

Current Biology

High Juvenile Mortality Is Associated with Sex-Specific Adult Survival and Lifespan in Wild Roe Deer

Highlights

- Sex differences in lifespan range from approximately 0%–30% in roe deer
- Sex differences in adult survival occur after exposure to high juvenile mortality
- High juvenile mortality leads to greater adult survival for those remaining females
- In males, high juvenile mortality is associated with a reduction in adult survival

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In Brief

Garratt et al. reveal that wild roe deer show sex-specific adult survival responses after exposure to high juvenile mortality. There is a positive association between the sex difference in lifespan and juvenile mortality, suggesting that this selection pressure and the associated environmental conditions contribute to sex-specific aging in the wild.



High Juvenile Mortality Is Associated with Sex-Specific Adult Survival and Lifespan in Wild Roe Deer

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Summary

Male mammals typically have shorter lifespans than females [1]. Sex differences in survival may result, in part, from sex-specific optima in investment in reproduction, with higher male mortality rates from sexual competition selecting for a “live-fast die-young” strategy in this sex [2]. In the wild, lifespan is also influenced by environmental conditions experienced early in life. Poor conditions elevate juvenile mortality, which may selectively remove individuals with a particular phenotype or genotype from a cohort [3], and can alter the subsequent phenotypic condition and fate of those that survive to adulthood [4]. Males and females can respond differently to the same early-life environmental experiences [5, 6], but whether such environmental pressures generate sex differences in lifespan has rarely been considered. We show that sex differences in adult survival and lifespan in cohorts of roe deer (*Capreolus capreolus*) range from virtually absent in some years to females living 30% longer than males in others. The extent of this sex difference in adult longevity is strongly linked to the level of mortality each cohort experiences as juveniles, with high juvenile mortality generating a strong sex difference in both adult survival and lifespan. In females, high juvenile mortality leads to increased adult survival for those remaining individuals, whereas in males survival is actually reduced. Early environmental conditions and the selective pressures they impose may help to explain variability in sex-specific aging across animal taxa.

Results and Discussion

Early environmental conditions can have long-lasting effects on the expression of subsequent adult phenotypes, including body mass, age at first reproduction, and lifetime reproductive success [5]. When early-life environmental conditions are harsh, this can elevate juvenile mortality [7, 8] and selectively remove particular individuals from a population, changing

the frequency of subsequent adult phenotypes [9–11]. There are several non-mutually exclusive predictions for how the risk of juvenile mortality, and the environmental conditions that cause juvenile mortality in the wild, could affect the subsequent lifespan of surviving individuals in a particular cohort or population. High juvenile mortality could selectively remove stunted, poor-performing individuals. If there is a positive correlation between early-life performance and late-life survival [12], this will leave a cohort of predominantly robust individuals with improved survival prospects (i.e., viability selection [13–15]) [3]. At the same time, however, harsh environmental conditions experienced early in life—those that generate high juvenile mortality—might have negative effects on survivors, causing them to acquire poor condition and, as a consequence, suffer a shorter lifespan (i.e., the negative corollary of silver spoon effects) [4, 16].

The life history and demography of two enclosed populations (Chizé and Trois Fontaines) of roe deer in France, which face contrasting environmental conditions (see the [Experimental Procedures](#)), have been monitored intensively for over 35 years [17]. This presents an opportunity to test how the magnitude of juvenile mortality experienced by each cohort of fawns influences subsequent adult lifespan and survival to old ages. Roe deer also provide a favorable species for examining sex-specific adult responses to early-life environments. Although adult roe deer males show territory-based polygyny and weigh slightly more than females (~10%) [18], no sex differences in phenotypic traits have been detected early in life. Males and females have the same mean birth date [19], size at birth and growth rate throughout the weaning period [20], and juvenile survival [8, 21, 22] ([Figure S1](#)). Thus, both sexes are exposed to equivalent environmental conditions and mortality rates early in life.

In both populations, juvenile mortality over the first 8 months of life (assessed by capture-mark-recapture methods [8]) is highly variable between years [23] ([Figure S1](#)). The degree of juvenile mortality experienced by fawns in a given year is not correlated with either the overall (sex-independent) subsequent mean cohort lifespan or the percentage of individuals living beyond 7 years ([Table 1](#)), the age at which survival starts to decrease in this species (i.e., survival to an age of actuarial senescence [24]). However, this lack of an overall effect is a consequence of the highly divergent responses of the sexes to the level of juvenile mortality ([Table 1](#); [Figures 1A and 1B](#)). With an increase in juvenile mortality, a greater proportion of females in a given cohort survived to an age of senescence (supporting the viability selection scenario; $F_{1,25} = 4.50$, $p = 0.044$), whereas male survival decreased (supporting the silver spoon hypothesis; $F_{1,19} = 6.47$, $p = 0.020$). This effect was consistent across both populations, and a similar pattern was found when average adult lifespan was examined ([Figure 1B](#); [Table 1](#)). High juvenile mortality is therefore a strong predictor of sex differences in adult survival and lifespan in roe deer: when juvenile mortality is elevated, females live longer than males and a greater proportion of females than males survive to senescent ages (relationship between juvenile mortality and sex difference in survival to senescence: estimate \pm SE = 0.81 ± 0.24 , $F_{1,22} = 11.53$, $p = 0.003$; [Figure 1C](#)).

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Table 1. Final Linear Mixed-Effects Models Examining the Effects of Sex, Cohort-Specific Juvenile Mortality, and Population on Average Survival to 8 Years of Age and Adult Lifespan in Roe Deer

Parameter	Estimate	SE	p Value
Survival to Senescence (8 Years of Age)			
Both sexes: intercept	0.35	0.47	0.90
Both sexes: sex	0.005	0.09	0.96
Both sexes: mortality	-0.40	0.18	0.78
Both sexes: sex × mortality	0.72	0.23	0.004
Males: intercept	0.36	0.41	0.85
Males: mortality	-0.43	0.17	0.020
Females: intercept	0.50	0.09	<0.001
Females: mortality	0.46	0.22	0.044
Average Adult Lifespan			
Both sexes: intercept	5.36	3.16	0.79
Both sexes: sex	1.42	0.62	0.12
Both sexes: mortality	-1.69	1.27	0.78
Both sexes: population	0.72	1.30	0.85
Both sexes: sex × mortality	3.97	1.50	0.014
Both sexes: sex × population	-0.96	0.52	0.076
Male: intercept	6.85	0.51	<0.001
Male: mortality	-0.45	1.26	0.73
Female: intercept	7.29	2.14	0.61
Female: mortality	1.91	1.54	0.23

Female parameter estimates are provided in relation to those of males. See also [Figure S1](#).

To further understand the underlying causes of these sex differences, we explored how juvenile mortality influenced subsequent adult body mass. Body mass shapes individual performance and correlates with adult survival [24] ([Table S1](#)), thus providing an indication of how juvenile mortality influences adult phenotypic quality. Furthermore, combinations of specific stressful early-life environmental conditions have been linked to a reduction in the adult body mass of both sexes [25]. The relationship between juvenile mortality and adult body mass differed between sexes ([Table 2](#); [Figures 2](#) and [S2](#)), suggesting that male and female body condition is indeed differentially impacted in years of high juvenile mortality. Males surviving from cohorts that experienced high juvenile mortality were lighter than males from cohorts in which juvenile mortality was less intense ([Figure 2](#)). Female body mass, by contrast, did not decline with increased juvenile mortality ([Figure 2](#)). When expressed in relation to their fawn mass at 8 months, producing a more accurate assessment of body mass gained since the juvenile mortality period, female body mass after high juvenile mortality slightly increased ([Figure S2](#)), although not significantly so ([Table 2](#)). There were no statistically significant effects of juvenile mortality on the fawn mass of either sex at 8 months or consistent interactions between sex and juvenile mortality on this trait ([Table S2](#)).

Male-specific declines in body mass with elevated juvenile mortality further highlight impaired adult condition in this sex. In highly polygynous species, poor-quality environments experienced by offspring and/or their mothers early in life usually generate sex differences in perinatal and early postnatal mortality, with juvenile males showing a dramatic reduction in survival when compared to females, potentially as a consequence of their greater early growth requirements [22]. However, roe deer are weakly polygynous [26], and the sexes have similar juvenile survival under all environmental conditions ([27] and [Figure S1](#)). Our results indicate that although poor conditions have minimal immediate effects on sex differences in early-life survival, they produce a reduction in male

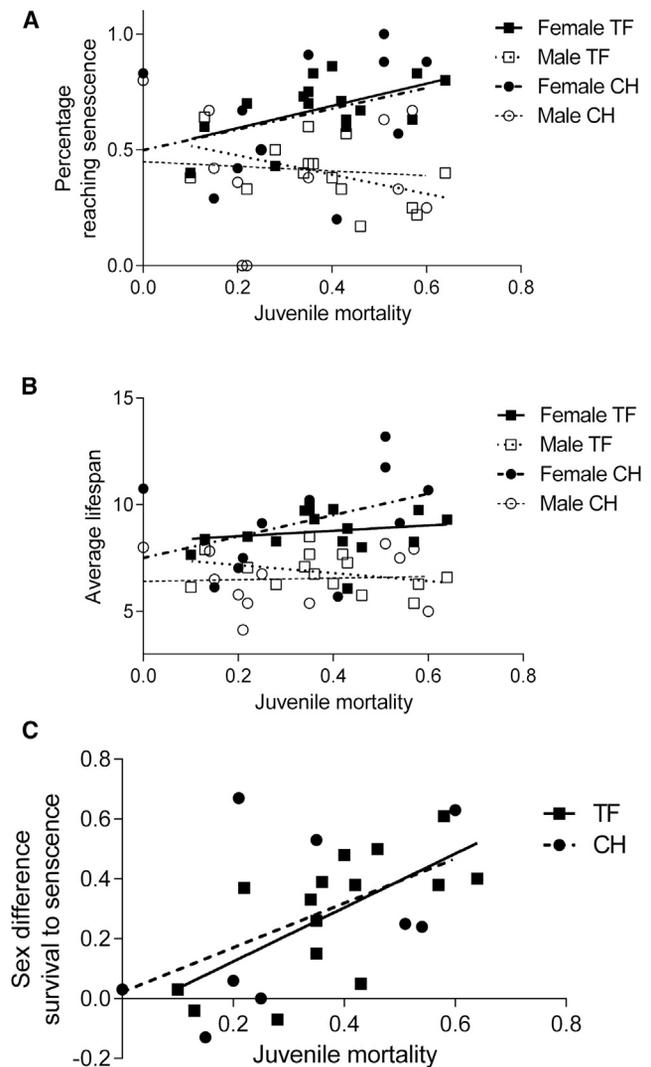


Figure 1. The Level of Juvenile Mortality in a Cohort Has Sex-Dependent Effects on Lifespan and Survival in Roe Deer

Cohort-specific juvenile mortality, lifespan, and survival were assessed at two sites: Trois Fontaines (TF) and Chizé (CH). When cohort-specific juvenile mortality is high, a strong sex difference is generated both in the percentage of animals reaching 8 years old (A), the age at onset of senescence in this species, and in average lifespan (B). These effects generate sex differences in adult survival when cohort-specific juvenile mortality is high (C). See also [Figure S1](#).

survival and body mass when compared to females in adulthood.

In some species, changes in adult condition can make early-life reproductive allocation more favorable, because it helps to maximize fitness, even though this reduces survival in late life [28]. However, in roe deer males, such a change is unlikely because the male mating tactic is invariant [18] and males are severely limited in their ability to maximize reproductive success over a short period of time. Long life is required for high fitness [29]. In contrast to red deer, in which a few males defend harems of up to 20 females [30], virtually all roe deer males show obligatory territoriality for about half the year, with a much smaller number of females overlapping each male's territory (two to three [31]). Because males from years of high juvenile mortality are lighter, the fixed allocation to

Table 2. Final Linear Mixed-Effects Models Examining the Effects of Sex, Cohort-Specific Juvenile Mortality, Population, and Fawn Mass on Adult Body Mass of Roe Deer

Parameter	Estimate	SE	p Value
Both sexes: intercept	1.37	0.009	<0.001
Both sexes: sex	-0.047	0.010	<0.001
Both sexes: mortality	-0.025	0.018	0.71
Both sexes: fawn mass	0.010	0.003	0.009
Both sexes: sex × mortality	0.060	0.026	0.018
Both sexes: sex × fawn mass	0.009	0.004	0.016
Both sexes: mortality × fawn mass	0.022	0.007	0.006
Both sexes: sex × mortality × fawn mass	-0.018	0.009	0.064
Males: intercept	1.42	0.006	0.001
Males: mortality	-0.030	0.016	0.073
Males: fawn mass	<0.001	0.002	0.84
Males: mortality × fawn mass	0.021	0.006	0.002
Females: intercept	1.37	0.013	<0.001
Females: mortality	0.032	0.020	0.11
Females: fawn mass	0.012	0.001	<0.001

Female parameter estimates are provided in relation to that of males. Fawn body mass was mean centered prior to inclusion as a covariate, and adult body mass was log transformed.

territory defense that all males exhibit could be more costly for these individuals than for heavier males. This might hasten physiological decline and contribute to their reduced survival.

Although specific stressful early-life environmental conditions have previously been linked to reduced body mass [25], females surviving high juvenile mortality do not have lower body mass in adulthood when compared to females from years of low juvenile mortality. Instead, females that survive from cohorts exposed to high juvenile mortality have a greater probability of reaching old age. Female survival could be expected to increase if females from cohorts experiencing high juvenile mortality are less able, or less willing, to allocate as much to reproduction, and as a consequence this reduces the damage or the survival costs of reproduction generated from a high investment in this life history trait [32], thereby allowing a longer lifespan. It is very unlikely that a change in the reproduction-lifespan tradeoff, in favor of increased lifespan, would be exerted through an alteration in age at first reproduction in this species, because female roe deer consistently give birth at 2 years of age under most environmental conditions [33]. In the Chizé population, age at first reproduction has been monitored through ultrasonography, and over this study period all 2-year-old females reproduced in all but four of the years. The proportion of females in a cohort reproducing at 2 years of age was not related to the level of mortality each cohort experienced as juveniles ($r_s = 0.11$, $p = 0.71$). It is conceivable that exposure to high juvenile mortality could reduce annual or lifetime fecundity. In Trois Fontaines, where lifetime reproductive success is known for many females [34], no detectable relationship was observed between juvenile mortality and either lifetime (estimate \pm SE = -1.55 ± 3.61 , $F_{1,34} = 0.19$, $p = 0.67$; Table S3) or mean annual (estimate \pm SE = -0.47 ± 0.47 , $F_{1,63} = 0.97$, $p = 0.33$; Table S4) reproductive success.

An alternative reason for increased female survival in cohorts exposed to high juvenile mortality, therefore, is that juvenile mortality is condition dependent and generates a strong viability selection. Juvenile mortality would thus selectively remove poor quality females from a given cohort—individuals in poor condition that would be expected to die at a young age as adults—thus leaving a pool of “high-quality” individuals that

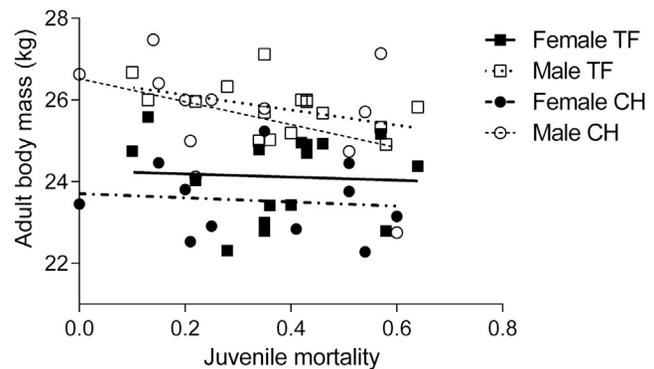


Figure 2. The Level of Juvenile Mortality in a Cohort Has Sex-Specific Effects on Adult Body Mass

Average adult body mass for each cohort of males (open symbols) and females (closed symbols) at Trois Fontaines (TF) and Chizé (CH). Female body mass is not markedly impacted by cohort-specific juvenile mortality, whereas males from cohorts with high juvenile mortality attain a smaller adult body mass. See also Figure S2.

should live longer. Such processes have recently been documented in nematodes, with condition-dependent mortality generating experimentally evolved populations with longer lifespans [15]. Likewise, guppies from populations exposed to high levels of predation had slower rates of aging in laboratory conditions than did guppies from populations with low predation risk [35].

If viability selection explains increased female lifespan after high juvenile mortality, we must consider why this would generate visible positive effects on survival in females and not males. Sexual selection is relatively weak in this species [18, 26, 29], and, as such, evolved differences in sex-specific reproductive investment, which lead to different mortality rates for the sexes, are expected to be slight. Indeed, in years of low juvenile mortality, males and females have similar levels of adult survival (Figure 1C), highlighting that differences in reproductive allocation between the sexes do not always generate sex differences in adult survival in this species. Although sexual selection is weak, the apparent obligatory requirement of male territory defense for half a year could make male survival more sensitive to poor environmental conditions. Any viability selection that is imposed over early life in this sex could be overridden by that fact that all surviving males, regardless of their genetic quality, are in poor body condition and show poor adult survival.

The low sexual selection found in roe deer might also make viability selection more likely to affect females than males. Although females are slightly smaller than males, patterns of sex allocation [36, 37] suggest that females show the greatest variability with regards to fitness [38], which would be expected to influence viability. If females show the greatest variability in these traits and juvenile mortality removes individuals of poor quality that are expected to die earlier, then we would predict that the mean quality of females in a cohort would show the greatest elevation after high selective mortality. To the extent that individual quality relates to viability, this could increase survival to a greater extent in females. Although neither female body mass nor reproductive success increased after high juvenile mortality, it is possible that female survival is enhanced through stronger selection on other traits that facilitate survival but are unrelated to size or reproduction. The home range quality of females is highly variable

and can influence performance in adulthood [34]. One explanation is that females surviving from cohorts of high juvenile mortality occupy the best quality home ranges (as reported in Chizé [39]), which may contribute to their increased adult survival.

Further examination of sex-specific lifespan responses to early-life environments across taxa will help to provide an insight into the causes of the patterns we reveal. If variability in individual quality influences the intensity of viability selection on each sex and the positive survival responses that result from this, then a greater increase in male survival might be expected in species where there is greater variance in male fitness. This would be expected in polygynous animals in which a few males monopolize much of the female mating and could dampen the sex differences in lifespan that are usually observed in such species [1]. If sex differences in reproductive allocation govern sensitivity in adult condition to poor-quality early-life environments, which masks the benefits of viability selection, then we would instead expect that polygynous species would show a similar or stronger version of the pattern that we document here. These species usually show the greatest sex differences in the timing and nature of reproduction. These ideas remain to be tested directly, but separate studies, conducted 10 years apart over different time scales, on the highly polygynous red deer (*Cervus elaphus*) tentatively suggest that these sex-specific patterns in adult survival could be reversed. Male red deer exposed to high juvenile mortality showed *increased* survival during adulthood [40], whereas in females, juvenile mortality was not detectably related to adult survival and variation in survival was much lower [41], although the number of cohorts over which this pattern was assessed was much smaller. Greater investigation of the relationships between early-life environments and sex differences in lifespan across taxa, coupled with controlled manipulations of condition in laboratory studies, may help to reveal the causes for these sex differences and their relationships to a species' mating system and ecology.

Experimental Procedures

Trois Fontaines is an enclosed 1,360 ha area of highly productive forest in the east of France, with cold winters and warm, wet summers. Chizé is an enclosed area of poorly productive forest in the west of France (2,614 ha), with mild winters and relatively dry, warm summers [17, 21, 25]. Data were available for cohorts from 1985–2000 for both juvenile mortality and cohort-specific adult body mass and lifespan. Adult body mass and survival were quantified as previously conducted [24, 42], with adult body mass being an average value from several samples across adult life and survival being assessed from yearly trapping sessions in spring and direct observations over the rest of the year. Juvenile mortality was assessed from fawning time (spring) to the onset of winter as previously reported [8, 43]. All handling and monitoring of animals were conducted under an official agreement provided by the ethics committee of the University of Lyon (agreement number DR2014-09).

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, two figures, and four tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.11.071>.

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