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**OVERWINTER SURVIVAL IN ALPINE IBEX: EFFECTS OF THE ENVIRONMENT AND  
OF INDIVIDUAL CONDITIONS**

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## RIASSUNTO

La sopravvivenza influisce sulle dinamiche di popolazione e sui cicli vitali; la sopravvivenza delle specie che vivono in habitat stagionali, come gli ungulati delle zone temperate, può essere fortemente influenzata dalle condizioni ambientali stagionali e dalla variabilità climatica. Inoltre, le dinamiche di popolazione degli ungulati sono determinate dalle differenze specifiche per età e sesso in diversi tratti della storia di vita delle specie, tra cui la condizione fisica degli individui.

Nel presente studio abbiamo analizzato quali variabili intrinseche e ambientali hanno maggiormente influenzato la sopravvivenza invernale in una popolazione di stambecchi. In particolare, abbiamo concentrato lo studio su individui marcati nell'ambito del progetto di monitoraggio a lungo termine attualmente condotto nel Parco Nazionale del Gran Paradiso. Abbiamo evidenziato un andamento della sopravvivenza fortemente strutturato in base all'età. In entrambi i sessi, abbiamo osservato tassi di sopravvivenza più elevati nei giovani, a partire dai 3 anni di età, un graduale declino durante l'età adulta e una marcata e improvvisa diminuzione nelle età avanzate. Nella popolazione esaminata, le probabilità di sopravvivenza invernale sono risultate favorite da specifiche condizioni meteorologiche e ambientali, in particolare temperature minime invernali più elevate e periodi nevosi e vegetativi più lunghi. Questi fattori migliorano le condizioni fisiche individuali e l'apporto nutrizionale, riducendo il dispendio energetico durante l'inverno e favorendo uno scioglimento più rapido della neve e la disponibilità anticipata di foraggio di alta qualità. I maschi della popolazione studiata sono stati pesati ripetutamente durante le stagioni estive tra il 2000 e il 2024. La massa corporea autunnale, ovvero la quantità di riserve di grasso con cui gli animali arrivano all'inverno, ha favorito i tassi di sopravvivenza, riducendo il rischio di mortalità durante l'inverno. Questo effetto positivo sulla sopravvivenza è stato osservato in modo differenziale in diverse classi di età. I giovani e i subadulti hanno dimostrato di trarre maggiori benefici da una maggiore massa corporea prima del periodo invernale, mentre gli adulti e gli anziani non hanno mostrato alcun vantaggio significativo da una maggiore dimensione corporea.

Sebbene sia nota da tempo la relazione tra condizioni ambientali e sopravvivenza negli ungulati, il ruolo combinato dei fattori climatici e della condizione fisica non è stato ancora indagato a fondo nei maschi di stambecco. L'integrazione delle variabili ambientali individuali e stagionali può essere efficace per identificare quali condizioni contribuiscono a un più alto rischio di mortalità negli stambecchi di diverso sesso ed età. I nostri risultati potrebbero rappresentare un importante contributo per una migliore comprensione delle influenze dei cambiamenti climatici sulla dinamica della popolazione dello stambecco e potrebbero avere un'applicazione rilevante ai fini della conservazione della specie.

## **ABSTRACT**

Survival affects population dynamics and life histories; survival of seasonal habitats' taxa, such as temperate ungulates, can be strongly influenced by seasonal environmental conditions and climate variability. Furthermore, ungulates population dynamics are shaped by age and sex-specific differences in several life-history traits, including individuals' body condition.

In the present study we analysed which intrinsic and environmental variables most influenced survival during winter in a population of Alpine ibex. Specifically, we focused our study on marked individuals in the framework of the long-term monitoring project currently conducted in the Gran Paradiso National Park. In the study population, we highlighted a strong age-structured survival pattern. In both sexes, we observed higher survival rates in juveniles, from the age of 4, a gradual decline during adulthood, and a marked and sudden decrease at older ages. In the population examined, overwinter survival probabilities resulted increased by specific meteorological and environmental conditions, in particular, higher minimum winter temperatures during winter and longer snowy and vegetative growing periods. These factors enhance the individual body condition and nutritional intake by reducing energetic costs of thermoregulation during winter by providing a faster snowmelt and an earlier high-quality forage availability. Males of the study population were weighted repeatedly during summer between 2000 and 2024. The autumn body mass, with which animals enter the winter season, reflects the amount of fat reserves accumulated and it increased survival rates, ultimately decreasing overwinter mortality risk. This positive effect on survival was differentially showed in males of different age classes. Juveniles and sub-adults proved to benefit more from a greater body mass before the winter period, while adults and senescent individuals showed no strong advantage from a larger body size.

A relationship between environmental conditions and survival of temperate ungulates has long been recognized, but the possible role of combined effects of external factors with individuals body conditions has not been explored yet, especially in male Alpine ibex, and could improve our knowledge on which potential limiting factors are most influential.

Integrating individual and seasonal environmental variables may be particularly effective in identifying which specific condition contribute to higher mortality risk in Alpine ibex across different sexes and age classes. Our results could represent an effective contribute to a better understanding of climate change influences on Alpine ibex population dynamic and could have also a relevant application for the conservation of the species.

# 1. INTRODUCTION

## *1.1 Life history and survival in wild vertebrates*

Survival is a fundamental component of population dynamics and life histories across all taxa and habitats. In wild animals it is shaped by a range of intrinsic (age, sex, health status and physical conditions) and extrinsic (predation, resource availability, population density and environmental conditions) factors.

Individual physical condition depends on environmental characteristics, individual health and behavioural adaptations (e.g. seasonal migration, thermoregulation and body reserves accumulation), and can vary across ages and between sexes. Age and sex-specific variations in survival determine the evolution of mammalian life-history strategies and has direct effects on population dynamics and size (Partridge and Harvey 1988; Garrott 1991; Stearns 2000).

In large vertebrates, population growth rate is more sensitive to adult survival than to any other demographic factor, as adult survival rates are higher and most of the individuals in a population are adults. (Gaillard et al. 1998, 2000; Coulson et al. 2005). Survival is expected to depend by age even though the relationship between age and survival is not always linear and some age classes may be more vulnerable to some factors than others (e.g., young individuals may be more subject to predation than adults). In general, however, in long-lived iteroparous vertebrates, survival typically increases during early life, depending mostly on maternal care, stabilises at prime age and then declines during senescence (age-related mortality) (Caughley 1966; Clutton-Brock 1988; Gaillard et al. 2000). Senescence has been documented in both domestic and natural populations, and manifests itself with a deterioration in individual physical conditions and fitness associated with an increase in mortality risk. Age-specific mortality in mammals may increase due to the physiological and physical decline, that can be exacerbated by other factors such as variabilities in climate, density and behaviour (Abrams 1991; Promislow 1991; Gaillard et al. 1994). Those other external factors as well as others (such as predation, diseases, food availability, social rank and climate variations) may indeed have strong influence on animal survival so that only few individuals reach an age susceptible to senescence (Loison et al. 1999b).

Also, across animal species, a sex-dependent variability in survival can occur. This has been explained in several works by various factors, such as the different genetic sex determination system and also the different reproductive effort between sexes. In fact, in numerous bird species, higher adult mortality has been associated to the heterogametic sex and to the sex that holds the higher costs of parental care, which in birds is the female in both cases. While in mammals, males represent the heterogametic sex and generally suffers higher mortality related to their competition during the

breeding period (Clutton-Brock and Vincent 1991; Liker and Székely 2005; Payevsky 2021). Generally, in most mammals, especially in highly polygynous and sexually dimorphic species, males are expected to exhibit lower survival rates and shorter lifespan, while females adopt a conservative approach to favour their own survival, ensuring future reproduction (Gaillard et al. 1998, 2000).

Variations in individual condition and lifespan are also associated with several ecological and population-dynamic factors, including body conditions (Peters 1983), population density (Clutton-Brock et al. 1992), evolutionary history (Harvey and Pagel 1991) and general ecological context (Calder 1984). For example, in some ungulates, the population size directly affects resource competition during favourable periods, influencing body mass and consequently the mortality risk during the adverse season (as seen in Soay sheep lambs, *Ovis aries*; Clutton-Brock 1992).

Survival in large herbivores is known to be influenced by environmental conditions associated to forage availability and this impact can vary across different sexes and ages (Gaillard 2000; Toïgo and Gaillard 2003; Bonenfant et al. 2009). In relation to the ecological context, males have been found more vulnerable than females to weather severity and, hence, forage shortage, and this is likely due to a higher energetic requirement (Clutton-Brock 1982; Gaillard et al. 1993; Jorgenson et al. 1997; Festa-Bianchet et al. 2003). Also, coherently with Caughley's (1966) pattern of age-dependent survival, environmental variations were proven to differently affect fitness in different ages: survival of adult large herbivores tends to be less sensitive to environmental fluctuations compared to that of juvenile or senescent individuals (as seen by Jorgenson et al. (1997) on bighorn sheep *Ovis canadensis*; by Gaillard et al. (2000, 2003) on different ungulate populations; by Bergeron et al. (2022) on eastern grey kangaroo *Macropus giganteus*; by Toïgo et al. (2007) on Alpine ibex *Capra ibex*).

Differences in mortality rates among capital breeders (i.e., species that rely on resources previously accumulated for reproductive investment and survival) can also result from the balance between reproductive effort and survival, mainly through a temporal separation between the time of energy gain and reproduction investment (Jönsson 1997). Life-history theories predict that mature individuals must allocate limited energy either to physiological maintenance, such as accumulating body reserves that enhance survival under harsh environmental conditions, or to reproduction. This creates a trade-off, particularly strong in seasonal environments, where resource scarcity and high population density can constrain reproductive effort and increase immediate mortality risks. In addition, population density can intensify this trade-off between body growth and reproduction, particularly in females, delaying the age of primiparity and often increasing the costs of reproduction, ultimately decreasing both survival and future reproductive success (Gaillard et al. 1998; Stearns 2000, Bonenfant et al. 2009). In many temperate or migratory taxa, including ungulates, the periods

of reserve accumulation and reproduction overlap so, to withstand the nutritional, and demographic, bottleneck that occurs during winter, individuals must calibrate their reproductive investment according to their body condition (Monteith et al. 2013; Ortega et al. 2022).

### *1.2 Survival in mountain ungulates*

Ungulates are considered particularly suitable for the investigation of survival and senescence since different species may vary significantly in life-history traits, mating system (Jarman 1983), fecundity (Bunnell 1987), and body size (Peters 1983). Also, large herbivorous mammals are highly appropriate species for demographic analysis because age classes are easily identifiable, and populations are strongly age-structured (Gaillard et al. 1998; Festa-Bianchet et al. 2003).

Survival in ungulates is strongly affected by age (Festa-Bianchet et al. 2003), as demonstrated in several works. For example, Loison et al. (1999b) provided strong evidence for the effects of senescence on survival rates, showing that survival decreased with age for both sexes in five wild ungulate populations, and underlined the deviation of senescence patterns among sexes, populations, and species. This age-dependent influence on survival allowed the identification of three main age-specific stages commonly recognized in mammalian survival dynamics: a juvenile stage, marked by highly variable survival; a prime-age adult stage, during which survival reaches its peak and remains relatively stable despite environmental variability; and a senescent stage, characterized by a decline in survival (Caughley 1966; Gaillard et al. 2000; Toïgo et al. 2007).

Ungulates populations show patterns coherent with this dynamic: because population growth rate is mainly sensitive to adult survival, high and stable survival rates of prime-aged adults minimize demographic risks and support population persistence, while newborn and yearling survival is generally lower and shows a stronger yearly variability (Clutton-Brock et al. 1982; Gaillard et al. 2000, 2003; Toïgo et al. 2007). Ungulates generally exhibit long generation times and growth rates, which means that changes in adult survival have a greater impact on population growth than equivalent changes in juvenile survival or reproduction rates (Gaillard 1998; 2000).

In most large ungulates, another factor influencing sex-specific differences in survival is sexual dimorphism. Males are larger than females and therefore, they have higher energy requirement. For this, they may be exposed to greater mortality during periods of resource scarcity (Clutton-Brock et al. 1985). In addition, social rank and mating competition introduce additional pressures that can influence negatively survival, particularly among males, whose survival is usually lower at all ages (as shown, for example, by Clutton-Brock et al. (1982) on red deer *Cervus elaphus*; Jorgenson et al. (1997) on bighorn sheep; Modafferi and Becker (1997) on moose *Alces alces*) and especially if the rut occurs during the unfavourable season. As a consequence, during unfavourable climatic seasons,

male survival is often more variable at all ages, typically lower, than female survival, as the latter remains relatively stable to maximize lifetime reproductive success (Clutton-Brock et al. 1982; Gaillard et al. 1993, 2000; Jorgenson 1997). For female ungulates living in temperate environments, the most energetically demanding period occurs from early spring to mid-summer, during late pregnancy and lactation, whereas for males it is the rut, occurring typically in late autumn and early winter, when food availability is already declining (Myserud et al. 2004; Parker et al. 2009). As a result, when resources are scarce, males usually lose more mass over winter (Apollonio et al. 2020) and allocate much of their resource to mating efforts, experiencing higher winter mortality (Barrett 1982). For instance, in female ungulates, during periods of resource scarcity and difficult environmental conditions, it has been observed a reduction in parental care to ensure their own overwinter survival and summer mass gain over their offspring's fat accumulation and, hence, survival. Consequently, female survival and mortality rates should remain more stable across different environmental conditions, as observed on bighorn sheep by Festa-Bianchet and Jorgenson (1998) and by Gaillard et al. (1998, 2000); on reindeer *Rangifer tarandus* by Simmonds et al. (2025). As for males' survival rates, Toïgo and Gaillard (2003) analysed survival data from several ungulate species and observed that males consistently showed lower survival rates than females during the adverse season. Their results highlighted that the main cause of this sex-biased survival is the environmental context, especially the severity of conditions and the degree of resource scarcity affecting the winter period, during which, reproductive effort is mainly concentrated and intra-sexual competition occurs, often resulting in direct injuries and increased energetic costs that ultimately diminish survival (Clutton-Brock et al. 1982; Clutton-Brock and Vincent 1991; Garrott 1991). Early studies linked rising male mortality in wild sheep to reproductive reasons, specifically to rut participation after 6–8 years of age (Hansen 1980). More recent research, however, suggest that younger males may as well engage in reproductive activities, as observed by Hogg (1987) on bighorn sheep, by Singer et al. (1991) on Dall sheep (*Ovis dalli*) or by Willis and Neuhaus (2009) on Alpine ibex, with the evolution of an alternative highly energy-demanding behaviour, the “coursing” tactic, mostly used by young Alpine ibex to access reproduction avoiding direct competition with larger dominant males. Understanding the age at which males first participate in the rut is therefore essential to explore patterns of age-dependent mortality among males.

### *1.3 Effects of seasonality on survival*

Climate affects population dynamics both directly, by influencing population survival rates, and indirectly through long-term changes in the individual life history (Bårdsen et al. 2011).

In seasonal environments, such as high-latitudes or mountainous areas, the main impacting factor is the seasonal climatic variability, that typically include the alternation between favourable springs and summers and harsh conditions during winters, including heavy snowfall and low temperatures, that can significantly affect food availability, the energetic costs of thermoregulation and acclimatization, leading to variations of survival rates. Animals living in these habitats experience a short plant-growing season for both reproduction and resource accumulation before the long and demanding winter season (Mautz 1978; Gaillard et al. 2000; 2003).

Most temperate and high latitudes mammals face seasonal periods of resource scarcity and stochastic meteorological changes, that affect body condition and survival. Several physiological and morphological adaptations are required and employed by these species, using thermoregulatory responses aimed at stabilizing body temperature and reducing energy consumption: large mammals' adaptations comprehend seasonal migration, reserves accumulation and reduced vital functions; in small mammals, such as rodents, hibernation and retreating to underground burrows can occur. However, seasonal acclimatization may correspond to a greater need for energy during a period of reduced availability of food and resources (Heldmaier 1989; Lovegrove 2005; Signer et al. 2011).

Variability of ecological factors can shape survival and reproduction in temperate ungulates: during the cold season the resources are limited, and individuals must adjust reproductive effort to promote survival over reproductive success (Gaillard et al. 1998; Stearns 2000; Pettorelli et al. 2007).

Winter severity (e.g., snow depth and temperature) strongly influences the energy balance of ungulates. The duration of snow cover determines how long individuals must endure a negative energy budget, while the fat reserves accumulated during previous foraging seasons define the amount of energy that can be consumed before mortality occurs due to resource scarcity or other causes associated with weakened body condition (Parker et al. 2009). Likewise, conditions during the favourable season are crucial for resource acquisition to ensure future survival but also, mostly in the case of females, to ensure successful reproduction and weaning. The biological cycles of species are indeed aligned with other ecological processes and, consequently, environmental changes and climatic variability can modify the timing of biological events, such as the correspondence of births and the peak availability of high-quality vegetation (Post et al. 2007; Both et al. 2009).

Alpine ecosystems have been facing rapid climate and environmental changes. Winter weather events include more often conditions such as unusually mild temperatures (Rebetez and Reinhard 2008) and reduced snowfalls (Gottlieb and Mankin 2024). Warmer springs and reduced snow cover influence

plant growth (Wang et al. 2020), thereby altering both the quantity and timing of resources available to herbivores (Pettorelli et al. 2007). In these ecosystems, the timing of spring vegetation emergence, largely driven by snowmelt, plays a key role in shaping the life-history strategies of ungulates (Rutberg 1987). Mountain ungulates rely on grasslands as their main food resource, and the spatial and temporal variability of vegetation strongly influences their annual survival: changes in vegetation phenology and forage quality, through its effect on body mass variation, can reduce survival rates, particularly among juvenile, ultimately decreasing recruitment (Pettorelli et al 2007; Garel 2011). These effects are especially pronounced in highly seasonal environments such as the Alps, where strong temporal and spatial fluctuations define foraging conditions throughout the year. In such regions, the nutritional quality of forage is highest during the early phenological stages, when newly emerged green leaves dominate the biomass (Crawley 1983). The onset and duration of this favourable period mainly depend on winter and spring weather conditions, particularly on temperature and precipitation patterns. These conditions, based on biological cycle, may have both positive and negative, direct and indirect, influence on animals' performance. Early and favourable spring conditions generally are expected to enhance the performance and survival of ungulates by providing milder temperatures and earlier access to high-quality forage. At the same, time this early availability access may shortens the time window during which individuals can exploit nutrient-rich forage, especially in the newborns. Conversely, snowy winters and late springs snowfall tend to delay the onset of spring and may therefore prolong the green-up period by slowing vegetation maturation, especially at higher elevations (Pettorelli et al. 2005, 2007; Brambilla et al. 2024).

#### *1.4 Body conditions in large vertebrates: causes and consequences on life-history traits*

Body condition depends on the relationship between an animal's food consumption and its nutritional demands and affect fitness components, such as survival and reproduction. In wild vertebrates, body mass loss in old age classes is a good predictor of senescence declines in survival and reproductive performance (Brunet-Rossinni and Austad 2006; Parker et al. 2009). Nussey et al. (2011) found interesting results analysing age-related variations in body mass of females in three ungulate populations: bighorn sheep, roe deer (*Capreolus capreolus*) and Soay sheep. All three species exhibited evidence of body mass senescence through time: in particular, bighorn and roe deer showed a gradual and accelerating decline in body mass with increasing age, while the Soay sheep displayed a sudden, terminal decline in the few years preceding death. In all species, lighter individuals had lower survival rates and heavier females tended to live longer. Despite the divergent patterns observed across these species, this study is particularly significant as it emphasizes the central role of age-related body mass loss, indicating that body mass is an important predictor of longevity and fitness-related traits.

Body mass reflects physiological condition and skeletal structure but also variations in muscle and fat reserves. In temperate environments, all these variables can be shaped by distinct selective pressures, such as the quality of forage, climatic conditions and density-dependent competition for food (Dobson 1992; Toïgo et al. 2006) and reproduction. For instance, the body mass of mountain goat kids (*Oreamnos americanus*) increased during lactation with a good quality diet of mothers (Côté and Festa-Bianchet 2001) and forage summer availability influenced the autumn body mass of moose calves (Ericsson et al. 2002).

Animals in good physiological condition accumulate adequate fat reserves during the favourable season to withstand the resource-limited winter period. Well-nourished individuals also exhibit a superior resistance to bacterial and parasitic infections and generally achieve greater reproductive success (Tataruch et al. 1996). The deposition and use of body fat vary according to physiological needs and environmental conditions, as species rely on both food intake and body reserves to balance the gains of summer with the energetic demands of winter. Individuals with access to high-quality nutritional resources typically achieve larger body sizes and better condition than those with limited nutrition, with consequent effects on survival and reproduction. Body mass is an indicator of individual quality but is also directly and indirectly influenced by environmental conditions and resource availability (Parker et al. 2009; Simmonds et al. 2025).

Body fat reserves are especially relevant in capital breeding species that suppress feeding and rely on previously accumulated fat reserves and depend on stored energy to sustain reproductive investment and survival. By contrast, income breeders continue collect resources during the reproduction period

(Jönsson 1997; Apollonio et al. 2020). In polygynous mammalian mating systems, male reproductive success is closely associated with the energy invested in intra-sexual competition. In these systems, the primary reproductive costs for males are expected to be the mate acquisition and reproduction. This competitive pressure is likely to reduce feeding activity, leading to the capital breeding strategy in highly polygynous species. By contrast, in systems with lower polygyny and limited competition, males can maintain regular feeding patterns, consistent with an income breeding strategy (Clutton-Brock 1989; Apollonio et al. 2020). The degree of polygyny influences the intensity of male intrasexual selection but also the amount of energy that must be accumulated in advance, and consequently shapes different male investment strategies: in capital breeders (with high level of polygyny and intrasexual competition, e.g., red deer and Alpine chamois *Rupicapra rupicapra*), males invest heavily in reproduction, and those with different initial body conditions lose weight at different rates (Apollonio et al. 2020). This leads to high variability in body condition during or immediately after the rut, suggesting that males calibrate their reproductive effort based on their body condition, as also observed in other ungulate species (Ortega et al. 2022). In income breeders (low level of polygyny and male-male competition, e.g., roe deer), the energy spent on reproduction is lower, and males maintain more consistent body mass before and after the rut. Therefore, in this case, variability in body mass among males remains minimal, reflecting inferior dependency on stored reserves and lower energy expenditure during the rut period (Apollonio et al. 2020).

In species whose mating period occur late in fall or at the beginning of winter, feeding suppression during the breeding season is an unfavourable phenomenon for the animals' fitness, as they enter the adverse season in poor body conditions and they could result more susceptible to death from predation, disease or starvation (Pelletier et al. 2005, 2009). Rut-induced hypophagia has been observed in a series of ruminant species, such as red deer (Clutton-Brock et al. 1982; Myrsterud et al. 2008), bighorn sheep (Pelletier 2005), Alpine chamois (Willisch and Ingold 2007) and mountain goat (Mainguy and Côté 2008). Adult males of highly polygynous ungulate species represent the age class in which hypophagia is most pronounced: in fact, prime-aged (sexually and socially mature) males deplete nearly all their fat reserves within a few weeks of the autumn rut, whereas younger and still-growing males exhibit a markedly smaller reduction in stored energy reserves consumption. This age-dependent variation in body mass loss is caused by a corresponding age-related decline in feeding activity during the rut (Myrsterud et al. 2004): adult males typically experience the greatest loss of body mass during the rut, whereas younger and socially immature males exhibit a more limited decline (Alpine chamois: Mason et al. 2011; moose: Myrsterud et al. 2005); this pattern may reflect the lower immediate reproductive opportunities for younger males when competing with older and larger individuals, leading them to prioritize growth to enhance future reproductive success (Brivio

et al. 2010; Mainguy and Côté 2008; Mysterud et al. 2003). Specifically, in the Alpine ibex, it has been observed that older males (>11 years) decrease food intake during the rut by 42%, while younger males exhibited a more moderate reduction of around 24% (Brivio et al. 2010).

Brivio et al. (2010) suggested five hypotheses to explain the phenomenon of temporary hypophagia: during the rut, males reallocate time typically devoted to feeding and resting toward mating activities (“foraging constraint hypothesis”; Pelletier et al. 2009); males cease feeding to conserve energy, particularly when forage quality is poor and the energetic cost of foraging outweighs its benefits (“energy-saving hypothesis”; Willisch and Ingold 2007); males reduce feeding time to recover physically and restore muscle energy, enabling them to sustain the intense reproductive activities (“physical rest hypothesis”; Mysterud et al. 2008); reduced feeding may be associated with scent-urination behaviour that suppresses appetite and aids reproduction (“physiological hypothesis”; Apollonio and Di Vittorio 2004); suppressed appetite may represent a trade-off between reproduction and immune defence (“parasite hypothesis”; Mysterud et al. 2008). This study allowed a full correspondence only between the first hypothesis (the “foraging constraint hypothesis”) and the specific case of the Alpine ibex, revealing only a partial reduction in foraging activity for this species, with males still foraging for 30–39% of daylight hours. These findings highlight the limits of a strict separation between energy acquisition and reproductive investment.

Regardless of the reason why ibex do not feed during winter, the accumulation of reserves during the preceding summer is crucial for this species both for reproduction success and winter survival. Only few studies have directly measured the effect of body condition on winter survival in capital breeder species: Kautz et al. (2020) found a weak effect of body mass on survival rates in females of white-tailed deer, while Parker et al. (2009) used a simulation model to assess the percentage body fat’s impact on winter survival in females of reindeer. However, no previous work of this kind has been conducted on male Alpine ibex yet.

A recent study (Brambilla et al. 2024) has shown that, male Alpine ibex, a capital breeder inhabiting the European Alps, in the last year tended to enter the new favourable growing season without fully depleting the body reserves accumulated during the previous summer. This reduced winter mass loss is primarily associated with spring resource availability, which is influenced by winter and spring meteorological conditions. In particular, the earlier onset of spring proved to be a key factor, as it mitigates the influence of snow conditions (e.g., snow depth and duration of snow cover) on survival. This study also revealed that male Alpine ibex in the study population, due to this reduced body mass loss, are now substantially heavier than they were two decades ago, with some age classes showing increases of up to 10 kg, corresponding to approximately 15%. Similar patterns have been noticed in other ungulates: Douhard et al. (2018) observed that in female bighorn sheep, changes in body mass

across seasons, particularly the winter loss and summer gain, are mainly affected by spring temperature trends. These studies ultimately evidenced that seasonal fluctuations in body mass among mountain ungulates are strongly influenced by seasonality and plant phenology, both affecting the forage quality, and more in general, by environmental conditions (Pettorelli et al. 2007; Brambilla et al. 2024).

Variation in body mass can provide important insights into individual fitness, energetic strategies, and population dynamics across vertebrate species (Toïgo et al. 2006). Although this relationship may vary across species, age classes and ecological context, a large body size in mammals is generally associated to higher survival probabilities and reproductive success (Stearns 2000). Autumn body condition is one of the strongest predictors of overwinter survival, especially for ungulates in seasonal habitats that mostly rely on the accumulated fat reserves to survive the winter season. In juveniles this is particularly emphasized, as the body size achieved early in life often determines also adult body size, primiparity and reproductive success (Loison et al. 1999a). A survival advantage for individuals with larger body mass has been assessed in ungulate populations with winter nutritional deficits such as red deer (Loison et al. 1999a) white-tailed deer (*Odocoileus virginianus*; Kautz et al. 2020) and bighorn sheep (Festa-Bianchet et al. 1997). Most of these studies in polygynous ungulates living in seasonal environments, however, have been conducted on females while less is known about the effect of body conditions on survival of males. Considering the higher reproductive cost experienced during winter by male mountain ungulates, the effect of their body conditions on overwinter survival is expected to be substantial. Nevertheless, not many studies have investigated the factors affecting survival in male ungulates. Despite changes in survival of females may have a greater impact on population dynamic of polygynous species, males' survival can also have profound effects on age-structure and life history of ungulate populations. The factors affecting survival in male ungulates should therefore be better understood.

### 1.5 Survival analysis

Due to its importance in population dynamic in wild species but mostly due to human-related implications, lot of research has been done on statistical tools to analyse survival patterns. Survival analysis is currently mostly used in medical studies (Ayele et al. 2017; Alomaish et al. 2021) but can also be applied to ecological studies (on white-tailed deer: DelGiudice et al. 2002; on red deer: Frair et al. 2007; on roe deer: Gehr et al. 2020).

Survival analysis is based on a range of statistical techniques designed to model the time passed until the occurrence of a particular event, such as death, commonly termed as “failure time”. The survival time represents the period during which an individual remains alive within the study’s follow-up interval. The hazard represents the risk of an event occurring and the hazard function  $h(t)$  describes the instantaneous rate at which the event occurs at time  $t$ . Formally, it represents the probability that an individual experiences the event in a small-time interval, given that they have survived to the beginning of that interval. The primary goal of survival analysis is to estimate and interpret the survival and hazard functions, while accounting for censoring and incorporating the effects of covariates.

The Cox proportional hazards model is a semi-parametric model that has been widely used in observational studies to analyse survival patterns, and it estimates hazard ratios (HR) of binary response data (for example alive or dead) and is expressed as follows:

$$h(t, X) = h_0(t) \times \exp(\beta_1 X_1 + \beta_2 X_2 + \dots + \beta_p X_p)$$

where  $h_0(t)$  is the baseline hazard function (the hazard when all covariates are equal to zero),  $X_i$  represents a collection of explanatory variables ( $X_1, X_2, \dots, X_p$ ), and  $\beta_i$  stands for the regression coefficients to be estimated ( $\beta_1, \beta_2, \dots, \beta_p$ ). The exponentiated coefficients,  $\exp(\beta)$ , represent the hazard ratio (HR), which quantifies the multiplicative effect of each covariate on the hazard. An  $HR > 1$  indicates an increased risk of the event,  $HR < 1$  indicates a protective effect, and  $HR = 1$  suggests no association with studied variables.

This model accounts for “censored data”, that occur when exact survival time is unknown. There are two types of censored data: left or right censorship. Left censorship, or left truncation, results from subjects entering the study at different times, while right-censoring can happen when subjects of the study do not experience the event before the study ends.

The model handles time with an interval notation  $(start, stop]$  to manage the cases when there are multiple events per subject. Each observation is represented by an interval  $(t_1, t_2]$ , where  $t_1$  is the start time and it is open on the left, while  $t_2$  is the stop time, closed on the right. This format allows

individuals to enter the study at different ages and to have multiple lines of data (Cox 1972; Cox and Oakes 1984; Kleinbaum and Klein 2012; Therneau et al. 2024).

Cox proportional-hazard model requires that the hazard ratio is constant over time and that the hazard for one individual is proportional to the hazard for any other individual and independent of time. This assumption can be verified graphically, plotting the residuals against time, and obtaining the Schoenfeld residuals for each predictor (Schoenfeld 1982; Kleinbaum and Klein 2012).

The extended Cox model has the same structure of the standard model but allows to include time-dependent covariates  $X_p(t)$  that change over the follow-up time. This is possible thanks to the structure of the model, which at each event time, compares the covariate values of the individual experiencing the event with the values of all others at risk during the same time period. This feature allows for the representation of dynamic processes in which an individual's state evolves over time, allowing the model to accurately capture risk and changes in survival throughout the observation period. An important assumption of the extended Cox model is that the effect of a time-dependent covariate on survival at time  $t$  is determined by its value at that exact time (Cox 1972; Kleinbaum and Klein 2012; Therneau et al. 2024).

The “stratified Cox model” is a modification of the Cox proportional hazards model that allows a stratification of a categorical predictor that does not satisfy the proportional hazards assumption. In this case, the predictor being stratified is not included in the model (Kleinbaum and Klein 2012).

The Cox proportional-hazard model is highly convenient for survival analysis, and it presents several advantages, as it allows to fully reflect the design required by survival analyses within long-term longitudinal studies: first of all, it enables the analysis to include right-censored data and time-dependent variables. Furthermore, the Cox model is a robust semiparametric model, as the baseline hazard is an unspecified function, so the results from using this model are reliable and approximate closely the result from a parametric one. Also, since the hazard function must range between zero and plus infinity, the structure of this model, particularly the exponential part of the product, allows to obtain always nonnegative hazard estimates. Cox models are generally preferred over logistic models, as the first requires less assumptions and, when available, uses more information, while the second considers a binary outcome (0, 1), ignoring survival times and censoring (Kleinbaum and Klein 2012). Several ecological studies have been taking advantage of these convenient model design to assess the causes of survival rates across different species. Gehr et al (2020) analysed the effect of spatial variation in predation risk on roe deer mortality with a stratified Cox model with different death cause as stratification factor. They used site familiarity as the time-dependent covariate and the Cox model allowed them to model when death occurred and what caused it, ultimately observing that animals with a low site familiarity suffered higher mortality rates, due both to predation but also to other

causes like human hunting and diseases and starvation. DelGiudice et al. (2002) explored the influence of the winter period severity on age-specific survival and cause-specific mortality rates (especially by wolf predation) of females white-tailed deer, using an extended Cox model to allow more flexibility in modelling complex survival data with periodic exit and re-entry of individuals in the study. They found a strong negative influence on survival rates particularly during harsh winters, from high snow depth levels, primarily by increasing the risk of wolf predation and starvation. Frair et al. (2007) evaluated the importance of forage quality, predator density and previous exposure to predators in determining mortality rates of newly translocated red deer. Since survival risk changed over time after translocation and the key predictors were time-varying, they used mortality hazard functions with Cox models. They confirmed that translocation success depended strongly on previous predator experience, as they registered higher mortality rates by predation in riskier landscapes and early after release.

## 2. AIM OF THE STUDY

Winter survival in mountain ungulates is influenced by multiple factors that have been analysed mostly in females as their survival and reproductive success are expected to be among the main drivers of population dynamic. However, due to the marked sexual dimorphism, spatial segregation and differences in survival rates that characterize many mountain ungulates, differences on the factors affecting winter survival in male and females are expected with possible consequences on population dynamic. Nevertheless, studies investigating winter survival in mountain ungulates remain scarce and even less evidence are available for survival of males.

One reason could be that obtaining accurate estimates of age- and sex-specific survival in long-lived mammals is challenging, as they require long-term monitoring of individuals of known age, and such longitudinal data are scarce. In mountain ungulates this is even more challenging due to the remote environment they live in, which make long-term data collection complex. Understanding how environmental factors affect seasonal changes in body mass and their demographic consequences necessitates instead of repeated measurements of marked individuals, which are rarely available for wild populations, especially for mountain ungulates (Douhard 2018).

Given their high and long-lasting survival rates, and the availability of long individual-based data series, the Alpine ibex represents a particularly suitable and interesting species for studying these aspects of population dynamics. The aim of this research is to use survival analysis to identify the biotic and abiotic conditions associated with overwinter mortality in male Alpine ibex, thereby addressing gaps in our understanding of mountain ungulate population dynamics and identifying potential factors limiting population growth. Identifying which conditions result in high mortality risk for male ibex during winter is one of the important factors to understand which mechanisms are potentially affecting population growth.

Taking advantage of the long-term monitoring project of Alpine ibex currently going on in Gran Paradiso National Park, we investigated, by means of Cox proportional hazards models, the factors affecting overwinter survival of the species and examined the relationship between male survival and biotic and abiotic factors. We expected both males and females survival to be affected by age and by environmental conditions. In the case of males, for which we could also test the effect of body conditions, we expected that body size at the beginning of autumn would influence the probability of winter survival.

We based our predictions on the hypothesis that male ibex survival during winter could be influenced by many variables, both intrinsic (age and individual body condition) and environmental (climatic and ecological conditions). These factors are strongly related with each other: first of all, male ibex

experience a negative energy balance during winter, during which also the rut occurs, the highest energy demanding period for males, and to survive over the cold season they rely heavily on fat reserves accumulated during the previous summer. The winter body mass loss, and therefore the ability to overcome harsh winters, is strictly dependent both on the autumn body mass and winter climatic conditions. Consequently, we expected that male overwinter survival depends both on the overall autumnal body condition, with which they enter the new winter season, but also on the timing of the spring onset after snowmelt (determined as well by winter and spring conditions), as it represents the moment that ibex can start foraging again and hence stop relying on fat reserves.

### 3. MATERIAL AND METHODS

#### 3.1 Study species

The Alpine ibex, focus of this work, is a species of the genus *Capra* inhabiting the Alps.

Today it is classified as “Least Concern” by the IUCN (International Union for Conservation of Nature; Toïgo et al. 2020), but, despite this, its distribution is still highly fragmented in the Alps (Fig. 1). The Alpine ibex holds significant conservation value due to its recent recovery from near extinction.

Less than two centuries ago, intense hunting had caused severe population declines, leaving only about 100 individuals that persisted in the Gran Paradiso region in the mid-1800s. Subsequent conservation measures were applied, including the creation of the Royal Hunting Reserve in 1756, of the National Park in 1922, captive-breeding programs and several successful translocation events. Conservation programs laid the foundation for ibex reintroduction efforts across the Alps during the following decades and now the species is found throughout most of the European central and southern high-alpine mountain ranges (Grodinsky and Stüwe 1987; Stüwe & Scribner 1989; Brambilla et al. 2020a, b).

The species mostly lives above the tree line in the alpine and subnivale zone, between 1500 and 3000 m a.s.l., characterised by alpine meadows and pastures and steep and rocky cliffs (Grignolio et al. 2003; Brambilla et al. 2020b).

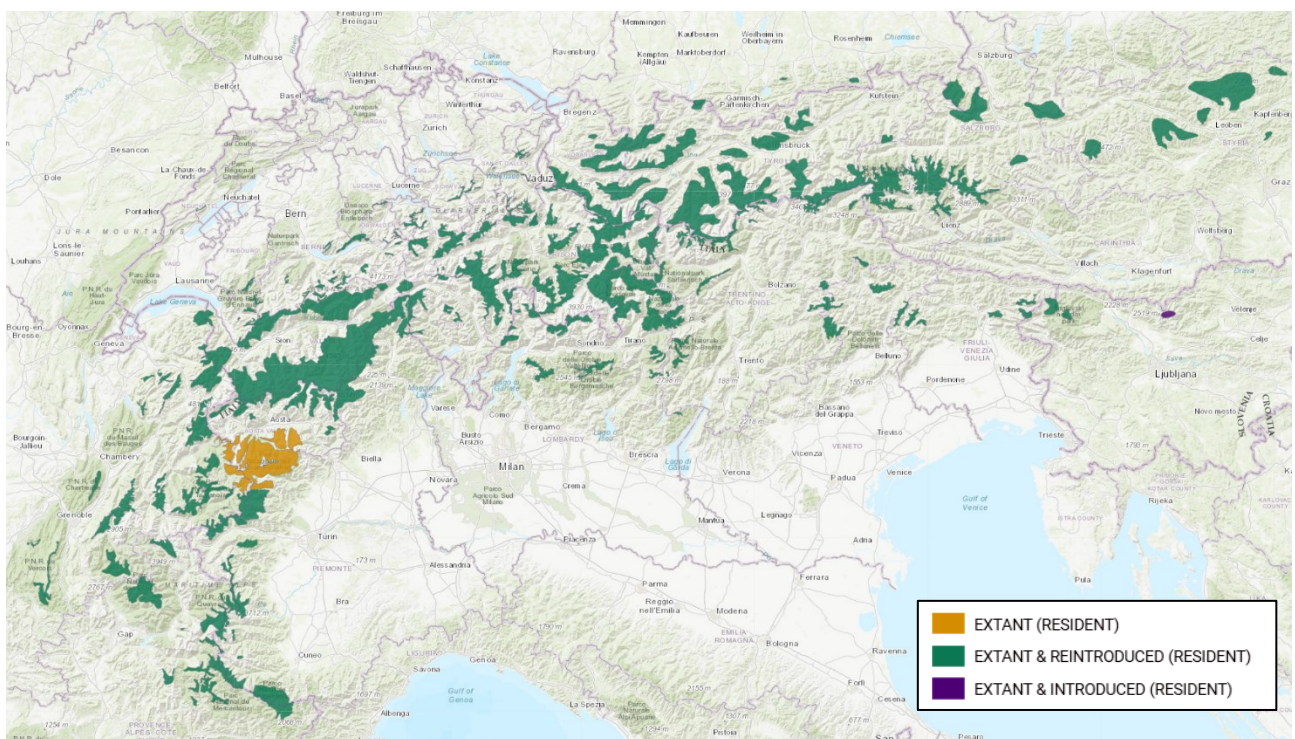
In this species, a pronounced sexual and spatial segregation occurs, mainly attributed to body size differences and to behavioural variations, with the only exception occurring during the rut period, when males join females’ groups on rocky cliffs. Adult males tend to feed on low inclination pastures where they find large amounts of biomass and are more likely to move into lower-altitude areas in winter. Due to their larger body mass and greater rumen volume, adult males can consume and digest larger amounts of fiber-rich forage (Villaret and Bon 1995; Villaret et al. 1997; Brivio et al. 2010, 2014; Brambilla et al. 2020a). The smaller body size and higher predation risk of females and kids lead them to select steeper and rocky environments close to cliffs, which offer both protection and suitable foraging grounds throughout most of the year. Younger males use similar areas and altitudes to females than to older males (Grignolio et al. 2007b, 2019). Both sexes show a conservative use of space but shifts between summer and winter home ranges occur and are mainly influenced by foraging conditions, snow cover, and thermoregulatory needs (Parrini et al. 2003; Abderhalden 2005; Mason et al. 2017).

Alpine ibex is a highly sex dimorphic species: males are significantly larger and heavier, with an average body mass of 75–95 kg, while females range between 35–45 kg, exceptionally reaching 60 kg. Sexual dimorphism is reflected in the spatial segregation with differences also in activities during

the day: males lay and rest for longer than females that allocate more time between feeding and ruminating, young males (Ruckstuhl and Neuhaus 2001; Brambilla et al. 2020a).

Growth patterns in male and female Alpine ibex reflect their sex-specific survival patterns. Females typically reach their maximum body size at around 5 years of age, whereas males continue growing until approximately 10–12 years, when they reach asymptotic body mass. Body growth comprehends the energy investment on horns, a secondary sexual character that grows lifelong, mainly during the favourable season with a pause each winter, during which an annual ring is developed enabling the age determination (Ratti and Habermehl 1977; Toïgo et al. 2002; Brambilla et al. 2020a).

In both sexes, survival is strongly age-dependent: both male and female kids generally show high survival rates until the onset of winter, but survival through the first winter varies greatly depending on weather conditions and predation pressure (Brambilla et al. 2020a; Grignolio et al. 2019; Pettorelli et al. 2007). Females exhibit high survival between until 8-9 years of age, followed by a gradual decline thereafter. Males instead maintain high survival rates up to 10-13 years, after which mortality increases sharply with advancing age, 5-20% higher than survival rates of males in other large herbivores. Average longevity is about 13–14 years in males and 16–17 years in females, although individuals may occasionally reach 17 and 22 years, respectively (Gaillard et al. 2003; Toïgo et al. 2007; Brambilla et al. 2020a).



**Figure 1.** Distribution map (IUCN 2024).

### *Adaptations to high altitude environments*

The Alpine ibex represents an excellent model for studying the effects of environmental variation on body condition and growth. Alpine ibex lives in an altitudinal range between 1500 and 3000 m a.s.l., depending on the season (Brambilla et al. 2020b). Consequently, it experiences some of the most extreme environmental conditions among all Alpine ungulates.

Ibex's morphology and physiology reflect the habitat they live in, a strong seasonal environment, with a series of adaptations to difficult conditions of high mountain habitat. The compact body structure, with short and strong legs and a robust neck, minimizes heat loss, and its dense, dark and well insulating fur provides effective thermal insulation during winter with one yearly moult during spring to replace the winter coat.

The species exhibits a series of specific adaptations to cope with the marked and highly seasonal conditions of high-altitude habitats. These adaptations include a high haematocrit, which facilitates oxygen transport in thin mountain air, a compact body morphology that minimizes heat loss, and a dense, dark winter coat that provides effective thermal insulation. Also, a 60% heart rate reduction, and breath and metabolic rates accordingly, occur. Body core temperature varies during the year with lower values registered in winter (38-38.2 °C) and peak values in summer (39.5 °C). To cope with this low internal temperature during winter, Alpine ibex bask in the sun in the morning and actively use external heat to increase the body heat (Signer et al. 2011).

A further important aspect of the adaptation traits of this species is migration, a key behavioral strategy to cope with seasonally varying environments and to prolong access to optimal climatic conditions (Rickbeil et al. 2019). Male alpine ibex exhibit both seasonal and daily altitudinal migration, to follow the progression of vegetation green-up and favorable environmental conditions (Aublet et al. 2009; Mason et al. 2017). During the favorable season, ibex follow the green wave upwards and move to the alpine pastures, where they are going to spend the whole summer to accumulate body fat reserves. In particular, during early spring (late April to May), males primarily forage on fresh vegetation in low-elevation grasslands ranging from 1500 to 2000 meters. By June, they typically move above the treeline to altitudes of 2300-2500 meters. Throughout summer and early autumn (July to September), their distribution is generally concentrated between 2700 and 3200 meters (Grignolio et al. 2003; Parrini et al. 2003; Aublet et al. 2009). Seasonal migration can provide survival and reproductive benefits, but the net fitness gain strongly depends on its timing (Chauveau et al. 2025).

These kinds of seasonal migrations in several species of ungulates are largely influenced by temperature and the relative environmental factors. In spring, rising temperatures, snowmelt, and vegetation growth induce the beginning of the migration (Gurarie et al. 2019; Candino et al. 2022),

while in autumn, declining temperatures and early snowfall drive animals to move before forage becomes inaccessible and predation risk increases (Rickbeil et al. 2019).

However, one of the most important adaptations of this species to the seasonality of the Alpine range is the accumulation of fat reserves during summer. This trait is not found in other ibex species across the world that inhabit different environments (e.g., *Capra nubiana* in the Sinai Peninsula, *Capra walie* in Ethiopia but also the *Capra sibirica* in the Himalaya and Mongolia regions that are characterized by similar temperature ranges as the Alps but drier and with less precipitations winter periods). Alpine ibex metabolism instead follows a seasonal cycle to accumulate large amounts of body fat during summer and to reduce energy loss and sustain metabolism during the resource-scarce winter period. During winter, food intake is extremely reduced because the vegetation is dry and fibrous, low in protein, and often covered by snow; body fat reserves therefore allow ibex to better survive by relying almost exclusively on the fat accumulated during the favourable months when nutritious vegetation is abundant. The fat reserves are crucial, as they enable the ibex to spend less than half the energy in winter compared to summer (Couturier 1962; Brivio et al. 2010; Signer et al. 2011, Brambilla et al. 2020a).

Collectively, these physiological and morphological traits confer the ability to survive and reproduce under some of the most extreme environmental conditions encountered by Alpine ungulates (Signer et al. 2011).

### 3.2 Study area

#### *Gran Paradiso National Park*

Gran Paradiso National Park, Italy's oldest national park, extends between 800 and 4061 m a.s.l., over an area of 71,044 hectares. It surrounds the Gran Paradiso massif along the Italian-French border and includes five valleys: three in the Aosta Valley (Cogne, Rhêmes, and Valsavarenche) and two in Piedmont (Orco and Soana). The Park was established in 1922, transforming a former royal hunting reserve into a protected area to prevent the extinction of the Alpine ibex.

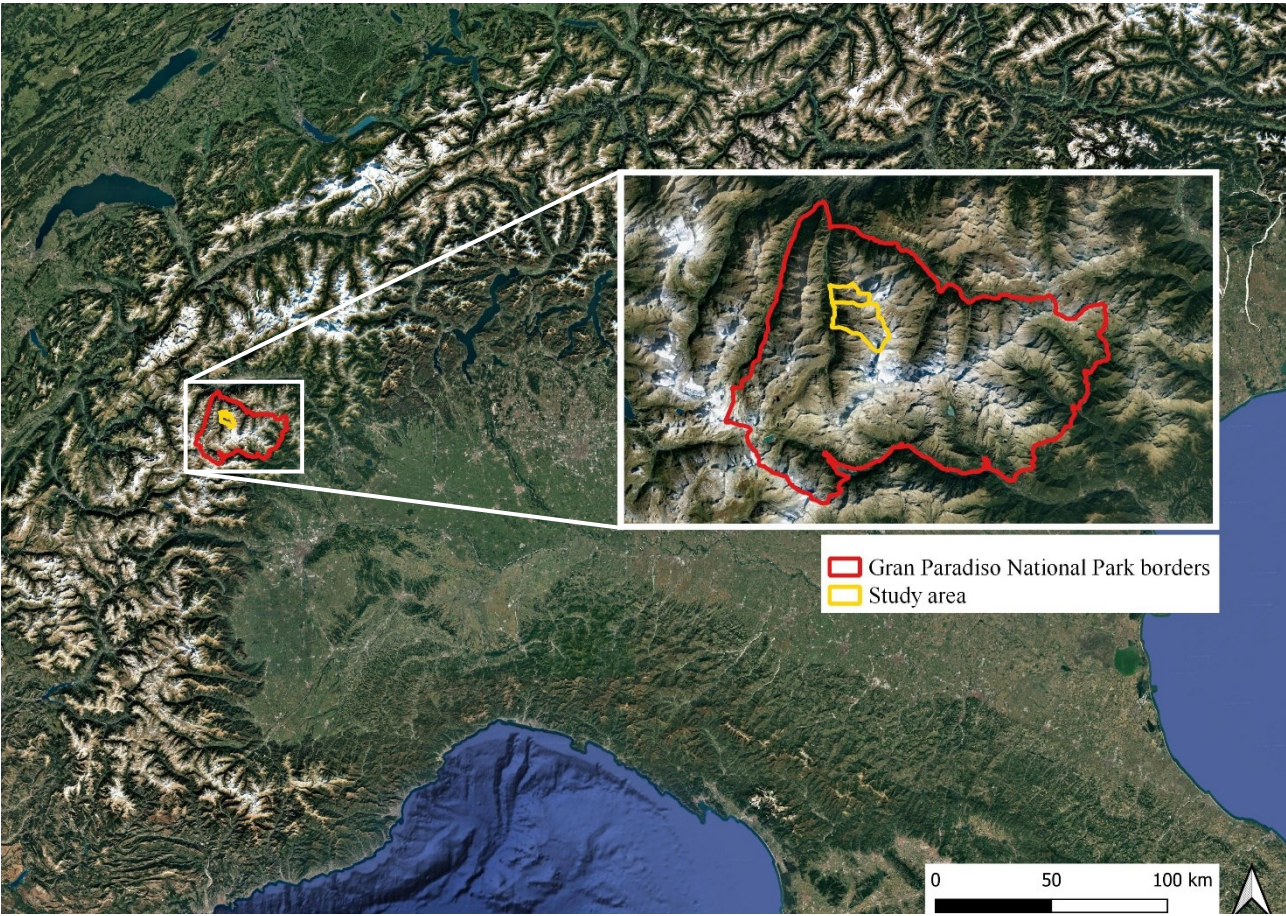
#### *The ibex Project*

In 1999, the Park initiated the ibex Project, a long-term program designed to study various ecological aspects of the Alpine ibex and support evidence-based conservation strategies. Implemented in collaboration with national and international academic institutions, the project addresses key topics such as behavioural ecology, life-history traits, population dynamics, and genetic diversity within the Levionaz study area. This research relies on individual-based monitoring, with animals identified through coloured ear tags or collars. This method allows for systematic collection of biological samples and detailed longitudinal data on behaviour, survival, reproduction, resource use, and population trends.

#### *Study site*

Data collection was carried out in Valsavarenche, in the core of the Gran Paradiso National Park (GPNP: 45°35'N, 7°12'E, northwestern Italy). The study site ranges from the valley bottom (Degioz and Tignet village at about 1600 m a.s.l.) to the Levionaz valley, located on the right side of Valsavarenche (AO) (Fig. 2). The lower parts of the study area are dominated by subalpine grasslands, transitioning at higher elevations into steep cliffs and coniferous forests. The Levionaz Valley is a sharply incised glacial valley covering around 1,700 hectares, with elevations ranging from 1700 to 3300 meters a.s.l. (Brivio et al. 2019). This valley is characterized by the presence of one major valley that branches off into three other valleys (Vallone del Lauson, Vallone dell'Inferno, Vallone del Timorion). This area, located above the tree line (2300 m a.s.l.), is dominated by rocks, scree slopes and is covered by meadows and alpine grassland (*Festuca varia*, *Poa alpina* and *Carex curvula*), conifer woods (*Picea abies*, *Larix decidua* and *Pinus cembra*) and bushes (*Rhododendron ferrugineum*, *Vaccinium myrtillus* and *Juniperus communis*). The only other widespread large herbivore in the study area is the Alpine chamois. The wolf (*Canis lupus*) has been present in the area since 2007, although the ibex is a secondary prey item for this large predator. Predation by golden eagles (*Aquila chrysaetos*) is usually limited to ibex kids. Hunting is not permitted in the National

Park. Domestic ungulates have not been present in the Levionaz Valley for about 50 years (Grignolio et al. 2003, 2007a).



**Figure 2.** Gran Paradiso National Park (red) and study area (Degioz, Tignet and Levionaz Valley, yellow) borders.

### *3.3 Data collection*

To investigate the factors influencing the animal survival during winter, three main kinds of data were collected: environmental conditions in the study area, individual survival and individual body mass changes of marked male Alpine ibex

#### *Environmental conditions data*

Daily meteorological data from 1985 to 2024 were gathered from a meteorological station (Iren S.p.A.) near Lake Serrù (Ceresole Reale, TO), located at 2240 m a.s.l., 10 km from the study area of Levionaz and aggregated in seasonal values (see Data handling paragraph for details). In addition, we obtained data on the onset of the green-up period and the total duration of the vegetative growing season using the Normalized Difference Vegetation Index (NDVI). The NDVI is a vegetation indicator derived from satellite imagery and is calculated as the ratio of reflectance in the red (RED) and near-infrared (NIR) portions of the electromagnetic spectrum ( $NDVI = [NIR - RED] / [NIR + RED]$ ; Myneni et al. 1995). NDVI provides valuable information on vegetation productivity and phenology across broad temporal and spatial scales and has been widely applied in ecological research as a proxy for these parameters (Pettorelli et al. 2005). The duration of the green-up period serves as an effective indicator of the rate of vegetation maturation.

#### *Individual-based data*

##### *Capture and marking*

As part of long-term research on ibex life-history and conservation in the Park, individuals aged 3-16 years are captured via chemical immobilization using tele-injection and subsequently marked for data collection. Captures are carried out by a highly experienced team, typically including Park wardens and a veterinarian. A CO<sub>2</sub> injection rifle is used to inject a mixture of xylazine and ketamine to tranquilize the animal while allowing its immobilization. The shot is done carefully measuring the distance to adjust dart pressure to minimize stress on the animals. Darting is performed from approximately 30 meters and in locations away from cliffs to ensure the safety of both the animals and the team. Once the ibex had lied down, the team approaches and, after immobilization, collects physiological parameters (heart and respiratory rate and body temperature), biological samples (blood and tissue), and biometric data (neck and chest girth, metatarsus length and wither height). Age is determined by counting the annual growth rings on the horns (Ratti and Habermehl 1977), after that, each individual is marked with color-coded ear tags (Allflex®) for identification during subsequent field observations. Throughout the procedure, the animal is continuously monitored for stress indicators and vital signs. Following measures and marking, an antagonist is administered to reverse sedation, and the ibex is released after approximately 45 minutes, with the team observing it until it

reaches a safe location and exhibits normal behaviour. Newly marked individuals are further monitored in the subsequent days to ensure their well-being. The entire capture and handling protocol was approved by the Italian Ministry of Environment (protocol no. 25114/04; Brivio et al. 2015).

### *Survival data*

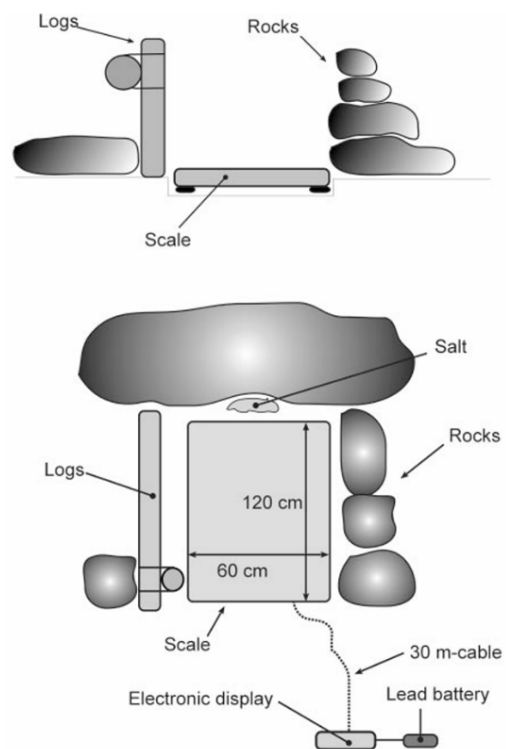
Alpine ibex survival has been monitored in the Park, since 1982. The data about marked animals' survival come from the daily monitoring of researchers in the study area of Levionaz as well as from warden's activity of surveillance in the entire Park and through the census of the population, conducted every year during the first week of September in the whole area since 1956 (von Hardenberg et al. 2000).

All individuals are reported in a database including individual information (animal code, cohort, sex, name and the specific-coloured ear tags) and the location (area and valley) in which the animal was marked. If an animal is observed alive at least once during a given year it is considered as alive and reported in the dataset as *alive* (code: 1). If it is not observed during the whole year, it is entered as *not seen* (code: 0). If it is found *dead*, it is assigned the code 2 in the year following death (and 1 in the year before when it was observed alive for at least part of the year). It has to be noted that the yearly interval of this dataset as well as of the models described below, does not correspond to the calendar year but to the biological year of the study species (that is usually considered to start in spring, when births occur, and end at end of the following winter). This means that each "ibex year" begins on June 1st and end on May 31st.

### *Body mass data*

Starting from 2000, marked animals were repeatedly weighed each summer, from late May-early June to September. Data on body mass of the marked male Alpine ibex were collected with remote observations that provide accurate and repeated weight measurements without handling the animals. The system consists of three scales located in different parts of the study area, in the Levionaz Valley. The scales consist of a remotely observed electronic platform. The wooden stand is fixed on a metal frame, connected by a cable to an electronic display suitable for outdoor use and baited with a salt block (Fig. 3 and 4). The system is powered by rechargeable batteries or solar energy. The lateral boards of the scales are placed in such a way that only one individual at a time can have access to it and that the animal must step on the scale with all four legs to access salt (Bassano et al. 2003). This posture allows the observer, located at about 20-30 meters, to record the mass values measured by the electronic platform (precision between 0.1 and 0.5 kg, depending on the instrument). In the study area ibex came to the three scales mostly in the early morning and late evening, until darkness, according to the daily migration habit. To ensure continuous monitoring of the scales, including during midday

and nighttime hours, since 2020, a wildlife camera and a video surveillance system (AlfredCamera Home Security app, developed by Alfred Systems Inc.) have been installed near one of the scales. Scales were monitored each morning and evening, corresponding to periods of peak animal activity, over the entire field season (from early June to early September); we collected data on the body mass of marked animals, the possible tare of the scale, and the amount of time each individual spent on the platform.



**Figure 3 and 4.** Picture of two individuals on one of the three scales and schematic project of the scale structure (Bassano et al. 2003).

## 4. DATA ANALYSIS

The statistical analysis was conducted using RStudio as interface of R software (version 4.5.0, R Core Team 2025). Data manipulation was performed using the *dplyr* (Wickham et al. 2023), *tibble* (Müller & Wickham 2023), *tidyr* (Wickham et al. 2024) and *corrplot* (Wei et al. 2017) packages. Graphical exploration and plots were produced with *ggplot2* (Wickham 2016), *visreg* (Breheny and Burchett 2017) and *survminer* (Kassambara et al. 2025). Linear mixed effects models were fitted using *lme4* (Bates et al., 2015) and survival analysis was conducted using the *survival* package (Therneau 2015).

### 4.1 Data handling and computation of variables

#### *Aggregation of environmental variables*

Meteorological variables (minimum and maximum temperatures, rain or snow precipitations, and snow depth on the ground) were calculated for each season from 1985 to 2024 using meteorological data gathered from a weather station (Iren S.p.A.) situated at Lake Serrù (Ceresole Reale, TO), in proximity of the study area.

Daily measures were aggregated into seasonal values for each year by averaging the daily values for the reference period. Seasons were defined as follows, also based on the yearly biological cycle of the study species: winter: from November (of the previous year) to March, spring: April and May, summer: from June to August, autumn: September and October. For the winter period we computed, for each year: mean minimum temperature ( $T_{min\ winter}$ , °C), mean maximum temperature ( $T_{max\ winter}$ , °C), mean snow depth ( $Snow\ depth$ , cm), number of days with snow cover ( $Snow\ days$ ), first day of snow cover ( $First\ snow$ ), and last day of snow cover ( $Last\ snow$ ). The first and last snow dates were calculated considering an extended period from September to June of the following year to capture the entire snow season. Snow dates were measured as day of year, and from these values we calculated, for each winter season, the total number of days between the first and last day of snow ( $length\ winter$ ). For spring and summer, we calculated mean minimum temperatures ( $T_{min\ spring}$  and  $T_{min\ summer}$ , °C), mean maximum temperatures ( $T_{max\ spring}$  and  $T_{max\ summer}$ , °C), and mean precipitations ( $Spring\ precipitation$  and  $Summer\ precipitation$ , mm).

Vegetation phenology indices were derived from NDVI (Normalized Difference Vegetation Index) data obtained from optical satellite images extracted from MODIS data (sensor TERRA, NASA LP DAAC 2014) available since 2000. This dataset provides daily composite raster images, where each pixel corresponds to an estimate of the surface spectral reflectance, representing how it would be measured at ground level without absorption by the atmosphere (Jiang et al. 2006).

The images were further processed as suggested by Ranghetti et al. (2016): we first selected grassland pixels from Corine Land Cover (© European Union, Copernicus Land Monitoring Service 2018,

European Environment Agency EEA). To obtain homogeneous time series and daily values, for each selected pixel we then smoothed the time series for each year of the study with a spline interpolation (using *npreg* R package (Helwig 2022)). From each pixel time series for each year, we finally extracted the day of the onset of spring (*onset of spring*), that is the day when NDVI reached 51% of its maximum that year, and it represents the day when spring forage starts to be available for the animals. We then considered also the day of NDVI maximum value (*NDVI max*), as a proxy for seasonal peak in vegetation fresh biomass and its quality. The *onset of spring* and *NDVI max* value were then used to determine the length of the green-up period (*length green-up*) for each year, calculated as the number of days between the two values.

Meteorological and phenological variables were then associated with the survival data described below. Winter variables were referred to the year of death of each individual, as we were interested in analysing factor affecting mortality which happened in winter. Conversely, spring and summer conditions were referred to the season preceding death, assuming that these factors may influence the physical condition with which animals enter the winter season.

To avoid potential collinearity issues in the meteorological variables, we examined correlations among all weather predictors and, based on our initial hypothesis, we selected only variables with correlation coefficients  $< 0.55$  for analysis. Correlations were then visualized using a correlation matrix plot with the *corrplot* package (Fig. S1; Wei et al. 2017).

#### *Estimates of autumn body mass and body mass changes*

To estimate body mass changes during the season, we built Linear Mixed Models (function *lmer* of the *lme4* package; Bates et al. 2015) for each year separately. In these models, we considered individual body mass repeatedly measured during summer as the dependent variable which varied as a linear function of the day of the year, which was included as predictor. As we had repeated measures for the same individuals and we expect individual variability in initial body mass and growth rate we included individual identity as random effect with random intercept and slope (days since 1<sup>st</sup> May). Specifically, we fitted two models per year: one with day centered on day 92 (1<sup>st</sup> September; *absolute mass September*) and one with day centered on day 32 (1<sup>st</sup> June; *absolute mass June*). By extracting the individual-specific coefficients from these models, we obtained estimates of absolute body mass for each individual at the beginning and at the end of the summer season. The intercept from each model represents the estimated body mass at the centered date, and the slope (*slope*) represents the individual rate of change in body mass per day. We used the slope coefficients extracted from the September model as a measure of individual variation in mass gain throughout the season. We also

calculated the relative mass gain (*increase*) during the entire favourable season as the percentage increase in body mass relative to the starting mass of each season.

### *Survival dataset*

To analyse survival patterns, we designed the dataset with each row representing an individual-year combination.

We converted the survival status from the 0/1/2 codification (not seen/alive/dead) previously described to binary 0/1 codification, as requested for Cox proportional hazards models, with 1 indicating the year when the event (death) occurred and 0 indicating a year when an animal was part of the study (i.e., after being marked) but no death occurred.

We acknowledge that the lack of observation of an animal during one year is no irrefutable evidence of death. However, as most of the animals (N=324) were never seen any more after the first year without being observed, we considered them as dead during the winter in which they disappeared (i.e., when their status went from alive in year  $t$  to not seen in year  $t+1$  and following years). We had however some cases (N=80, most of them in the first years of the study, i.e., before 2000, not in the long-term study area, and with a higher proportion of females) where an animal was not observed in a specific year but then was observed again in following years. In those cases, we assumed that the animal was alive also during the year when it was not observed.

In addition, we excluded from the analysis individuals unsuitable to answer our question about the variables affecting overwinter survival, such as animals that died during capture, were predated, died during summer, (N = 15 individuals). These individuals can be related to a “non-responder group”, a group of animals whose deaths were unrelated to the conditions under study (Therneau et al. 2017). We also excluded individuals that had not been seen for the first time in the last year of the study.

We finally created two datasets: the largest dataset (survival 1985-2024) included all individuals (males and females) monitored in the Park between 1985 and 2024. The second dataset (survival m 2000-2024) spans for a shorter time and only included male individuals monitored in the study site of Levionaz since 2000, when body mass data collection started.

## 4.2 Survival analysis

### *Age-related survival curves*

To represent age-related survival curves for Alpine ibex we used the Kaplan-Meier (KM) curves. Kaplan-Meier estimator is a non-parametric statistical method allowing to estimate the survival function also in presence of right-censored data. It calculates the probability of surviving until a certain point in time using data on when the event of interest (death in the case of the present study) occur. The result is a survival curve, where the x-axis is time and the y-axis is the probability of survival (Kaplan and Meier 1958). We built a KM curve using data on all individuals monitored in Gran Paradiso National Park from 1985, including females and we also built separate curves for males (in total 2507 observations for 430 males) and females (in total 621 observations for 95 females). We also used a log-rank tests to compare survival curves and probabilities between sexes.

### *Survival models*

To examine the effects of intrinsic (age and body conditions) and extrinsic factors (environmental variables) on animals' mortality risk, we modelled ibex survival in the study period with a Cox proportional hazards model, to predict the probability (hazard rate) for an individual, based on a series of predictor variables, of dying at a specific time.

All continuous variables were standardized to permit direct comparisons among the effects of each variable. The model was fitted both on standardized variables, to allow coefficients comparison, and also on non-standardized variables, to facilitate their biological interpretation.

We fitted the Cox model using the *coxph* function from the survival package (Therneau 2015) to assess the effects of individual and environmental covariates on survival probability.

We used a staggered entry design (left truncation) to account for varying capture dates of the individuals, as they contribute to the survival analysis only after their entry into the study. We also had right-censored data that occur an animal did not experience the event, i.e., animals still alive at the end of the study.

In our study, the data were structured with annual time intervals, allowing us to account for changes in individual characteristics (such as age and body condition) and environmental factors (such as temperature or snow conditions) across years. Specifically, covariates were measured annually and remained constant within each interval. We created time intervals by assigning  $t_1$  (starting time) and  $t_2$  (ending time) for each year, where  $t_1$  represents the cumulative years since first observation, i.e., the year of the animal's capture, and  $t_2$  represents the end of the time interval ( $t_2 = t_1 + 1$ ). As explained before, for each interval, each individual was assigned a status 0 if he did not experience the event (i.e. if he was alive) or 1 if he died during that interval.

We modelled the baseline hazard,  $h_0(t)$ , using a “time since capture” model so that time for each animal started from its capture date. This means that each individual is assigned  $t_I = 0$  in the year when it was captured. We chose the “time since capture” model for statistical reasons, as it allows, using parametrical assumptions, the variable *age* to be included as a continuous covariate, considering that different extrinsic factors (such as environment) could cause individuals of the same age, but different cohorts, to show different mortality rates (Fieberg and DelGiudice 2009).

We tested the proportional hazard assumption of the models, using scaled Schoenfeld residuals (*cox.zph* function; Kleinbaum and Klein 2012).

To further confirm the results of previous models, we also run “age-based” models. This model is based on animals’ birth year as the time origin, but the influence of age is modelled nonparametrically and is derived implicitly by the model as time intervals. The outputs of this second model can be found in Supporting Information and are shown in table S6 (standardized variables) and table S7 (non-standardized variables), along with the results of the Schoenfeld residual p-values (table S8) and the corresponding plots (figure S5).

As body mass data were available only since 2000, we fitted two separate models on the two datasets described before.

*Model survival 1985-2024*: this model included males and females monitored in the whole Park. In addition to age and sex, we added covariates possibly affecting survival patterns the following annual environmental conditions: spring and summer maximum temperatures, spring precipitations, minimum winter temperature, mean snow cover and the length of the winter and green-up period. Since the variable sex included in this model did not respect the proportionality assumption, we used a Cox proportional hazards model stratified by sex to address the violation of assumption and to account for different baseline mortality rates between males and females. The output of the original model can be found in Supporting Information (tables S1 and S2), in addition to the results of the Schoenfeld residual analysis (table S3) and the associated diagnostic plots (figure S2).

*Model survival m 2000-2024*: this model only included males for which body mass data were available. In addition to the variables included in the previous model (excluding sex), we added the effect of body mass at the end of summer (absolute mass September) and its interaction with age as covariates affecting survival. By including product terms in the linear predictor, we examined the interaction between age and body condition to assess whether the effect of body mass on survival varied across different ages.

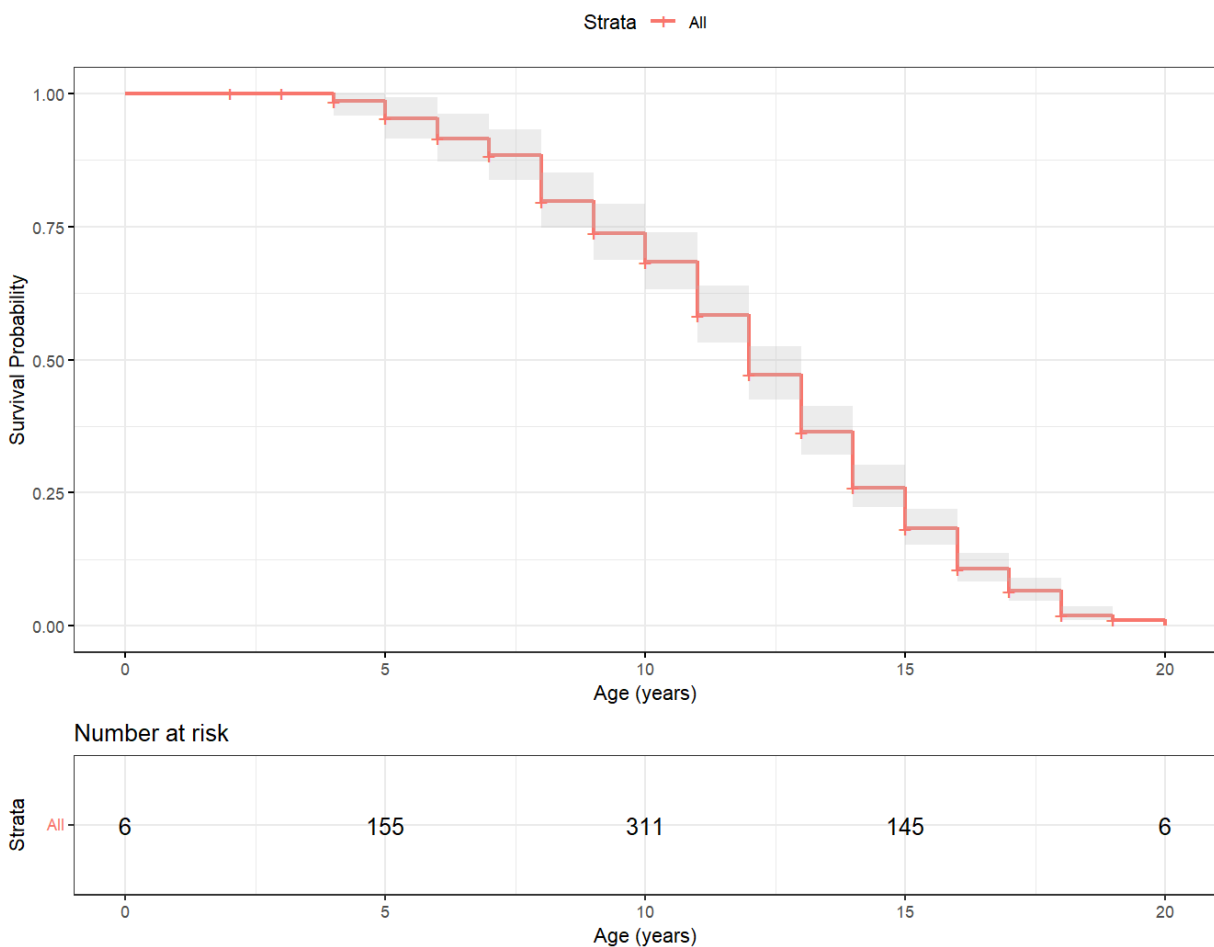
## 5. RESULTS

In total, the *survival 1985-2024* dataset included 3138 observations, referred to the period from 1985 to 2024, with a total of 525 individuals and a number of 468 deaths events. The subset *survival m 2000-2024* included 1446 observations on 245 individuals, among which 193 died.

As for the body mass data, a total number of 4138 body mass data were collected in the field between 2000 and 2024 and resulted in 829 estimates of autumn body mass that were used as covariate in the model.

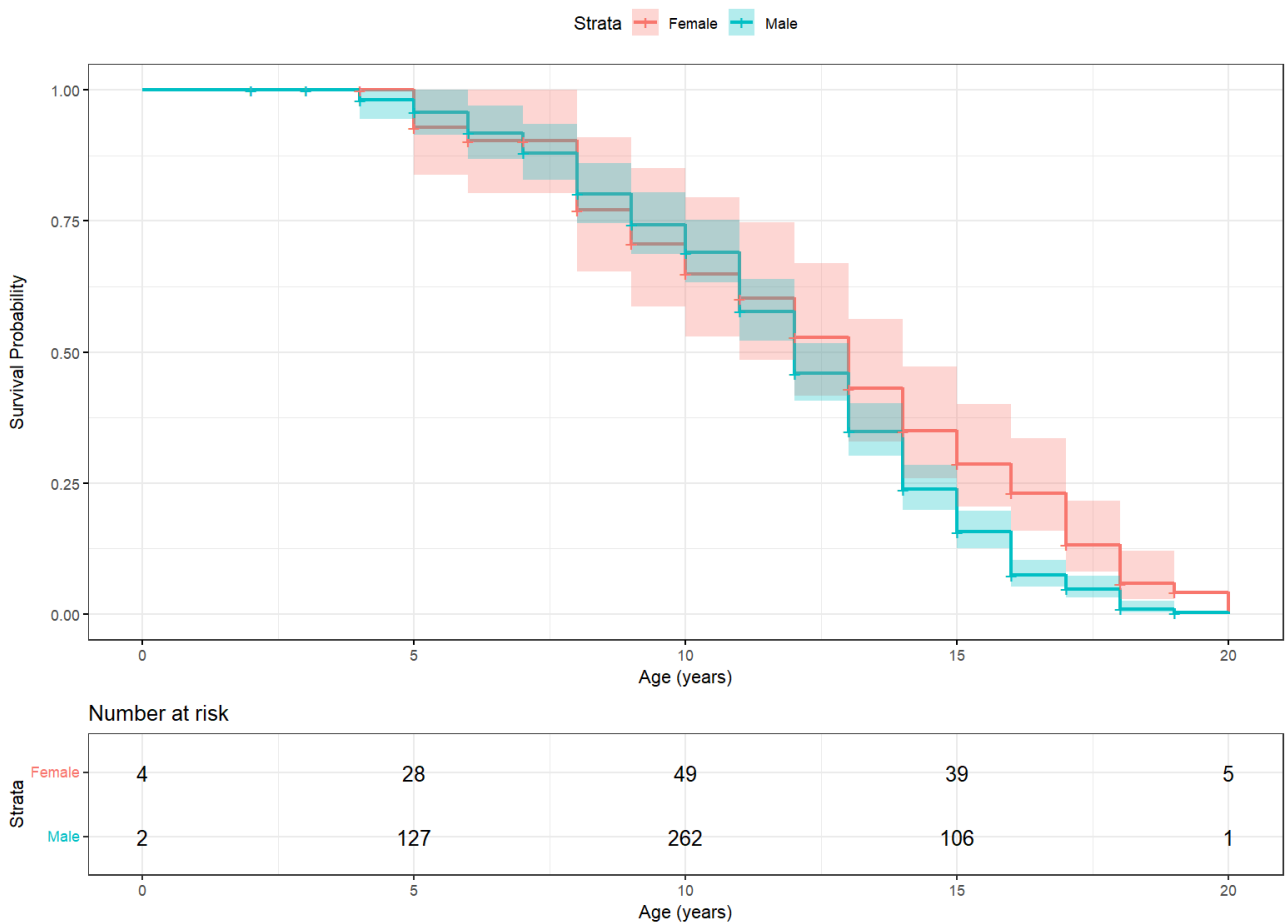
### 5.1 Age related survival curves

We investigated the age-dependent influence on ibex survival rate in the entire ibex population. We visualized the age influence on survival with a Kaplan-Meier survival curve (Fig. 5) using the complete dataset of all marked animals, including both males and females, across the entire Park since 1985 (*survival 1985-2024*).



**Figure 5.** Kaplan-Meier survival curve showing survival probability for the entire Ibex population, both males and females, during the period 1985-2024. For representation purposes we chose to exclude a male (V15/99), that exceptionally reached the age of 23.

The distinction in survival patterns across sexes has been graphically explored and it is shown in the Kaplan-Meier curve below (Fig. 6):



**Figure 6.** Kaplan-Meier survival curve showing survival probability of males (blue) and females (red), during the period 1985-2024. For representation purposes we chose to exclude a male (V15/99), that exceptionally reached the age of 23. Log-rank test:  $p = < 0.001$ .

We examined the distinction in survival patterns between the two sexes and the respective number of events and survival probabilities, for each age group. The values are reported in the table 1.

Age	MALES		FEMALES	
	Number of events	Survival probability	Number of events	Survival probability
4	1	0.98	0	NA
5	3	0.96	2	0.93
6	8	0.92	1	0.90
7	10	0.88	0	NA
8	23	0.80	7	0.77
9	19	0.74	4	0.71
10	19	0.69	4	0.65
11	43	0.58	4	0.60
12	48	0.46	7	0.53
13	48	0.35	10	0.43
14	50	0.24	9	0.35
15	36	0.16	7	0.29
16	37	0.07	7	0.23
17	11	0.05	12	0.13
18	16	0.01	9	0.06
19	3	0.002	2	0.04
20	1	0	5	0

**Table 1.** Distribution of different survival probabilities between males and females, across different ages.

Kaplan-Meier survival analysis revealed a significant sex difference in survival probability (log-rank test:  $\chi^2 = 40.9$ ,  $df = 1$ ,  $p < 0.001$ ). Females exhibited higher survival rates than males, with 90 observed deaths compared to 148 expected if there were no sex effect, whereas males showed 377 observed deaths against 319 expected. It has to be noted that the data refer to animals beyond the age of 3, because information on the individual survival of juveniles and yearlings is not available.

In juveniles and sub-adults (3-7 years) the survival rates, in both males and females, were remarkably high and similar across sexes: the rates were high, over 0.90, and varied little over time. In prime-aged adult (8-10 years) the survival probabilities were still high but more variable, decreasing from approximately 0.80 to 0.65-0.70. Both sexes showed very similar survival patterns with a rapid decrease in survival rates with survival values ranging widely from 0.80 to 0.58 for males and from 0.77 to 0.65 for females. Finally, senescent adults (> 10 years) showed a rapid and sharp decrease in survival probabilities. Beyond the age of 11, females showed higher survival probabilities than males. Males experienced particularly high mortality during this period, while females showed more moderate but consistent losses. This decrease, after age 14, was much more pronounced and sudden in males. At very old ages, around 20 years old, survival probabilities for both males and females dropped to nearly zero.

Despite the statistical significance, the survival graphical representation displayed overlapping trajectories, especially in juveniles and sub-adults, with survival probability declining progressively from age 4 in both groups. The decline in survival probabilities was relatively gradual up to about 7-8 years, after which it accelerates in both sexes.

## 5.2 Survival models

### *Influence of environmental conditions on survival rates*

We assessed the effects of age and environmental variables on survival rates of Alpine ibex using the complete dataset (*survival 1985-2024*), based on their age and stratified by sex.

The outputs of the stratified Cox model assessing the effects of age and environmental conditions on survival rates are shown in table 2 (standardized variables) and 3 (non-standardized variables).

	$\beta$	$\exp(\beta)$	$p$ -value
<b>Age</b>	<b>0.68</b>	<b>1.98</b>	<b>&lt; 0.001</b>
T max spring	- 0.05	0.95	0.35
<b>Spring precipitation</b>	<b>0.17</b>	<b>1.18</b>	<b>&lt; 0.01</b>
T max summer	0.02	1.02	0.70
<b>T min winter</b>	<b>- 0.21</b>	<b>0.81</b>	<b>&lt; 0.001</b>
Snow depth	- 0.04	0.96	0.44
Length winter	- 0.06	0.95	0.40

**Table 2.** Results of the stratified Cox proportional hazards model to test the effects of standardized age and environmental conditions on mortality rates, in both males and females. Total number of observations = 3138. Total number of events = 468. Variables in bold are statistically significant ( $p < 0.05$ ).

	$\beta$	$\exp(\beta)$	$p$ -value
<b>Age</b>	<b>0.20</b>	<b>1.22</b>	<b>&lt; 0.001</b>
T max spring	- 0.04	0.96	0.35
<b>Spring precipitation</b>	<b>0.06</b>	<b>1.06</b>	<b>&lt; 0.01</b>
T max summer	0.02	1.02	0.70
<b>T min winter</b>	<b>- 0.14</b>	<b>0.87</b>	<b>&lt; 0.001</b>
Snow depth	- 0.0009	1.00	0.44
Length winter	- 0.002	1.00	0.40

**Table 3.** Results of the stratified Cox proportional hazard model to test the effects of non-standardized age and environmental non-standardized conditions on mortality rates, in both males and females. Total number of observations = 3138. Total number of events = 468. Variables in bold are statistically significant ( $p < 0.05$ ).

Using a sex-stratified Cox model, we found that age, spring precipitation, and minimum winter temperature significantly affected survival.

Age emerged as the main predictor of mortality, with a strong positive effect on mortality risk in the study population; more in particular, for each year the risk of death rises by approximately 22%. This means that older individuals have higher mortality rates.

Most of the environmental variables were non-significant. Only spring precipitations and the mean minimum winter temperature proved to be significantly correlated to survival, both with strong coefficients but with opposite directions: precipitations had a positive effect, which means each additional mm of average daily precipitations during the spring period increased the hazard by 6%, while winter temperatures showed the most negative effect, as higher minimum temperatures reflect a decreasing mortality risk by 13%.

The proportional hazards assumption of the model was tested using Schoenfeld residuals and graphically examined. Each hazard proved to be proportional and independent of time, except for the variable of minimum winter temperatures, that showed a minimal borderline  $p$ -value ( $p = 0.04$ ),

however, the visual inspection of the residuals revealed no clear pattern of non-proportionality. (table S4 and figure S3).

*Influence of individual and environmental conditions on survival rates*

We tested the combined effects of individual absolute body mass and climatic variations on survival rates, based on animals' age, on the restricted dataset (*survival m 2000-2024*), from 2000 to 2024. In table 4 and 5, we can see the outputs of the model, with both standardized and non-standardized variables.

	$\beta$	$\exp(\beta)$	$p$ -value
<b>Age</b>	<b>1.23</b>	<b>3.44</b>	<b>&lt; 0.001</b>
<b>Absolute mass September</b>	<b>- 0.53</b>	<b>0.58</b>	<b>&lt; 0.001</b>
T max spring	- 0.06	0.94	0.74
Spring precipitation	0.38	1.47	0.08
T max summer	0.26	1.30	0.08
<b>T min winter</b>	<b>- 0.62</b>	<b>0.54</b>	<b>&lt; 0.001</b>
Snow depth	- 0.09	0.91	0.55
<b>Length winter</b>	<b>- 0.42</b>	<b>0.66</b>	<b>0.01</b>
<b>Length green-up</b>	<b>- 0.28</b>	<b>0.75</b>	<b>0.04</b>
Age: absolute mass September	0.25	1.29	0.05

**Table 4.** Results of the Cox proportional hazards model to test the influence of standardized age, individual body mass and environmental conditions on survival rates. Total number of observations = 729. Total number of events = 99. Likelihood ratio test=79.57. Variables in bold are statistically significant ( $p < 0.05$ ).

	$\beta$	$\exp(\beta)$	$p$ -value
Age	- 0.08	0.92	0.72
<b>Absolute mass September</b>	<b>- 0.08</b>	<b>0.92</b>	<b>&lt; 0.01</b>
T max spring	- 0.04	0.96	0.74
Spring precipitation	0.16	1.17	0.08
T max summer	0.20	1.23	0.08
<b>T min winter</b>	<b>- 0.46</b>	<b>0.63</b>	<b>&lt; 0.001</b>
Snow depth	- 0.001	0.99	0.55
<b>Length winter</b>	<b>- 0.01</b>	<b>0.98</b>	<b>0.01</b>
<b>Length green-up</b>	<b>- 0.04</b>	<b>0.95</b>	<b>0.04</b>
Age: absolute mass September	0.005	1.00	0.05

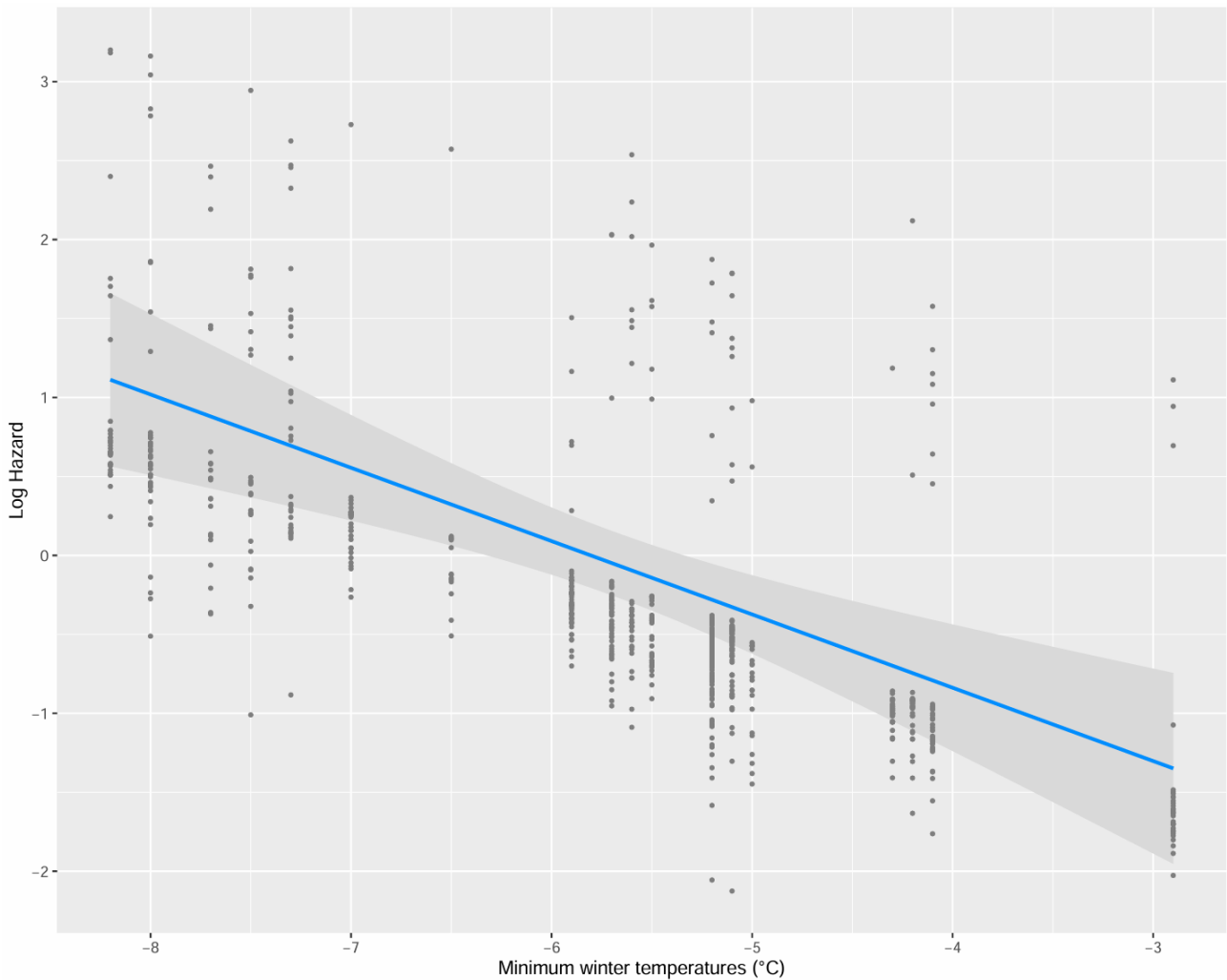
**Table 5.** Results of the Cox proportional hazards model to test the influence of age, individual body mass and environmental non-standardized conditions on survival rates. Total number of observations = 729. Total number of events = 99. Likelihood ratio test=79.57. Variables in bold are statistically significant ( $p < 0.05$ ).

Similarly to the previous model, there was strong evidence of the effect of age on mortality in the study population. Age showed a high and positive coefficient suggesting that, as expected, older males have higher mortality rates.

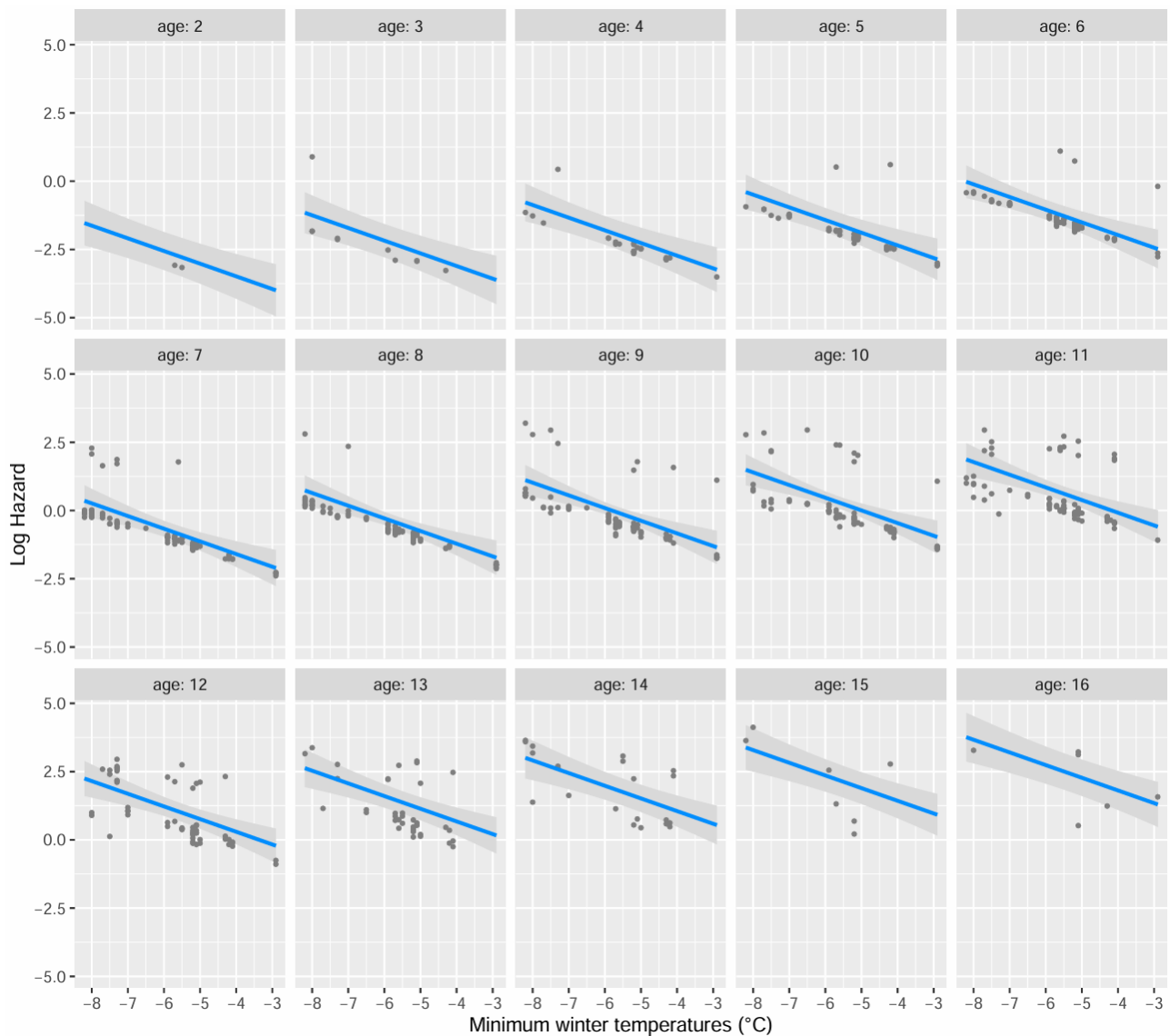
The absolute mass proved to be highly significant and correlated with mortality risk, with a negative effect, determining a decrease of the risk of 8%, for each additional kilogram.

Among the environmental covariates, the minimum winter temperatures showed the highest correlation with survival rates: higher values of minimum winter temperatures reduced the hazard risk by 37%. We visualized this effect in figure 7 and in figure 8, separated per ages. As statistically proved by the strong negative coefficients of this variable, also graphically, it is possible to assess that higher minimum temperatures during winter (i.e., warmer winters) are associated with inferior

mortality risk and higher survival rates and that this relationship is constant across age classes, showing a similar and consistent pattern in all ages. As for the other environmental variables, the total length of the winter and the vegetative period resulted significantly correlated, but showing negative effects. That means that longer winter periods decrease the risk by 2%, and that to longer vegetative seasons corresponds a decrease of mortality by 5%.



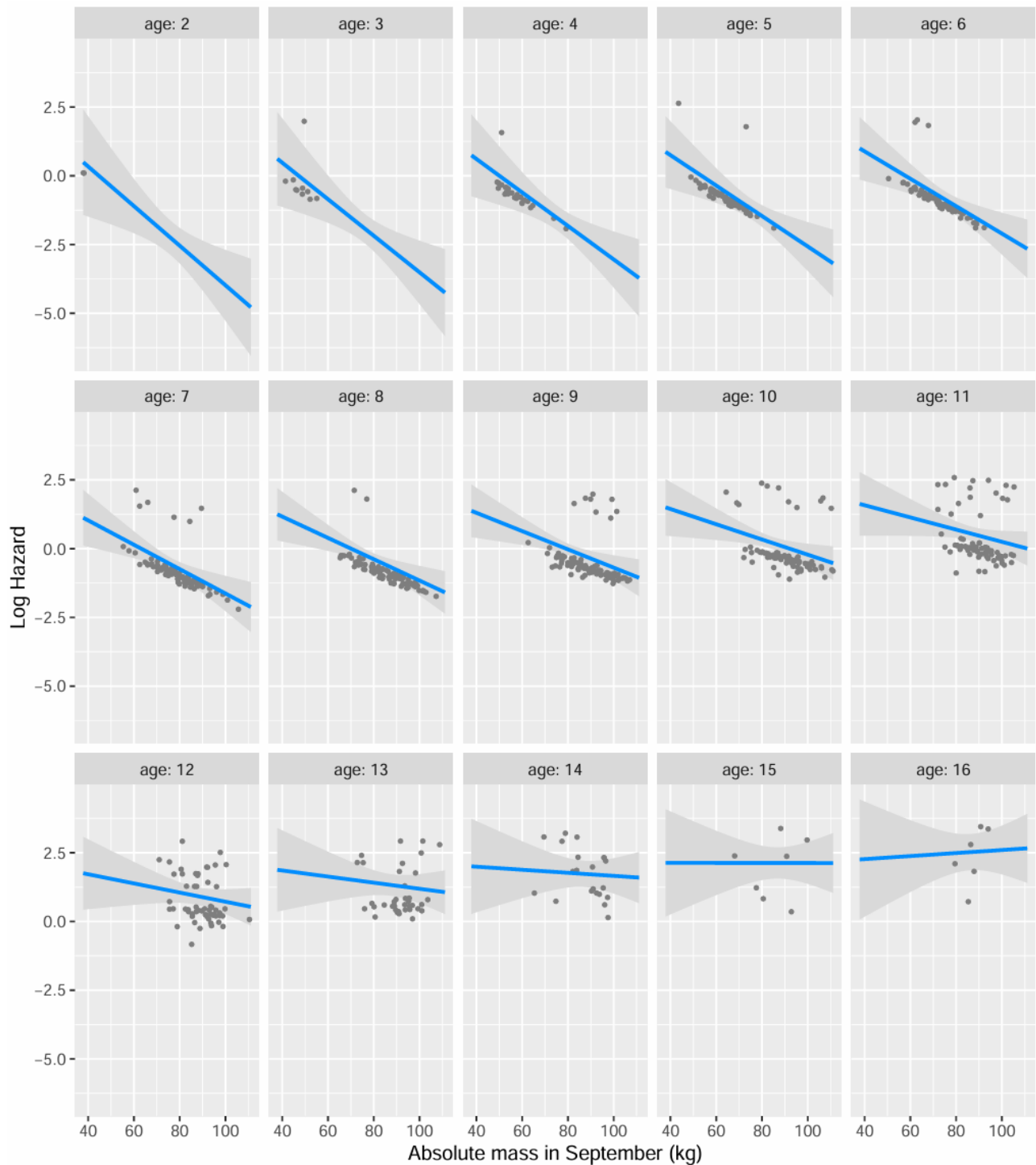
**Figure 7.** Graphical representation of the influence of minimum winter temperatures (°C) on mortality rates.



**Figure 8.** Graphical representation of the influence of minimum winter temperatures ( $^{\circ}\text{C}$ ) on mortality rates.

The model revealed a significant influence of the age-absolute mass interaction, displaying a positive coefficient and indicating that the effect of individuals' conditions is dependent on individuals' age. This relationship, between animal's age and their body mass on survival probability, is illustrated in figure 9, separated by different ages. The figure illustrates the clear effect of body mass on the hazard risk across different age classes, highlighting how this relationship changes over the animal's lifetime. In juveniles, from 2 to 7 years of age, we can see a marked negative relationship of the two predictors, highlighting the strong and positive effect of a higher body mass on reducing mortality risk. In prime-aged adults (7-11 years), the relationship still shows a moderately negative slope, while the senescent individuals' (> 12 year) slope flattens, suggesting the minor effect of body mass on senescent individual survival. Beyond 15 years of age, the relationship shows a slope that becomes slightly

positive, suggesting a modest negative effect of higher body mass on survival rates in older individuals. However, data for individuals reaching such advanced ages are limited.



**Figure 9.** Graphical representation of the interaction between animal's age and their absolute body mass, measured in September, stratified by age

The proportional hazards assumption of the model was tested using Schoenfeld residuals and graphically examined (table S5 and figure S4). Only one variable, minimum winter temperatures, showed a borderline  $p$ -value ( $p = 0.047$ ), but the visual inspection of the residuals did not show any clear pattern of non-proportionality, suggesting only a minimal and non-meaningful violation of the assumption.

## 6. DISCUSSION

In the present study we analysed which intrinsic and environmental variables affected male ibex survival during winter. In the study population overwinter survival resulted influenced by climate conditions, mainly spring and winter weather and vegetation phenology, as well as by the individual autumn body mass, representing the condition with which animals face winter season. We also highlighted a strong age-structured survival pattern, with relatively high survival rates in early ages, followed by a gradual decline in adults and a marked and sudden decrease at older ages.

Combining individual and seasonal environmental variables allowed us to identify which specific factor or condition could result in higher mortality risk in the Alpine ibex, across sexes and ages. Specifically, we found that the autumn body mass and the seasonal environmental conditions influencing the individual body condition and body fat use during winter, strongly affected survival, but this effect varied with age.

In mammals, survival is expected to vary across ages. Age-related mortality may increase from physiological and physical decline but also be exacerbated by environmental or density-dependent factors (Abrams 1991; Promislow 1991; Gaillard et al. 1994). Mountain ungulates populations are strongly age-structured (Gaillard et al. 1998; Festa-Bianchet et al. 2003) and the age-related influence on survival has been largely explored also in other ungulate populations (Loison et al. 1999b).

In our study, Kaplan-Meier survival estimates suggested that mortality rates in both sexes, were strongly shaped by age, providing evidence for effects of senescence on survival. In particular, survival probability decreased with age and the survival curves showed a net and progressive decline in survival probability with increasing animal's age. Males and females' survival rates proved to be different. This pattern is consistent with other studies in ungulate populations, where it was found that senescence commonly affected both sexes but with different rates and timing. Survival remained high during the first 6 years of life for both sexes, with minimal mortality events recorded. In both sexes, juveniles and sub-adults had the highest survival rate, over 90%. However, it has to be noted that this result only refers to animals from the age of 3, since data on newborns and yearling of the study population were not available. Between ages 8-10, survival probability decreased, corresponding to a notable increase in mortality events. Prime-aged adults (8-11 years), both males and females, showed very similar survival patterns with a rapid decrease in survival rates. Males' values were slightly higher but show a higher decrease than females. Up to the age of 10, males and females showed very high and similar survival probabilities. This is confirmed by nearly overlapping mean values and very wide confidence intervals in the females' survival curve, likely due to the limited amount of data. This overlap may indicate that survival rates were comparable between sexes during the juvenile and sub-adult stages. Beyond the age of 11, females showed a much higher survival

probability than males. Males reached 50% survival probability between 11-12 years compared to 12-13 years for females, indicating overall reduced male longevity. Between ages 11-14 males experienced particularly high mortality during this period, while females showed more moderate but consistent losses. After the age of 15, survival probability declined steeply in both sexes and around 20 years of age, survival probabilities for males and females were almost zero. This reflects also the fact that animals in the study population are not likely to reach such old ages, especially males.

Different life-history traits introduce sex-specific differences in survival rates of highly dimorphic and polygynous ungulate populations. Evidence of higher survival rates in females, at all ages, have been found in several ungulate species, due to various factors such as, reproductive effort, mating competition, level of the species' polygyny and energy requirements (Clutton-Brock et al. 1982, 1985; Gaillard et al. 1993, 2000; Jorgenson 1997). Age-specific mortality among polygynous males is expected to be linked to reproductive effort during the breeding season (Bonenfant et al. 2009). In our results, we did not find a constant higher survival rate in females, on the contrary, males, up to 9 years of age, showed slightly higher survival probabilities than females. This result may reflect the different reproductive investment and strategy of young and sub-adult males, who do not immediately engage intensively in rutting activities. Young males, because of the competition with older and bigger males, are less exposed to the high energetic expenditure and elevated injury risk that characterize the rut (Willisch et al. 2012), while in females, age of primiparity generally can vary between 2-4 years of age (Toïgo et al. 2002), experiencing earlier and higher energetic demands for reproduction, ultimately reducing survival. We observed a strong sex-related difference in survival rates among senescent individuals, more in particular beyond the age of 10. After this age, females showed higher probabilities to survive and less yearly variation across age groups, compared to males. This sexual difference in mortality rates could be caused by the different reproductive effort during the breeding season, occurring at the beginning of the winter period, when food resources are already declining and weather conditions tend to be harsh. During these adverse periods, females of ungulate population are known to maintain a conservative approach, decreasing reproductive effort and maternal care, to favour its own survival and body condition maintenance, rather than immediate breeding success (Gaillard et al. 1998, 2000; Simmonds et al. 2025). Also, in females, reproductive success increases during early life, stabilizes at prime-ages, and then declines from age 13 (Toïgo et al. 2002). On the other hand, adult and sexually mature males, allocate more energy to the breeding investment and physically risk more during the rut period, as intra-sexual competition occurs to gain access to females. This includes intense physical male-male confrontations, increased energy expenditure, hypophagia, and higher exposure to accidents while following females across steep terrains (Festa-Bianchet and Jorgenson 1998). It is known that male ibex reaches its maximum reproductive success

around 10-11 years of age but remains actively reproductive up to the age of 12-13 (Willisch et al. 2012; Apollonio et al. 2013), so this sex-related survival differences from female in old ages could arise from these different energy allocation patterns during the reproductive period. This analysis shows coherent results as in similar studies on other herbivores, reported by Gaillard et al. (1998, 2000), Festa-Bianchet et al. (2003) and by Toïgo et al. (2007) on the same study species, although, with some differences. While their study population reported exceptionally high male survival up to 13 years, similarly to females, our results indicate that sex differences emerge earlier, with males already showing a marked decline in survival after 10 years of age, reaching 50% survival probability at 11-12 years compared to 12-13 years for females.

Previous studies on many ungulate species observed more sensitivity to environmental variability in senescent individuals, being more fragile and physically susceptible, than juveniles and prime-aged adults (Jorgenson et al. 1997; Gaillard et al. 2000, 2003; Bergeron et al. 2022; Toïgo et al. 2007). In contrast to previous findings, we did not detect age-specific differences in the effects of environmental conditions. Minimum winter temperatures, for example, showed a consistent influence across all age classes (Fig. 8). Hence, the potential effect of environmental variability seems not to affect older male ibex, as equally as in other ungulates and different age classes proved to be equally resistant to fluctuations in environmental conditions.

The sex-specific differences in old individuals' survival rates that we obtained, could also be influenced by the limited number of data and events in our study, relative to females, specifically low in early ages. Also, the Kaplan-Meier curves showed very wide confidence intervals, especially for the females' curve in the first years of age. Such limited data for young females may therefore hide the true female-specific survival pattern, potentially showing larger differences in age-specific survival rates between females and males.

Survival in mammals can also depend on environmental conditions that ultimately can shape reproduction, forage availability, fat reserves accumulation and behavioural adaptations to climate variability (Gaillard 1998, 2000; Toïgo and Gaillard 2003; Bonenfant et al. 2009).

As expected, both spring and winter weather conditions influenced Alpine ibex mortality risk. The model including all individuals showed a positive effect of spring precipitation on the hazard risk, meaning that higher spring precipitations reduced survival probability over the following winter. This could be related to the fact that the precipitations in early spring periods mainly occurred as late snowfall. Temperate ungulates, after maintaining a negative energy budget during the winter period, stay in relatively poor condition for several weeks after snowmelt before fully recovering nutritionally (Kautz et al. 2020). Consequently, late and heavy spring precipitation (especially if they occur as snowfall), can determine addition snow cover on the ground, determining a temporal shift in the

beginning of the nutritional season. In the model including only males and a shorter time-span, spring precipitations maintained a positive effect on mortality rates but did not result significantly correlated. This could result from the different number of animals present in the two datasets, but also from the presence of females in the first one, that could be more susceptible than males to late precipitations during spring. In fact, in other mountain ungulates (Heffelfinger et al. 2017), it has been assessed the positive effect of spring precipitations on survival of females and juveniles. Spring rains during this period could enhance the green-up phase and increase forage quality, therefore becoming an important factor for animals emerging from a period of negative energy balance after the winter. Also, another difference between the effects in the two models, considering that the first model covers the years 1985–2024, while the second refers to a narrower period, 2000–2024, could arise from the general decreasing trend of this variable across years, due to a global climate change (Fig. S6).

Minimum winter temperatures showed a consistent negative effect on hazard rates in both models, meaning that milder temperature during winter decreased mortality rates and that this influence was constant over time in different ages and sexes. This result has also been confirmed by the visual inspection of this relationship, showing a consistent negative slope, also across different ages (Fig. 8). Higher minimum winter temperature can occur in strongly seasonal habitats, such as the Alps, suffering environmental and climate changes and relative extreme events. Higher temperatures during winter can provide a reduced snow cover and a faster snowmelt, hence an earlier access to forage resources, and overall advantageous effects during a period of poor body condition and negative energy balance. Moreover, milder temperatures allow temperate ungulates to save energy, reducing energy expenditure of thermoregulation (Signer et al. 2011).

We expected the snow depth at ground and the total duration of the winter period to have a negative direct impact on ibex mortality risk, by impeding to move or reach females during the rut, to feed when snow starts to fall and to escape predation or sudden events like avalanches. The second model showed a significant correlation between the duration of the snowy season and mortality rates, while in the first model, including only environmental variables, the amount of snow cover at ground and the total duration of the winter period did not have a great influence on survival probability. In both models, contrary to our expectations, snow cover and the duration of the winter period showed a negative effect on the hazard risk, meaning that higher snow cover and longer winters seemed to reduce mortality risks. Our results are found in contrast with other studies on mountain ungulates, which found that high levels of snowfall, resulting in prolonged snow cover during winter, negatively affected the survival of young individuals (Chirichella et al. 2020). Since we were more interested in the age-related differences in the effect of individual body condition on survival, we did not include the interaction of each environmental variable with age, so, from our results, it is not possible to

determine whether this variable might have different effects for specific age classes. However, this would be an interesting analysis to predict the effect of climate change on specific climatic and meteorological variables across different ages of the Alpine ibex. The positive influence on survival that we found could also arise from the fact that snowy winters with abundant snow cover increases the length of the green-up period, providing herbivores high-quality forage for a longer time (Pettorelli et al 2007; Cooper et al 2011). This could also be justified by the temporal trends of these variables in the last decades, showing a slow decrease, both in the level of snow cover, and also in the number of days with snowy precipitations, as well determined by a general increase in minimum winter temperatures and an earlier snowmelt (Fig. S6). Since climate change is likely to promote earlier phenology and faster plant growth (Wang et al. 2020), these conditions could enhance survival rates in herbivores, determining an earlier access to food resources in earlier spring periods.

The total length of the growing season negatively affected mortality rates, as longer vegetative period provides a much longer time-window of access to good-quality forage after the winter season. If snow starts to melt earlier, animals have an earlier access to high-quality forage and the period when animals need to rely on accumulated body fat is shorter, as higher spring temperatures and earlier snowmelts ultimately determine longer growing seasons. It has been observed, in the same study area, a temporal shift of the vegetative season during the last two decades and that, due to these earlier spring conditions, male ibex lost less mass during winter and started the new vegetative season with a higher body mass, decreasing also the summer mass gain (Brambilla et al. 2024). Given current climate-change trends, and the positive effect of longer growing seasons on survival, this relationship is expected to become even stronger.

Other environmental predictors, such as average maximum spring and summer temperatures, did not show significant effects on survival. Even though these variables showed non-significant weak effects on mortality rates, their directions were that one we expected. Spring maximum temperatures showed a negative effect on mortality risk, as higher spring temperatures determine a faster snowmelt and a earlier access to high-quality forage. Summer maximum temperatures proved to be positively associated with mortality rates, as warmer temperatures during the favourable season determine a variation in habitat selection, forcing animals to more rapid migration to higher altitudes, where the quality and abundance of forage is low. As also seen by Chirichella et al. (2020) in Alpine chamois, increasing summer temperatures could decrease survival rates, as animals could be led to spend more time resting than foraging, as ungulates reduce activities during the warmest hours of the day. This different allocation of time could affect the amount of stored body fat required to survival during the following winter (Brivio et al. 2016, Mason et al. 2014, 2017). However, due to the non-significance

of such variables in our model, no conclusion can be drawn about their effect on the population object of this study.

Overwinter survival in capital breeders rely especially on previously accumulated body fat reserves. Especially during a low energy balance period like winter, a large body size and good individual body conditions are associated to higher survival probability. In particular, the individual autumn body condition, including the amount of fat stored, can improve overwinter survival rates (Loison et al. 1999a; Stearns 2000; Apollonio 2020; Simmonds 2025). Evidence for this were, however, not available for male mountain ungulates, and our study addressed this gap in the literature. Our results confirmed what was expected, i.e., that body conditions at the end of winter affected overwinter survival in a male polygynous ungulate and that the effect was not constant in all age classes. In younger and sub-adult individuals (3-7 years), a higher body mass at the end of the favourable season was strongly associated with reduced mortality risk. Adults (8-12 years), having already reached the maximum body size and being at their prime, showed a diminishing influence of body mass on survival outcomes. This suggest that at this age, animals are more robust and less susceptible to environmental conditions and, since body condition is more stable at this age, it is no longer influential on survival rates. Senescent individuals (>12 years) showed an even more diminishing influence of body mass on survival outcomes: this means that at very old ages, more difficult to reach, individual body condition do not influence in mortality rates.

The general pattern we observed could indicate that, while body condition remained important, its relative contribution to survival decreased with age. Body condition is not an equally important predictor of survival across the animals' lifespan but rather shows age-specific patterns: it appears to be a significant predictor mainly in young individuals, while its role becomes marginal with increasing age. The combined influence of individual body mass and environmental conditions seemed to only affect positively the survival of juveniles and sub-adults, coherently with what is already known about the age-related survival differences in this species (Toigo and Gaillard 2003, 2007). This substantial age-related different impact on survival rates probably occurs because, at old ages, mortality rates are more stochastic and other variables, more than individual body condition, could have stronger effects, like senescence and susceptibility to diseases and to environmental conditions. This unfavourable positive relationship may also include greater energy expenditure and physiological stress resulting from maintaining a large body size, also because it may occur in individuals whose immune system is already compromised, due to senescence. Supporting this interpretation, Brambilla et al. (2024) revealed contrasting trends in body mass across age classes of male Alpine ibex: while younger males (7-8 years) increased autumn body mass by up to 15% between 2000-2022, the oldest individuals (13 years) showed significant declines over the same

period. This divergent pattern coincides with the ages (10-13 years) at which yearly survival starts to decline rapidly in this species (Toïgo et al. 2007), suggesting that senescent males experience higher costs of maintaining a larger body mass.

The observed strong effect of a larger body mass in juvenile survival could however also be overestimated due to the challenges of identifying the relative contribution to body mass of stored fat reserves and actual body growth. Young males indeed invest less in fat storage and more in skeletal growth than adult males. Since ibex growth rates are slow and reach adult size late, allocating less energy to early growth may allow them to invest more in maintenance, supporting higher survival rates. So, considering that, in juveniles, an increase in body mass includes not only body fat storage but also skeletal and horn growth, it would be important to distinguish the real potential beneficial effects of a greater body fat accumulation during winter. Adults, on the other hand, have already reached the maximum body size at the age of 10-12 years, so any variation in body mass reflects primarily changes in fat reserves rather than structural growth (Toïgo et al. 2007; Brambilla et al 2020a).

To assess the influence of the individual body condition on survival rates we used the value of the absolute autumnal mass, as a measure of animals' size. This variable could not necessarily be the most adequate to account for the real variability in the accumulated fat reserves during summer. One option could also be to use the value of the percentage increase in body mass, even though this estimate could be misleading, as it is based on the individuals' initial mass. Consequently, an animal that weighs less at the beginning of the season, for example a young one, will tend to accumulate proportionally more fat reserves than an adult or senescent individual that starts the season at a higher initial mass, ultimately overestimating the effect of the body mass. Ideally, it would be best to find a method that allows to accurately estimate the amount of body fat accumulated during each season.

More recent research in the Gran Paradiso National Park found an increase in survival rates (GPNP unpublished data) and also an increased body mass trend (Brambilla et al. 2024) in the last decades in the same study population. This is perfectly in line with our results, which allow us ultimately to state the strong and positive effect of higher body mass on survival rates.

It is important to underline that data for females were scarce compared to the males' data, due to a small number of marked individuals, especially in the last decade. However, given the possible interest on population dynamic variations and the presence of the long-term longitudinal study on the Alpine ibex population in the National Park, it would be important to apply the same analysis on an equal number of marked females. Young females do not adopt as riskier growth strategy as young males, that allocate more energy to skeletal growth and less resources to body fat storage. It is also

known that females' survival is less sensitive to harsh environmental conditions than the males' survival and that during rut females do not display the same food reduction rate (Clutton-Brock et al. 1985; Toïgo and Gaillard 2007; Brivio et al. 2010). Since these different patterns in reproductive effort and a consequent different energy expenditure during the breeding season, it would be interesting to explore the specific effects of the environment on females' mortality rates, considering also the individual body conditions and the body mass loss occurring during winter. Female survival rates could not be as affected by these variables as males' rates, but they would rather be more influenced by other factors such as the habitats they use, steep and rocky slopes, that can provide better protection for their offspring from potential predation, but, on the other hand can represent a higher hazard and lower forage availability.

## 7. CONCLUSIONS AND FUTURE PERSPECTIVES

This represents the first empirical study about male Alpine ibex variability in survival rates, based on estimates obtained from individually based data.

Our study demonstrated that overwinter survival in male Alpine ibex is shaped by a combination of intrinsic and seasonal environmental conditions and that the relationship between these variables and life-history traits, like survival, is complex and varies across different sexes and ages. Autumn body mass emerged as a key predictor of overwinter survival of male ibex, highlighting the importance of body condition in determining the individuals' ability to withstand adverse winter conditions and energetic limits. Seasonal weather and vegetational conditions, especially during winter and spring, influenced both individuals' body conditions and their survival probabilities, suggesting that resources availability and winter severity influence individual physical conditions. We also found a strong age-structured survival pattern, with higher survival probabilities in younger individuals, a progressive decline in adults and a sharp decrease at very old ages. This emphasizes the importance to consider age-specific differences when analysing mortality risk. In the end, these results show that combining individual traits with environmental conditions proved to be highly effective to understand mortality patterns in Alpine ibex. A better understanding of the future population dynamics of this species could be enhanced by future research also including environmental variations induced by climate change. Considering the rapid environmental changes affecting alpine ecosystems, a better knowledge of how climate change will alter winter severity and vegetation phenology is essential for predicting future survival patterns in Alpine ibex. In particular, modifications in temperatures and precipitations patterns could strongly influence survival and behavioural adaptations, like acclimatization and seasonal and altitudinal migration, of this species. To further confirm the results that we obtained here, in a long-term study perspective, it would be interesting to predict survival probabilities based on the animals' body condition at the end of the favourable season, in order to compare these predictions with the observed outcomes in the following year.

Furthermore, for future conservation purposes of the species, since the great relevance of individuals body condition resulted here, it would be important to continue the monitoring of individuals' body mass in the study population, to ultimately improve our understanding of the population dynamics and health status of this species.

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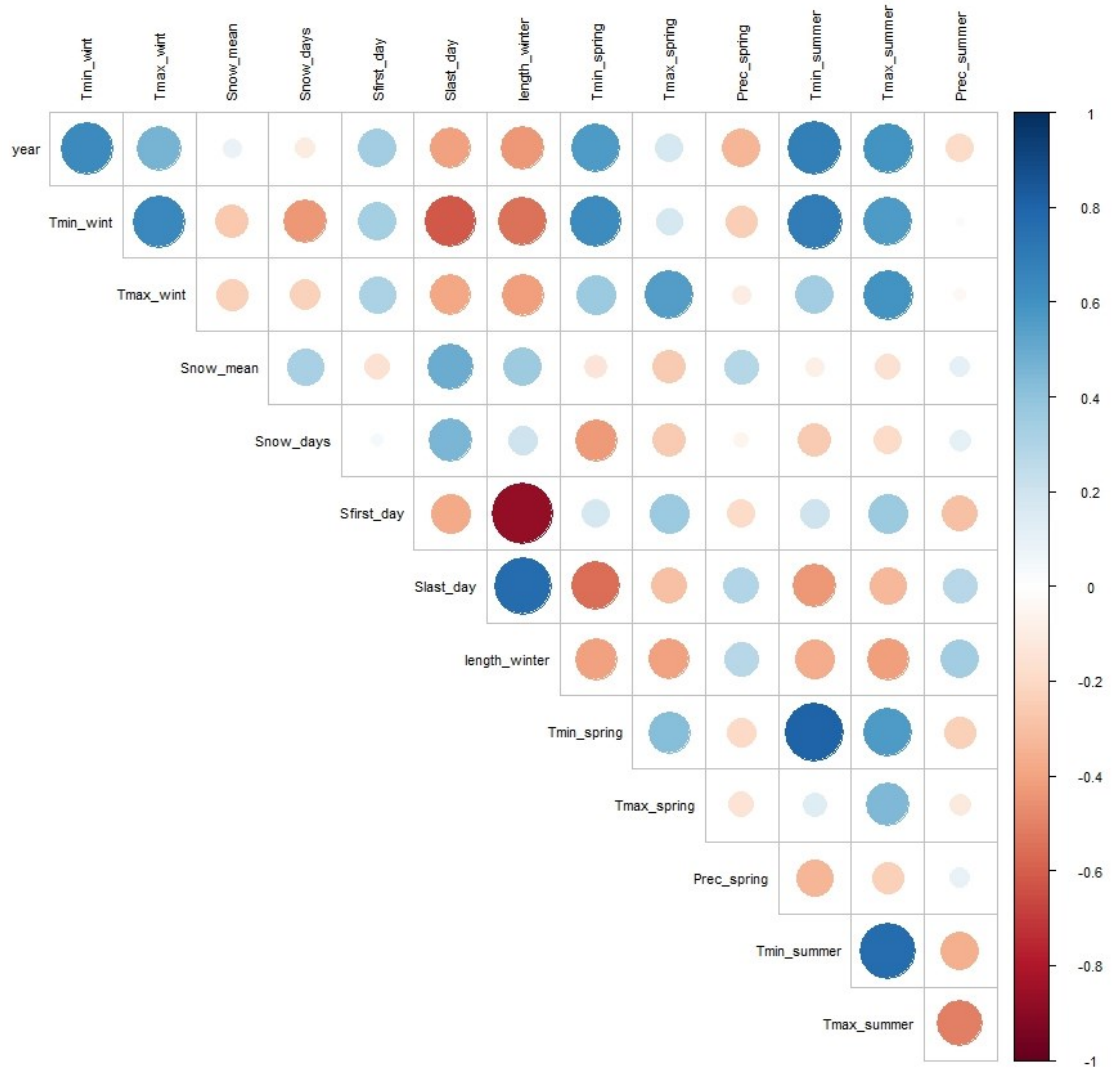
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## 9. SUPPORTING INFORMATION



**Figure S1.** Correlation matrix of the meteorological and climatic variables in Gran Paradiso National Park, in the framework of the present study (1985-2024).

	$\beta$	$\exp(\beta)$	$p$ -value
<b>Age</b>	<b>0.69</b>	<b>1.99</b>	<b>&lt; 0.001</b>
Sex male	0.30	1.34	0.08
T max spring	- 0.05	0.95	0.37
<b>Spring precipitation</b>	<b>0.17</b>	<b>1.18</b>	<b>&lt; 0.01</b>
T max summer	0.03	1.03	0.61
<b>T min winter</b>	<b>- 0.20</b>	<b>0.82</b>	<b>&lt; 0.01</b>
Snow depth	- 0.03	0.97	0.53
Length winter	- 0.05	0.95	0.42
Age: sex male	0.02	1.02	0.87

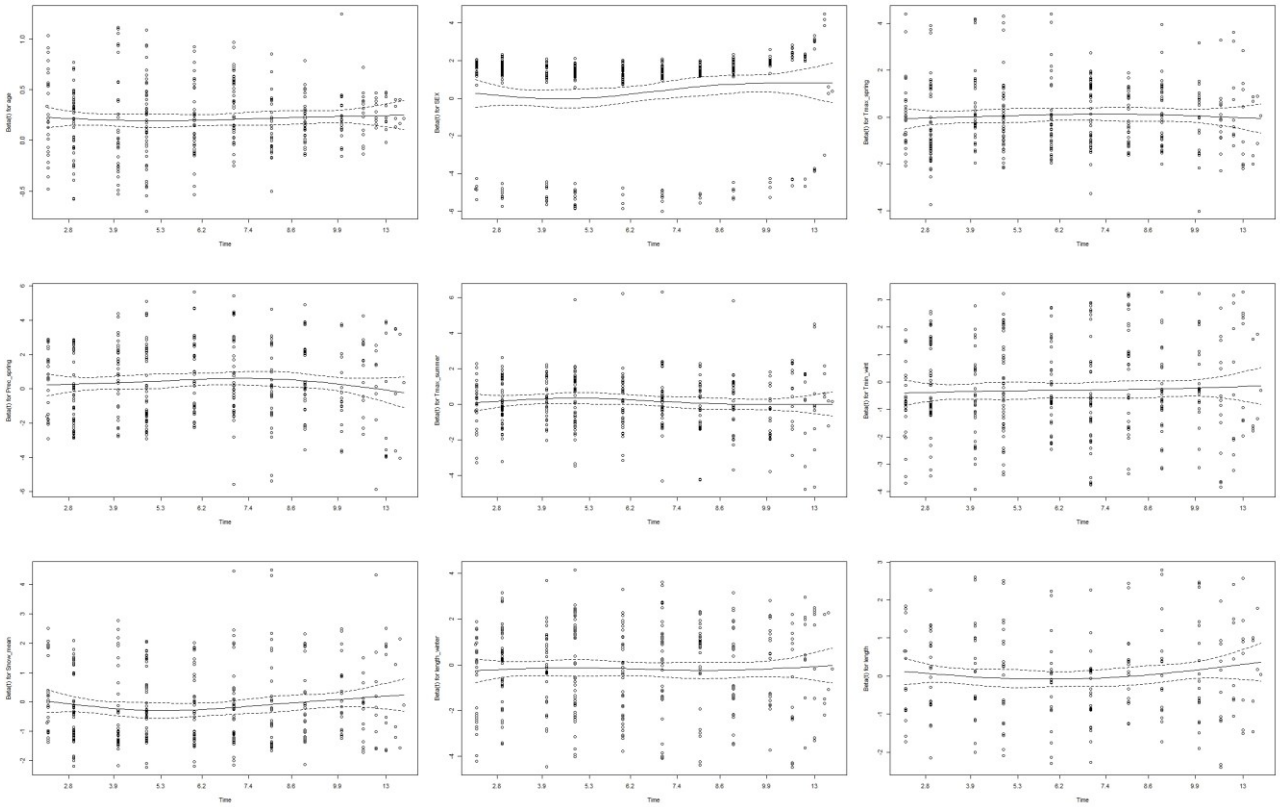
**Table S1.** Results of the Cox proportional hazards model to test the effects of standardized age and environmental conditions on mortality rates, in both males and females. Total number of observations = 3138. Total number of events = 468. Likelihood ratio test=178.4. Variables in bold are statistically significant ( $p < 0.05$ ).

	$\beta$	$\exp(\beta)$	$p$ -value
<b>Age</b>	<b>0.20</b>	<b>1.22</b>	<b>&lt; 0.001</b>
Sex male	0.25	1.28	0.57
T max spring	- 0.03	0.97	0.37
<b>Spring precipitation</b>	<b>0.06</b>	<b>1.06</b>	<b>&lt; 0.01</b>
T max summer	0.02	1.02	0.61
<b>T min winter</b>	<b>- 0.13</b>	<b>0.88</b>	<b>&lt; 0.01</b>
Snow depth	- 0.0006	1.00	0.53
Length winter	- 0.002	1.00	0.42
Age: sex male	0.006	1.00	0.87

**Table S2.** Results of the Cox proportional hazards model to test the effects of non-standardized age and environmental non-standardized conditions on mortality rates, in both males and females. Total number of observations = 3138. Total number of events = 468. Likelihood ratio test=178.4. Variables in bold are statistically significant ( $p < 0.05$ ).

	<i>p</i> -values
Age	0.70
<b>Sex male</b>	<b>0.0007</b>
T max spring	0.42
Spring precipitation	0.56
T max summer	0.67
T min winter	0.06
Snow depth	0.41
Length winter	0.44
<b>Age: sex male</b>	<b>0.002</b>
<b>GLOBAL</b>	<b>0.009</b>

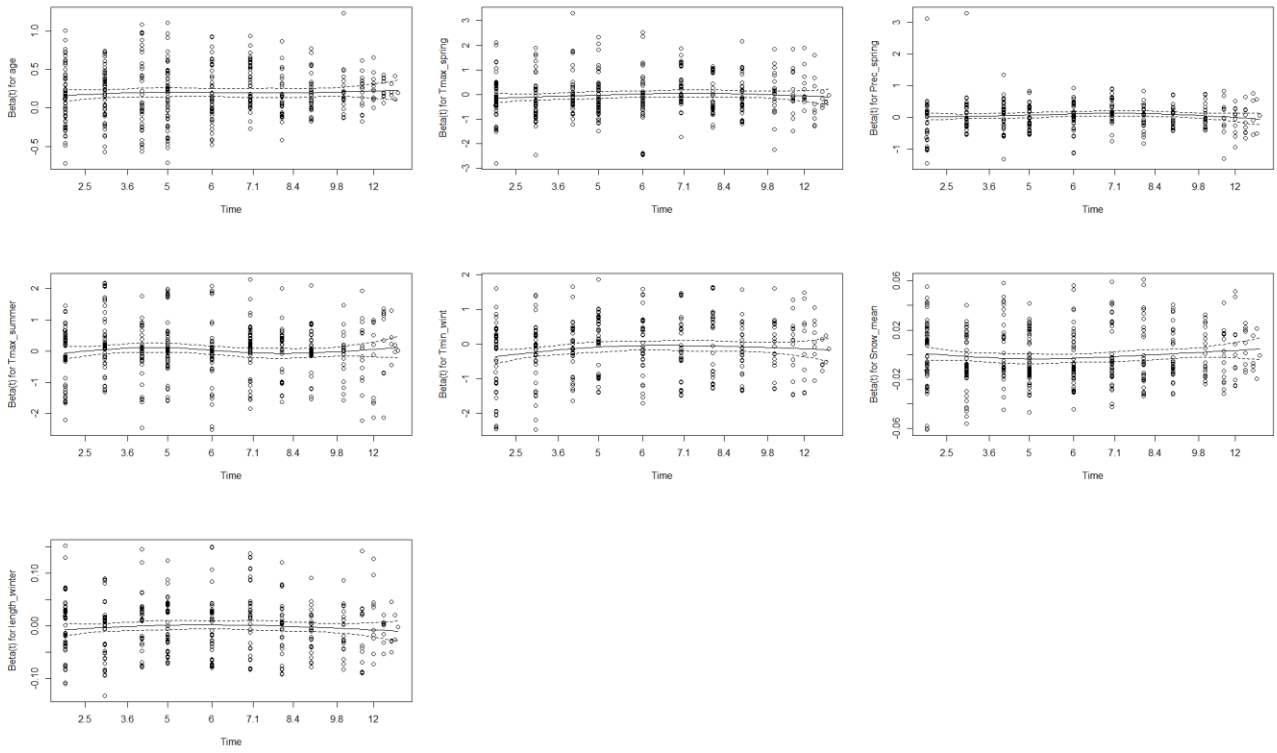
*Table S3. p-values from the Schoenfeld residuals test assessing the proportional hazards assumption for each covariate for the first original model. Variables in bold are statistically significant and violated the proportionality assumption ( $p < 0.05$ ).*



**Figure S2.** Schoenfeld residual plots for each covariate used to assess potential violations of the proportional hazards assumption in the first original model.

	<i>p</i> -values
Age	0.53
T max spring	0.43
Spring precipitation	0.62
T max summer	0.68
<b>T min winter</b>	<b>0.04</b>
Snow depth	0.56
Length winter	0.33
<b>GLOBAL</b>	0.28

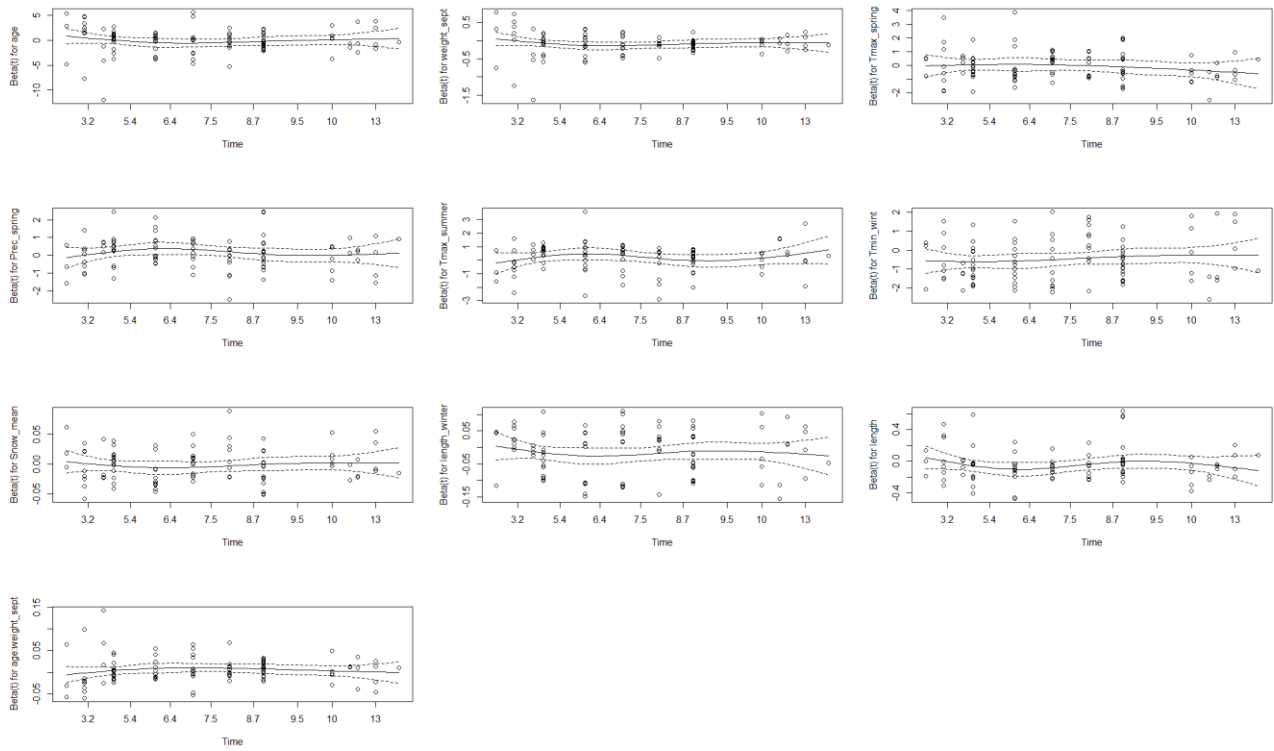
**Table S4.** *p*-values from the Schoenfeld residuals test assessing the proportional hazards assumption for each covariate for the first stratified model. Variables in bold are statistically significant and violated the proportionality assumption ( $p < 0.05$ ).



**Figure S3.** Schoenfeld residual plots for each covariate used to assess potential violations of the proportional hazards assumption in the first stratified model.

	<i>p</i> -values
Age	0.35
Absolute mass September	0.76
T max spring	0.24
Spring precipitation	0.85
T max summer	0.86
<b>T min winter</b>	<b>0.047</b>
Snow depth	0.95
Length winter	0.28
Length green-up	0.40
Age: absolute mass September	0.33
<b>GLOBAL</b>	<b>0.73</b>

**Table S5.** *p*-values from the Schoenfeld residuals test assessing the proportional hazards assumption for each covariate in the second model. Variables in bold are statistically significant and violated the proportionality assumption ( $p < 0.05$ ).



**Figure S4.** Schoenfeld residual plots for each covariate used to assess potential violations of the proportional hazards assumption in the second model.

	$\beta$	$\exp(\beta)$	$p$ -value
Age	NA	NA	NA
Absolute mass September	- 1.42	0.24	0.05
T max spring	- 0.14	0.87	0.42
Spring precipitation	0.36	1.44	0.10
<b>T max summer</b>	<b>0.30</b>	<b>1.35</b>	<b>0.04</b>
<b>T min winter</b>	<b>- 0.70</b>	<b>0.49</b>	<b>&lt; 0.001</b>
Snow depth	- 0.01	0.99	0.93
<b>Length winter</b>	<b>- 0.55</b>	<b>0.57</b>	<b>0.001</b>
<b>Length green-up</b>	<b>- 0.29</b>	<b>0.74</b>	<b>0.03</b>
Age: absolute mass September	0.09	1.10	0.14

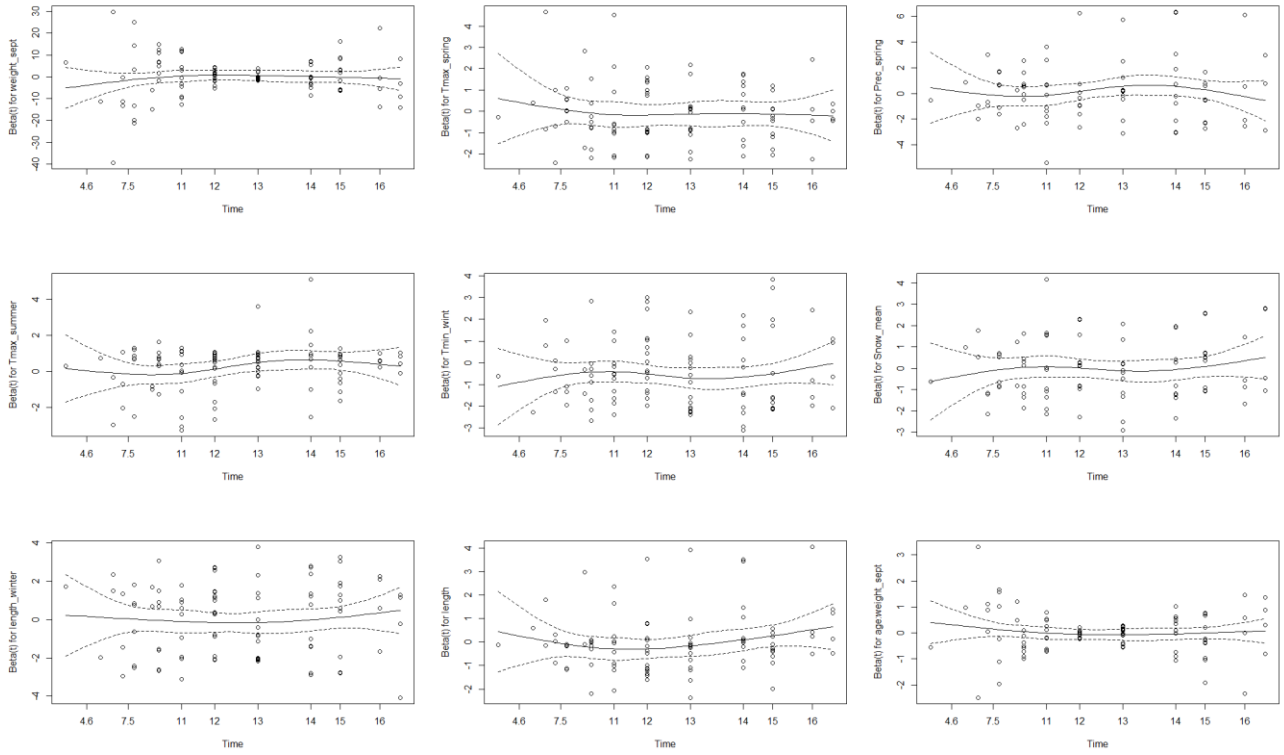
**Table S6.** Results of the standardized age-based model to test the correspondence with the time since capture model. Likelihood ratio test = 44.81. Variables in bold are statistically significant ( $p < 0.05$ ).

	$\beta$	$\exp(\beta)$	$p$ -value
Age	NA	NA	NA
Absolute mass September	- 0.10	0.90	0.05
T max spring	- 0.10	0.91	0.42
Spring precipitation	0.15	1.16	0.09
<b>T max summer</b>	<b>0.23</b>	<b>1.26</b>	<b>0.04</b>
<b>T min winter</b>	<b>- 0.52</b>	<b>0.59</b>	<b>&lt; 0.001</b>
Snow depth	- 0.0002	1.00	0.93
<b>Length winter</b>	<b>- 0.02</b>	<b>0.98</b>	<b>0.001</b>
<b>Length green-up</b>	<b>- 0.05</b>	<b>0.95</b>	<b>0.03</b>
Age: absolute mass September	0.007	1.00	0.14

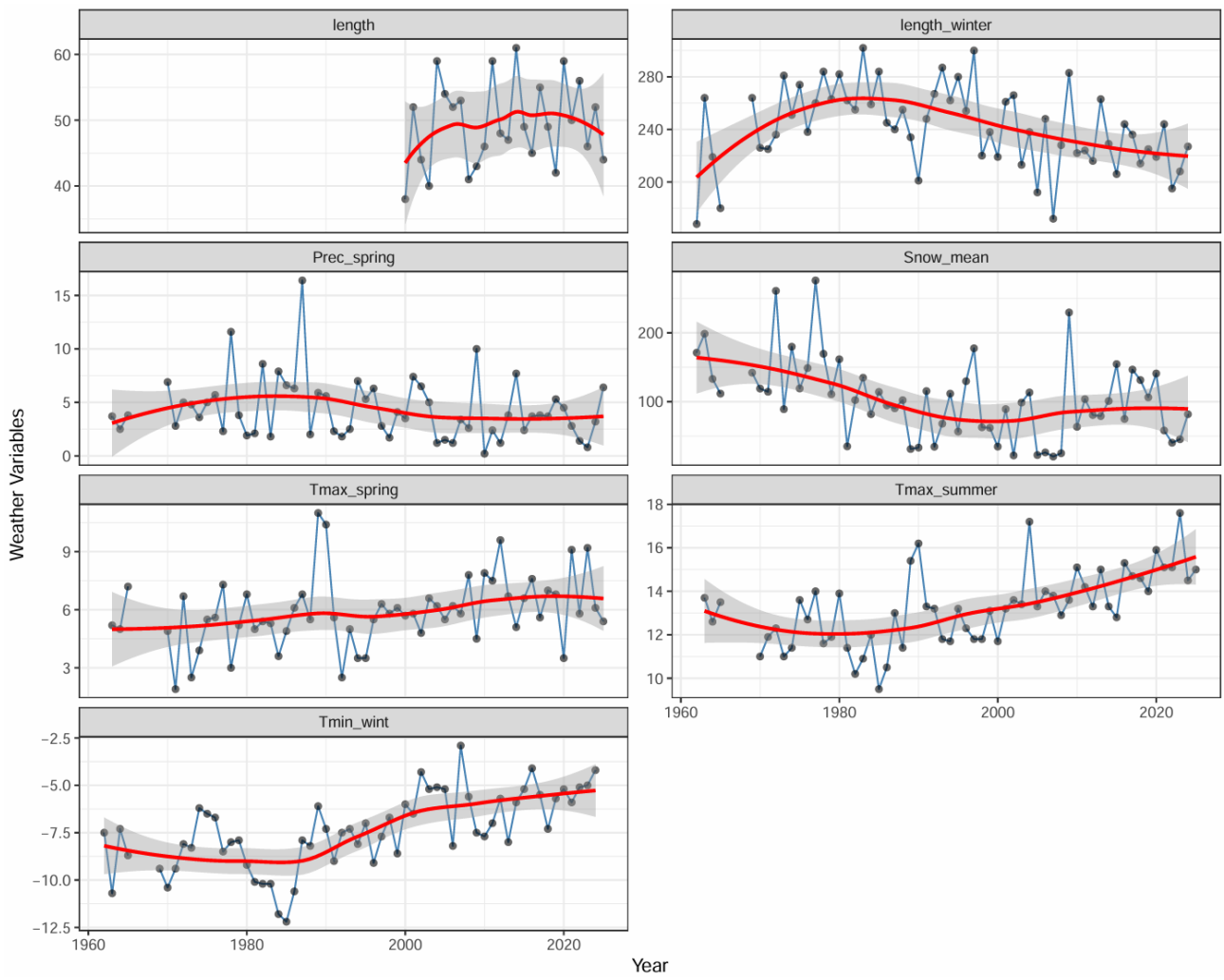
**Table S7.** Results of the non-standardized age-based model to test the correspondence with the time since capture model. Likelihood ratio test = 44.81. Variables in bold are statistically significant ( $p < 0.05$ ).

	<i>p-values</i>
Age	NA
Absolute mass September	0.16
T max spring	0.11
Spring precipitation	0.24
T max summer	0.10
T min winter	0.86
Snow depth	0.05
Length winter	0.28
Length green-up	0.07
Age: absolute mass September	0.31
<b>GLOBAL</b>	0.09

*Table S8. p-values from the Schoenfeld residuals test assessing the proportional hazards assumption for each covariate in the age-based model.*



**Figure S5.** Schoenfeld residual plots for each covariate used to assess potential violations of the proportional hazards assumption in the age-based model.



**Figure S6.** Temporal trends of phenological (2000-2024) and meteorological (1985-2024) variables in Gran Paradiso National Park.