table S2.

## 3.2 | Overall mortality

Pooling natural and hunting mortality, early environment strongly influenced adult male mortality: an improvement of environmental quality by 1 kg increased the risk of death at every adult age by 10% ($\beta_M$ = 0.090 ± 0.032, $p$ = 0.004). As a result, we found marked sex differences in the effects of early environment on overall mortality risk ($\beta_M - \beta_F$ = 0.14 ± 0.039, $p$ < 0.001, Figure 2b).

## 3.3 | Path analysis

In females, early environment influenced age at first reproduction, which, in turn, influenced adult mortality (Figure 3). There was a twofold reduction in age of primiparity between females born in very poor and very favourable conditions (Supporting Information Figure S3). Delaying age at first reproduction was associated with an increase in the risk of death at adult age. The risk of death decreased by 5% per additional kg at age 4, but early environment did not influence adult mass (Figure 3). We found no evidence for a direct effect of early environment on adult mortality of females.

In males, early environment had an indirect effect on adult mortality through adult horn length (Figure 4a). Adult horn length and mass increased by 34% and 22%, respectively, comparing males born in very poor and very favourable environmental conditions (Supporting Information Figure S4). The risk of death at every adult age increased by 4% per cm of horn at age 4. The positive relationship between horn length and mortality was due to trophy hunting: neither horn length nor mass influenced natural mortality of adult males (Figure 4b).

# 4 | DISCUSSION

In long-lived vertebrates, adult males usually die younger than females, partly because males suffer higher baseline mortality and stronger actuarial senescence (Clutton-Brock & Isvaran, 2007). Although recent studies have advanced our understanding of sex differences in life span and senescence (Brooks & Garratt, 2017; Clutton-Brock & Isvaran, 2007; Lemaître & Gaillard, 2013; Maklakov & Lummaa, 2013), it is not clear whether and how early environmental conditions generate sex differences in life-history traits such as mortality. Our results in a wild population of bighorn sheep show that early environment influences adult mortality of females and males in opposite directions. Good early environment reduced adult mortality in females, consistent with the silver-spoon hypothesis, but increased mortality in males because of the trophy hunt.

Contrary to our prediction, there was no "filtering effect" (Figure 1b) in bighorn males. At Ram Mountain, late birth decreased survival to 1 year in males but not in females, likely because males require more resources than females for growth and survival in this highly seasonal environment (Feder et al., 2008). We expected that poor early environment would selectively remove stunted male lambs, thus leaving a cohort of robust males that lived longer. We found no evidence to support this, as natural mortality of adult males was independent of early environment. Furthermore, males born in good environments were heavier and had longer horns as adults than those born in poor environments. In roe deer (*Capreolus capreolus*), cohorts with high juvenile mortality then have greater adult survival for females but not males, presumably because female fawns are more susceptible to condition-dependent mortality than males (Garratt et al., 2015). Thus, adult female roe deer from cohorts that experienced high juvenile mortality tended to be heavier (Garratt et al., 2015). The apparent lack of "filtering effect" in bighorn sheep may be due to their higher and less variable juvenile survival compared to roe deer (Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toïgo, 2000).

In addition to sex-specific effects of early environment on overall mortality, the patterns relating adult body mass and early conditions
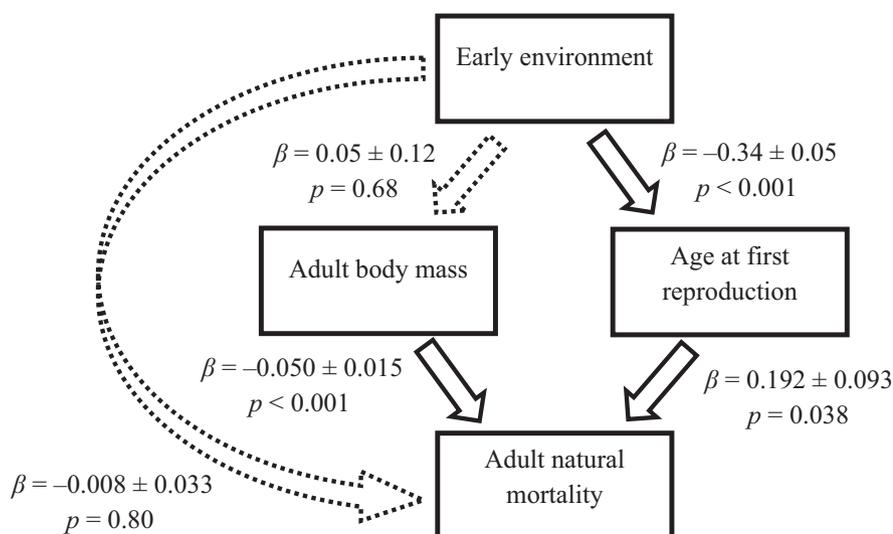


**FIGURE 3** Path diagram describing the direct and indirect effects of early environment on adult mortality of female bighorn sheep. Unstandardized path coefficients are reported with their associated standard errors and $p$-values. Solid lines indicate statistically supported effects ($p$ ≤ 0.05) and dotted lines non-statistically supported effects ($p$ > 0.05)
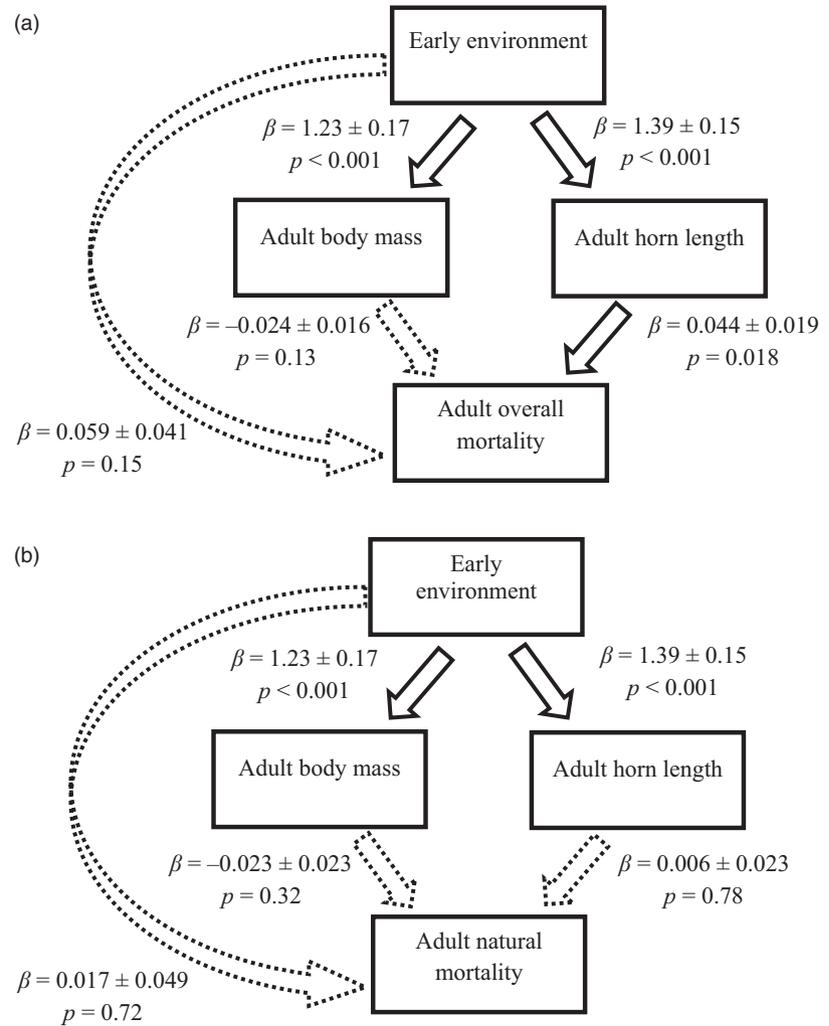
(a)

Early environment

$\beta = 1.23 \pm 0.17$
$p < 0.001$

$\beta = 1.39 \pm 0.15$
$p < 0.001$

Adult body mass

Adult horn length

$\beta = -0.024 \pm 0.016$
$p = 0.13$

$\beta = 0.044 \pm 0.019$
$p = 0.018$

Adult overall mortality

$\beta = 0.059 \pm 0.041$
$p = 0.15$

(b)

Early environment

$\beta = 1.23 \pm 0.17$
$p < 0.001$

$\beta = 1.39 \pm 0.15$
$p < 0.001$

Adult body mass

Adult horn length

$\beta = -0.023 \pm 0.023$
$p = 0.32$

$\beta = 0.006 \pm 0.023$
$p = 0.78$

Adult natural mortality

$\beta = 0.017 \pm 0.049$
$p = 0.72$

**FIGURE 4** Path diagrams describing the direct and indirect effects of early environment on (a) overall mortality and (b) natural mortality of adult male bighorn sheep. Unstandardized path coefficients are reported with their associated standard errors and P-values. Solid lines indicate statistically supported effects ($p \leq 0.05$) and dotted lines non-statistically supported effects ($p > 0.05$)

differ between males and females. Contrary to males, there was no influence of early environment on the mass of adult females. These differences likely result from different sexual selection pressures. In polygynous species, like bighorn sheep (Coltman et al., 2002), some males can monopolize many mating opportunities and male–male competition is intense. Consequently, there is strong selection for traits that increase competitive ability, such as body mass or horn length. Early growth can have a greater influence on reproductive success in males than in females, as shown in red deer (*Cervus elaphus*, Kruuk, Clutton-Brock, Rose, & Guinness, 1999). Males with poor early growth typically remain small through life (Carvalho et al., 2017; Solberg, Loison, Gaillard, & Heim, 2004). The potential to catch up after a bad start (sensu Hector & Nakagawa, 2012) is stronger in females (Festa-Bianchet, Jorgenson, & Réale, 2000). At Ram Mountain, small young females do not show compensatory growth but prolong their growth, so that the mass difference between females that are heavier and lighter than the median mass as yearlings decreases from 20% to 4% between 1 and 7 years of age (Marcil-Ferland, Festa-Bianchet, Martin, & Pelletier, 2013). We found that heavier females lived longer, consistent with previous findings for this population (Gaillard, Festa-Bianchet, Delorme, & Jorgenson,

2000). However, adult mass was not the phenotypic link between early environment and adult mortality of females.

Females that experienced a favourable early environment started to reproduce earlier, and early primiparity was associated with reduced adult mortality. The strong relationship between early environment and age at first reproduction may be attributed to the manner in which early environment was estimated. Body mass of yearling females, used to calculate early environmental index, affected their age at first reproduction (Martin & Festa-Bianchet, 2012). However, the slope of the relationship between early environment and age at first reproduction did not vary much when accounting for individual yearling mass ($-0.29 \pm 0.05$ vs. $-0.33 \pm 0.05$). In this population, females born at low density are at a reproductive advantage compared to those born at high density (Pigeon et al., 2017). Overall, these results support the existence of silver-spoon effects in females. Both the disposable soma (Kirkwood & Rose, 1991) and the antagonistic pleiotropy (Williams, 1957) theories predict negative covariation between allocation to reproduction in early adulthood and life-history traits at a later age. Age at first reproduction is often used to measure allocation to early reproduction (Lemaître et al., 2015). We found, however, no evidence of a trade-off between age at

primiparity and adult survival. Inter-individual variation in resource acquisition (van Noordwijk & de Jong, 1986) seems unlikely to fully explain this negative result because our path analysis included adult mass. Possibly, females start to reproduce only when they can do so without suffering survival costs (Martin & Festa-Bianchet, 2012). Long-lived species such as ungulates usually do not show survival costs of reproduction (Hamel et al., 2010).

Our results also do not support the internal PAR, which predicts earlier primiparity for individuals born under poor conditions in response to a shorter life expectancy (Nettle et al., 2013). We suggest that strong developmental constraints force females born under poor environment to delay primiparity. In large mammalian herbivores, young females must reach a threshold body mass to ovulate (about 45 kg in bighorn sheep, Jorgenson, Festa-Bianchet, Lucherini, & Wishart, 1993). In these species, however, the predictions of internal PAR may apply to other reproductive traits (Berghänel, Heistermann, Schülke, & Ostner, 2016; Douhard et al., 2016) such as maternal care. Testing this hypothesis is beyond the scope of this study, but remains an important topic for future investigation. The internal PAR hypothesis seems more likely to apply than external PAR to long-lived species, because environmental autocorrelation must be almost perfect for external PAR to evolve (Nettle et al., 2013). Contrary to what the external PAR hypothesis predicts, we found no interaction between early and current environmental conditions on mortality risk in either sex. In addition, the external PAR does not hold for annual reproductive success in female bighorn sheep (Pigeon et al., 2017). There is an overall lack of support for the external PAR in long-lived species (humans: Hayward, Rickard, & Lummaa, 2013; roe deer: Douhard et al., 2014; baboons: Lea, Altmann, Alberts, & Tung, 2015; mountain goats: Panagakis, Hamel, & Côté, 2017), as well as in a range of other organisms (Briga, Koetsier, Boonekamp, Jimeno, & Verhulst, 2017; Uller, Nakagawa, & English, 2013).

In males, early environment and adult mortality were linked by an indirect effect through horn length. Adult males that experienced a favourable early environment had longer horns and died earlier because hunting regulations prohibit the harvest of rams with small horns (Festa-Bianchet et al., 2014). Males that experienced good early environment were also heavier by 4 years of age. Although ram mass and horn length are moderately correlated, mass is not a direct target of trophy hunting (Pigeon et al., 2016). Survival costs of growing large horns in ungulates are predicted (Geist, 1966) but generally not observed (Bonenfant et al., 2009). A trade-off between horn growth and natural longevity was only documented in male Soay sheep (*Ovis aries*) (Robinson et al., 2006), likely because large male lambs participate in rutting activities. Once hunting mortality was excluded, neither mass nor horn length influenced adult mortality of bighorn rams. Our results confirm that trophy hunting does not mimic natural mortality (Bonenfant et al., 2009).

The findings on natural mortality of bighorn males must, however, be interpreted with caution. By definition, rams available for harvest are not a random sample of the population because they must reach a minimum degree of horn curl (4/5 curl before 1996 and full curl between 1996 and 2011). Hunting pressure was high: these males had a 40% yearly probability of being shot (Coltman, O'Donoghue, Jorgenson, Strobeck, & Festa-Bianchet, 2003). Without hunting, rams growing large horns early in life may reach the oldest age group. In unhunted Alpine ibex (*Capra ibex*), males growing large horn annuli in a given year had higher survival probability in the following year (von Hardenberg, Bassano, del Pilar Zumel Arranz, & Bogliani, 2004). The data used in our analyses might not reflect the mortality response observed in complete cohorts of bighorns that die of natural causes. Because hunting continued to 2011, the numbers of cohorts over which this hypothesis may be assessed are not yet sufficient.

There is growing evidence that harvest-induced selection may cause rapid evolutionary changes (Allendorf & Hard, 2009; Darimont et al., 2009; Kvalnes, Sæther, Haanes, Engen, & Solberg, 2016). These life-history changes can have a strong impact on populations, communities and ecosystems (Palkovacs, Moritsch, Contolini, & Pelletier, 2018). Our results suggest that trophy hunting can also profoundly alter the link between ecology and sex differences in mortality. These results may occur in other species because trophy hunting is widespread world-wide (Palazy, Bonenfant, Gaillard, & Courchamp, 2012). Thus, changes in sex-specific mortality according to early environment can be caused by factors other than differences in viability selection during early life (Garratt et al., 2015). Although only a few studies have tested whether variation in early environment can drive sex differences in adult survival, the diversity of observed responses (Table 1, this study) stresses the potential pitfalls of extrapolating across species. We thus encourage additional studies on the influence of early environment on adult survival and actuarial senescence of both sexes.

## AUTHORS' CONTRIBUTIONS

M.F.-B. and F.P. collected and collated the data; M.D. conceived the ideas; M.D. and J.L. analysed the data; M.D. led the writing of the manuscript. All authors contributed critically to the drafts and gave approval for publication.

## DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.6bm4228 (Douhard, Festa-Bianchet, Landes, & Pelletier, 2019).

## ORCID

*Mathieu Douhard* 🔟 https://orcid.org/0000-0001-9422-7270

*Julie Landes* 🔟 https://orcid.org/0000-0002-1845-4970

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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