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LETTER

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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

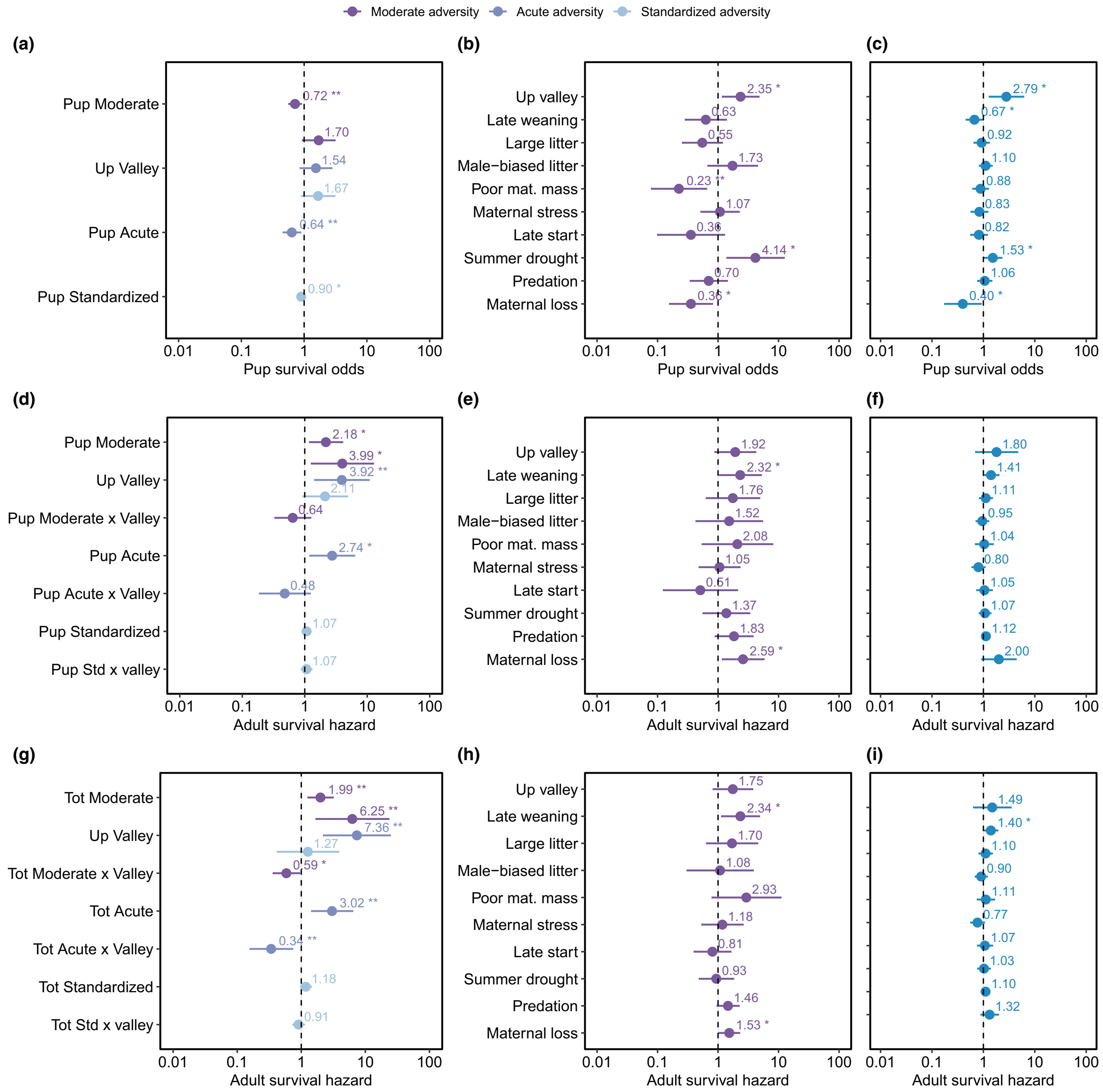

FIGURE 1 (a) Results of our pup survival models, the figure includes all three models (moderate CAI, acute CAI, and standardized CAI) and the fixed effect of valley (up and down). The pup survival odds ratio represents the odds of survival to year 1, therefore an increase in odds ratio represents increased 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.

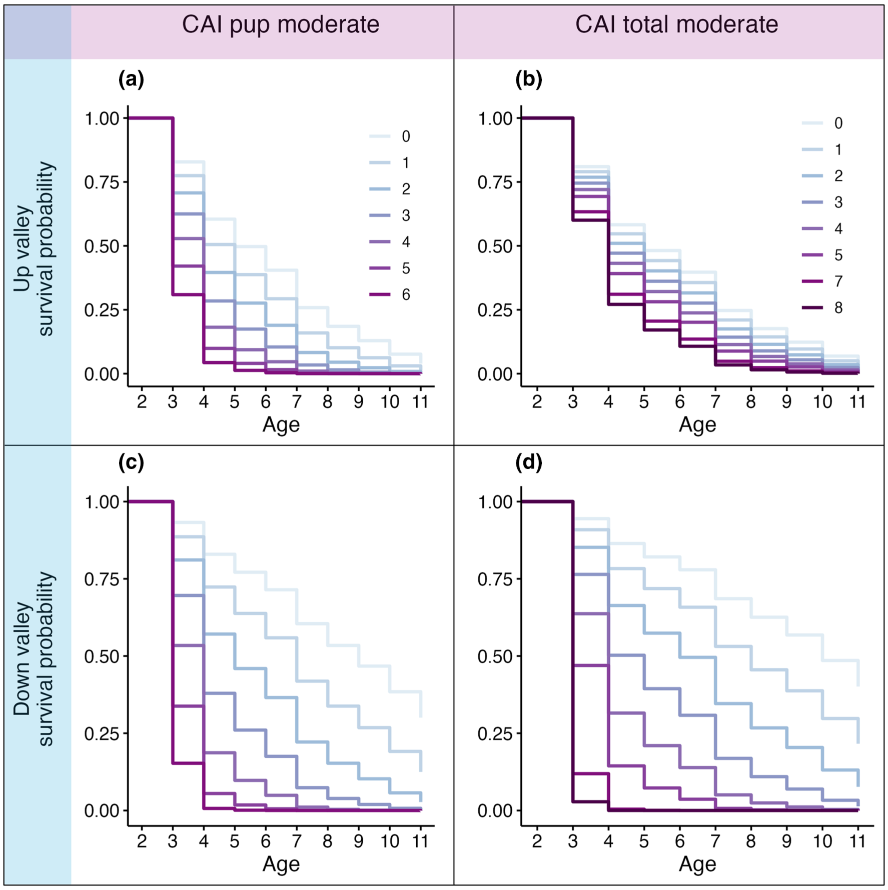

FIGURE 2 Survival probability under low predation up valley (a, b) and down valley (c, d) for each CAI moderate pup adversity (a, c) and each CAI moderate total adversity (b, d). Valley was included as a fixed effect to account for site differences due to elevation. Colonies up-valley tend to experience 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 up-valley 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 ($\Delta > 10$) 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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SUPPORTING INFORMATION

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

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