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The Fitness and Life-History Consequences of Early-Life Adversity in a Wild Mammal: A Cumulative Impacts Approach

A dissertation submitted in partial satisfaction of the

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by

Xochitl Ortiz Ross

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ABSTRACT OF THE DISSERTATION

The Fitness and Life-History Consequences of Early-Life Adversity in a Wild Mammal: A Cumulative Impacts Approach

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Xochitl Ortiz Ross

Doctor of Philosophy in Biology

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Professor Daniel T. Blumstein, Chair

Early-life adversity (ELA) can shape survival, reproduction, and fitness long after development, yet wild animals typically encounter multiple ecological, social, and parental challenges whose cumulative consequences remain difficult to quantify. This dissertation develops and applies a cumulative adversity framework to determine how the total burden of ELA affects fitness and life-history outcomes in free-living female yellow-bellied marmots (*Marmota flaviventer*). Using more than six decades of longitudinal data, I constructed cumulative adversity indices (CAIs) spanning ecological, demographic, and maternal exposures before sexual maturity and evaluated their relationships with survival, lifetime reproductive success, annual breeding probability, and reproductive onset decisions. Cumulative adversity predicted lower pup survival

and shorter adult lifespan, whereas indices that allowed favorable conditions to offset adverse experiences performed poorly. Greater adversity was also associated with lower lifetime reproductive success, but this effect was largely explained by reduced lifespan: females with comparable lifespans produced similar numbers of offspring regardless of adversity exposure. Yet, adversity also reduced annual breeding probability and altered age-specific reproductive patterns, indicating trends and costs to reproduction that were not evident from total lifetime output alone. Finally, I found that ELA was associated with contrasting life-history patterns at first reproduction. Greater adversity delayed first reproduction, consistent with developmental or energetic constraints. However, females that began reproducing later after high adversity also weaned larger first litters, suggesting partial compensation through increased initial reproductive investment. Together, these findings show that cumulative ELA primarily constrains fitness by reducing survival and limiting reproductive opportunities. However, shifts in life-history trade-offs that increase early output could mitigate these costs, indicating how other fitness traits can be less constrained and more responsive. Some developmental costs appear irreversible, but individuals may retain limited capacity to adjust reproductive allocation when opportunities arise. A cumulative framework therefore provides a tractable way to connect complex early environments with later-life fitness and may help reshape how environmental risks are evaluated and provide novel avenues for conservation actions.

The dissertation of Xochitl Ortiz Ross is approved.

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2026

Dedication

To curiosity, stubbornness, and the people who fueled both.

And to Helen, who pushed me to ask again.

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List of abbreviations

AICc	Akaike information criterion corrected for small sample size
CAI	Cumulative adversity index
ELA	Early-life adversity
ICC	Intraclass correlation coefficient
iPAR	Internal predictive adaptive response
IRR	Incidence rate ratio
LRS	Lifetime reproductive success
RMBL	Rocky Mountain Biological Laboratory

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Chapters 2 and 3 have both been prepared for submission to academic journals with Daniel T. Blumstein as senior author. I am the first author and primary researcher of these manuscripts. The data and analyses used in these papers will be made publicly available on the OSF repository after publication.

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Ortiz-Ross, X., Blumstein, D.T. 2024. Cumulative adversity and survival in the wild. Ecology Letters 27

Ortiz-Ross, X., Taha, H. B., Press, E. [*], Rhone, S.[*], Blumstein, D. T. 2024. Validating an immunoassay to measure fecal glucocorticoid metabolites in yellow-bellied marmots. Comparative Biochemistry and Physiology Part A 298

Kong, A.Y.[*], **Ortiz-Ross, X.**, Blumstein, D.T. 2025. Is early life adversity associated with adult stress in a wild rodent? Ecology and Evolution 15

Blumstein, D. T., Johnson, N. A., Katz, N. D., Kharpatin, S., **Ortiz-Ross, X.**, Parra, E., Reshke, A. 2023. Biological lessons for strategic resistance management. Evolutionary Applications 16

Nicholson, D.J., Knell, R.J., Folfas, E., Neel, L.K., Degon, Z., DuBois, M., **Ortiz-Ross, X.**, Chung, A.K., Curlis, J.D., Thurman, T.J., McMillan, W.O., Garner, T.W.J., Cox, C.L., Logan, M.L. 2023. Island colonisation leads to rapid behavioural and morphological divergence in Anolis lizards. Evolutionary Ecology 37

Ortiz-Ross, X.[*], Thompson, M. E., Salicetti-Nelson, E., Vargas-Ramírez, O., Donnelly, M. A. 2020. Oviposition site selection in three glass frog species. Copeia 108

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IN THE MEDIA

American Society of Naturalists Press Release. Weather the storm by spreading your investments—the benefits of bet-hedging in Sonoran Desert plants. By X. Ortiz-Ross, Eds. S. Subramanian. June 23, 2025. *Link*

Science Friday radio interview with X. Ortiz-Ross. Measuring the effects of early life adversity—in marmots. November 8, 2024. *Link*

The Conversations article. Wild animals can experience trauma and adversity too – as ecologists, we came up with an index to track how it affects them. By X. Ortiz-Ross. October 21, 2024. *Link*

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INTRODUCTION

The conditions individuals experience early in life can influence their health, survival, and reproduction long after those conditions have passed (Lindström, 1999). The quality of their early environment and experiences determines the resources and opportunities that will be available to them throughout their lives (Metcalfe and Monaghan, 2001; Monaghan, 2008). However, it can also influence how they navigate challenges and adapt to difficult situations, determining their ability to mitigate costs and realize their fitness potential (Fawcett and Frankenhuis, 2015; Nettle et al., 2013). Given that even individuals within the same population may experience different ecological, social, or parental conditions, these early differences can explain much of the observed variation in adult phenotype, survival, reproduction, and lifetime fitness. By understanding how early experiences shape these outcomes we can gain better insight into how populations respond to environmental change and their capacity for resilience.

A cumulative adversity approach

The long-lasting effects of early environmental conditions, from conception to maturity, have long been established across fields and taxa (Lindström, 1999; Lummaa and Clutton-Brock, 2002; Monaghan, 2008). However, most of this research has focused on the independent effect of any given environmental stressor. Single-stressor studies are essential for identifying mechanisms, but they do not capture the range of simultaneous challenges faced by wild populations in their natural environments. Yet, we still do not have a good understanding of how or when the number of stressors experienced affects the ecology of natural populations (Orr et al., 2020).

Given the increasing number of threats faced by wild populations due to rapidly changing climate and human encroachment, interest in the cumulative impact of multiple stressors has been growing (Orr et al., 2020; Pirotta et al., 2022; Tyack et al., 2022). However, estimating these cumulative effects remains a challenge due to the statistical and conceptual complexity of interactions among stressors (Gunn et al., 2014; Jarvis et al., 2024; Mahon and Pelech, 2021).

Cumulative risk models offer a promising way forward (Rutter, 1983). Developed for human studies, the model measures the total burden of early-life adversity (ELA) by summing the number of intrinsic and extrinsic risks an individual experienced into a single, cumulative adversity index (CAI). By using a CAI as a single predictor, these models result in more amenable statistical analyses (Evans et al., 2013). In humans, CAIs (or adverse childhood experiences, ACEs) effectively predict mortality and health risks in adults (Berens et al., 2017; Evans, 2003; Seeman et al., 2010), often better than individual exposures (Beckie, 2012; Edes and Crews, 2017; Mauss et al., 2015).

Therefore, this approach does not ask how each stressor impacts individual health, but rather whether the accumulation of stressors itself an impact/predict an individual's state or prospects. While few have attempted to apply these models to wild animals, recent studies have shown that cumulative early-life adversity can predict adult performance and longevity, although the strength and direction of these effects vary among populations and species (Gicquel et al., 2022; Morrison et al., 2023; Tung et al., 2016). These differences make cumulative approaches useful for identifying general patterns, but also for asking when and how populations can withstand adversity.

A cumulative index is deliberately coarse. It cannot identify the mechanism of every exposure, and it should complement rather than replace studies of specific stressors. Its advantage is that it captures a property that is otherwise easy to miss: developing organisms must respond to their whole environment at once (Ortiz-Ross and Blumstein, 2024). It can also make complex questions tractable when sample sizes do not support a model containing every stressor and interaction (Pirotta et al., 2022). This is especially important in longitudinal studies of wild animals, where complete lifetime records are valuable but inevitably limited. By placing diverse experiences on a common scale, a cumulative adversity index provides a way to compare their combined consequences across life stages, fitness components, and, eventually, study systems.

Opportunity costs and trade-offs

The cumulative stress hypothesis predicts that stressful experiences have accruing costs that become increasingly detrimental to fitness (Stewart, 2006). These costs derive from “wear and tear” of the stress-response, physiological mechanisms that are continuously activated by repeated environmental stressors (McEwen and Wingfield, 2007). This repeated activation then reduces the organism’s capacity to respond to future demands. From a life-history perspective, similar costs arise through developmental trade-offs: the more challenges individuals encounter, the more resources they must divert from growth and future reproduction into responding to immediate threats (Monaghan, 2008). Both explanations agree that exposure to multiple or repeated stressors will inevitably reduce lifetime fitness.

Lifetime reproductive success (LRS) is often considered the ultimate, or truest, fitness measure. It represents a combination of longevity, or survival, which also

contributes the number of breeding opportunities, and reproductive success, as the total number of offspring produced. However, lifespan is the better predictor of LRS (Clutton-Brock, 1988; Vasilieva and Tchabovsky, 2020; Weibel et al., 2020). Focusing on LRS, especially when not controlling for lifespan, risks ignoring how adversity impacts lifetime fitness through reproduction (Pigeon and Pelletier, 2018). While total effects describe the population-level consequences of adversity; lifespan-conditioned effects help identify the pathways that produce them. Together, they can show whether adversity primarily limits survival, reproduction, or both. Evidence that cumulative ELA is strongly associated with lifespan has been found in studies of multiple mammals (Gicquel et al., 2022; Gonzalez et al., 2023; Ortiz-Ross and Blumstein, 2024; Patterson et al., 2021; Tung et al., 2016; Weibel et al., 2020), but other reproductive aspects have yielded mixed results and are still underexplored (Dettmer and Chusyd, 2023; Drake et al., 2025; Hamel et al., 2009; Monaghan, 2008).

Life-history theory dictates that growth, survival, and reproduction represent competing demands on limited resources (Stearns, 1992). Therefore, poor early conditions can influence not only the availability of resources, but also their allocation. While flexibility in reallocating energy can help individuals respond to immediate threats, the energy spent on survival can no longer be used for growth. This trade-off can place those individuals at a competitive disadvantage against individuals who were instead able to prioritize their growth (Metcalfe and Monaghan, 2001; Monaghan, 2008).

The early-life effects literature can be broadly split into two camps: those who predict persistent fitness losses from poor early conditions (Cooper and Kruuk, 2018; also the “silver spoon” effect; Lindström, 1999), and those who predict a compensatory

adaptive response that maintains fitness (Ancona et al., 2018; Nettle et al., 2013). One of the most popularly studied compensatory responses involves shifting life-history strategies, or energy trade-off decisions (Ellis, 2004; Fawcett and Frankenhuis, 2015; Metcalfe and Monaghan, 2001; Nettle and Frankenhuis, 2020). Life-history theory (Stearns, 1992) predicts that, under unfavorable conditions, long-lived species should favor growth and survival (or future reproduction) over current reproduction; longer lifespans mean greater future breeding opportunities. Those with shorter lifespans, and lower prospects for future reproduction, should instead take advantage of early breeding opportunities even if it threatens their future survival, since their mortality risk is already high. Therefore, changes in longevity are coupled with changes in other life-history traits such as the timing of reproduction (Stearns, 1992). As such, under an adaptive-response framework, individuals with reduced survival prospects should increase investment in current or early reproduction (Nettle et al., 2013); this strategy is often described as “accelerated reproduction”. Early adversity may therefore influence not only how long an individual lives or how many offspring it produces, but also when it reproduces, how often it breeds, and how much it invests when an opportunity arises.

Ultimately, the fitness consequences of early-life conditions can be interpreted under two different frameworks: early developmental adversity may irrevocably impair fitness, but it could also induce adaptive phenotypic changes that allow organisms to compensate for adversity costs. The two predictions are usually treated as alternatives, but reproductive success is not a single trait and need not have a uniform response. Age at first reproduction, body condition, annual breeding probability, litter size, and lifetime output can have different drivers and different levels of plasticity (Ellis, 2004;

Nettle and Frankenhuis, 2020; van Noordwijk and de Jong, 1986). Reproductive onset may be under greater developmental control and more likely to be constrained, while fertility may be more plastic and responsive to environmental conditions (Charmantier and Garant, 2005; Stearns, 1992), allowing adative shifts in reproductive output. Constraint and compensation may therefore operate simultaneously on different components of reproduction (Ellis, 2004; Nettle and Frankenhuis, 2020).

A long-term study of yellow-bellied marmots

In the following chapters I use ELA to describe the range of challenges faced by individuals prior to reaching sexual maturity. More specifically, I define adversity as any ecological, demographic, and parental condition that can reduce an individual's access to resources or otherwise have detrimental consequences for fitness (Ortiz-Ross and Blumstein, 2024). This definition is intentionally broad. Adversity may arise from the physical environment, from interactions with conspecifics and predators, or from maternal state and loss. Importantly, natural populations are likely to experience multiple forms of adversity throughout their development. While they may differ in their mechanism, they each place an additional burden on the individual. This dissertation will explore how the number of adverse experiences, regardless of their nature, can impact lifetime fitness, including survival, reproductive success, and life-history strategy.

I address these questions using a long-term study of wild yellow-bellied marmots (*Marmota flaviventer*) near the Rocky Mountain Biological Laboratory in Colorado. This population has been monitored for more than six decades, providing detailed behavioral, demographic, physiological, and life-history data on individually marked animals (Armitage, 2014). Such long-term, individual-based studies are essential for

linking experiences during development to outcomes that may not appear until years later (Clutton-Brock and Sheldon, 2010).

Yellow-bellied marmots are large, facultatively social ground squirrels that live in a highly seasonal, high-elevation montane environment. After hibernating for approximately seven months, they have a short active season to reproduce, grow, and accumulate sufficient fat reserves to survive their next hibernation (Armitage, 2014). Females generally reach sexual maturity at age two, but their ability to breed depends strongly on their body condition after hibernation (Armitage, 2017; Oli and Armitage, 2004). Their harsh environment and slow life history impose considerable weight and energetic constraints on both annual survival and reproduction, lending an excellent opportunity to study trade-offs.

Additionally, this study population must contend with many other environmental risks which can vary substantially in their threat level across years, location, and an elevation. Extensive studies on this population have determined that their fitness varies with a variety of ecological and maternal conditions, including snowmelt, summer precipitation, predation pressure, litter composition, maternal condition, maternal stress, and maternal survival (see Ortiz-Ross and Blumstein, 2024). The range and number of scientifically grounded possibilities for early adverse experiences make this system also well suited for testing a cumulative adversity approach.

Summary of findings

Across the following three chapters, I explore the benefits of adopting a cumulative impact approach to ELA. I begin by proposing a systematic framework for developing a system-based CAI. Applying this approach, I detail the cumulative fitness costs of

increasing ELA exposures from early survival through adult longevity, including LRS. I then proceed to investigate the early life-history pathways through which that cost may be expressed and/or mitigated (i.e., the reproductive onset, condition, and output).

In Chapter 1, I develop and evaluate a cumulative adversity framework for wild yellow-bellied marmots (Ortiz-Ross and Blumstein, 2024). I combine ecological, demographic, and maternal adversities experienced before sexual maturity and ask whether their accumulation (or sum) predicts survival. Cumulative adversity was associated with lower survival through the first year of life and shorter adult lifespan. Importantly, indices that allowed positive experiences to offset negative ones did not predict adult longevity compared to indices focused on adverse exposure. This suggests that positive conditions may buffer some immediate costs, but they do not fully erase the long-term consequences of early adversity. Lastly, adult longevity models that used a single binary index for ELA performed substantially better than multivariate models with independent adversity measures. Biologically, these findings add support for the cumulative stress hypothesis (but see Kong et al., 2025) and highlight the value of focusing on adverse experiences. Methodologically, the chapter shows that cumulative indices can reveal persistent fitness costs that are not apparent when stressors are modeled separately, thereby opening new research avenues. Furthermore, by systematically following the outlined approach, researchers can also test how cumulative impacts might vary by adversity type, severity, and timing, while still retaining a common conceptual framework to ease cross-taxa comparisons.

Chapter 2 shows a detrimental impact of ELA on LRS but driven by lifespan. Females with shared lifespans achieved similar LRS regardless of the adversity they

experienced, suggesting that the lifetime fitness costs of ELA act primarily by constraining survival probability rather than limiting total reproductive output. Yet, a closer view revealed that ELA reduced annual breeding probability, constraining the breeding opportunities normally gained with age. Taken together, these findings show that the independent reproductive costs of ELA are not fully evident when comparing total lifetime output. At the same time, it raises the question of how females who survive to any given age do not incur adversity costs on their lifetime reproductive output despite their annual decrease in the likelihood of breeding successfully. Therefore, these findings reveal the possibility that females can compensate for the annual breeding costs of ELA.

Chapter 3 seeks to identify potential avenues for reproductive compensation in response to ELA by examining three distinct expressions of female reproductive investment at its onset: timing, body condition, and output. Greater ELA was associated with delayed reproductive onset, consistent with developmental or energetic constraints. However, those same females (late breeders who experienced high ELA) were also more likely to wean larger first litters, consistent instead with a compensatory response. Adversity was therefore associated with delayed reproductive timing but also increased reproductive output, showing that opposing life-history patterns can operate simultaneously on different traits. More specifically ELA compromised the ability to initiate reproduction in early adulthood, but this impediment weakened later in life, when females were able to gain enough resources to boost their first litter size. Indeed, while ELA was not strongly associated with body mass at first reproduction, females that delayed reproduction tended to be heavier when they bred. Therefore, individually,

reproductive timing and reproductive investment told different stories, but complemented each other when examined together. This finding could explain how females with similar lifespans maintain similar lifetime reproductive success despite lower annual breeding probability.

Together, the chapters show that cumulative ELA primarily reduces fitness by decreasing survival and reproductive opportunities; annual costs that cannot be fully recovered even as conditions become more favorable. However, ELA constraints are not uniform across fitness traits. Some traits may be more sensitive to developmental costs, such as reproductive onset, while others can be more readily adapted to fit changing conditions, such as reproductive output (or fertility). Therefore, females can make the best of a bad situation by weathering the initial storm, conserving their energy, and taking full advantage of the first viable opportunity to breed. While perhaps not enough to overcome the heavy mortality costs, this adaptive breeding response to ELA identifies one form of resilience.

In the end, a poor start may indeed result in a poor end, but this does not prevent one from still making the best of a bad situation. Early adversity changes the amount of time and the set of opportunities available to an individual. Some losses are irreversible and cannot be changed, but individuals can still choose how to take advantage of the opportunities they do encounter.

Take-aways

Overall, this dissertation advances a cumulative perspective on environmental adversity in wild populations, recognizing the complex combination of stressors they experience and the need to consider their cumulative burden. It also highlights that cumulative ELA

does not act uniformly across fitness traits (e.g., survival, reproductive opportunity, and reproductive investment), which, individually, can exhibit different life-history patterns. Importantly, we show that individuals can experience persistent ELA constraints while still showing trait-specific opportunities for compensation, or resilience. Responses to adversity should therefore be evaluated across multiple fitness components to uncover which paths, if any, provide opportunities for recovery. To show resilience, an individual is not required to escape every cost or match an unconstrained phenotype in every respect, they need only mitigate some of those losses. By combining a feasible cumulative method with a trait-specific life-history perspective, this work provides a framework for studying how wild populations respond to increasingly complex environments and for translating long-term ecological data into more useful predictions and management decisions.

Conservation decisions often focus on identifying and reducing the largest individual threat. However, population persistence may depend more on total adversity than on any one stressor. A cumulative adversity framework can help identify which populations are experiencing a higher burden and may require a different management approach. By understanding which life-history traits are more vulnerable or more resilient to developmental constraints and when improving conditions can benefit recovery, managers can also adjust the type and timing of mitigation strategies to increase their effectiveness.

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LETTER

Cumulative adversity and survival in the wild

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Abstract

Protecting populations contending with co-occurring stressors requires a better understanding of how multiple early-life stressors affect the fitness of natural systems. However, the complexity of such research has limited its advancement and prevented us from answering new questions. In human studies, cumulative risk models predict adult health risk based on early adversity exposure. We apply a similar framework in wild yellow-bellied marmots (*Marmota flaviventer*). We tested cumulative adversity indices (CAIs) across different adversity types and time windows. All CAIs were associated with decreased pup survival and were well supported. Moderate and acute, but not standardized CAIs were associated with decreased lifespan, supporting the cumulative stress hypothesis and the endurance of early adversity. Multivariate models showed that differences in lifespan were driven by weaning date, precipitation, and maternal loss, but they performed poorly compared with CAI models. We highlight the development, utility, and insights of CAI approaches for ecology and conservation.

KEYWORDS

allostatic load, cumulative adversity index, cumulative risk, cumulative stress, developmental plasticity, developmental stress, early-life adversity, early-life effects, environmental change, multiple drivers

INTRODUCTION

Natural populations live in complex environments in which they are exposed to many co-occurring stressors that can compound and interact in a variety of ways. Yet, we do not have a good understanding of how or when the number of stressors experienced affects the ecology of natural populations. Early-life experiences in particular are known to have lifelong consequences (Lindström, 1999), but little is known about the cumulative impact of multiple early-life stressors on adult fitness. In many ways, this gap in our knowledge has been defined by constraints in data analysis and availability (Pirotta et al., 2022). A better understanding requires more longitudinal studies and the shared application of feasible methods.

While the importance of cumulative effects has been gaining recognition across fields (Orr et al., 2020), estimating them remains a challenge (Gunn et al., 2014; Jarvis et al., 2024; Mahon & Pelech, 2021; Orr et al., 2020; Pirotta et al., 2022; Tyack et al., 2022). Many of these effects, and especially their interactions, are context dependent, which makes it harder to generalize across populations (Côté et al., 2016; Kroeker et al., 2017; Orr et al., 2020) and over time (Darling & Côté, 2008; Debecker et al., 2017; Lange et al., 2018). While some frameworks have been highlighting the importance of understanding stressor interactions (Hale et al., 2017), such variable effects are hard to capture at higher, more complex scales (Orr et al., 2022). We suggest that a more general and widely applicable approach can yield novel insights even when the specific mechanisms are unknown or uncertain.

To quantify the impact of multiple adverse childhood experiences on adult health risks, human studies developed a cumulative risk model (Rutter, 1983). The model combines organismal traits with characteristics of the social and physical environment into a single, cumulative adversity index (CAI). In these models, risk exposure becomes binary by either a statistical cut-off (e.g., upper quartile) or a conceptual categorization (e.g., below the poverty line). Each exposure is then summed into a single cumulative risk score. By using a CAI as a single predictor, these models result in more amenable statistical analyses (Evans et al., 2013). CAIs have been effective in demonstrating that adverse childhood experiences are strongly associated with adult allostatic load (an indicator of cumulative stress, Box 1) and related health risks (Berens et al., 2017; Evans, 2003; Seeman et al., 2010). Furthermore, CAIs were repeatedly found to be a better predictor of mortality and health decline than individual biomarkers alone (Beckie, 2012; Edes & Crews, 2017; Mauss et al., 2015). While effective in humans, few have attempted to apply these models to wild animals (Gicquel et al., 2022; Gonzalez et al., 2023; Morrison et al., 2023; Patterson et al., 2021; Tung et al., 2016).

In a dynamically changing Anthropocene, we need better ways to evaluate the impact of cumulative stressors. CAIs can yield both ecological insights and aid conservation management (Pirotta et al., 2022) by highlighting important survival and demographic patterns. They can be a great tool to test the cumulative stress hypothesis (Stewart, 2006; Box 1) in wild animals, evaluate the importance of the number of early stressors, and identify at-risk individuals and populations. However, to be effective, CAIs must be applied using an accessible, reliable, and consistent framework that allows for better comparisons across systems. A clear framework is paramount because the few prior studies that used CAIs in wild animals have varied considerably in their development.

In this article, we aim to (1) determine the utility of using a CAI to predict survival in wild yellow-bellied marmots (*Marmota flaviventer*) and (2) provide a structure that others can follow to develop bespoke CAIs in their own study species (Figure S1).

We begin by describing our framework. We: (a) define adversity and how to identify it; (b) discuss best practices for quantifying adversity; (c) evaluate how well different methodologies predict early survival and adult longevity in yellow-bellied marmots (hereafter, marmots); and (d) discuss what inferences can be made and which types of studies would benefit from this kind of analysis. More specifically we ask: Does greater cumulative early adversity decrease early survival and adult longevity? Can the survival costs of cumulative early adversity be compensated by positive early experiences? Which CAI performs best? Do models using a single CAI perform better than multivariate 'full' models?

BOX 1 The importance of cumulative adversity: cumulative stress, allostatic load, and developmental constraints

Within the field of developmental plasticity, the cumulative stress hypothesis (Stewart, 2006) has been underexplored. Based on the concept of allostatic load (McEwen, 1998), the cumulative stress hypothesis posits that stressful situations have accruing costs that become increasingly detrimental to fitness. As individuals interact with their environment, they overcome challenges by adjusting their physiology. This ability to 'maintain stability through change' has been termed allostasis (McEwen & Wingfield, 2007). Allostatic load occurs when excessive use of these regulatory systems results in 'wear and tear' rendering them less effective with use. Therefore, allostatic load refers to the cost of repeated exposure to environmental challenges through over-activation of the stress response (Guidi et al., 2021).

Allostatic load has been extensively investigated in human health, where it has been associated with increased risk for a range of diseases, from cardiovascular diseases to neurological disorders (for a review, see Guidi et al., 2021). Several studies have identified allostatic load through biological markers (McEwen, 2015; Seeman et al., 1997, 2001), such as cortisol and resting systolic and diastolic blood pressure. While biomarkers focus on the physiological evidence of allostatic load, clinical studies have focused on its underlying experiential factors (e.g., significant hardship and distress). Identifying the adverse environment allows us to not only identify at-risk individuals but also proactively address the root cause and reduce the load for future generations.

From a life-history theory perspective, the detrimental effects of cumulative stress arise not from a loss of efficiency but from developmental trade-offs (Monaghan, 2008). The more challenges individuals encounter, the more energy they must divest from growth into survival. This trade-off places them at a competitive disadvantage at maturity (developmental constraint), compared with individuals who were able to prioritize their growth. According to both hypotheses, exposure to multiple or repeated stressors leaves individuals in a suboptimal state that reduces relative fitness. If true, to better understand the fitness options available to individuals, we must focus specifically on the detrimental effect of multiple

BOX 1 (Continued)

stressors on developing individuals. While it may appear like two sides of the same coin (e.g., 'silver spoon' effect; Grafen, 1988), we assert the distinction is important.

MATERIALS AND METHODS

Study system and field site

We capitalize on 62 years of studying a population of yellow-bellied marmots (Armitage, 2014; Blumstein, 2013) around the Rocky Mountain Biological Laboratory (RMBL, 38°57′N, 106°59′W) in Gunnison County, Colorado, U.S.A. These decades provided us with a deep understanding of the ecology and life history of its individuals, but in our study, we used only 17–18 years of data comprised of females born after 2001 (when we started quantifying physiological stress) and who remained in one of our colonies until 2019, to guarantee an accurate record of their pedigree, age, and lifetime experiences.

The RMBL population of marmots is spread across a 300 m elevational gradient and is characterized by high annual and colony-level variation in environmental and demographic conditions (Armitage, 2014). Based on their elevational difference, colonies are subdivided into up- and down-valley (respectively at higher and lower elevations), groupings with demonstrated environmental, ecological, and demographic differences (Armitage, 2014). Data collection occurs during times of peak activity (0800–1200 h and 1600–1900 h) from mid-April to mid-September. Individuals in this population have been trapped biweekly, uniquely marked, and systematically observed daily (Blumstein et al., 2016) by many trained students and volunteers (authors included), who collected behavioural, morphological, and physiological data (details in S1).

Defining adversity

We define adversity as any external or internal environmental condition that can have a detrimental effect on the fitness of the individual who experiences it, often by directly or indirectly limiting their access to resources. In this well-studied system, we were able to reduce our assumptions about what marmots might experience as adverse by choosing to only consider factors known to affect a component of fitness (Table S1). To do so in a systematic manner, we proceeded using the following approach (Figure S1).

The cumulative adversity index framework

Time window

Adversity can occur at any life stage. Therefore, a CAI can be built annually or it can consider a discrete life period, such as sensitive periods—developmental periods during which certain experiences or stimuli have a particularly strong effect on the phenotype (Fawcett & Frankenhuis, 2015; Stamps & Luttbeg, 2022). Marmots reach sexual maturity at the age of 2, therefore we consider these first two years as their early life. Given we have not determined sensitive periods in marmots, we chose to build three different indices to investigate the importance of the timing of early adversity. (1) The *Pup CAI* only includes adversity experienced during the first year of life, (2) the *Yearling CAI* only includes adversity experienced during the second year, and (3) the *Total Early CAI* sums the adversity experienced across both years.

Fitness measures

Given our definition of adversity (i.e., having a detrimental effect on fitness), we first considered which fitness measures were relevant for marmots. We identified the following: winter survival, body mass, summer survival, reproductive success, longevity, and dispersal (more details in Table S1). Therefore, to identify adversity measures we then looked for factors that had been shown to affect said fitness measures in some way (see below).

Sources of adversity

We identified determinants of the above fitness measures (i.e., sources of adversity) by conducting an informal search of the marmot literature. We include the following ecological, demographic, and maternal measures: late start of season, summer drought, predation pressure, large litters, male-biased litters, late weaning, poor maternal mass, high maternal stress, and maternal loss (Table 1).

By adopting the term 'adversity', we emphasize risks that are detrimental to fitness. However, when deciding which factors to list as adversity measures, we considered *any* variable that had been shown to impact the fitness measures identified above, even if the reported effect was positive. For example, we found that summer precipitation was reported as having a positive effect on fitness; we still considered summer precipitation as a source of adversity because of its opposite detrimental effect, summer drought, even though the effect of drought per se had not been reported. In such cases, to better interpret the results the measure was reversed. For example,

TABLE 1 We describe how each adversity measure was selected based on its association with a fitness outcome (in bold). More detailed data collection in the Supporting Information (1).

Adversity type and measure	Demonstrable effect on a relevant fitness measure	References
Ecological		
Late start of season (SOS)	Longer winters and shorter growing seasons are associated with lower **body mass** at hibernation which results in lower **winter survival** and lower **reproductive success**	Ozgul et al., 2006, 2010; Cordes et al., 2020
Summer drought	Summer drought is associated with lower food availability that results in lower **body mass** at hibernation, lower **winter survival**, and lower **reproductive success**	Cordes et al., 2020
Predation pressure	Predation is a major determinant of **summer mortality** and has also been indirectly linked to lower **reproductive success** and higher rates of **dispersal**	Van Vuren, 2001; Monclús et al., 2011
Demographic		
Large litter size	Larger litters likely result in higher competition among littermates and have been associated with smaller **weaning mass** in pups, which results in a lower likelihood of **survival**	Armitage, 2014
Male-biased litters	Females born in male-biased litters have lower **overwinter survival**, lower **reproductive success**, and increased probability of **dispersal**	Monclús & Blumstein, 2012
Parental		
Late weaning	Earlier weaning dates lead to offspring with higher **body mass** at hibernation which in turn increases pup **winter survival**	Ozgul et al., 2010
Poor maternal mass	Maternal mass in June is associated with **weaning mass** in pups (body mass at weaning)	Armitage, 2013
Maternal stress	High maternal stress during pregnancy and lactation has been linked to higher stress in pups, which is also associated with lower pup **winter survival**	Pinho et al., 2019
Maternal loss	Offspring are nearly twice as likely to **disperse** if their mother is absent	Armitage, 2014

summer precipitation was multiplied by −1 such that larger values indicated a summer drought.

Composite indices often do not consider interactions. We wanted to avoid omitting potentially important interactions and were mindful of how we could incorporate them. For example, predation pressure could be costly when population density is low but not when high (i.e., overcompensation; Neale & Juliano, 2019). In such a case, we were prepared to pair each term and include the interaction as its own measure (high predation + low density = adverse; high predation + low density = not adverse). However, our informal search of the marmot literature yielded no clear-cut, proven interactions and we decided not to make further assumptions. Perhaps this is a gap within the marmot literature and more potential interactions could be investigated, or perhaps the existing interactions are too complex. Nevertheless, we made sure none of our adversity measures were correlated with each other before performing our analyses.

Weighing adversity across measures

We explored whether to treat measures equally or assign them weights (e.g., based on the standardized effect size of their impact on fitness). A review of the organizational sciences literature (Bobko et al., 2007) found that indices that use unweighted (or unit-weighted) measures gave similar results as those that use weighted measures, whereas weighted measures provided more accurate results when based on accurate data, they otherwise tended to increase the margin of error and introduce false assumptions without increasing accuracy (Pirotta et al., 2023). Based on this literature and our available data, we chose to weigh all adversity equally.

Quantifying adversity within measures

To create a composite index containing both categorical and continuous data, it is recommended to turn them

into a similar scale (Bobko et al., 2007). We chose to use binary levels (e.g., adverse or not). While we could have considered multiple levels of adversity (e.g., high, medium, and low) we felt we did not have enough data to justify those decisions; furthermore, the literature suggests binary measures yield similar results with fewer assumptions (Bobko et al., 2007), and we were interested in the utility of its simplicity. Binary measures have also been used in other CAIs in humans and other animals (e.g., Tung et al., 2016).

In deciding how to determine when an experience was adverse, we aimed to be conservative and consistent. Thus, we explored two thresholds for determining when a continuous variable is adverse: the upper quartile and the upper decile. When converting a continuous measure into a binary one, we only considered an experience as adverse when it fell above a threshold. We explored whether this threshold could be empirically obtained (e.g., critical maximum temperature), but we did not have this level of evidence in our system. Following human and wildlife examples (Evans, 2003; Tung et al., 2016), we chose an upper quartile threshold—an experience was considered adverse when it fell above the upper quartile of the population distribution. In other words, an experience that matched that of 75% of the population (below the upper quartile) was not considered adverse. However, we were concerned about how sensitive our results would be to the type of threshold chosen. We therefore explored a more extreme threshold, the upper decile, to represent acute adversity.

In this index, we assumed that adversity accrues and *cannot be buffered* by the benefits of a positive environment, which aligns with the concept of allostatic load and developmental constraints but may not be true under other paradigms (e.g., 'silver spoon' effect; Grafen, 1988; Box 1). Alternatively, it is possible to standardize measures, for instance by calculating z-scores. Literature advocating for the use of unit-weighted measures in composite index scores indicates that such measures are most appropriate when they are each standardized (the data are rescaled to have a mean of 0 and a standard deviation of 1; Bobko et al., 2007). However, when used in an adversity index, standardized measures imply that positive experiences can cancel (or buffer) the effects of negative experiences. To avoid creating an inappropriate buffering effect, adversity measures could be standardized following two alternative methods: (a) standardize only adverse experiences: in this method, only negative experiences are scaled, so anything above 0 (positive experiences) remains 0, whereas negative experiences are standardized. Or (b) normalize values from 0 to 1: instead of centering the values around 0, each value is normalized to a range from 0 to 1 (e.g., Patterson et al., 2021). Each method is associated with a slightly different interpretation of adversity and the mechanisms by which it can yield negative outcomes. It is also possible that different kinds of adversity follow different patterns (e.g., non-linear relationships), but specific data would be required to make that determination. To evaluate our hypothesis that positive experiences could not significantly buffer negative ones, we created an index that summed standardized scores (categorical variables were first made binary as 0 and 1 and then rescaled).

In summary, we created three CAI indices: one binary with an upper-quartile cut-off (hereafter moderate adversity); one binary with an upper-decile threshold cut-off (hereafter acute adversity); and one continuous and standardized.

Evaluating the cumulative adversity indices

All data manipulation and analyses were carried out using R Statistical Software (version 4.3.1; R Core Team, 2023) and were freely available (see Data Availability). To evaluate whether any of the indices explained variation in marmot longevity, we fitted mixed-effects Cox proportional hazard models using the 'coxme' package (version 2.2.20; Therneau, 2024b) that included survival of adult individuals as the response variable and each CAI (in separate models) as the predictor variable. We used a total of nine indices representing three time windows—pup CAI, yearling CAI, and total CAI—and three different types of adversity—moderate, acute, and standardized adversity. Unlike most other studies, we decided to control for the present environment; we included the fixed effects of valley position (up and down) and its interaction with the CAI, since the conditions up-valley tend to be consistently harsher than those down-valley, current predation pressure, a major determinant of summer survival, and August mass, a major determinant of winter survival. Variables we initially considered as random effects were colony, dam ID, litter, and cohort year. However, after a structured exploration, we excluded litter, because 92% of litters in our dataset only had 1 remaining individual, and dam ID (nested within colony) because it showed a negligeable amount of variance (0.0097). Our final models included colony and cohort year as random effects.

To test whether CAIs were associated with survival to age 1 (hereafter pup survival) we fitted generalized linear mixed-effects models using the package 'lme4' (version 1.1.35.1; Bates et al., 2015) with pup survival as the response variable, and the pup CAI and valley position as fixed effects. We investigated the suitability of random effects in the pup survival models and found that colony had negligeable variance compared with dam ID. Our final model included litter ID nested within dam ID and cohort year as random effects. We did not explore survival to adulthood because differentiating between dispersal and death proved difficult.

To determine which index best explained marmot survival, we compared the corrected Akaike Information Criterion (AICc) scores of each model (following Burnham et al., 2011) using the package 'performance' (version 0.11.0; Lüdecke et al., 2021). The model with the lowest AICc

represents the estimated best model, every other model is evaluated as how different it is from the best model. To better evaluate the utility of a cumulative index, we also compared the cumulative models with mixed-effects Cox regression model that included each adversity measure as a separate fixed effect (hereafter the *full models*), both in their binary and raw structures (Figure 1; Tables S4–S7). Model diagnostics on survival models were performed

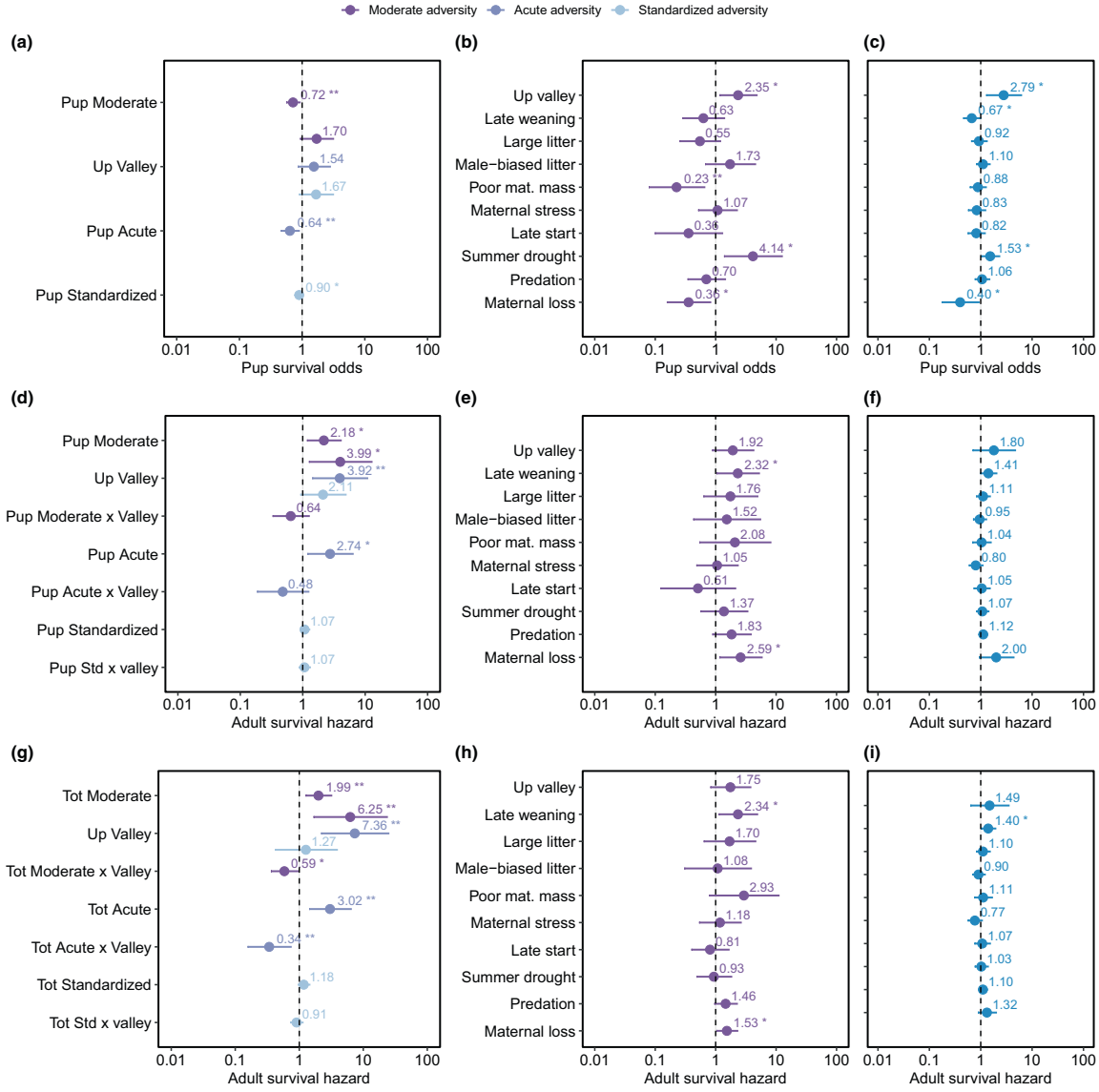

FIGURE 1 (a) Results of our pup survival models, the figure includes all three models (moderate CAI, acute CAI, and standardized CAI) and the fixed effect of valley (up and down). The pup survival odds ratio represents the odds of survival to year 1, therefore an increase in odds ratio represents increased survival probability. (b, c) show the results of the full pup survival models with moderate adversity and raw, untransformed values respectively. All pup survival models included 471 female pups from 2002 to 2018. (d) and (g) show the results of our adult longevity models for all three types of adversity (moderate, acute, standardized) experienced during the first year (pup adversity) and summed across both years of early life (total adversity) respectively. The figures omit the current variables of predation and August mass for ease of reading the figure and because they were not significant (Tables S5 and S6). As the hazard ratio increases, survival probability decreases. All adult longevity models included 229 observations of 79 adult females from 2004 to 2019. The models included random effects of colony ($n=11$) and birth-year cohort ($n=15$). Similarly to (b) and (c), we show the results of the full adult longevity models for pup moderate adversity (e), raw values of pup adversity (f), total moderate adversity (h), and raw values of total adversity (i). Asterisks represent significance values (*$p<0.05$; **$p<0.01$).

using the 'cox.zph()' function from the 'survival' package (version 3.5.8; Therneau, 2024a), and the functions 'check_collinearity()' from the 'performance' package; the function 'check_model()' from the 'performance' package was used for all other models.

RESULTS

Pup survival

Data were collected between 2002 and 2018 and included 471 females from 197 litters and 112 unique mothers. 54% of pups survived their first year. All four models yielded similar results (Figure 1a; Table S2); all CAIs were positively associated with reduced odds of survival. Moderate and acute CAIs decreased odds by 30 and 40% for each additional adversity respectively ($p = 0.008$), whereas standardized adversity decreased them only by 10% each ($p = 0.047$). Of the three, the moderate and acute adversity models were equally likely to be the best model (ΔAICc<1) and both explained ca. 40% of the variation (Table S2).

The full models showed that pup survival odds were significantly higher up-valley for all models (OR = 1.85–2.79; Table S4; Figure 2b,c). Maternal loss significantly decreased survival odds in all models (OR = 0.36–0.63), showing a 64% decrease in the moderate adversity model. Poor maternal mass decreased them by 77% only in the moderate adversity model, whereas late weaning decreased them by 33% only in the standardized and raw models. Surprisingly, drought increased the odds of survival across all but the acute adversity model (OR = 4.14–1.52), with the greatest effect observed in the moderate adversity model. The standardized and raw models were virtually indistinguishable. When comparing AICc, the full model of moderate adversity was comparable to the moderate CAI model (ΔAICc<2), whereas all other models had a larger AICc (Table 2). We conclude that a CAI effectively captures short-term survival risk in yellow-bellied marmots, but full models, when available, may be more informative.

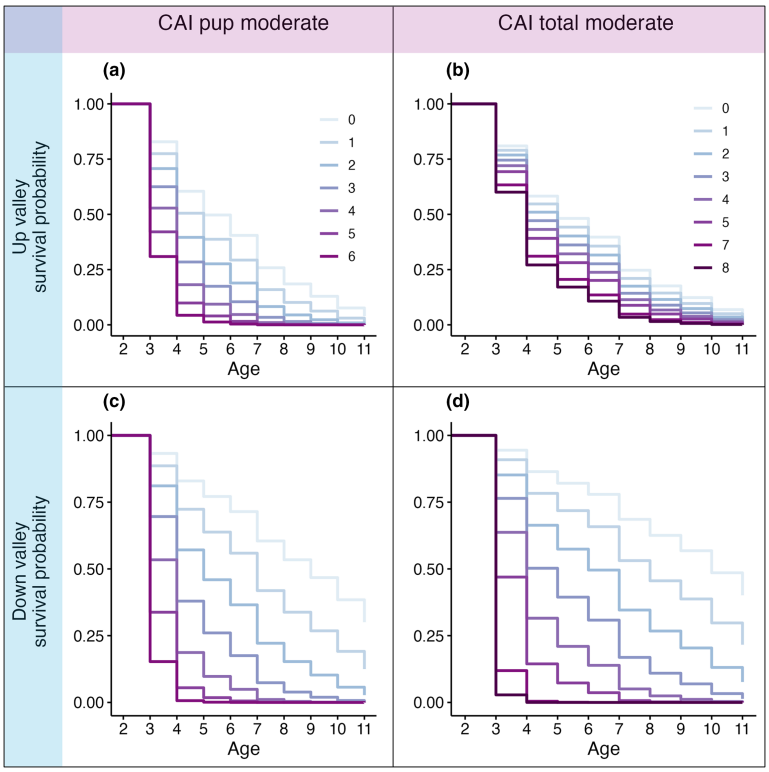

FIGURE 2 Survival probability under low predation up valley (a, b) and down valley (c, d) for each CAI moderate pup adversity (a, c) and each CAI moderate total adversity (b, d). Valley was included as a fixed effect to account for site differences due to elevation. Colonies up-valley tend to experience harsher weather conditions. All adult longevity models included 229 observations of 79 adult females from 2004 to 2019. Survival plots were generated using a Cox proportional hazards model without random effects; all other elements remained the same. Full results of the mixed-effects models are found in Tables S5 and S6.

TABLE 2 List of all the pup survival and adult longevity models we fit and their relative AICc values for model comparison.

Model	Adversity	Window	AICc	Weight	Cum weight	ΔAICc	Evidence ratio	R^2 (cond)	R^2 (marg)
Pup survival									
Full	Moderate	Pup	604.3	0.464	0.464	*best estimate*	*best estimate*	0.414	0.139
CAI	Moderate	Pup	605.7	0.232	0.696	1.4	2.00	0.400	0.049
CAI	Acute	Pup	605.7	0.238	0.934	1.4	1.95	0.408	0.049
CAI	Standardized	Pup	609.3	0.040	0.974	5.0	11.6	0.379	0.027
Full	Acute	Pup	611.2	0.015	0.989	6.9	30.9	0.412	0.115
Full	Raw	Pup	611.7	0.012	1.001	7.4	38.7	0.405	0.120
Adult longevity									
CAI	Moderate	Pup	376.7	0.430	0.430	*best estimate*	*best estimate*	-	-
CAI	Moderate	Total	377.4	0.294	0.724	0.7	1.46	-	-
CAI	Acute	Total	378.9	0.143	0.867	2.2	3.01	-	-
CAI	Moderate	Yearling	381.0	0.050	0.917	4.3	8.60	-	-
CAI	Acute	Pup	381.1	0.046	0.963	4.4	9.35	-	-
CAI	Acute	Yearling	383.4	0.015	0.978	6.7	28.7	-	-
CAI	Standardized	Total	384.4	0.009	0.987	7.7	47.8	-	-
CAI	Standardized	Pup	384.7	0.008	0.995	8.0	53.8	-	-
CAI	Standardized	Yearling	386.4	0.003	0.998	9.7	143	-	-
Full	Moderate	Pup	387.4	0.002	1.000	10.7	215	-	-
Full	Moderate	Total	391.5	<0.001	1.000	14.8	>430	-	-
Full	Acute	Total	394.5	<0.001	1.000	17.8	>430	-	-
Full	Raw	Pup	394.6	<0.001	1.000	17.9	>430	-	-
Full	Moderate	Yearling	394.8	<0.001	1.000	18.1	>430	-	-
Full	Acute	Pup	395.5	<0.001	1.000	18.8	>430	-	-
Full	Acute	Yearling	395.9	<0.001	1.000	19.2	>430	-	-
Full	Raw	Total	396.7	<0.001	1.000	20.0	>430	-	-
Full	Raw	Yearling	399.3	<0.001	1.000	22.6	>430	-	-

Note: Model: CAI models are those that include an adversity index, while the Full models include each adversity measure as an independent variable. Adversity: Moderate adversity is quantified as binary with a threshold of 0.75; Acute adversity is quantified as binary with a threshold of 0.90; Standardized adversity is quantified using a z-score; Raw adversity uses the raw, untransformed data. Window: Time windows include pup as the first year, yearling as the second year, and total as the sum of the first 2 years. Weight: AICc weights represent the probability that the model represents reality based on the data. Cum weight: The cumulative weight from the best to worst model. The *estimated best* model represents the model with the lowest AICc and highest probability of being the best model to approximate reality. ΔAICc: Quantifies the difference in AICc from this estimated best and represents how different the models are from each other (or how much information is lost between them). Evidence ratio: Calculated as the ratio between the estimated best model and the current model; it represents how many times stronger the evidence for the estimated best model is compared with the current model (Burnham et al., 2011). All pup survival models included 471 female pups from 2002 to 2018. All adult longevity models included 229 observations of 79 adult females from 2004 to 2019. The models included random effects of colony (11) and birth-year cohort (15).

Adult survival

The dataset included those pups who survived to adulthood (age 2) and remained in their natal colony: 79 adult females, 56 of which died during the study period (2004–2019). The average adult lifespan was 3.8 years (range: 2–11 years). Moderate and acute CAIs significantly increased the hazard across all three time windows (Table S3; Figures 1 and 2). Increases ranged from a factor of 1.99–2.21 for each additional moderate CAI, with the lowest effect found looking across both years. Acute CAIs increased hazard even more, by a factor of 2.53–3.02, with the highest effect found under total adversity. In the absence of adversity, up valley marmots had an increased hazard of 3.92–7.36, increasing from pup to total adversity. A significant interaction between adversity and valley was found in both moderate and acute CAI models, but not for pup adversity (Figure 1d,g). The interaction showed that increases in adversity up-valley resulted in a lower hazard than increases in adversity down-valley (Figures 1g, 2b,d), with the difference becoming more pronounced under acute adversity (*estimate*=0.34, CI=0.16–0.74). None of our predictors explained significant variation in adult survival for the standardized CAI model.

Overall, there was a trend of lower AICc scores for moderate CAIs, followed by acute ones, and trailed by

standardized CAIs (Table 2). Among the nine models, the moderate pup CAI had the lowest AICc, but only had a 43% probability of being the best model. It was closely followed by the moderate total CAI, with a 30% probability, and the acute total CAI with a 14% probability. It is likely that there is valuable information contained in each of these models that is not fully being captured by any one of them. Indeed, many of the CAI models were within a ΔAICc of 7–8 (Table 2).

Among full models, the moderate total and moderate pup adversity full models were the most similar and had the lowest AICc values (Table 2). They showed that late weaning and maternal loss significantly increased the adult survival hazard (Figure 1e,f,h,i; Tables S5 and S6). No effect was apparent in the yearling adversity full model, but late weaning was a significant hazard when using the raw values for yearling and total adversity (Tables S5 and S7). Residing upvalley was the only significant hazard in all acute adversity full models (*estimates* = 2.72–3.04)—in strong contrast to acute CAIs, which had a strong effect on adult longevity—but was not a hazard in the other models. Lastly, all the AICc values of the full models were considerably higher (Δ > 10) than those of the models that used an index (except in pup survival models; Table 2). However, we were unable to test the interaction between each adversity measure and valley in the full models of adult longevity because the models became too complex—this may help explain why no adversity measure was found hazardous in the full model of acute adversity. Together, our results support our hypothesis that a CAI is a useful tool in yellow-bellied marmots to evaluate the long-term survival impact of multiple early life stressors; a CAI also allows the inclusion of interactions with other variables while avoiding unfeasible, over-fitted models.

DISCUSSION

Most species face various co-occurring stressors in their lives, with those experienced early in life being particularly impactful. While developmental plasticity can increase an individual's adaptability to adversity, life-history theory predicts it will require trade-offs. The greater the number of adverse experiences encountered, the greater the trade-offs, the higher the likelihood of long-term fitness costs (Monaghan, 2008). Similarly, the cumulative stress hypothesis posits that increased stressors result in higher allostatic load, which reduces fitness. Research on cumulative impacts in global change ecology has indeed suggested that increases in the number of stressors experienced often lead to adaptive constraints and reduced population fitness (Orr et al., 2022). However, such studies have not incorporated more than three co-occurring stressors. In part, this is due to difficulties in determining the effect of complex interactions among stressors (Hale et al., 2017) and the requirement of large sample sizes.

To address these challenges, we described a framework for how we built and evaluated CAIs in yellow-bellied marmots. While CAIs are well established in human studies (but note, Lanoue et al., 2020), they are not widely used to study the health and ecology of wild populations, especially in terrestrial systems. Our results add support to the idea that a single CAI can be used to study cumulative impacts in wild animals, thereby opening such analyses to studies where sample sizes do not support many covariates. Importantly, CAIs can capture accrued costs despite complex interactions and uncertainty among stressors. Indeed, the analyses of our full models showed that few of our chosen adversities had a significant effect on survival. Furthermore, contrary to expectation, we found a positive effect of summer drought on pup survival—one of our measures was a benefit rather than an adversity! Nevertheless, our CAIs still captured the survival consequences of cumulative adversity.

While large datasets may allow more thorough evaluation of CAIs (e.g., Gicquel et al., 2022), we suggest that CAIs will be especially useful to those with less data (who may be unable to fit full models) by using a single indicator of an individual's 'state' at the end of development; this can then also be used to identify individuals who are at higher risk and/or are more likely to adopt 'reactive strategies' (Grafen, 1988). Future work could help determine up to which CAI value an individual can recover and when it cannot, as well as compare such values among populations and taxa.

Index type

Standardized adversity represented a framework in which the costs of negative experiences could be 'recovered' by positive experiences. Interestingly, we found that this relationship may be true for pup survival, but not for adult longevity. Nevertheless, within pup survival standardized adversity models still did not perform as well as the full raw or moderate CAI models. Perhaps this shows the short-term adaptability benefits of plasticity compared with its long-term consequences. Thus, we conclude that standardized CAIs are not a good predictor of marmot longevity, although some early costs could be buffered. Importantly, we see that the long-term costs of early adversity cannot be fully recovered by positive experiences but rather result in persistent fitness costs. This exciting finding supports the cumulative stress hypothesis and the developmental constraints paradigm (Monaghan, 2008; Stewart, 2006). Our results also support the importance of talking about 'adversity' in contrast to more general early-life effects or 'silver spoon' effects, since the impact of adverse experiences appears greater than that of positive ones. This suggests

that positive and adverse experiences should perhaps be analysed separately because there is a fundamental difference between good and bad effects.

Acute and moderate CAIs were similarly supported in pup survival models, while we found some support for moderate CAIs in longevity models, but only when considering pup adversity (Table 2). This is likely due to the stronger effect of acute adversity on pup survival. While results are similar, acute adversity tends to have moderately greater effect sizes (Tables S2–S5). We conclude that acute adversity is associated with higher immediate risks, but moderate adversity is a slightly better predictor of longevity. Overall, CAIs may not be as sensitive to the chosen threshold cut-off as we originally thought (although Gicquel et al., 2022 used mean cut-offs and found indices less informative). More detailed investigations on threshold cut-offs can help us better understand how to choose an appropriate threshold. So far, the upper quartile seems to be an appropriate and meaningful cut-off for yellow-bellied marmots and some primates (e.g., Patterson et al., 2021; Tung et al., 2016).

Time window

All three of our time windows had a significant effect of adversity on survival, except when using standardized indices. The pup moderate CAI performed the best but was very similar to the total moderate adversity (ΔAICc<1), followed by total acute adversity. Interestingly, the effects of pup adversity and yearling adversity do not appear to be additive. This suggests that while there is value in looking across the entirety of early life, moderate adversity experienced in the first year may have the strongest effect on longevity. Notably, the interaction between valley and adversity varies across time windows—the hazard associated with pup adversity does not change between valleys (Figure 1d), but that of total adversity is lower up valley (Figure 1g). This may indicate that harsher conditions up valley result in only the most resilient individuals surviving, therefore showing a decreased hazard associated with adversity later in life. A similar pattern in pup adversity may have instead indicated inherent local adaptation to harsher conditions.

Index vs. full model

Our full models provided novel evidence that maternal loss is a significant contributor to both short and long-term marmot survival. This is an interesting finding in a species with a relatively short dependence period compared with similar studies in primates (Zipple et al., 2019). We also found that different adversity measures had an impact on early but not later survival (poor maternal mass) and vice-versa (late weaning). Nevertheless, most of our full models did not significantly explain adult survival, while our CAI models did. This strongly supports our prediction that exposure to multiple early life stressors can have cumulative impacts on both adult and pup survival that would not be apparent when adversity measures are analysed separately. This is especially evident when considering long-term consequences of early adversity—all full longevity models performed considerably worse than those with a CAI.

Recommendations for future applications

We have shown the feasibility of using a CAI framework to study the long-term fitness impacts of multiple early life stressors. We suggest that a wider application of this approach within ecology can yield new and exciting insights that will expand our understanding of developmental plasticity, demography, and population viability, and by doing so, will also support concrete conservation strategies. By thoroughly describing our thought process and steps, we hope our paper will be particularly beneficial to novel studies interested in adopting a CAI approach.

We recognize that this approach may not be well-suited to all studies. It certainly requires sufficient ecological knowledge to identify appropriate adversity measures, and multiple generations of data if one is to answer questions about long-term fitness. However, as previously discussed, using an index composed of binary measures may identify important fitness consequences of adversity that emerge specifically from adopting a cumulative approach. Furthermore, using an index requires less data than a model with many covariates and we have shown its utility for answering both short- and long-term survival questions.

While CAIs can only address broad questions about the impact of multiple early stressors, and not the specific impact of each stressor, we have demonstrated that such cumulative analyses can still yield novel insights and help focus areas of future research. A CAI approach is meant to complement, not replace studies that investigate the mechanisms by which key environmental features or experiences impact fitness. Nevertheless, we have shown that it may be important to account for multiple stressors across multiple traits. Furthermore, our framework explicitly calls for deeper reflection on what can be considered adversity, why, and how research questions and analyses will account for them. We propose this framework as a generative process that can highlight both broad trends and novel questions.

Cumulative, not simply specific, perturbations may influence population persistence which is both theoretically important as well as having substantial applied importance. When adopting a CAI approach, we

can evaluate resiliency thresholds by determining how many stressors are too many stressors or, at what point an environmental variable becomes adverse. While current conservation management approaches require the identification of the highest threat, we emphasize the importance of cumulative stressors. If our results hold for other systems, and from an applied perspective, it may be more important to reduce cumulative adversity than to try to reverse single stressors if we are trying to increase population persistence. Only by broadening our understanding and applying comparable methodologies across taxa can we better understand how different populations will cope with increasing stressors.

AUTHOR CONTRIBUTIONS

XOR and DTB discussed concepts and ideas together. XOR and past field teams collected the data. XOR analysed the data, created the figures, and wrote the first draft of the manuscript. DTB contributed substantially to revisions.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data and code for the analyses and figures that support the findings of this study are available on OSF at https://osf.io/2tmdz/ (DOI: 10.17605/osf.io/2tmdz).

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REFERENCES

Armitage, K.B. (2013) Climate change and the conservation of marmots. *Natural Science*, 05(5), 36–43.
Armitage, K.B. (2014) *Marmot biology. Sociality, individual fitness, and population dynamics*. Cambridge: Cambridge University Press.
Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48.
Beckie, T.M. (2012) A systematic review of allostatic load, health, and health disparities. *Biological Research for Nursing*, 14, 311–346.
Berens, A.E., Jensen, S.K.G. & Nelson, C.A. (2017) Biological embedding of childhood adversity: from physiological mechanisms to clinical implications. *BMC Medicine*, 15, 1–12.
Blumstein, D.T. (2013) Yellow-bellied marmots: insights from an emergent view of sociality. *Philosophical Transactions of the Royal Society B*, 368, 1–9.
Blumstein, D.T., Keeley, K.N. & Smith, J.E. (2016) Fitness and hormonal correlates of social and ecological stressors of female yellow-bellied marmots. *Animal Behaviour*, 112, 1–11.
Bobko, P., Roth, P.L. & Buster, M.A. (2007) The usefulness of unit weights in creating composite scores: a literature review, application to content validity, and meta-analysis. *Organizational Research Methods*, 10, 689–709.
Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65(1), 23–35.
Cordes, L.S., Blumstein, D.T., Armitage, K.B., CaraDonna, P.J., Childs, D.Z., Gerber, B.D. et al. (2020) Contrasting effects of climate change on seasonal survival of a hibernating mammal. *Proceedings of the National Academy of Sciences of the United States of America*, 117, 18119–18126.
Côté, I.M., Darling, E.S. & Brown, C.J. (2016) Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B*, 283, 20152592.
Darling, E.S. & Côté, I.M. (2008) Quantifying the evidence for ecological synergies. *Ecology Letters*, 11, 1278–1286.
Debecker, S., Dinh, K.V. & Stoks, R. (2017) Strong delayed interactive effects of metal exposure and warming: latitude-dependent synergisms persist across metamorphosis. *Environmental Science & Technology*, 51, 2409–2417.
Edes, A.N. & Crews, D.E. (2017) Allostatic load and biological anthropology. *American Journal of Physical Anthropology*, 162(Suppl 63), 44–70.
Evans, G.W. (2003) A multimethodological analysis of cumulative risk and allostatic load among rural children. *Developmental Psychology*, 39, 924–933.
Evans, G.W., Li, D. & Whipple, S.S. (2013) Cumulative risk and child development. *Psychological Bulletin*, 139, 1342–1396.
Fawcett, T.W. & Frankenhuis, W.E. (2015) Adaptive explanations for sensitive windows in development. *Frontiers in Zoology*, 12, S3.
Gicquel, M., East, M.L., Hofer, H. & Benhaiem, S. (2022) Early-life adversity predicts performance and fitness in a wild social carnivore. *The Journal of Animal Ecology*, 91, 2074–2086.
Gonzalez, S.J., Sherer, A.J. & Hernández-Pacheco, R. (2023) Differential effects of early life adversity on male and female rhesus macaque lifespan. *Ecology and Evolution*, 13, e10689.
Grafen, A.T.H. (1988) On the uses of data on lifetime reproductive success. In: Clutton-Brock, T.H. (Ed.) *Reproductive success: studies*

of individual variation in contrasting breeding systems. Chicago: University of Chicago Press.
Guidi, J., Lucente, M., Sonino, N. & Fava, G.A. (2021) Allostatic load and its impact on health: a systematic review. *Psychotherapy and Psychosomatics*, 90, 11–27.
Gunn, A., Russell, D. & Greig, L. (2014) *Insights into integrating cumulative effects and collaborative co-management for migratory tundra caribou herds in the Northwest Territories*. Ecol Soc: Canada, p. 19.
Hale, R., Piggott, J.J. & Swearer, S.E. (2017) Describing and understanding behavioral responses to multiple stressors and multiple stimuli. *Ecology and Evolution*, 7, 38–47.
Jarvis, L., Rosenfeld, J., Gonzalez-Espinosa, P.C. & Enders, E.C. (2024) A process framework for integrating stressor-response functions into cumulative effects models. *Science of the Total Environment*, 906, 167456.
Kroeker, K.J., Kordas, R.L. & Harley, C.D.G. (2017) Embracing interactions in ocean acidification research: confronting multiple stressor scenarios and context dependence. *Biology Letters*, 13, 20160802.
Lange, K., Bruder, A., Matthaei, C.D., Brodersen, J. & Paterson, R.A. (2018) Multiple-stressor effects on freshwater fish: importance of taxonomy and life stage. *Fish and Fisheries*, 19, 974–983.
Lanoue, M.D., George, B.J., Helitzer, D.L. & Keith, S.W. (2020) Contrasting cumulative risk and multiple individual risk models of the relationship between adverse childhood experiences (ACEs) and adult health outcomes. *BMC Medical Research Methodology*, 20, 239.
Lindström, J. (1999) Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, 14, 343–348.
Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P. & Makowski, D. (2021) Performance: an R package for assessment, comparison and testing of statistical models. *J Open Source Softw*, 6(60), 3139.
Mahon, C.L. & Pelech, S. (2021) Guidance for analytical methods to cumulative effects assessment for terrestrial species. *Environmental Reviews*, 29, 201–224.
Mauss, D., Li, J., Schmidt, B., Angerer, P. & Jarczok, M.N. (2015) Measuring allostatic load in the workforce: a systematic review. *Industrial Health*, 53, 5–20.
McEwen, B.S. (1998) Stress, adaptation, and disease: allostasis and allostatic load. *Annals of the New York Academy of Sciences*, 840, 33–44.
McEwen, B.S. (2015) Biomarkers for assessing population and individual health and disease related to stress and adaptation. *Metabolism*, 64, S2–S10.
McEwen, B.S. & Wingfield, J.C. (2007) Allostasis and allostatic load. *Encyclopedia of Stress*, 135–141.
Monaghan, P. (2008) Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 363, 1635–1645.
Monclús, R. & Blumstein, D.T. (2012) Litter sex composition affects life-history traits in yellow-bellied marmots. *The Journal of Animal Ecology*, 81(1), 80–86.
Monclús, R., Tiulim, J. & Blumstein, D.T. (2011) Older mothers follow conservative strategies under predator pressure: the adaptive role of maternal glucocorticoids in yellow-bellied marmots. *Hormones and Behavior*, 60, 660–665.
Morrison, R.E., Eckardt, W., Stoinski, T.S. & Rosenbaum, S. (2023) Cumulative early-life adversity does not predict reduced adult longevity in wild gorillas. In brief. *Current Biology*, 33, 2307–2314 e4.
Neale, Z.R. & Juliano, S.A. (2019) Finding the sweet spot: what levels of larval mortality lead to compensation or overcompensation in adult production? *Ecosphere*, 10, 1–15.
Orr, J.A., Luijckx, P., Arnoldi, J.F., Jackson, A.L. & Piggott, J.J. (2022) Rapid evolution generates synergism between multiple stressors: linking theory and an evolution experiment. *Global Change Biology*, 28, 1740–1752.
Orr, J.A., Vinebrooke, R.D., Jackson, M.C., Kroeker, K.J., Kordas, R.L., Mantyka-Pringle, C. et al. (2020) Towards a unified study of multiple stressors: divisions and common goals across research disciplines. *Proceedings of the Royal Society B*, 287, 20200421.
Ozgul, A., Armitage, K.B., Blumstein, D.T. & Oli, M.K. (2006) Spatiotemporal variation in survival rates: implications for population dynamics of yellow-bellied marmots. *Ecology*, 87, 1027–1037.
Ozgul, A., Childs, D.Z., Oli, M.K., Armitage, K.B., Blumstein, D.T., Olson, L.E. et al. (2010) Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, 466, 482–485.
Patterson, S.K., Hinde, K., Bond, A.B., Trumble, B.C., Strum, S.C. & Silk, J.B. (2021) Effects of early life adversity on maternal effort and glucocorticoids in wild olive baboons. *Behavioral Ecology and Sociobiology*, 75, 114.
Pinho, G.M., Ortiz-Ross, X., Reese, A.N. & Blumstein, D.T. (2019) Correlates of maternal glucocorticoid levels in a socially flexible rodent. *Hormones and Behavior*, 116, 104577.
Pirotta, E., Schick, R.S., Hamilton, P.K., Harris, C.M., Hewitt, J., Knowlton, A.R. et al. (2023) Estimating the effects of stressors on the health, survival and reproduction of a critically endangered, long-lived species. *Oikos*, 2023, e09801.
Pirotta, E., Thomas, L., Costa, D.P., Hall, A.J., Harris, C.M., Harwood, J. et al. (2022) Understanding the combined effects of multiple stressors: a new perspective on a longstanding challenge. *Sci Tot Environ*, 821, 153322.
R Core Team. (2023) *R: A language and environment for statistical computing*.
Rutter, M. (1983) Statistical and personal interactions: facets and perspectives. In: Magnusson, D. & Vernon, L.A. (Eds.) *Human development: an interactional perspective*. New York: Academic Press, pp. 295–319.
Seeman, T., Epel, E., Gruenewald, T., Karlamangla, A. & Mcewen, B.S. (2010) Socio-economic differentials in peripheral biology: cumulative allostatic load. *Annals of the New York Academy of Sciences*, 1186, 223–239.
Seeman, T.E., McEwen, B.S., Rowe, J.W. & Singer, B.H. (2001) Allostatic load as a marker of cumulative biological risk: MacArthur studies of successful aging. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 4770–4775.
Seeman, T.E., Singer, B.H., Rowe, J.W., Horwitz, R.I. & McEwen, B.S. (1997) Price of adaptation—allostatic load and its health consequences. *Archives of Internal Medicine*, 157, 2259–2268.
Stamps, J.A. & Luttbeg, B. (2022) Sensitive period diversity: insights from evolutionary models. *The Quarterly Review of Biology*, 97, 243–295.
Stewart, J.A. (2006) The detrimental effects of allostasis: allostatic load as a measure of cumulative stress. *Journal of Physiological Anthropology*, 25, 133–145.
Therneau, T. (2024a) A package for survival analysis in R. *R Package Version*, 3, 5–8.
Therneau, T.M. (2024b) *Coxme: mixed effects cox models. CRAN R package*.
Tung, J., Archie, E.A., Altmann, J. & Alberts, S.C. (2016) Cumulative early life adversity predicts longevity in wild baboons. *Nature Communications*, 7, 1–7.
Tyack, P.L., Thomas, L., Costa, D.P., Hall, A.J., Harris, C.M., Harwood, J. et al. (2022) Managing the effects of multiple stressors on wildlife populations in their ecosystems: developing a cumulative risk approach. *Proceedings of the Royal Society B*, 289, 2–15.

Van Vuren, D.H. (2001) Predation on yellow-bellied marmots (*Marmota flaviventris*). *The American Midland Naturalist*, 145, 94–100.

Zipple, M.N., Archie, E.A., Tung, J., Altmann, J. & Alberts, S.C. (2019) Intergenerational effects of early adversity on survival in wild baboons. *eLife*, 8, 591248.

SUPPORTING INFORMATION

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

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CHAPTER 2. THE IMPACT OF EARLY ADVERSITY ON LIFETIME REPRODUCTIVE SUCCESS

ABSTRACT

Early experiences have important ecological and fitness consequences for wild animals. Exposure to multiple, adverse, early-life experiences can reduce lifespans and lower lifetime reproductive success (LRS). Although both are key fitness metrics, it is less clear how early-life adversities (ELAs) impact lifetime reproduction independently of lifespan and whether reproductive compensation strategies can mitigate longevity costs. Here, we evaluated (1) how cumulative ELA affects LRS both including and conditioning on lifespan, and (2) its influence on annual breeding probability and timing in free-living yellow-bellied marmots (*Marmota flaviventer*). Using a cumulative adversity index from birth to sexual maturity, we found no effect of ELA on LRS independent of lifespan, suggesting that survival costs overwhelm reproductive costs. However, we also found that females' odds of breeding decreased sharply with each ELA, suggesting that ELA likely affects breeding opportunities rather than total output. Finally, we found that exposure to ELA reduced the breeding gains otherwise associated with age, meaning adults with high ELA were less likely to breed as they got older. We conclude that female marmots facing high survival costs may favor early reproduction such that their LRS is comparable to that of females of similar lifespan who did not experience adversity.

INTRODUCTION

The developmental period of life, often referred to as early life, is an important time for the growth and learning that shape individuals into their adult form. Early-life adversity

(ELA) describes the range of challenges faced by developing individuals prior to reaching sexual maturity (Henry and Ulijaszek, 1996), such as resource scarcity, predation risk, or social and parental dynamics. These developmental challenges have lasting effects on the physiology, behavior, and life-history trajectories of both humans and wild animals (Lindström, 1999; Lummaa and Clutton-Brock, 2002; Metcalfe and Monaghan, 2001; Monaghan, 2008) contributing to the observed variation in lifetime fitness.

Most wildlife research on ELA (also referred to as developmental stress or early-life effects) has focused on how individuals respond to single stressors (Orr et al., 2020). However, understanding the cumulative effect of multiple adverse experiences is crucial for a comprehensive view of wildlife fitness (Orr et al., 2020; Pirotta et al., 2022; Tyack et al., 2022). This is especially true when trying to determine the extent to which experiencing multiple ELAs gives rise to adaptive (or compensatory) responses or generates developmental constraints (Lea and Rosebaum, 2020). An effective metric for quantifying such cumulative impacts is a cumulative adversity index (CAI), which sums each adversity exposure into a single measure to better assess the overall burden of early-life challenges (Berens et al., 2017; Evans, 2003). Adapted from the human literature, this novel method has recently been used to link cumulative ELA with adult longevity in a handful of wild animal populations (Gicquel et al., 2022; Gonzalez et al., 2023; Morrison et al., 2023; Ortiz-Ross and Blumstein, 2024; Patterson et al., 2021; Tung et al., 2016). However, the relationship between ELA and reproductive metrics has historically been less clear (Dettmer and Chusyd, 2023; Drake et al., 2025; Hamel et al., 2009; Lindström, 1999; Monaghan, 2008).

Lifetime reproductive success (LRS) is often considered a more direct fitness measure than longevity, but it is challenging to estimate in long-lived species without long-term monitoring. While prospective longitudinal studies are essential for understanding changes in lifetime fitness, such studies are rare and heavily biased towards primates (Dettmer and Chusyd, 2023). To gain a better understanding of the impact of multiple stressors on the lifetime fitness of wild animals, more studies across a greater diversity of taxa are necessary.

While ELA has been shown to reduce lifespan and/or LRS (Gicquel et al., 2022; Ortiz-Ross and Blumstein, 2024; Patterson et al., 2021; Tung et al., 2016), it remains less clear whether ELA constrains lifetime reproduction independently from lifespan. Given that much variation in LRS is explained by lifespan, especially in long-lived individuals (Clutton-Brock, 1988), the strength of that relationship can mask any other reproductive consequences of ELA. Yet, few studies distinguish the role of longevity when studying what influences LRS. Controlling for lifespan reveals how reproductive success changes when survival is constrained. In other words, it reveals whether changes in reproduction mitigate longevity costs; if an early death cannot be avoided, increases in early reproduction could provide an alternative pathway through which to increase fitness within a short lifespan.

Studies that investigate how ELA influences LRS conditioned on lifespan also provide an avenue to examine the pace of life theory. According to this theory, species exist on a slow-fast life-history spectrum based on their lifespan and reproductive strategy (Stearns, 1983). Fast life histories are characterized by short lives and early reproduction— “live fast, die young” (Promislow and Harvey, 1990)— while slow ones

are characterized by long lives and slow reproduction, echoing r- and K-selection (MacArthur and Wilson, 2001; Pianka, 1970). In terms of energy allocation, species with fast life histories invest greater energy in early reproduction than future survival (accelerated reproduction) because their expected lifespan is short. Those with slow life histories tend to be long-lived, with more opportunities for future reproductive success. Therefore, when conditions are unfavorable, slow-paced species allocate energy to survival and maintenance to increase their reproductive success later.

The theory has expanded to include differences within populations (Réale et al., 2010) by recognizing plastic responses to environmental conditions (Ricklefs and Wikelski, 2002; Wikelski et al., 2003). With this expansion, individuals are expected to follow their species life-history strategy (slow or fast) under typical environmental conditions; but they are also allowed to shift life-history strategy in response to changes in environmental pressures that impact their survival or reproductive prospects. Importantly, a certain level of reproductive plasticity is required to allow such shifts.

Here, we ask how life history trade-off decisions shift in response to the limited developmental resources imposed by ELA in a species with a slow life history. Given that ELA reduces lifespan and opportunities for future reproduction, the pace of life framework would suggest individuals divert energy towards immediate reproduction (the “accelerated reproduction” of fast life histories) at the expense of survival. On the other hand, ELA may pose insurmountable reproductive constraints such that all available energy is needed to maintain critical life processes.

Support for accelerated reproduction has been found in humans (Ellis, 2004; Ellis et al., 2009; Nettle et al., 2013) and other species (Lindström, 1999; Metcalfe and

Monaghan, 2001; Taborsky, 2006), but is limited in wild animals (Nettle and Frankenhuis, 2020), especially those with longer lifespans. Accelerated reproduction has been operationalized in several ways, and it need not reference merely timing but a deprioritizing of future reproduction or survival. Common metrics include age at various phases (e.g., weaning, sexual maturity, first reproduction), inter-birth interval, and litter size or fertility (Ellis, 2004). In Amboseli olive baboons (*Papio anubis*), cumulative ELA is associated with shorter lifespans (Tung et al., 2016) but not with early starts to or increased rates of reproduction (as inter-birth-intervals), which did increase LRS when adversity was absent (Weibel et al., 2020). Similarly, rhesus macaques (*Macaca mulatta*) who experienced a major hurricane in early life were less likely to breed successfully in early adulthood but more successful in their prime than females who did not experience that early adversity (Luevano et al., 2022). To better evaluate the impact of multiple early stressors on the life history and demography of wildlife populations, more studies are needed, across taxa, that account for the cumulative impacts of ELA on lifetime fitness independent on survival and instead focusing on different aspects of reproduction.

Yellow-bellied marmots (*Marmota flaviventer*) are an excellent model with which to study the life-long impacts of ELA due to their highly seasonal life-history and the availability of long-term data on individual LRS (Armitage, 2014). They are a large, facultatively social ground squirrel that inhabits montane meadows. Individuals hibernate for ~7 months, emerging in late spring to breed in a short annual window (Armitage, 2014). Therefore, females need to evaluate the risk of breeding based on their likelihood of recuperating enough resources to survive the next hibernation in early

Fall (Ozgul et al., 2010). Yellow-bellied marmots begin breeding at age 2 (in the absence of reproductive suppression (Armitage, 2014)) and can live for up to 16 years in the wild. However, adult females live an average of 3-4 years (Ortiz-Ross and Blumstein, 2024).

As hibernators, their lower metabolism, slower reproduction, and longer lifespan for their body size places marmots on the “slow” side of the pace of life spectrum (K-selected (Armitage, 2017)). However, if individuals who experience high ELA can predict their high risk for early mortality (Ortiz-Ross and Blumstein, 2024), such as by assessing their “internal state” (as suggested by the internal predictive adaptive response (iPAR) hypothesis (Nettle et al., 2013)), then they could shift their typical energy allocation to maximize early reproduction and deprioritize survival or future reproduction. Yellow-bellied marmots could accelerate reproduction by breeding more often than expected at younger ages, since older females tend to be more successful (Kroeger et al., 2020). They could also breed at lower body mass, jeopardizing their survival in favor of earlier reproduction. While several other pathways are possible, here we focus on these two.

To study the reproductive consequences of cumulative ELA in yellow-bellied marmots, we first ask whether ELA affects LRS beyond what is explained by lifespan to identify any additional costs to reproduction. We then examine whether ELA impacts the age and mass at which individuals are likely to breed to examine whether females attempt to mitigate longevity costs by prioritizing early reproduction (effectively switching life-history strategy). This study provides insights on how ELA shapes reproductive outcomes across lifespans and its impact on individual’s LRS (Clutton-Brock and

Sheldon, 2010). Beyond individual fitness, our findings also inform how early exposure to multiple environmental challenges influences how the pace of life theory relates to population growth and dynamics (Clutton-Brock and Sheldon, 2010; Coulson et al., 2006). We encourage practitioners to use this information to help identify vulnerable populations and to better determine their needs and opportunities for recovery (Tyack et al., 2022).

METHODS

Study system and field site

Yellow-bellied marmots are a large, facultatively social, matrilineal ground-squirrel. They have been studied in and around the Rocky Mountain Biological Laboratory (RMBL, 38º57´N, 106º59´W; ca 2900 m elevation) in Gothic, CO, USA, for over six decades (Armitage, 2014). We used 22 years of data collected between 2002 and 2024. For all the analyses we only considered females with known CAI that survived to sexual maturity (age 2; Oli and Armitage, 2004) by 2018. Our dataset for LRS only included females who died in a known year (data were not right censored). This enabled us to evaluate their entire lifetime. The study period included multiple generations and therefore extended beyond a single lifetime. All field procedures were approved by a UCLA research protocol (2001-191, renewed annually) and under permits issued by the Colorado Division of Wildlife (TR-519, renewed annually).

Cumulative adversity index

To quantify ELA, we used a previously developed CAI that is closely associated with adult longevity in our marmot population (Ortiz-Ross and Blumstein, 2024). The index

includes nine potential sources of adversity known to impact marmot fitness, and they vary from ecological (late snowmelt, summer drought, high predation pressure) to socio-demographic (large, male-biased litters) and parental (late-season birth, poor maternal condition, high maternal stress, and maternal loss). The CAI is the total number of adversities encountered in early life. Each adversity is a binary measure indicating whether the adversity was present or absent during the first and/or second year of life (marmots reach sexual maturity at age 2). An adversity measure was considered such when it fell within the upper quartile of the population distribution and, therefore, did not match the 'typical' experience of 75% of the population. This is the same method established in the human literature, where it was conceived (Rutter, 1983), and has been deemed robust for our system (Ortiz-Ross and Blumstein, 2024).

Female reproduction

Lifetime reproductive success was measured as the total number of weaned offspring. Annual breeding probability was based on whether each female was identified as the mother of an emerged litter. Therefore, a female was only considered to have bred if she successfully weaned a litter, since this was the best way to confirm breeding events. Maternity was observationally inferred and then confirmed via genetic analysis (Blumstein et al., 2010).

Analyses

To determine the effect of ELA on LRS independent of lifespan, we compared two negative binomial zero-inflated models (fit using the R package *glmmTMB*; Brooks et al., 2017; McGillycuddy et al., 2025). One model estimated the impact of ELA on LRS

independent of lifespan by including it as a separate predictor. This model included both a linear and non-linear term for lifespan, which was then centered to avoid collinearity and ease interpretation. The other estimated the total effect of ELA, implicitly including its indirect impact through survival (Ortiz-Ross and Blumstein, 2024). In the lifespan-adjusted model, zero-inflation was also modelled as a function of lifespan. In the total-effect model, zero-inflation was modelled stochastically (zi ~ 1). We evaluated the fit of maternal ID, cohort, and colony as random effects, but they showed negligible variance and were therefore excluded.

To test whether females with high ELA tended to breed more often at younger ages and lower masses we fit a generalized binomial mixed model with two interaction terms that allowed the effect of ELA (quantified with a CAI) to vary with age and June mass (both of which were centered). We also included a non-linear term for age. Our final model also included random effects of year and individual ID. Maternal ID, cohort, and colony were considered but were not supported by the model. As a post-hoc analysis, we also compared this interaction model with a simpler additive model, in which the effect of ELA was constant across age and body mass (no interactions).

All analyses were run using R (version 4.5.2). We used the packages glmmTMB (Brooks et al., 2017; McGillycuddy et al., 2025) to fit the zero-inflated models; lme4 (Bates et al., 2015) to fit the GLMMs; bbmle (Bolker and R Development CoreTeam, 2023) to compare AICc, and DHARMa (Hartig, 2024) for model diagnostics.

RESULTS

The final dataset for our LRS model included N = 95 unique females with known histories who reached sexual maturity (age 2) between 2004 and 2018. The mean adult

lifespan was 4 years (SD = 2.43) and ranged 2-11. The mean LRS was 7 (SD = 8.81) and ranged 0-37. Mean CAI was 2.5 (SD = 1.74) and ranged 0-8. The final dataset for our breeding probability model included 280 observations of 89 unique individuals between 2002 and 2024. Mean breeding probability was 0.55 (SD = 0.5), mean age was 4 (SD = 2.1), and mean June mass was 2.63Kg (SD = 0.41Kg).

Lifetime reproductive success

Lifetime reproductive success (LRS) was best described by the zero-inflated negative binomial model that included both ELA and lifespan (linear and quadratic terms) rather than just ELA (ΔAICc ≈ 108). Therefore, variation in LRS is strongly influenced by lifespan. Longer lifespans increased LRS by 33%, while short lifespans nearly doubled the odds of never reproducing (Table 2.1). When controlling for these effects, ELA had no detectable impact on LRS (β = -0.06713, SE = 0.042, p = 0.111). However, when lifespan was excluded from the model (and included in the total effect of ELA), we found a clear negative association between ELA and LRS (β = -0.211, SE = 0.064, p= 0.001). Taken together, these results indicate that the LRS costs associated with ELA are primarily mediated by the latter's impact on survival rather than independent impacts on reproductive output.

Effect of ELA on annual reproduction

We found consistent support for a negative association between ELA and breeding probability (odds decreased by 28% per adversity) across mean age and June mass in both the additive and interaction models (Table 2.2). The interaction model lent some support for a buffering effect of age on the breeding costs of ELA (β = -0.134, SE =

0.067, p = 0.045; Table 2.2), such that older individuals had a higher chance of breeding (contrary to an accelerated reproduction prediction). The interaction between ELA and mass was weaker and not statistically discernible (β= 0.515, SE = 0.292, p = 0.078). Nevertheless, this result suggests a potential advantage associated with better body condition in lowering ELA costs (Figure 2.2C-D). The interaction model showed only a small improvement in model fit (ΔAICc < 1; marginal R^2 increased from 0.087 to 0.141), meaning both models are similarly supported (Burnham et al., 2011). Therefore, the interactions do explain some of the data structure. The extent to which these are biologically significant remains to be determined.

Predictably, both models had an asymptotic relationship between age and breeding probability (Figure 2.2). After age ~6, marmots tend to consistently breed annually. Somewhat more surprisingly, we found no independent effect of June mass on breeding probability.

DISCUSSION

We found that cumulative early-life adversity (ELA) decreases the lifetime reproductive success (LRS) of breeding female yellow-bellied marmots, but the relationship was largely explained by lifespan (Table 2.1; Figure 2.1A-B). These results align with studies in other wild taxa in which ELA had negative impacts on both lifespan and LRS, generally measured independently of one another, and the close relationship between the two fitness metrics (Gicquel et al., 2022; Pigeon and Pelletier, 2018; Vasilieva and Tchabovsky, 2020; Weibel et al., 2020).

Given that LRS was unaffected by ELA (when conditioned on survival), ELA seems to have negligeable impact on reproductive output. In other words, breeding

females with the same lifespan achieve similar LRS regardless of their ELA exposure. Therefore, individuals who experience ELA appear capable of matching the reproductive success of those without ELA if they survive to the same age.

Somewhat contrary to what is often assumed, these findings contribute to our understanding of the pathways by which ELA impacts lifetime fitness—they suggest ELA acts primarily on survival mechanisms rather than reproductive ones. However, given the strong influence of survival, focusing on total lifetime output alone risks missing the more nuanced effects of ELA on reproduction and life history.

Indeed, a closer look shows that the annual breeding probability of an average female decreases with increasing ELA, costs that seem to accumulate and amplify with age (Figure 2.2A). While the odds of breeding usually increase considerably (non-linearly) with age, the annual benefit decreases for each additional adversity. Additionally, ELA appears to induce earlier reproductive senescence as age begins to quickly lower breeding probability (Figure 2.2A-B). Therefore, the breeding opportunity costs of ELA are felt more strongly in older individuals than young ones, meaning females who experience high ELA are most likely to breed at younger ages than those without ELA. While this may cautiously indicate a form of reproductive acceleration, the overall breeding probability remains consistently lower at higher ELAs. Furthermore, given the high mortality risk associated with greater ELA, this pattern could also reflect a form of terminal investment rather than a life-history shift per se. Similarly, it could also emerge from viability selection or selective disappearance early in life , which is hard to avoid in natural studies.

In contrast, other studies on long-lived mammals have associated ELA with impaired reproduction but with no evidence of an accelerated pace. In Amboseli baboons (Weibel et al., 2020), females with higher instances of ELA did not start breeding earlier or show higher early fecundity. Similarly, captive rhesus macaques showed that ELA increased interest towards infants but was not associated with reproductive timing (Maestripieri, 2005). Our results offer novel insights by suggesting a potential pattern of accelerated reproduction at higher ELAs despite clear cumulative constraints. Notably, compared to other studies, we used not only a CAI that sums multiple exposures, but also a wider range of CAIs in our analyses, allowing us to better detect changes in reproductive pace. For example, Figure 2.2A shows how the shift in the age of peak fertility in response to ELA becomes more evident at higher ELA exposures.

Our results highlight that the reproductive costs of ELA are not fully evident in females' total reproductive output but rather in their number of breeding opportunities, which tend to diverge with age. The different impacts ELA has on distinct reproductive aspects, and the extent to which they can be detected depending on the metrics used, may help explain the mixed results found across studies (Metcalfe and Monaghan, 2001; Nettle and Frankenhuis, 2020; Taborsky, 2006). On the one hand, higher ELA reduces breeding probability and the relative gains offered by age (Figure 2.2A-B). On the other, females with similar lifespan but higher ELA can still achieve comparable LRS to those without (Figure 2.1B).

Taken together these results suggests that, while ELA may impose strong constraints on early survival that cannot be recovered, the reproductive success of

individuals who survive could be at least partially recoverable. Further research is necessary to uncover the mechanisms underlying these patterns; in particular, studies distinguishing early vs late reproductive decisions could provide other interesting insights on how the accumulation of ELAs impacts fitness across the lifespan (Dettmer and Chusyd, 2023; Gaillard et al., 2000; Lea et al., 2017). We also highlight that relative fitness should be carefully considered when comparing the fitness of individuals rather than relying solely on total fitness. Under constrained conditions, individuals may adopt alternative strategies that increase their fitness and mitigate costs despite yielding lower outcomes than their unconstrained peers (Ellis and Del Giudice, 2019; Lea et al., 2017; Nettle and Bateson, 2015).

Accelerated reproduction is one strategy by which such a recovery could be achieved; if time is short, individuals may attempt to maximize early output. While we found some evidence of accelerated reproduction in response to adversity, it was most evident at high adversity numbers and, therefore, lower sample sizes. Nevertheless, accelerated reproduction is also most expected under severe resource scarcity (Metcalfe and Monaghan, 2001; Nettle and Frankenhuis, 2020), when survival prospects are sufficiently low (Nettle and Frankenhuis, 2020; Stearns, 1992) and accelerated reproduction becomes a form of terminal investment (Clutton-Brock, 1984). Therefore, it is possible that a pattern of accelerated reproduction emerges only under extreme adversity, which would be consistent with our study.

Another aspect that is often overlooked in many life-history trade-off studies is the distinction between resource allocation (Williams, 1966) and variation in resource acquisition (Tamian et al., 2024). In natural populations, both acquisition and allocation

are likely to vary with individual state and environmental context, including age, body condition, habitat quality, and climate (Hamel et al., 2009; MacNulty et al., 2009a, 2009b; McLoughlin et al., 2007; Moyes et al., 2009). Such variation can obscure predicted trade-offs unless resources are strongly limiting or environmental conditions are highly predictable (Hamel et al., 2010; van Noordwijk and de Jong, 1986). As a result, adaptive reproductive acceleration may be restricted to specific ecological contexts rather than representing a general response to early adversity.

When investigating shifts in life-history strategies, it is also important to consider that such shifts require an adequate level of plasticity; but developmental plasticity is still a constrained process. Although it can be advantageous for individuals to respond to environmental changes quickly, appropriately, and with maximal flexibility throughout their lives, high levels of responsiveness are not always either possible or desirable. Therefore, the mechanisms controlling reproductive energy allocation may not be very flexible or plastic in certain species. For example, yellow-bellied marmots must exceed a threshold minimum body mass for successful breeding (Armitage, 2014) which could be why we did not find a clear association with body condition.

Regardless, accelerated reproduction may not be a common or easily detectable response to ELA in species with slow life histories. This should not be surprising given that, in such species, fitness increases considerably with increasing breeding opportunities, which are themselves contingent on continued survival. Therefore, long-lived species may be programmed to prioritize future reproduction, making it hard to detect significant life-history shifts even if they are present. However, in such cases, developmental constraints or viability selection may better explain the reproductive

impacts of ELA (Luevano et al., 2022; van de Crommenacker et al., 2022; Weibel et al., 2020).

Clearly, simple pace-of-life predictions are more complicated and harder to identify in natural populations of long-lived species. Although we found some support for increased breeding probability at younger ages in response to ELA, the impact of adversity on lifetime fitness may depend less on shifting reproductive pace than on the heavy constraints on survival. More broadly, our results highlight the importance of distinguishing between total lifetime effects and lifespan-conditioned reproductive effects when evaluating the fitness consequences of early adversity. Without that distinction, important reproductive costs may be obscured.

TABLE AND FIGURES

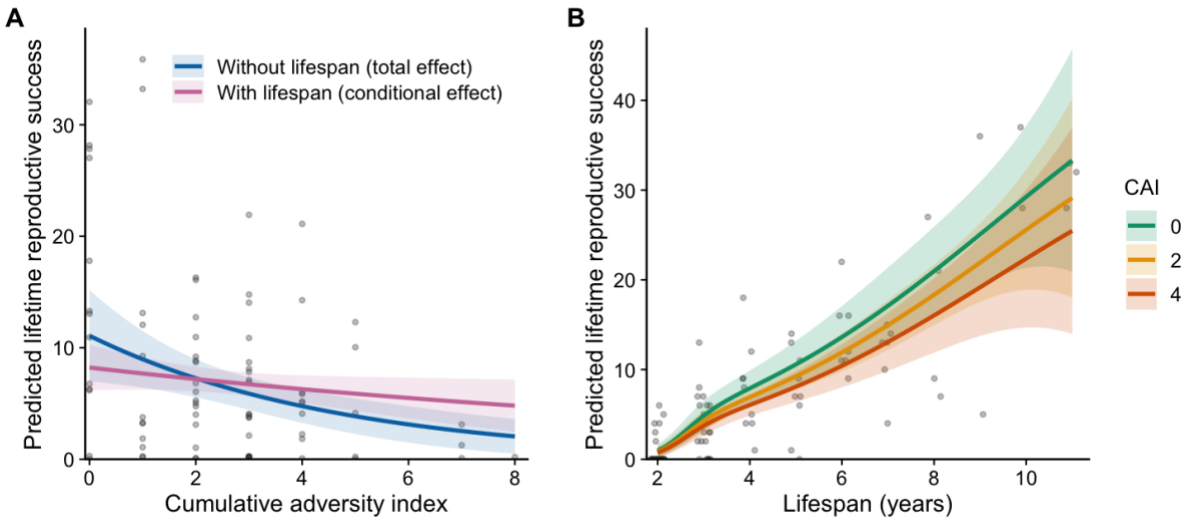

Figure 2.1. Lifespan is the primary driver of LRS. Early-life adversity (ELA), quantified using a cumulative adversity index (CAI), predicts lifetime reproductive success (LRS) primarily through its effect on lifespan in adult female yellow-bellied marmots. Predictions are from zero-inflated negative binomial GLMMs (n = 95; years = 2004–2018; CAI range: 0–8; lifespan range: 2–11 years). (**A**) compares the total predicted effect of ELA on LRS (steeper blue line) with predictions conditional on lifespan (flatter pink line). Only the total effect is negatively associated with LRS in a statistically significant way ($p<0.05$). (**B**) shows a positive association between lifespan and LRS which remains largely consistent across different levels of adversity. Shaded ribbons indicate 95% confidence intervals. Raw data points, in grey, are slightly jittered vertically).

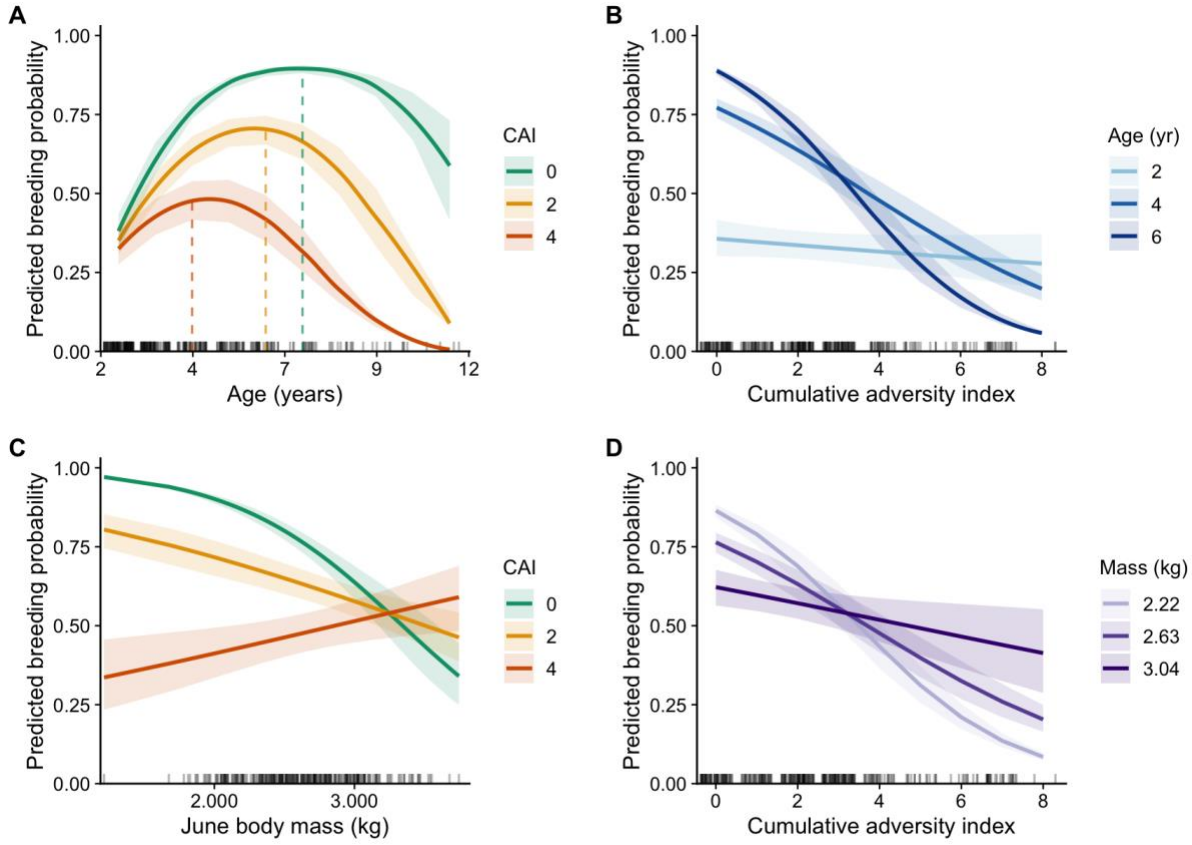

Figure 2.2. State-dependent changes in annual breeding probability. The effect of early-life adversity on annual breeding probability varies with age but perhaps not mass in adult female yellow-bellied marmots. Changes in the effect of early-life adversity (as a cumulative adversity index, or CAI) on predicted annual breeding probability as a function of age (**A, B**) and June mass (**C, D**). Predictions are estimated from a binomial GLMM (*n* = 280; unique individuals = 89; years = 2004–2024), with age and mass centered. (**A**) breeding probability follows a hump-shaped relationship with age, with the peak shifting to younger ages at higher adversity, when it also decreases more sharply. (**B**) an alternative perspective; breeding probability increases with age at low adversity but decreases at high adversity. (**C**) although higher June body mass (kg) tended to increase breeding probability at low adversity and decrease it at higher adversity, such

that breeding probability becomes more similar at higher mass, the CAI × mass interaction was not statistically significant (p = 0.078). Similarly, (**D**) shows how lighter individuals tended to be more likely to breed at lower CAI and less at higher CAI, with this effect potentially attenuating with increasing mass. Overall, higher adversity was associated with decreased breeding probability in females of mean age and mass. All groupings represented the mean value of that variable and one SD above and below the mean. Shaded ribbons indicate 95% confidence intervals. Green, higher lines represented 0 adversity increasing with yellow and red (overall lower). For age and mass, darker shades indicate higher values.

Table 2.1. Lifetime reproductive success (LRS). Zero-inflated negative binomial models of the effects of cumulative early-life adversity (ELA) on the LRS of adult female yellow-bellied marmots. We compare models with and without lifespan. Shown are incidence rate ratios (IRR) with 95% confidence intervals (CI); p-values < 0.05 (computed using a Wald z-distribution approximation) are bolded. The lifespan term was centered to avoid collinearity and ease interpretation. The sample comprised 95 unique individuals born between 2004 and 2018, the cumulative adversity index (CAI) for ELA ranged 0-8, and lifespan ranged 2-11.

	Lifetime Reproductive Success					
Count Model	**Independent ELA effect**			**Total ELA effect**		
Predictors	*IRR*	*CI*	*p*	*IRR*	*CI*	*p*
(Intercept)	8.31	6.50 – 10.6	**<0.001**	15.4	11.0 – 22.0	**<0.001**
CAI	0.94	0.86 – 1.02	0.111	0.81	0.71 – 0.92	**0.001**
Lifespan	1.33	1.21 – 1.47	**<0.001**			
Lifespan^2	0.99	0.97 – 1.01	0.185			
Zero-Inflated Model						
(Intercept)	0.01	0.00 – 0.11	**<0.001**	0.39	0.24 – 0.65	**<0.001**
Lifespan	0.06	0.02 – 0.24	**<0.001**			
Observations	95			95		
R^2 / R^2 adjusted	0.985 / 0.984			0.838 / 0.835		

Table 2.2. Annual breeding probability. Results from the binomial mixed-effects models showing how the effect of early-life adversity (ELA) on the annual breeding probability of adult, female yellow-bellied marmots varies with and without age and June mass. Age and June mass were both centered, to avoid collinearity and ease interpretation. The total sample size was 280, including 89 unique individuals and 21 years (2004-2024). The cumulative adversity index (CAI) for ELA ranged 0-8. The table includes 95% confidence intervals (CI) and bolded p-values (computed using a Wald z-distribution approximation) when $p < 0.05$.

Breeding Probability	**With interactions**			**Without interactions**		
Predictors	*Odds Ratios*	*CI*	*p*	*Odds Ratios*	*CI*	*p*
(Intercept)	3.37	1.20 – 9.45	**0.021**	2.71	0.97 – 7.53	0.057
CAI	0.72	0.56 – 0.92	**0.009**	0.72	0.58 – 0.90	**0.005**
June mass	0.19	0.03 – 1.36	0.099	0.66	0.20 – 2.19	0.496
Age	1.88	1.22 – 2.90	**0.004**	1.39	1.03 – 1.88	**0.032**
Age^2	0.90	0.82 – 0.98	**0.013**	0.92	0.85 – 0.99	**0.034**
valley [up]	1.39	0.58 – 3.35	0.460	1.48	0.65 – 3.38	0.349
CAI × June mass	1.67	0.94 – 2.97	0.078			
CAI × Age	0.87	0.77 – 1.00	**0.045**			
Random Effects						
σ^2	3.29			3.29		
T_{00}	0.24 $_{uid}$	1.60 $_{year}$		0.14 $_{uid}$	2.04 $_{year}$	
ICC	0.36			0.40		
Marginal / Conditional R^2	0.141 / 0.449			0.087 / 0.451		
AICc	343.809			344.651		

CHAPTER 3. DELAYED LIFE-HISTORY SHIFTS MITIGATE EARLY ADVERSITY COSTS

ABSTRACT

Early-life adversity (ELA) can have lasting consequences for survival and reproduction, often interpreted as developmental constraints that reduce fitness. However, some individuals may partly offset these costs by altering reproductive strategies. From a life-history perspective, individuals with reduced future reproductive opportunity may shift early investment to favor current (or early) reproduction, whereas developmental constraints may delay or limit reproduction. We tested these alternatives using long-term data from wild female yellow-bellied marmots (*Marmota flaviventer*) and a cumulative adversity index previously shown to predict lifespan. We asked whether ELA was associated with age, body mass, and litter size at first reproduction. We found that greater ELA was associated with delayed age at first reproduction, consistent with developmental or energetic constraints. While body mass at first reproduction was not significantly associated with ELA, females tended to be heavier when they delayed reproduction. Among these late breeders, those with high ELA weaned larger first litters, but they weaned smaller first litters when they bred early. Our results suggest that females who delay reproduction (and survive) could compensate for lost breeding opportunities by increasing their reproductive output. Together, we show that the impact of ELA on reproduction is not uniform. Instead, our findings support a trait-specific life-history framework in which delayed and accelerated reproduction can operate simultaneously on different components of reproduction. Therefore, this study highlights

the importance of separating reproductive timing and output when evaluating how early-life conditions shape life-history strategies in wild animals.

INTRODUCTION

It has long been observed that early-life conditions can have persistent consequences for survival, reproduction, and lifetime fitness (Lindström, 1999) in both wild animals and humans (Lummaa and Clutton-Brock, 2002; Monaghan, 2008). Recent studies investigating the cumulative impacts of early-life adversity (ELA) agree that the number, and not only the type, of early-life stressors is associated with decreased lifespan and, consequently, lifetime reproductive success (LRS; Gicquel et al., 2022; Ortiz-Ross and Blumstein, 2024; Patterson et al., 2023; Tung et al., 2016). However, their impact on other aspects of reproduction is less clear. Some studies on early-life effects show persistent reproductive costs, such as reduced reproductive success, late reproductive onset, or earlier reproductive senescence (Nussey et al., 2007; Pigeon et al., 2017; Spagopoulou et al., 2020). Others find that such costs are either absent or explained by the qualities of either the adult environment or individuals' somatic state (Hamel et al., 2009; Moyes et al., 2011; Rosenbaum et al., 2025; Taborsky, 2006). Few have investigated whether such variation in reproductive responses depends on individual's survival probabilities (Weibel et al., 2020).

From a life-history perspective, developing individuals must distribute limited resources among growth, maintenance, survival, and reproduction (Metcalfe and Monaghan, 2001; Stearns, 1992). Therefore, early adverse conditions could influence not only survival, but also how young individuals allocate their reduced energy supply. When encountering high adversity, they could either prioritize growth and survival,

aiming for better future reproductive success, or allocate those energy reserves towards immediate reproduction but risking the success of future opportunities. If individuals adjust energy allocation in response to early conditions and perceived survival prospects in a way that maximizes realized fitness, such trade-offs could provide an opportunity to compensate for some of the fitness costs of adversity (Fawcett and Frankenhuis, 2015; Nettle et al., 2013; Nettle and Frankenhuis, 2020). While support for this adaptive-response model can be found in the human literature (Ellis, 2004; Nettle et al., 2013), there is mixed support in wild animals.

The dominant expectation in the early-life effects animal literature is that adverse developmental conditions impose fitness constraints that persist into adulthood and cannot be recovered. Under this “silver-spoon” framework, favorable early environments confer lasting advantages over adverse ones, which instead impair fitness and often lead to a variety of reproductive costs (Cooper and Kruuk, 2018; Lindström, 1999; Monaghan, 2008). Reproductive costs have been identified as delayed reproductive onset (Martin and Festa-Bianchet, 2012), poor body condition at first reproduction (Douhard et al., 2014), and reduced reproductive output (Pigeon et al., 2021).

Reproductive success is not a single, uniform response, but is instead composed of different aspects that can have different drivers across the life course. Age at maturity, reproductive effort, and fecundity are related but distinct components of life-history and fitness (Stearns, 2000). Therefore, ELA may have a different impact on each, potentially explaining some of the lack of consensus among studies. In wild collared flycatchers (*Ficedula albicollis*), experimentally lowered natal conditions decreased early-life fitness but were also associated with slower reproductive

senescence (Spagopoulou et al., 2020). Similarly, female rhesus macaques (*Macaca mulatta*) who experienced a major hurricane in early life were less likely to breed successfully in early adulthood but more successful in their prime than females who did not experience that early adversity (Luevano et al., 2022). While ELA may result in significant costs to early reproduction, it can also shape later reproductive outcomes that compensate for some of those costs. This pattern also parallels the life-history trade-offs between current and future reproduction (Stearns, 2000). Considering multiple reproductive components together may reveal patterns that could be otherwise missed when reproductive performance is quantified with a single outcome.

To better understand the relationship between ELA and reproduction, and whether they are based on changes in life-history trade-offs, we must concurrently investigate not only how different aspects of reproduction change with developmental conditions but also with life expectancy. While the latter is usually hard to determine accurately, cumulative ELA approaches have consistently found decreased lifespans with increasing adversities (Gicquel et al., 2022; Ortiz-Ross and Blumstein, 2024; Patterson et al., 2023; Tung et al., 2016). As such, cumulative ELA can be a reliable indicator of life expectancy, regardless of the environmental conditions encountered in adulthood. Here, we build on this framework to ask whether cumulative ELA is associated not only with survival costs, but also with changes in reproductive timing, state, and output.

Yellow-bellied marmots (*Marmota flaviventer*) are a useful system for asking life-history questions because they are long-lived, iteroparous mammals that reproduce during a short season after a long hibernation. Females must carefully balance how to

allocate limited time and resources between the high energetic demands of reproduction and growth, since replenishing enough fat stores is essential for hibernation (Armitage, 1991; Monclús et al., 2014; Monclús and Blumstein, 2012). Prior work in a long-term study population in Colorado also showed that cumulative ELA reduced not only longevity (Ortiz-Ross and Blumstein, 2024) but also annual breeding probability (chapter 2). Yet, despite these reproductive costs, ELA was not associated with any significant difference in the LRS of females of similar lifespan (chapter 2). This discrepancy suggests females might be able to compensate for some reproductive costs to match the expected LRS. This finding presents a perfect opportunity to address which reproductive traits are constrained and which allow compensatory shifts in breeding responses.

We addressed this question by examining three components of first reproduction: age, body condition (mass), and litter size (or number of weaned offspring). These traits capture distinct aspects of reproductive strategy. Age at first reproduction reflects the capacity to start breeding, which may be more sensitive to developmental, energetic constraints (but can also be under hierarchical control). Age at first reproduction is also a key determinant of LRS in iteroparous species, including marmots (Oli and Armitage, 2003). Body mass at first reproduction indicates the state in which females initiate reproduction, which can suggest whether trade-off decisions favor growth or early reproduction. However, given the energetic demands of reproduction, breeding condition may be tightly constrained. Indeed, female marmots below an adequate mass threshold cannot reproduce successfully (Armitage, 2014). First-litter size reflects initial reproductive output, which could provide an excellent route to compensate for delayed

onset or reduced reproductive opportunities. However, it may also be constrained by the high energetic demand.

To determine whether our findings support constrained vs. adaptive life-history responses, we make the following predictions (summarized in **Table 3.1**): if early adversity primarily imposes insurmountable constraints, (a) females with greater adversity will initiate reproduction later, reproduce at a typical body mass, and produce smaller first litters; on the other hand, if females associate ELA with shorter life expectancy and adaptively shift their reproductive allocation, then (b) greater adversity will be associated with earlier reproduction, reproduction at lower mass, and increased first-litter size. However, by separating reproductive timing, reproductive state, and reproductive output, we also test whether early adversity produces uniform or trait-specific responses. The latter would suggest that reproductive traits vary in the extent to which they are either constrained by developmental costs or are responsive to shifts in reproductive potential.

METHODS

Study system and field site

Yellow-bellied marmots are a large ground-squirrel that lives in matrilineal colonies of varying size. Our study used data collected on individuals living in and around the Rocky Mountain Biological Laboratory (RMBL, 38º57′N, 106º59′W) in Gunnison County, Colorado, USA, where they have been studied for over six decades. Individuals in this population are observed near daily from mid-April to mid-September—their active season—both in the morning and late afternoon, when they are most active. They are also trapped biweekly, when possible, to collect physiological and morphological data.

All field procedures were approved by a UCLA research protocol (2001-191, renewed annually) and under permits issued by the Colorado Division of Wildlife (TR-519, renewed annually).

Our analyses focused on adult females (age ≥2) monitored between 2002-2020 with known annual survival, reproductive history, body mass, and weaned offspring. Given that this population was studied across an elevational gradient (~300 m) that presents very different environmental conditions, when considering the geographic location of colonies we categorized them as either located “up valley”, at higher elevation, or “down valley,” at lower elevation. Importantly, this difference has been associated with differences in life history (Schwartz and Armitage, 2005; Van Vuren and Armitage, 1991).

Cumulative adversity index

To quantify ELA, we used a previously developed cumulative adversity index (CAI) that is closely associated with adult longevity in our marmot population (Ortiz-Ross and Blumstein, 2024). The index includes 9 potential sources of adversity known to impact marmot fitness, and they vary from ecological (late snowmelt, summer drought, high predation pressure) to socio-demographic (large, male-biased litters) and parental (late weaning, poor maternal condition, high maternal stress, and maternal loss). The CAI is the total number of adversities encountered in early life. Each adversity is a binary measure indicating whether the adversity was present or absent within the first two years of life, when marmots reach sexual maturity (Oli and Armitage, 2004). Early experiences were considered adverse when they fell within the upper quartile of the

population distribution. Therefore, non-adverse or 'typical' conditions were those experienced by 75% of the population across the entire study period.

Reproductive traits

All females in our study were monitored annually from birth, but we only used data collected after maturation (age 2). Female reproductive status was assessed annually throughout the season. We considered two separate measures of reproductive onset: the first breeding attempt (that resulted in a pregnancy), and the successful weaning of a litter. The first was determined based on nipple development or the emergence of a litter. The second only considered the emergence of weaned offspring. The main distinction being that the first allows for reproductive onset to occur even if it fails before offspring are weaned.

Offspring are counted as soon as they emerge (once they are weaned), with different litters usually emerging at different times or from different maternal burrows. Therefore, maternity could often be behaviorally inferred but was also confirmed via genetic analysis using 12 microsatellite loci (details in Blumstein et al., 2010).

Individuals were weighted during each trapping event. Since marmot body mass varies greatly as the season progresses, BLUPs were used to estimate the mass of each individual on June 1st and August 15th (following (Maldonado-Chaparro et al., 2015). To quantify mass at first reproduction, we used mass estimates for June 1st.

Statistical analysis

To test the effect of ELA on age at first reproduction we fit discrete-time hazard, or event history, models for both of our definitions of reproductive onset. More specifically,

we fit generalized binomial linear models with a complementary log-log (cloglog) link. The dataset included an annual assessment of the breeding status (bred or not) of each individual beginning at age 2 and ending at first reproduction or last observation. Age was modelled both as a factor, with ages ≥5 grouped, and as a continuous variable with a linear and quadratic terms to allow for a non-linear hazard. Since the results were unaffected, we only show age as continuous. Valley location (up or down) was included as a fixed effect in these and all other models to account for spatial variation in environmental conditions. A random effect of year was considered but excluded from final models due to near-zero variance.

The effects of ELA on mass at first reproduction (based on successfully weaning a litter) were analyzed with a linear mixed-effects model that included year as a random effect, linear and quadratic terms for age at first reproduction, and an interaction between age at first reproduction and ELA. The same fixed effects were used to model how the number of offspring weaned in the first litter varied with ELA, fit as a Poisson generalized linear model with a log link.

All analyses were conducted in R (v 4.5.0). Mixed models were fit with the *lme4* package (v 1.1-38; Bates et al., 2015), while the other linear models used the native stats package (v 4.5.0). Model assumptions were verified using the *performance* package (v 0.15.2; Lüdecke et al., 2021). The sjPlot package (v 2.9.0; Lüdecke, 2025) was used to aid in the tabular reporting of the results.

RESULTS

The final dataset included N = 102 unique females with known histories who reached sexual maturity (age 2) between 2002-2018, and 67 unique litters between 2004-2020.

During the study period, 74 females became reproductive at ages 2-5 (median = 2), with 63.55% initiating reproduction by age 2. Maternal mass on 1 June the year they weaned their first litter ranged from 1.67-3.47 kg (mean ± SD = 2.47 kg ± 0.36). First-litter size varied from 1-9 pups (median = 4), and mean pup mass by August 15 ranged from 0.56-2.18 kg (mean ± SD = 1.24 kg ± 0.32) across litters. Across our two valley locations, 65 females (63.73%) were located up valley, the higher elevation site. Sample sizes for individual analyses varied due to trait-specific data availability and censoring but were consistently restricted to first reproductive events for maternal and offspring traits.

Age at first reproduction (AFR)

In both of our discrete-time hazard models, the probability of first reproduction increased sharply in younger females but declined with age, indicating a baseline hazard that favors early reproduction. This hazard decreased with each additional ELA, resulting in delayed reproduction (**Table 3.2**). When reproductive onset was triggered by a likely pregnancy (based on nipple assessment if a litter did not emerge), each ELA was mildly associated with a 12% reduction in breeding probability (risk ratio = 0.88, 95% CI: 0.77–0.99, $p = 0.045$). When triggered by the weaning of a litter, ELA was associated with a 23% reduction in breeding probability (risk ratio = 0.77, 95% CI: 0.66–0.89, $p < 0.001$). Therefore, ELA delayed reproductive onset regardless of whether the pregnancy successfully yielded weaned offspring or not, increasing our confidence in the signal. Valley location did not shift reproductive timing (**Table 3.2**). The interaction between age and ELA did not improve the model and had no impact on the results, so it was removed from the final model. Since reproductive onset is conditional on survival to

maturity, the effects of ELA on reproductive timing are limited to surviving females and therefore subject to some selective filtering. Furthermore, the breeding hazard at older ages is estimated from fewer observations, increasing uncertainty at that end. However, both models were right censored to include those who had yet to initiate reproduction.

Mass at first reproduction

Early-life adversity was not significantly associated with body mass at first reproduction (β = −0.01, 95% CI: −0.06-0.03, $p = 0.52$), which was more closely associated with age and valley position (**Table 3.3**). Females who delayed reproduction (older age) were substantially heavier (β = 0.24, 95% CI: 0.14-0.33, $p < 0.001$), as were those living at lower elevation (β = −0.29, 95% CI: −0.44-−0.15, $p < 0.001$). Annual environmental variation also explained a meaningful proportion of variance in maternal mass (ICC = 0.36; Table 3.3). While we did not detect a significant effect of ELA on mass at first reproduction, this could be influenced by selective filtering of surviving females with minimum required weight for successful reproduction (see discussion).

Offspring weaned in first litter

Female marmots who delayed reproduction and experienced high ELA weaned larger first litters (significant ELA × age interaction; IRR = 1.14, 95% CI: 1.02–1.28, $p = 0.02$; Table 3.3). Offspring number also varied with location, with females living up valley producing smaller first litters (IRR = 0.76, 95% CI: 0.59–1.00, $p = 0.049$). Once again, our sample sizes are limited to successful breeders and biased towards younger ages at first reproduction. Therefore, our results are still conditional on survival to reproduction and may underestimate total adversity costs at the population level.

DISCUSSION

Adult female yellow-bellied marmots who experienced greater ELA had later reproductive onset (**Figure 3.1**) but weaned larger first litters (**Figure 3.3**). While the initial delay in reproduction is consistent with developmental constraints, the following increase in output is consistent with an adaptive or compensatory life-history shift to recover costs. Importantly, these findings show that the impacts of early adversity on female reproduction were not uniform. Instead, opposite patterns emerged between timing of onset and investment in output, or fertility (**Table 3.1**). Therefore, different components of reproductive performance may vary in their sensitivity to developmental constraints and reflect distinct life-history responses.

Delayed reproductive onset as a developmental constraint

The reproductive delay we found in response to ELA is consistent with other wild animal studies on early environmental conditions (Douhard et al., 2016; Monaghan, 2008; Pigeon and Pelletier, 2018), although many focused on annual cohort effects and environmental stressors were considered independently. However, our use of a CAI uniquely shows the constraint that arises from the additive number of ELAs encountered, regardless of kind. By broadening the scope, CAIs can provide overlooked insights into the simultaneous mechanisms that lead to the clear cumulative fitness costs of ELA (Gicquel et al., 2022; Kong et al., 2025; Ortiz-Ross and Blumstein, 2024; Patterson et al., 2023; Tung et al., 2016). Consequently, we also address the difficulty but need to estimate multiple-stressor impacts (Orr et al., 2020; Pirotta et al., 2022; Tyack et al., 2022).

While our results are also consistent with our previous study on the same population, which showed an annual decrease in breeding probability associated with greater ELAs (Chapter 2; unpublished work), a few other studies that incorporated cumulative effects show mixed results. For example, Cayo Santiago rhesus macaques (*Macaca mulatta*; Petersen et al. 2026) also delayed reproduction, but Weibel et al. (2020) did not find any association between cumulative, or specific, ELAs and age at first birth in Amboseli yellow baboons (*Papio cynocephalus)*. We suggest this discrepancy could be due to differences in reproductive periodicity that would change how selective pressure shapes reproduction, even though all have relatively slow life-histories (Boyce, 1979; Shivani et al., 2025). While delayed reproduction is consistent with the slower life-history of long-lived species, expected to prioritize future reproduction (Roff, 1992; Stearns, 1992), differences in breeding biology still exist within these larger groups and may become more relevant when making within-population comparisons.

Unlike yellow baboons, both marmots and rhesus macaques are obligate seasonal breeders with a restricted breeding window that imposes stronger constraints on the timing of reproduction (Oli and Armitage, 2003; Shivani et al., 2025), limiting opportunities to “get ahead” by breeding earlier. Furthermore, marmot’s reproductive energy availability is defined by the fat reserves gathered the previous season, since they breed right before emergence. Therefore, body condition at the start of the breeding season is most likely to constrain their ability to breed (more so than their fertility). This has been supported in yellow-bellied marmots, where studied have found a minimum weight threshold required to breed (Armitage, 1991; Monclús et al., 2014;

Schwartz et al., 1998). This strict threshold may also explain why we did not find a strong association between ELA and mass at first reproduction. The additional constraints imposed on seasonal breeders over continuous breeders, like yellow baboons, may explain why reproductive delays have been more often observed in the former.

Yellow-bellied marmots are also particularly sensitive to energetic constraints because of the considerable energy demands of hibernation, which means their survival, not just reproductive success, is strongly reliant on accumulating enough energy reserves throughout the breeding season, which would only begin after weaning offspring (Armitage, 2014). A compromised body condition may leave them no other choice than to redirect efforts towards survival and thus delay reproductive efforts until conditions improve. Taken together, we show that certain reproductive traits are tightly regulated, with little to no room for alternative energy trade-offs. But the same may not be true for all reproductive traits.

Increasing reproductive output after delay—an opportunity to compensate?

While delayed reproduction is consistent with energetic constraints, it need not reflect a suboptimal response to such constraints. Although limited resources are likely to impede an individual's ability to breed successfully, this hurdle can be overcome once they regain enough resources. Delaying reproduction can provide the opportunity to gain greater energy reserves, take advantage of potential windfalls, and increase future reproductive success. Indeed, our study found that females who delayed reproduction, regardless of ELA, reproduced in better body condition that those who reproduced earlier (**Figure 3.2**). Since better body condition is often associated with increased

reproductive success (Van Vuren and Armitage, 1994), this increased energy stored may be what enables those with high ELA to produce larger first litters (**Figure 3.3**) and compensate for the missed breeding opportunities of delaying reproduction. However, this hypothesis must be formally tested.

Support for recovery from an initial delay can be found in other studies; for example, rhesus macaques (*Macaca mulatta*) that delayed reproduction were still able to keep reproductive pace with other females (Luevano et al., 2022), and North American red squirrels (*Tamiasciurus hudsonicus*) that experienced a bad start were able to take advantage of later food booms to recover those costs (Petrullo et al., 2024). We conclude that when conditions are poor, delaying reproduction in favor of future opportunity may remain the better bet than reproducing early (West-Eberhard, 2003), at least in longer-lived species.

Despite the initial delay, the increased number of first-weaned offspring associated with ELA indicates a greater investment in the first viable breeding opportunity, a pattern consistent with accelerated reproduction, albeit one that only emerges once breeding begins. Importantly, it does not support a pure constraint model in which ELA only imposes insurmountable developmental limitations. If so, high ELA individuals would be expected to always produce smaller litters.

Accelerated reproduction predicts trade-off decisions that reflect increased energy allocation towards immediate vs. future reproduction when opportunities for the latter are reduced. While evidence in support of accelerated reproduction is more commonly sought in shifts in the timing (or start of) reproduction (Ellis, 2004; Petersen et al., 2026; Weibel et al., 2020), our findings highlight that such evidence can instead

be found in the extent of early investment once breeding can begin. This important distinction should inform how the field frames and tests adaptive life-history shifts in wild animals. Reproductive onset alone, while tightly associated with LRS, may not accurately reflect the cumulative reproductive success of individuals up-to any given survival age. Given that ELA reduces lifespan, comparing fitness measures within a lifetime would better reflect evidence of compensation based on life expectancy.

The timing of reproductive peaks is another avenue worth investigating. For example, a recent marmot study found that, while high ELA was associated with lower annual breeding probability, it tended to peak earlier (chapter 2). This finding is again consistent with an earlier increase in reproductive investment. Combined with larger first litters, it can suggests that individuals, when compromised, take maximum advantage of early opportunities; a pattern also found in other species (Hämäläinen et al., 2017).

Opposite life-history patterns across reproductive dimensions

Taken together, these results suggest that developmental constraints and adaptive shifts in energy allocation can operate simultaneously on different components of reproduction through different pathways (Nettle and Frankenhuis, 2020). Although reproductive onset is often used to quantify accelerated reproduction, a delayed start may not represent an overall slower reproductive pace, only a slow start. As previously discussed, competing selection pressures may influence onset vs. investment, operating through different mechanisms during different life periods, or time windows. Reproductive timing may be especially sensitive to developmental or energetic constraints, whereas reproductive output once breeding begins may be more responsive to current state, reproductive value, or allocation decisions (Charmantier and

Garant, 2005; Ellis, 2004; Shivani et al., 2025). In this study, the reproductive constraints associated with higher ELA seem to primarily influence breeding opportunities, by delaying the start of reproduction, rather than the reproductive output.

This trait-specific perspective may help explain why studies of early-life adversity often find mixed effects across taxa and fitness components. Similarly, our previous study on the same population found that LRS among females of similar lifespan did not vary with ELA (chapter 2), suggesting the notable lifetime fitness cost of ELA were felt only through decreased survival and not reproduction. Yet, ELA was also associated with a lower breeding probability in any given year, a clear reproductive cost. A similar pattern of ELA causing reproductive costs without decreasing LRS was also found in other populations (Cartwright et al., 2014). Our finding that mothers with high ELA produce more offspring when they start breeding may explain that discrepancy by offering an avenue for compensation, although the quality or survival of those offspring was not explored. Importantly, this finding was only evident when age at first reproduction was included, emphasizing the need to simultaneously account for multiple life-history traits (Petersen et al., 2026). Future work can better evaluate whether this pattern of early delay followed by a greater push reflects adaptive trade-off decisions, state-dependent responses, or selective disappearance, which is hard to avoid in animal studies.

Conclusions

In summary, our findings suggest that early adversity may be an important source of within-population variation in life-history tactics, but its varied effects cannot be understood from any single measure of fitness. Early adversity can simultaneously

generate both constraints and compensatory responses across different life-history components. At lower taxonomic levels, the conventional slow–fast life–history continuum framework may be less informative. Expected lifespan may still shape the value of current versus future reproduction, but other ecological and phenological pressures, may further determine which trade-offs are possible. Among seasonal breeders, reproductive timing is highly constrained, therefore an adaptive response to ELA is less likely to manifest in aspects of reproductive timing than output. Testing this idea across species with different breeding schedules could help explain why evidence for adversity-induced life-history shifts has been inconsistent across taxa. As seasonal cycles become increasingly disrupted by climate change, a deeper understanding of how seasonality can shape resilience will provide valuable insights (Burtschell et al., 2023).

Finally, using a CAI of the total burden of multiple early-life challenges, revealed additive systematic changes across reproductive traits regardless of the specific adversities. This approach provides a practical and effective way to connect increasingly complex early environments with later life-history variation. Combining cumulative adversity measures with comparative life-history data could therefore help identify which traits and species are most capable of compensating for increasingly variable and multi-stressor environments.

TABLE AND FIGURES

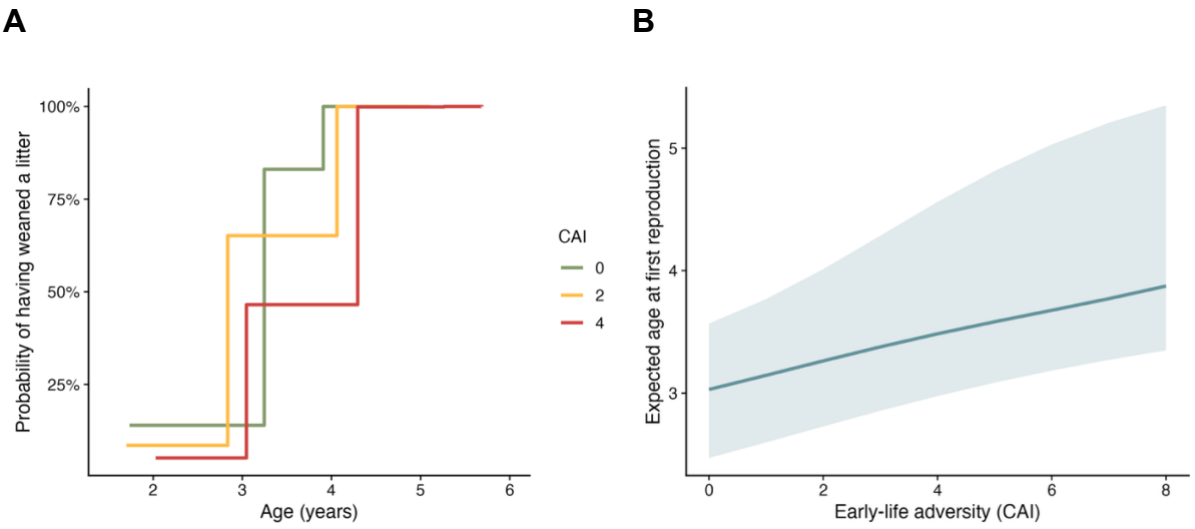

Figure 3.1. Early-life adversity delays age at first reproduction. (**A**) Cumulative probability of females weaning their first litter by a given age when their cumulative adversity index (CAI) values are 0, 2, or 4 (mean ±1 SD). (**B**) Expected age at first reproduction across the observed range of CAI; the shaded band represents a 95% confidence interval. Estimates for (**A**) and (**B**) were derived from a discrete-time event-history model of first successful weaning that included linear and quadratic effects of age and valley location as a 2-level factor. Greater early-life adversity was associated with a lower annual probability of becoming a breeder and, consequently, a later expected age at first reproduction. The analysis included 161 female-year observations from 102 females aged ≥2 years.

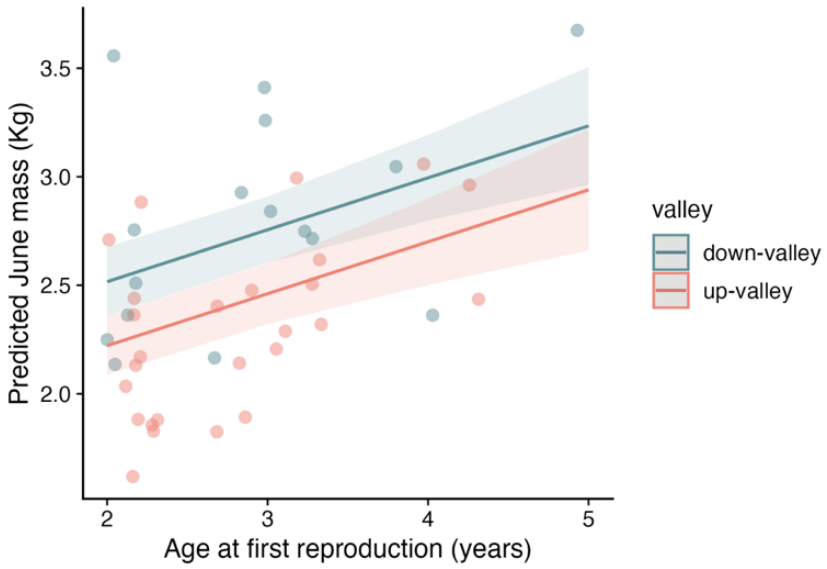

Figure 3.2. June body mass increased with age at first reproduction. Females living up-valley initiated reproduction at a lower body mass than those living down-valley. Points represent individual observations, while lines and shaded bands show fitted values and 95% confidence intervals from a linear mixed-effects model that included CAI, age at first reproduction, and valley location as fixed effects and year as a random intercept. Early-life adversity was not associated with body mass at first reproduction. The analysis included 66 females across 15 years.

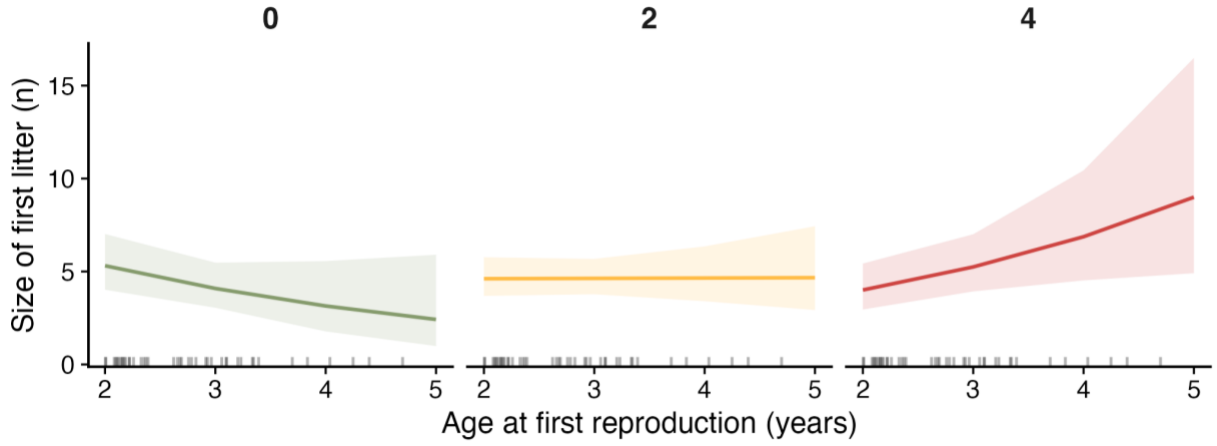

Figure 3.3. Late breeders with high ELA weaned larger first litters. Females exposed to greater early adversity weaned larger first litters when they began reproducing later. Lines show the predicted number of offspring weaned in a female's first litter as a function of age at first reproduction when their CAI values were 0, 2, or 4 (mean ±1 SD). and shaded bands represent predictions and 95% confidence intervals from a Poisson generalized linear model that also included valley location. Grey marks on the x-axis show the distribution of observed ages at first reproduction. The analysis included 66 females that successfully weaned at least one litter across 15 years.

Table 3.1. Predicted trends and findings. Predictions compare expected trends in age, mass, and litter size at first reproduction under a constraint-only or an adaptive shift hypothesis.

	Response to increasing early-life adversities (ELAs)		
At first reproduction	**Constraint predicts**	**Adaptive shift predicts**	**Our findings**
Age	Delay (later)	Acceleration (earlier)	Delayed
Mass	No change or higher	Lower	Unchanged
Litter size	Smaller	Larger	Increases with delay

Table 3.2. Age at first reproduction. Results of two discrete-time event history models (generalized binomial models with a cloglog link) estimating the effects of early-life adversity (ELA) on the annual probability of reproductive onset, conditional on survival. Reproductive onset was quantified based on either nipple development or the successful weaning of a litter. Time was quantified in annual age intervals, using both linear and quadratic terms. Valley location was included as factor with 2 levels (up and down) representing elevational variation. Risk ratios greater than 1 indicate a higher hazard (risk) of reproductive onset. Sample sizes reflect individual-year observations (N =139 for nipple development only; n=161 for first successful weaning), but they both included 102 unique adult females (age≥2). The reported β coefficients and 95% confidence intervals (CIs) are for standardized (std) covariates enabling direct comparisons. P-values ≤ 0.05 are bolded.

	Risk of reproductive onset (pregnancy)				Risk of weaning a first litter			
Predictors	Risk Ratios	β (std)	CI (std)	p	Risk Ratios	β (std)	CI (std)	p
(Intercept)	0.92	0.63	0.39 – 0.97	0.738	0.73	0.32	0.19 – 0.52	0.250
Age	19.20	7.99	1.95 – 50.63	0.011	10.79	13.68	1.71 – 188.9	0.027
Age^2	0.66	0.15	0.02 – 0.64	0.031	0.69	0.05	0.00 – 0.53	0.036
ELA	0.88	0.75	0.57 – 0.98	0.045	0.77	0.56	0.39 – 0.77	<0.001
[Up] valley	1.29	1.29	0.74 – 2.30	0.363	1.63	1.63	0.93 – 2.91	0.093

Table 3.3. Mass at first reproduction. Results of the linear mixed-effects model estimating the effect of early-life adversity (ELA) on body mass at first reproduction. Mass was estimated for June 1st for all individuals. Fixed effects included age at first reproduction, and valley location (up or down). Year was included as a random intercept. The β coefficients and 95% confidence intervals (CIs) are standardized to facilitate comparison of effect sizes. The sample included 66 unique females who successfully weaned at least one litter. Represented are 15 years (2005-2020; excluding 2011).

	June mass (Kg) at first reproduction			
Predictors	Estimates	β (std)	CI (std)	p
(Intercept)	2.07	0.44	0.04 – 0.85	<0.001
ELA	-0.01	-0.07	-0.29 – 0.15	0.523
[Up] valley	-0.29	-0.81	-1.21 – -0.40	**<0.001**
Age	0.24	0.46	0.28 – 0.65	**<0.001**
Random Effects				
σ^2	0.06			
$\tau_{00\ year}$	0.03		Marginal R^2	0.388
ICC	0.36		Conditional R^2	0.608

Table 3.4. Size of first litter. Results of a Poisson generalized linear model estimating the effects of early-life adversity (ELA), age, and valley location (up or down) on the size of a female's first litter. An interaction between ELA and age was also included to allow for different life-history responses. Incidence rate ratios (IRR) greater than 1 indicate larger litters. The β coefficients and 95% confidence intervals (CIs) have been standardized. The sample included 66 unique females who successfully weaned at least one litter across 15 years (2005-2020; excluding 2011).

	Number of offspring weaned in the first litter			
Predictors	IRR	β (std)	CI (std)	p
(Intercept)	8.97	4.61	3.74 – 5.61	<0.001
ELA	0.71	0.99	0.86 – 1.13	**0.020**
Age	0.77	1.04	0.92 – 1.16	0.131
[Up] valley	0.76	0.76	0.59 – 1.00	**0.049**
ELA × Age	1.14	1.17	1.02 – 1.34	**0.021**

References

Ancona, S., Zúñiga-Vega, J.J., Rodríguez, C., Drummond, H., 2018. Experiencing El Niño conditions during early life reduces recruiting probabilities but not adult survival. R. Soc. Open Sci. 5. https://doi.org/10.1098/rsos.170076

Armitage, K.B., 2017. Hibernation as a major determinant of life-history traits in marmots. J. Mammal. 98, 321–331. https://doi.org/10.1093/jmammal/gyw159

Armitage, K.B., 2014. Marmot Biology. Sociality, individual fitness, and population dynamics. Cambridge University Press.

Armitage, K.B., 1991. Factors affecting corticosteroid concentration in yellow bellied marmots. Comp. Biochem. Physiol. - Part Mol. Integr. Physiol. 98, 47–54. https://doi.org/10.1016/0300-9629(91)90576-X

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Beckie, T.M., 2012. A systematic review of allostatic load, health, and health disparities. Biol. Res. Nurs. 14, 311–46. https://doi.org/10.1177/1099800412455688

Berens, A.E., Jensen, S.K.G., Nelson, C.A., 2017. Biological embedding of childhood adversity: From physiological mechanisms to clinical implications. BMC Med. 15, 1–12. https://doi.org/10.1186/s12916-017-0895-4

Blumstein, D.T., Ebensperger, L.A., Hayes, L.D., Vásquez, R.A., Ahern, T.H., Burger, J.R., Dolezal, A.G., Dosmann, A., González-Mariscal, G., Harris, B.N., Herrera, E.A., Lacey, E.A., Mateo, J., McGraw, L.A., Olazábal, D., Ramenofsky, M., Rubenstein, D.R., Sakhai, S.A., Saltzman, W., Sainz-Borgo, C., Soto-Gamboa, M., Stewart, M.L., Wey, T.W., Wingfield, J.C., Young, L.J., 2010. Toward an integrative understanding of social behavior: New models and new opportunities. Front. Behav. Neurosci. 4. https://doi.org/10.3389/fnbeh.2010.00034

Bolker, B., R Development CoreTeam, 2023. bbmle: Tools for general maximum likelihood estimation. R package version 1.0.25.1.

Boyce, M.S., 1979. Seasonality and patterns of natural selection for life histories. Am. Nat. 114, 569–583. https://doi.org/10.1086/283503

Brooks, M., E., Kristensen, K., van Benthem, K., J., Magnusson, A., Berg, C., W., Nielsen, A., Skaug, H., J., Mächler, M., Bolker, B., M., 2017. glmmTMB balances

speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9, 378. Https://doi.org/10.32614/RJ-2017-066

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65, 23–35. https://doi.org/10.1007/s00265-010-1029-6

Burtschell, L., Dezeure, J., Huchard, E., Godelle, B., 2023. Evolutionary determinants of reproductive seasonality: A theoretical approach. Peer Community J. 3, e56. https://doi.org/10.24072/pcjournal.286

Cartwright, S.J., Nicoll, M.A.C., Jones, C.G., Tatayah, V., Norris, K., 2014. Anthropogenic natal environmental effects on life histories in a wild bird population. Curr. Biol. https://doi.org/10.1016/j.cub.2014.01.040

Charmantier, A., Garant, D., 2005. Environmental quality and evolutionary potential: lessons from wild populations. Proc. R. Soc. B Biol. Sci. 272, 1415–1425. https://doi.org/10.1098/rspb.2005.3117

Clutton-Brock, T., Sheldon, B.C., 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends Ecol. Evol. 25, 562–573. https://doi.org/10.1016/j.tree.2010.08.002

Clutton-Brock, T.H. (Ed.), 1988. Reproductive success: studies of individual variation in contrasting breeding systems. The Univ. of Chigaco Pr, Chicago.

Clutton-Brock, T.H., 1984. Reproductive effort and terminal investment in iteroparous animals. Am. Nat. 123, 212–229. https://doi.org/10.1086/284198

Cooper, E.B., Kruuk, L.E.B., 2018. Ageing with a silver-spoon: A meta-analysis of the effect of developmental environment on senescence. Evol. Lett. 2, 460–471. https://doi.org/10.1002/evl3.79

Coulson, T., Benton, T.G., Lundberg, P., Dall, S.R.X., Kendall, B.E., Gaillard, J.-M., 2006. Estimating individual contributions to population growth: evolutionary fitness in ecological time. Proc. R. Soc. B Biol. Sci. 273, 547–555. https://doi.org/10.1098/rspb.2005.3357

Dettmer, A.M., Chusyd, D.E., 2023. Early life adversities and lifelong health outcomes: A review of the literature on large, social, long-lived nonhuman mammals.

Neurosci. Biobehav. Rev. 152, 105297. https://doi.org/10.1016/j.neubiorev.2023.105297

Douhard, M., Loe, L.E., Stien, A., Bonenfant, C., Justin Irvine, R., Veiberg, V., Ropstad, E., Albon, S., 2016. The influence of weather conditions during gestation on life histories in a wild Arctic ungulate. Proc. R. Soc. B Biol. Sci. 283. https://doi.org/10.1098/rspb.2016.1760

Douhard, M., Plard, F., Gaillard, J.-M., Capron, G., Delorme, D., Klein, F., Duncan, P., Loe, L.E., Bonenfant, C., 2014. Fitness consequences of environmental conditions at different life stages in a long-lived vertebrate. Proc. R. Soc. B Biol. Sci. 281, 20140276. https://doi.org/10.1098/rspb.2014.0276

Drake, E.D., Ravindran, S., Bal, X., Pemberton, J.M., Pilkington, J.G., Nussey, D.H., Froy, H., 2025. Sex-specific effects of early-life adversity on adult fitness in a wild mammal. Proc. R. Soc. B Biol. Sci. 292, 20250192. https://doi.org/10.1098/rspb.2025.0192

Edes, A.N., Crews, D.E., 2017. Allostatic load and biological anthropology. Am. J. Phys. Anthropol. 162, 44–70. https://doi.org/10.1002/ajpa.23146

Ellis, B.J., 2004. Timing of pubertal maturation in girls: an integrated life history approach. Psychol. Bull. 130, 920–958. https://doi.org/10.1037/0033-2909.130.6.920

Ellis, B.J., Del Giudice, M., 2019. Developmental adaptation to stress: An evolutionary perspective. Annu. Rev. Psychol. 70, 111–139. https://doi.org/10.1146/annurev-psych-122216-011732

Ellis, B.J., Figueredo, A.J., Brumbach, B.H., Schlomer, G.L., 2009. Fundamental dimensions of environmental risk: The impact of harsh versus unpredictable environments on the evolution and development of life history strategies. Hum. Nat. 20, 204–268. https://doi.org/10.1007/s12110-009-9063-7

Evans, G.W., 2003. A multimethodological analysis of cumulative risk and allostatic load among rural children. Dev. Psychol. 39, 924–933. https://doi.org/10.1037/0012-1649.39.5.924

Evans, G.W., Li, D., Whipple, S.S., 2013. Cumulative risk and child development. Psychol. Bull. 139, 1342–1396. https://doi.org/10.1037/a0031808

Fawcett, T.W., Frankenhuis, W.E., 2015. Adaptive explanations for sensitive windows in development. Front. Zool. 12, S3. https://doi.org/10.1186/1742-9994-12-S1-S3

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., Toïgo, C., 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annu. Rev. Ecol. Syst. 31, 367–393. https://doi.org/10.1146/annurev.ecolsys.31.1.367

Gicquel, M., East, M., Hofer, H., Benhaiem, S., 2022. Early-life adversity predicts performance and fitness in a wild social carnivore. J. Anim. Ecol. 91, 1–13. https://doi.org/10.1111/1365-2656.13785

Gonzalez, S.J., Sherer, A.J., Hernández-Pacheco, R., 2023. Differential effects of early life adversity on male and female rhesus macaque lifespan. Ecol. Evol. 13. https://doi.org/10.1002/ece3.10689

Gunn, A., Russell, D., Greig, L., 2014. Insights into integrating cumulative effects and collaborative co-management for migratory tundra caribou herds in the Northwest Territories, Canada. Ecol. Soc. 19.

Hämäläinen, A., McAdam, A.G., Dantzer, B., Lane, J.E., Haines, J.A., Humphries, M.M., Boutin, S., 2017. Fitness consequences of peak reproductive effort in a resource pulse system. Sci. Rep. 7, 9335. https://doi.org/10.1038/s41598-017-09724-x

Hamel, S., Gaillard, J.-M., Festa-Bianchet, M., Côté, S.D., 2009. Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. Ecology 90, 1981–1995. https://doi.org/10.1890/08-0596.1

Hamel, S., Gaillard, J.-M., Yoccoz, N.G., Loison, A., Bonenfant, C., Descamps, S., 2010. Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. Ecol. Lett. 13, 915–935. https://doi.org/10.1111/j.1461-0248.2010.01478.x

Hartig, F., 2024. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. https://doi.org/10.32614/CRAN.package.DHARMa

Henry, C.J.K., Ulijaszek, S.J., 1996. Long-Term Consequences of Early Environment: Growth, Development and the Lifespan Developmental Perspective, in: Henry, C.J.K., Ulijaszek, S.J. (Eds.), Society for the Study of Human Biology Symposium Series; 37. Cambridge University Press, Cambridge, pp. 1–249.

Jarvis, L., Rosenfeld, J., Gonzalez-Espinosa, P.C., Enders, E.C., 2024. A process framework for integrating stressor-response functions into cumulative effects models. Sci. Total Environ. 906, 167456. https://doi.org/10.1016/J.SCITOTENV.2023.167456

Kong, A.Y., Ortiz-Ross, X., Blumstein, D.T., 2025. Is early life adversity associated with adult stress in a wild rodent? Ecol. Evol. 15, e71065. https://doi.org/10.1002/ece3.71065

Kroeger, S.B., Blumstein, D.T., Armitage, K.B., Reid, J.M., Martin, J.G.A., 2020. Older mothers produce more successful daughters. Proc. Natl. Acad. Sci. U. S. A. 117, 4809–4814. https://doi.org/10.1073/pnas.1908551117

Lea, A.J., Rosebaum, S., 2020. Understanding how early life effects evolve: progress, gaps, and future directions. Curr. Opin. Behav. Sci. 36, 29–35. https://doi.org/10.1016/j.cobeha.2020.06.006

Lea, A.J., Tung, J., Archie, E.A., Alberts, S.C., 2017. Developmental plasticity: Bridging research in evolution and human health. Evol. Med. Public Health 2017, 162–175. https://doi.org/10.1093/emph/eox019

Lindström, J., 1999. Early development and fitness in birds and mammals. Trends Ecol. Evol. 14, 343–348. https://doi.org/10.1016/S0169-5347(99)01639-0

Lüdecke, D., 2025. sjPlot: Data visualization for statistics in social science (manual).

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., Makowski, D., 2021. performance: An R package for assessment, comparison and testing of statistical models. J. Open Source Softw. 6. https://doi.org/10.21105/joss.03139

Luevano, L., Sutherland, C., Gonzalez, S.J., Hernández-Pacheco, R., 2022. Rhesus macaques compensate for reproductive delay following ecological adversity early in life. Ecol. Evol. 12, e8456. https://doi.org/10.1002/ece3.8456

Lummaa, V., Clutton-Brock, T., 2002. Early development, survival and reproduction in humans. Trends Ecol. Evol. 17, 141–147. https://doi.org/10.1016/S0169-5347(01)02414-4

MacArthur, R.H., Wilson, E.O., 2001. The Theory of Island Biogeography. Princeton University Press.

MacNulty, D.R., Smith, D.W., Mech, L.D., Eberly, L.E., 2009a. Body size and predatory performance in wolves: Is bigger better? J. Anim. Ecol. 78, 532–539.

MacNulty, D.R., Smith, D.W., Vucetich, J.A., Mech, L.D., Stahler, D.R., Packer, C., 2009b. Predatory senescence in ageing wolves. Ecol. Lett. 12, 1347–1356. https://doi.org/10.1111/j.1461-0248.2009.01385.x

Maestripieri, D., 2005. Effects of early experience on female behavioural and reproductive development in rhesus macaques. Proc. R. Soc. B Biol. Sci. 272, 1243–1248. https://doi.org/10.1098/rspb.2005.3059

Mahon, C.L., Pelech, S., 2021. Guidance for analytical methods to cumulative effects assessment for terrestrial species. Environ. Rev. 29, 201–224. https://doi.org/10.1139/ER-2020-0037

Maldonado-Chaparro, A.A., Martin, J.G.A., Armitage, K.B., Oli, M.K., Blumstein, D.T., 2015. Environmentally induced phenotypic variation in wild yellow-bellied marmots. J. Mammal. 96, 269–278. https://doi.org/10.1093/jmammal/gyu006

Martin, J.G.A., Festa-Bianchet, M., 2012. Determinants and consequences of age of primiparity in bighorn ewes. Oikos 121, 752–760. https://doi.org/10.1111/j.1600-0706.2011.19962.x

Mauss, D., Li, J., Schmidt, B., Angerer, P., Jarczok, M.N., 2015. Measuring allostatic load in the workforce: a systematic review. Ind. Health 53, 5–20. https://doi.org/10.2486/indhealth.2014-0122

McEwen, B.S., Wingfield, J.C., 2007. Allostasis and allostatic load. Encycl. Stress 135–141. https://doi.org/10.1016/B978-012373947-6.00025-8

McGillycuddy, M., Warton, D.I., Popovic, G., Bolker, B.M., 2025. Parsimoniously fitting large multivariate random effects in **glmmTMB**. J. Stat. Softw. 112. https://doi.org/10.18637/jss.v112.i01

McLoughlin, P.D., Gaillard, J.-M., Boyce, M.S., Bonenfant, C., Messier, F., Duncan, P., Delorme, D., Moorter, B.V., Saïd, S., Klein, F., 2007. Lifetime reproductive success and composition of the home range in a large herbivore. Ecology 88, 3192–3201. https://doi.org/10.1890/06-1974.1

Metcalfe, N.B., Monaghan, P., 2001. Compensation for a bad start: grow now, pay later? Trends Ecol. Evol. 16, 254–260. https://doi.org/10.1016/S0169-5347(01)02124-3

Monaghan, P., 2008. Early growth conditions, phenotypic development and environmental change. Philos. Trans. R. Soc. B Biol. Sci. 363, 1635–1645. https://doi.org/10.1098/rstb.2007.0011

Monclús, R., Blumstein, D.T., 2012. Litter sex composition affects life-history traits in yellow-bellied marmots. J. Anim. Ecol. 81, 80–86. https://doi.org/10.1111/j.1365-2656.2011.01888.x

Monclús, R., Pang, B., Blumstein, D.T., 2014. Yellow-bellied marmots do not compensate for a late start: The role of maternal allocation in shaping life-history trajectories. Evol. Ecol. 28, 721–733. https://doi.org/10.1007/s10682-014-9705-z

Morrison, R.E., Eckardt, W., Stoinski, T.S., Rosenbaum, S., 2023. Cumulative early-life adversity does not predict reduced adult longevity in wild gorillas. Curr. Biol. 33. https://doi.org/10.1016/j.cub.2023.04.051

Moyes, K., Morgan, B.J.T., Morris, A., Morris, S.J., Clutton-Brock, T.H., Coulson, T., 2009. Exploring individual quality in a wild population of red deer. J. Anim. Ecol. 78, 406–413.

Moyes, K., Nussey, D.H., Clements, M.N., Guinness, F.E., Morris, A., Morris, S., Pemberton, J.M., Kruuk, L.E.B., Clutton-Brock, T.H., 2011. Advancing breeding phenology in response to environmental change in a wild red deer population. Glob. Change Biol. 17, 2455–2469. https://doi.org/10.1111/j.1365-2486.2010.02382.x

Nettle, D., Bateson, M., 2015. Adaptive developmental plasticity: what is it, how can we recognize it and when can it evolve? https://doi.org/10.1098/rspb.2015.1005

Nettle, D., Frankenhuis, W.E., 2020. Life-history theory in psychology and evolutionary biology: one research programme or two? Philos. Trans. R. Soc. B Biol. Sci. 375, 20190490. https://doi.org/10.1098/rstb.2019.0490

Nettle, D., Frankenhuis, W.E., Rickard, I.J., 2013. The evolution of predictive adaptive responses in human life history. Proc. R. Soc. B Biol. Sci. 280, 20131343. https://doi.org/10.1098/rspb.2013.1343

Nussey, D.H., Kruuk, L.E.B., Morris, A., Clutton-Brock, T.H., 2007. Environmental conditions in early life influence ageing rates in a wild population of red deer. Curr. Biol. 17, R1000–R1001. https://doi.org/10.1016/j.cub.2007.10.005

Oli, M.K., Armitage, K.B., 2004. Yellow-bellied marmot population dynamics: demographic mechanisms of growth and decline. Ecology 85, 2446–2455. https://doi.org/10.1890/03-0513

Oli, M.K., Armitage, K.B., 2003. Sociality and individual fitness in yellow-bellied marmots: insights from a long-term study (1962-2001). Oecologia 136, 543–550. https://doi.org/10.1007/s00442-003-1291-7

Orr, J.A., Vinebrooke, R.D., Jackson, M.C., Kroeker, K.J., Kordas, R.L., Mantyka-Pringle, C., Van den Brink, P.J., De Laender, F., Stoks, R., Holmstrup, M., Matthaei, C.D., Monk, W.A., Penk, M.R., Leuzinger, S., Schäfer, R.B., Piggott, J.J., 2020. Towards a unified study of multiple stressors: divisions and common goals across research disciplines. Proc. R. Soc. B Biol. Sci. 287, 20200421. https://doi.org/10.1098/rspb.2020.0421

Ortiz-Ross, X., Blumstein, D.T., 2024. Cumulative adversity and survival in the wild. Ecol. Lett. 27. https://doi.org/10.1111/ele.14485

Ozgul, A., Childs, D.Z., Oli, M.K., Armitage, K.B., Blumstein, D.T., Olson, L.E., Tuljapurkar, S., Coulson, T., 2010. Coupled dynamics of body mass and population growth in response to environmental change. Nature 466, 482–485. https://doi.org/10.1038/nature09210

Patterson, S.K., Hinde, K., Bond, A.B., Trumble, B.C., Strum, S.C., Silk, J.B., 2021. Effects of early life adversity on maternal effort and glucocorticoids in wild olive baboons. Behav. Ecol. Sociobiol. 75, 114. https://doi.org/10.1007/s00265-021-03056-7

Patterson, S.K., Petersen, R.M., Brent, L.J.N., Snyder-Mackler, N., Lea, A.J., Higham, J.P., 2023. Natural animal populations as model systems for understanding early life adversity effects on aging. Integr. Comp. Biol. 63, 681–692. https://doi.org/10.1093/ICB/ICAD058

Petersen, R.M., Patterson, S.K., Widdig, A., Turcotte, C.M., Antón, S.C., Williams, S.A., Romero, A.N., Bauman Surratt, S.E., Ruiz-Lambides, A., Cayo Biobank Research Unit, Montague, M.J., Snyder-Mackler, N., Brent, L.J.N., Higham, J.P., Lea, A.J., 2026. Early-life adversity shapes the relationship between growth and reproduction in free-ranging female rhesus macaques. Proc. Natl. Acad. Sci. 123, e2524909123. https://doi.org/10.1073/pnas.2524909123

Petrullo, L., Delaney, D., Boutin, S., Lane, J.E., McAdam, A.G., Dantzer, B., 2024. A future food boom rescues the negative effects of early-life adversity on adult

lifespan in a small mammal. Proc. R. Soc. B Biol. Sci. 291, 20232681. https://doi.org/10.1098/rspb.2023.2681

Pianka, E.R., 1970. On r- and K-selection. Am. Nat. 104, 592–597. https://doi.org/10.1086/282697

Pigeon, G., Festa-Bianchet, M., Pelletier, F., 2017. Long-term fitness consequences of early environment in a long-lived ungulate. Proc. R. Soc. B Biol. Sci. https://doi.org/10.1098/rspb.2017.0222

Pigeon, G., Landes, J., Festa-Bianchet, M., Pelletier, F., 2021. Do early-life conditions drive variation in senescence of female bighorn sheep? Front. Cell Dev. Biol. 9. https://doi.org/10.3389/fcell.2021.637692

Pigeon, G., Pelletier, F., 2018. Direct and indirect effects of early-life environment on lifetime fitness of bighorn ewes. Proc. R. Soc. B Biol. Sci. 285, 20171935. https://doi.org/10.1098/rspb.2017.1935

Pirotta, E., Thomas, L., Costa, D.P., Hall, A.J., Harris, C.M., Harwood, J., Kraus, S.D., Miller, P.J.O., Moore, M.J., Photopoulou, T., Rolland, R.M., Schwacke, L., Simmons, S.E., Southall, B.L., Tyack, P.L., 2022. Understanding the combined effects of multiple stressors: A new perspective on a longstanding challenge. Sci. Total Environ. 821, 153322. https://doi.org/10.1016/J.SCITOTENV.2022.153322

Promislow, D.E.L., Harvey, P.H., 1990. Living fast and dying young: A comparative analysis of life-history variation among mammals. J. Zool. 220, 417–437. https://doi.org/10.1111/j.1469-7998.1990.tb04316.x

Réale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V., Montiglio, P.-O., 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. Philos. Trans. R. Soc. B Biol. Sci. 365, 4051–4063. https://doi.org/10.1098/rstb.2010.0208

Ricklefs, R.E., Wikelski, M., 2002. The physiology/life-history nexus. Trends Ecol. Evol. 17, 462–468. https://doi.org/10.1016/S0169-5347(02)02578-8

Roff, D.A., 1992. The evolution of life histories: theory and analysis. Chapman & Hall, New York London.

Rosenbaum, S., Malani, A., Lea, A.J., Tung, J., Alberts, S.C., Archie, E.A., 2025. Testing early life effects frameworks: developmental constraints and adaptive

response hypotheses do not explain fertility outcomes in wild female baboons. Proc. R. Soc. B Biol. Sci. 292, 20242485. https://doi.org/10.1098/rspb.2024.2485

Rutter, M., 1983. Statistical and personal interactions: Facets and perspectives, in: Magnusson, D., Vernon L., A. (Eds.), Human Development: An Interactional Perspective. Academic Press, New York, pp. 295–319.

Schwartz, O.A., Armitage, K.B., 2005. Weather influences on demography of the yellow-bellied marmot (*Marmota flaviventris*). J. Zool. 265, 73–79. https://doi.org/10.1017/S0952836904006089

Schwartz, O.A., Armitage, K.B., Van Vuren, D., 1998. A 32-year demography of yellow-bellied marmots (*Marmota flaviventris*). J. Zool. 246, 337–346. https://doi.org/10.1111/j.1469-7998.1998.tb00163.x

Seeman, T., Epel, E., Gruenewald, T., Karlamangla, A., Mcewen, B.S., 2010. Socio-economic differentials in peripheral biology: Cumulative allostatic load. Ann. N. Y. Acad. Sci. 1186, 223–239. https://doi.org/10.1111/j.1749-6632.2009.05341.x

Shivani, Malaivijitnond, S., Meesawat, S., Schülke, O., Ostner, J., 2025. Females prioritize future over current offspring in wild seasonally breeding Assamese macaques. Proc. R. Soc. B Biol. Sci. 292, 20250024. https://doi.org/10.1098/rspb.2025.0024

Spagopoulou, F., Teplitsky, C., Chantepie, S., Lind, M.I., Gustafsson, L., Maklakov, A.A., 2020. Silver-spoon upbringing improves early-life fitness but promotes reproductive ageing in a wild bird. Ecol. Lett. 23, 994–1002. https://doi.org/10.1111/ele.13501

Stearns, S.C., 2000. Life history evolution: successes, limitations, and prospects. Naturwissenschaften 87, 476–486. https://doi.org/10.1007/s001140050763

Stearns, S.C., 1992. The evolution of life histories. Oxford University Press, Oxford.

Stearns, S.C., 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. Oikos 41, 173–187. https://doi.org/10.2307/3544261

Stewart, J.A., 2006. The detrimental effects of allostasis: Allostatic load as a measure of cumulative stress. J. Physiol. Anthropol. 25, 133–145. https://doi.org/10.2114/jpa2.25.133

Taborsky, B., 2006. The influence of juvenile and adult environments on life-history trajectories. Proc. R. Soc. B Biol. Sci. 273, 741–750. https://doi.org/10.1098/rspb.2005.3347

Tamian, A., Viblanc, V.A., Dobson, F.S., Saraux, C., 2024. Population density and vegetation resources influence demography in a hibernating herbivorous mammal. Oecologia 205, 497–513. https://doi.org/10.1007/s00442-024-05583-2

Tung, J., Archie, E.A., Altmann, J., Alberts, S.C., 2016. Cumulative early life adversity predicts longevity in wild baboons. Nat. Commun. 7, 1–7. https://doi.org/10.1038/ncomms11181

Tyack, P.L., Thomas, L., Costa, D.P., Hall, A.J., Harris, C.M., Harwood, J., Kraus, S.D., Miller, P.J.O., Moore, M., Photopoulou, T., Pirotta, E., Rolland, R.M., Schwacke, L.H., Simmons, S.E., Southall, B.L., 2022. Managing the effects of multiple stressors on wildlife populations in their ecosystems: developing a cumulative risk approach. Proc. R. Soc. B Biol. Sci. 289, 2–15. https://doi.org/10.1098/rspb.2022.2058

van de Crommenacker, J., Hammers, M., Dugdale, H.L., Burke, T.A., Komdeur, J., Richardson, D.S., 2022. Early-life conditions impact juvenile telomere length, but do not predict later life-history strategies or fitness in a wild vertebrate. Ecol. Evol. 12, e8971. https://doi.org/10.1002/ece3.8971

van Noordwijk, A.J., de Jong, G., 1986. Acquisition and allocation of resources: Their influence on variation in life history tactics. Am. Nat. 128, 137–142.

Van Vuren, D., Armitage, K.B., 1991. Duration of snow cover and its influence on life-history variation in yellow-bellied marmots. Can. J. Zool. 69, 1755–1758. https://doi.org/10.1139/z91-244

Van Vuren, D.H., Armitage, K.B., 1994. Reproductive success of colonial and noncolonial female yellow-bellied marmots (*Marmota flaviventris*). J. Mammal. 75, 950–955.

Vasilieva, N.A., Tchabovsky, A.V., 2020. Early predictors of female lifetime reproductive success in a solitary hibernator: evidence for “silver spoon” effect. Oecologia 193, 77–87. https://doi.org/10.1007/s00442-020-04649-1

Weibel, C.J., Tung, J., Alberts, S.C., Archie, E.A., 2020. Accelerated reproduction is not an adaptive response to early-life adversity in wild baboons. Proc. Natl. Acad. Sci. 117, 24909–24919. https://doi.org/10.1073/pnas.2004018117

West-Eberhard, M., 2003. Developmental plasticity and evolution. Oxford University Press.

Wikelski, M., Spinney, L., Schelsky, W., Scheuerlein, A., Gwinner, E., 2003. Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. Proc. R. Soc. Lond. B Biol. Sci. 270, 2383–2388. https://doi.org/10.1098/rspb.2003.2500

Williams, G.C., 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am. Nat. 100, 687–690. https://doi.org/10.1086/282461