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Environmental and individual-level drivers of movements and space use in three ungulate species

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**Déterminants environnementaux et individuels des
mouvements et de l'utilisation de l'espace chez trois espèces
d'ongulés sauvages**

**Environmental and individual-level drivers of
movements and space use in three ungulate species**

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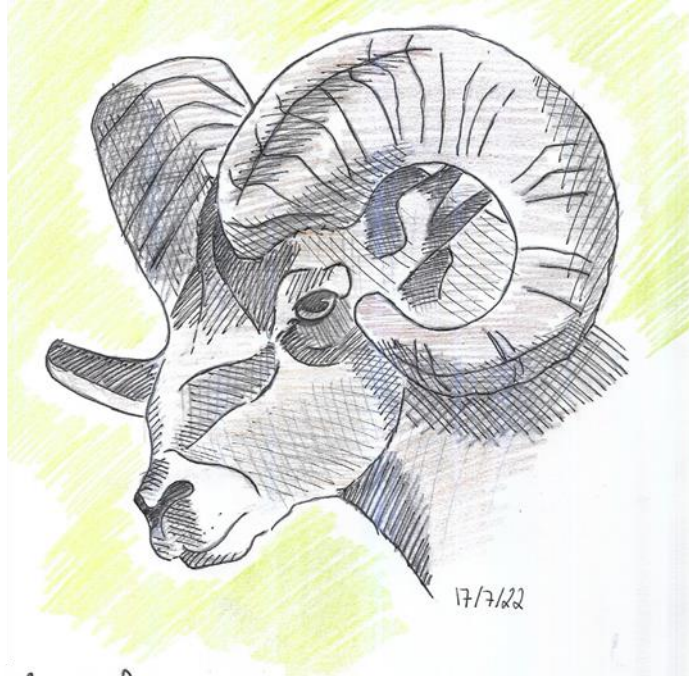


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Chapter 1:

General context

1. An era of major and fast global changes: the Anthropocene

Human activities profoundly affect and transform land surfaces and the composition of the atmosphere, to such an extent that many experts now suggest to refer to the present epoch as the Anthropocene, the “epoch of Man” (Lewis & Maslin, 2015). Whilst the start date of this new epoch is still debated (Zalasiewicz, 2015), many authors argue that the intensification of human activity in the mid-20th century has, in addition to major geochemical changes, lead to irreversible changes in the Earth’s biosphere, which will probably be observable in the geological stratigraphic record for millions of years into the future (Lewis & Maslin, 2015; Zalasiewicz et al., 2017). Indeed, since the 16th century, extinction rates increased consistently, with a dramatic acceleration since the beginning of the 19th century (Waters et al., 2016), to such an extent that current extinction rates are estimated be a 100 up to a 1000 times higher than background rates (Ceballos et al., 2015; De Vos et al., 2015), and could lead, if maintained, to the extinction of 75% of species in the next centuries (Waters et al., 2016). The main causes of current day biodiversity losses are associated with human activities. Overexploitation through hunting or fishing is one of the most documented causes of known extinctions for the past two centuries (Otto 2018). For example, the Food and Agriculture Organization of the United Nations (FAO 2020) reported in 2017 that only 65.8 % of commercially exploited fish stocks were within biologically sustainable levels, while this number was about 90% in 1974, and that 75% of the Mediterranean and Black Sea fisheries remain subject to overfishing (FAO-General Fisheries Commission for the Mediterranean 2020), which may lead to a risk of extinction for many species (Crookes & Blignaut, 2019). Another key driver of extinctions and current extinction threats is habitat loss and degradation (Figure 1). Habitat loss is indeed a prolonged process where habitat patches preferred by humans are changed first, leaving a fragmented mosaic of suitable patches where species may persist over a short term, but be subject to a longer term risk of extinction, due to declining genetic diversity and local perturbations (Otto, 2018). This phenomenon is referred to as “extinction debt” (Kuussaari et al., 2009), although it still remains challenging to assess accurately the number of threatened

species, as many remain unknown to science (Otto, 2018). In addition to overexploitation and habitat loss, the intensification of global trade and transport during the last decades has facilitated the spread of invasive species (Banks et al., 2015), which are also considered one of the major threats for biodiversity (Figure 1). Invasive species are indeed recorded as the sole driver of extinction in about 20% of known species extinctions, and are considered a risk to 27% of the currently threatened terrestrial vertebrate species and between 14 to 40% of the critically endangered species included in the IUCN Red list (Bellard et al., 2016; Dueñas et al., 2021). By altering ecosystems processes and function like nutrient cycling, seed dispersal, pollination and trophic interactions, through predation, competition and hybridization with native species (Pyšek & Richardson, 2010; Vilà et al., 2011), invasive species are responsible for major environmental damages and economic losses, which amount to \$120 billion annually in the United States alone (Pimentel et al., 2005). Finally, greenhouse gas emissions caused by human activities are responsible for the rise of global average surface temperatures, which have increased by 0.95-1.20°C since the late 1800's and are predicted to increase further by 1.5°C to 4°C by 2100 (IPCC, 2021), with critical consequences for ecosystems and human systems (Hoegh-Guldberg et al., 2018). Climate change is for example already affecting plant distributions and phenology, with increasing temperatures and shorter winters inducing altitudinal shifts, earlier green-up and senescence (Cremonese et al., 2017; Vitasse et al., 2021), as well as accelerating habitat loss (Mantyka-Pringle et al., 2012) and disease spread (Caminade et al., 2019; Ogden & Gachon, 2019). Increasing frequencies and severity of extreme weather events such as heatwaves (and associated wildfires), droughts, cyclones, floods or hurricanes (Ummenhofer & Meehl, 2017), lead to further population declines and local extinctions (Mantyka-Pringle et al., 2012; Maxwell et al., 2019). Not only is climate change a direct driver of biodiversity change but it increasingly exacerbates the impact of the other key drivers of biodiversity loss, especially land use change, overexploitation of natural resources, invasive species etc., and the compounding effects of these drivers pose the major threats for biodiversity in the 21st century (IPBES 2019).

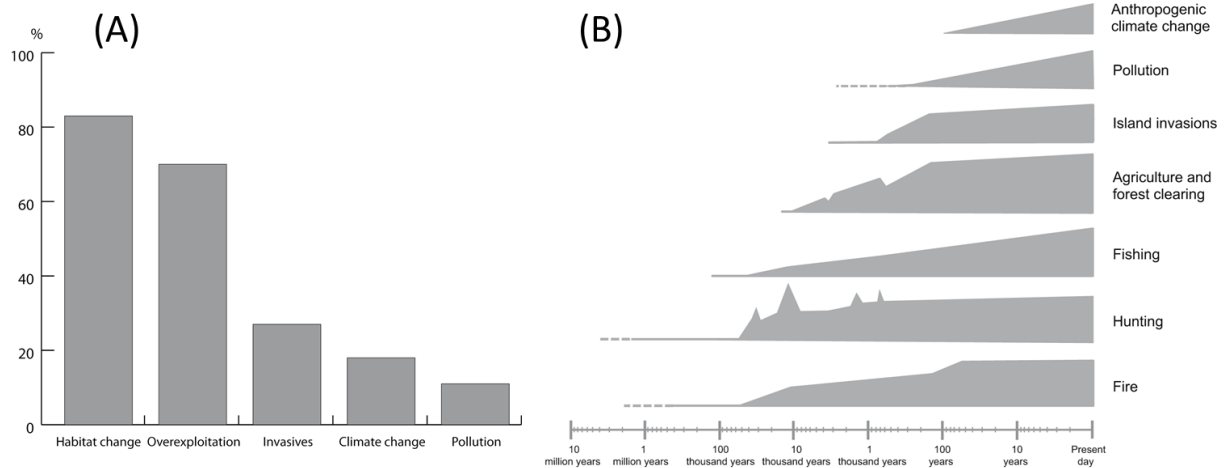


Figure 1: (A) Proportion of threatened species affected by each driver. Threatened species ($n = 4,259$) include mammals, birds, and amphibians in the following Red List categories: critically endangered, endangered, and vulnerable. Main threats are classified as habitat change (i.e., residential and commercial development, agriculture and aquaculture, energy production and mining, transportation and service corridors, and natural system modifications), overexploitation, invasive species, climate change, and pollution. Several threatened species are affected by multiple threats. (B) Qualitative representation of the temporal evolution of the main anthropogenic drivers of biodiversity change. References used for dating the pressure trend of each driver: fire, hunting, fishing, agriculture and forest clearing, species invasions on islands, pollution, and anthropogenic climate change. Figures extracted from Pereira et al. (2012).

2. Investigating the capacity of animals to cope with disruptive environmental changes: the role of behavioural ecology

Under current rapid global change scenarios it is important to investigate how species, which have evolved and adapted to their habitat over thousands to millions of year, may adapt to current rapid environmental change. Organisms respond to environmental variation by either local adaptation or phenotypic plasticity. Local adaptation occurs at the population level over longer time scales, through spatial matching of adaptive genetic variation and environmental variation and leads to populations to have traits allowing higher survival and reproduction in the local environment than elsewhere.

Phenotypic plasticity, i.e. the ability of one genotype to produce multiple phenotypes across different environmental conditions, is instead a more rapid response by individual organisms altering their behaviour, morphology or physiology in response to environmental variation and may buffer species from extinction by “buying them time” to evolve through local adaptation (Diamond & Martin, 2021). In particular, research has been increasingly focusing on behavioural plasticity, due to its important role in explaining species differences in the ability

to cope with human induce rapid environmental changes (HIREC, Sih et al., 2011). Indeed, behaviourally plastic species may better cope than behaviourally “rigid” species with HIREC, by either showing a wider array of innate behaviours for each environmental context (i.e. “contextual plasticity”, Stamps, 2016), or increased learning capacities that may enable individuals to modify or develop new behaviours in response to novel environmental conditions (i.e. “behavioural flexibility”, Stamps, 2016; van Schaik, 2013). For example “rigid” species may show maladaptive responses, such as insufficient behavioural responses to new predators (i.e. prey naivety, Moseby et al., 2015; Rödl et al., 2007), or preference for habitats where their fitness is lower, based on formerly informative cues which have become misleading under HIREC (“ecological traps”, Hale & Swearer, 2016; Sih, 2013). Inversely, plastic species are expected to be better able to respond to novel predators (Quinn & Cresswell, 2005) or parasites (Koprivnikar et al., 2012; Ruiz-Raya & Soler, 2017), to use novel resources or habitats (e.g. exploiting novel opportunities in anthropogenic landscapes, (Bressler et al., 2020; Fleming & Bateman, 2018); or to avoid or cope with novel stressors such as pollution (e.g. noise pollution, Duquette et al., 2021; light pollution, Da Silva et al., 2016; chemical pollution, (Araújo et al., 2020; Bertram et al., 2022). Moreover, behavioural plasticity is also expected to directly influence the ability of individuals to cope with climate change and represents a key factor to predict species resilience or susceptibility to this threat (Beever et al., 2017). However, studies documenting behavioural responses to climate stressors are relatively recent and further work investigating their implication in fitness and population dynamics is still needed to assess the potential of behavioural plasticity to buffer species from climate change (Beever et al., 2017).

The study of the spatial behaviour of animals is expected to be crucial to obtain a mechanistic understanding of how species distributions and abundance respond to climate change (Grémillet & Boulinier, 2009; Morales et al., 2010). Indeed, while phenomenological models have been developed to forecast changes in species distributions, their low predictive power, and the coarse spatial scales and level at which they are carried out, have made most of them unsuccessful to adequately predict population-level responses to climate change (Buchholz et al., 2019; Matthiopoulos et al., 2015). In fact, population dynamics and distributions are mediated by the fine scale movement decisions of individuals, in relation for example to foraging (e.g. Höner et al., 2005; Weimerskirch, 2018) or the avoidance of risk (i.e. predation and human disturbance), allowing individuals to track shifting biotic (e.g. conspecifics, predators, preys) and abiotic (e.g. precipitations, temperature) environmental conditions. Such adaptive changes in individual movements and habitat use should translate into energetic and

fitness benefits (DeCesare et al., 2014), allowing species to persist in modified or novel habitats (Sih, 2013). While the links between movement behaviour, individual performance (i.e. survival and reproductive success) and population dynamics have long been discussed by ecologists (Frederick & Ogden, 1997; Gaillard et al., 2010; Pulliam & Danielson, 1991), progress in the past decades in technologies to track animals (GPS and biologgers, Wilson et al., 2014) and the computing power to process the data and fit novel statistical methods (Demšar et al., 2015) is increasingly enabling researchers to collect and process the required information about animal movement trajectories, habitat selection, physiology (e.g. energy expenditure) and demographic parameters (i.e. survival and reproductive success). Thus, the study of animal movement offers new and exciting avenues to improve our understanding of how individual decisions influence demographic parameters and ultimately translate into population dynamics (Morales et al., 2010, Figure 2).

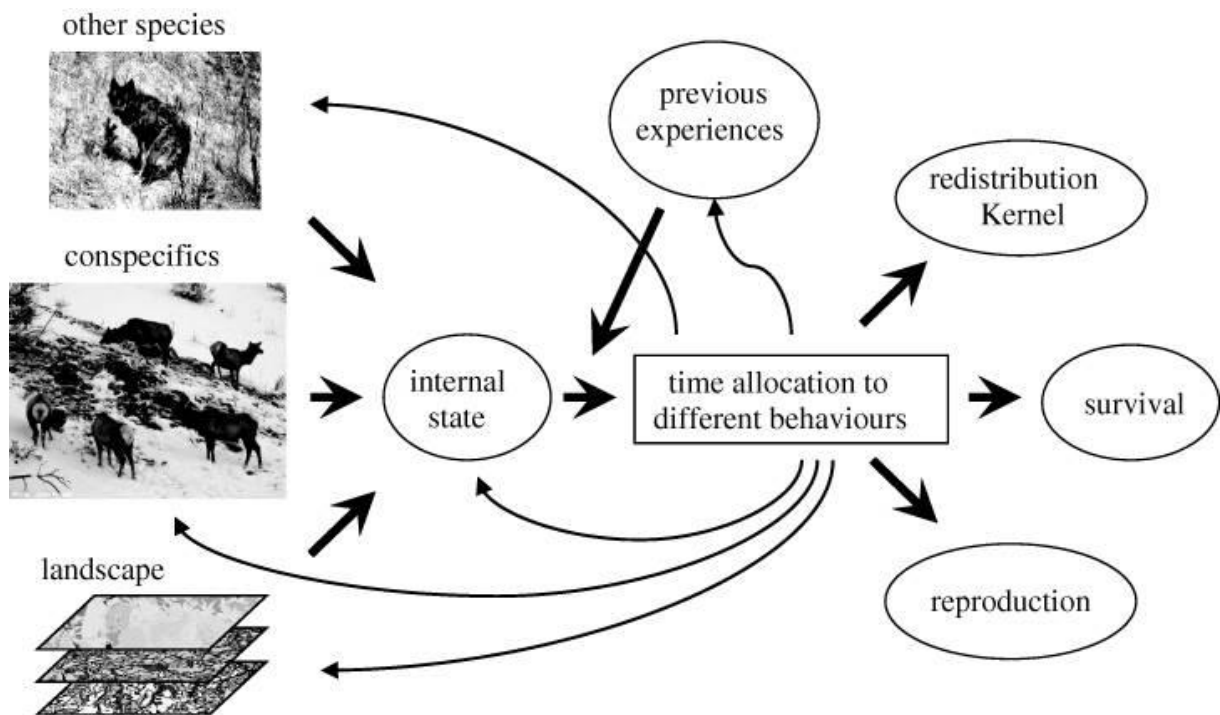


Figure 2: Sketch for developing mechanistic links between animal movement and population dynamics (Morales et al., 2010). Authors consider a catch-all, and usually unobserved, individual internal state that integrates body condition (reserves, reproductive status, etc.). Several factors affect the dynamics of this internal state, including social interactions with conspecifics, trophic or other interaction with other species and surrounding landscape attributes. Internal state dynamics determines the organism's time allocation to different behaviours such as food acquisition, predator avoidance, homing, landscape exploration and so on, but this is also modulated by previous experiences and phenotypic traits such as behavioural predispositions. As these different behaviours imply different movement strategies, the time budget determines the properties of the redistribution kernel that describes space use. Time allocation to different behaviours will also affect individual survival and reproduction and thus overall population dynamics.

3. The case of ungulates: an ubiquitous group with multiple conservation and management challenges

Among mammal species, ungulates, i.e. “hoofed animals”, are some of the most studied ones, which can be explained by their high ecological, economical and socio-cultural importance. Ungulates are a keystone species in the functioning of many ecosystems, as they occupy a central place in trophic networks (Ripple et al., 2015), including predator-prey dynamics (Gebo et al., 2022; Vucetich et al., 2011) and the structure, composition and dynamics of vegetation (Bernes et al., 2018). Through their different activities, ungulates may directly alter their habitat and have facilitative effects on other herbivore species, by enhancing habitat heterogeneity via their feeding behaviour (Kanga et al., 2013), or by creating habitats for other species, e.g. for amphibians through the formation of temporal pools via wallowing (e.g. Baruzzi & Krofel, 2017). In addition, ungulates may also influence ecosystem processes such as seed dispersal, nutrient cycling or fire regimes, resulting in ungulates being often considered as “ecosystem engineers” (Ripple et al., 2015).

The influence of ungulates on human and natural systems directly depends on their density, which is strongly affected also by anthropogenic factors. In Africa and Asia, large herbivores are faced with many threats related to human activities, such as hunting (and poaching), competition with livestock, and habitat loss related to land-use (e.g. human encroachment, cultivation, and deforestation), to the extent that 43 of the 74 largest terrestrial herbivores (~58%) are subject to population declines, and 44 of them (~60%) are listed as threatened with extinction (Ripple et al., 2015). As keystone species and ecosystem engineers, the decline of large herbivores populations may have cascading effects on biodiversity and ecosystem process such as a decline in the abundance of predators, scavengers or other herbivores species (Gordon et al., 2019), decreased tree growth and reproduction through liana encroachment (Coverdale et al., 2021) and the loss of other ecosystem services like seed dispersal (Poulsen et al., 2013), nutrient cycling (Sitters et al., 2020) and fire control (Waldram et al., 2008). The decline of large herbivores may also have socio-economic; as 1 billion of the poorest inhabitant of the planet rely on wild meat, often through hunting of ungulates, as their main source of protein (Brashares et al., 2014), with subsistence hunting being still very important in several human populations (e.g. Rao et al., 2010; Wilfred & MacColl, 2014). The decline of charismatic herbivores species and their related predators may also affect the income obtained by rural populations from ecotourism (Ripple et al., 2015). Finally, the decline of large herbivores may also further worsen related wildlife trade and even human trafficking and organized crime issues (e.g.

Janjaweed, Lord's Resistance Army, al-Shabab, and Boko Haram in Africa, Brashares et al., 2014).

Contrary to Africa and Asia, no large herbivore species in North America, and only one in Europe, the European bison (*Bison bonasus*), are threatened by extinction (Ripple et al., 2015). This is mostly due to the fact that the majority of North American and European megaherbivores has been extirpated during the late Quaternary megafauna extinctions, probably due to human expansion on the continent (Sandom et al., 2014). By the end of the 19th and the beginning of the 20th century, ungulate populations in Europe reached their historical minimum, mostly due to hunting, deforestation and competition with livestock (Putman et al., 2011). During the second half of the 20th century instead ungulates populations in Europe drastically recovered, mainly thanks to numerous reintroduction programs and changes in management and hunting practices (Maillard et al., 2010; Putman et al., 2011), but also to the renaturalisation/reforestation of habitats due to the abandonment of agricultural land (Acevedo et al., 2011) and the extirpation of local predators such as wolves or bears (Okarma, 1995; Schwartz et al., 2003). Roe deer (*Capreolus capreolus*) for example may represent the species with the most extensive recovery, being present now in about 74% of Europe with an estimated population of 10 to 15 million individuals (Burbaiteè & Csányi, 2009), while it nearly faced extinction in some countries like England or Sweden at the beginning of the 20th century (Putman et al., 2011). Other large herbivores like red deer (*Cervus elaphus*) or moose (*Alces alces*) have also considerably increased in population size and the omnivorous wild boar (*Sus scrofa*) is now present in 71% of the European continent (Linnell et al., 2020).

Mountain ungulate populations have also largely benefitted from these changes in socio-ecological factors, the most iconic example being ibex (*Capra ibex*). While there were no more than a hundred individuals left in Europe at the beginning of the 19th century, located in the Gran Paradiso Massif in Italy, the prohibition of ibex hunting in 1821 and the institution of of the Gran Paradiso Royal Hunting Reserve by King Vittorio Emanuele II in 1856, prevented the species from going extinct and even enabled the population to increase to up to 3000 individuals at the beginning of the 20th century (Brambilla et al., 2020). It is then thanks to the numerous reintroductions during the second half of the 20th century that ibex populations were able to recover and recolonize the entire Alpine arc, with an estimated over 55000 individuals living in the Alps in 2015 (Brambilla et al., 2020). Similarly, chamois (*Rupicapra rupicapra*), which were only present in the Alps in the 19th century, began to reappear naturally in the Jura Massif by the end of the 19th century, and were successfully reintroduced, just like the European

mouflon (*Ovis aries musimon*), to various massifs in France and across Europe (Corlatti et al., 2022; Maillard et al., 2010). However, in contrast with cervids and wild boar, the range and size of mountain ungulate populations increased much more slowly (% of Europe surface), and some species have even been experiencing recent declines. For example, five out of the 10 subspecies of chamois are listed as threatened by the IUCN, and 3 of them are currently experiencing population declines (i.e. *Rupicapra rupicapra asiatica, balcanica & caucasica*, (Corlatti et al., 2011; IUCN, 2020). The threats for the conservation of chamois are numerous and common to other ungulates. Among them we can mention diseases (Iacopelli et al., 2020; Loison et al., 1996), competition with livestock (Brivio et al., 2022; Chirichella et al., 2014) or other wild ungulates (Ferretti et al., 2015), overharvesting and poaching, and climate change (Chirichella et al., 2021; Semenzato et al., 2021).

Thus, the conservation and management of ungulates species is a critical issue in Europe, as these species hold a high social, cultural, economic and ecological value (Figure 3). A key socio-economic role of ungulates is as game species for hunters, with more than 7 million ungulates harvested each year in Europe, the majority of them roe deer and wild boar (3 million each), followed by red deer (over 720 000), moose (around 190 000), other deer (around 250 000) and finally mountain ungulates (around 100 000 individuals across all species, Linnell et al., 2020). However, the demographic explosion of ungulates, especially cervid species and wild boar, has started to cause conflicts with human activities (Valente et al., 2020), especially in human-dominated landscapes. Linnell et al. (2020) estimated that more than 560 000 animals were involved in vehicle collisions in Europe, each year with more than 360 000 of them being caused by roe deer, followed by wild boar with around 73 000 collisions. Damages to agriculture by wild boar were estimated to amount to around 80 million of euros per year (Apollonio et al., 2010) and forest damages made by other ungulates species in European countries species may range from 150 000 euros in Sweden, up to more than 15 million euros in Poland (Linnell et al., 2020). In addition, wild ungulates are an important reservoir of diseases (e.g. sarcoptic mange, Iacopelli et al., 2020 ; keratoconjunctivitis, Loison et al., 1996 ; brucellosis, White et al., 2011), and their high densities may accelerate the appearance and spread of zoonoses, as more than 70% of these originates from wildlife (Jones et al., 2008), . Deer species, for example, represent an important reservoir of tick-borne diseases and are one of the factors influencing the prevalence of Lyme disease (Mysterud et al., 2016).

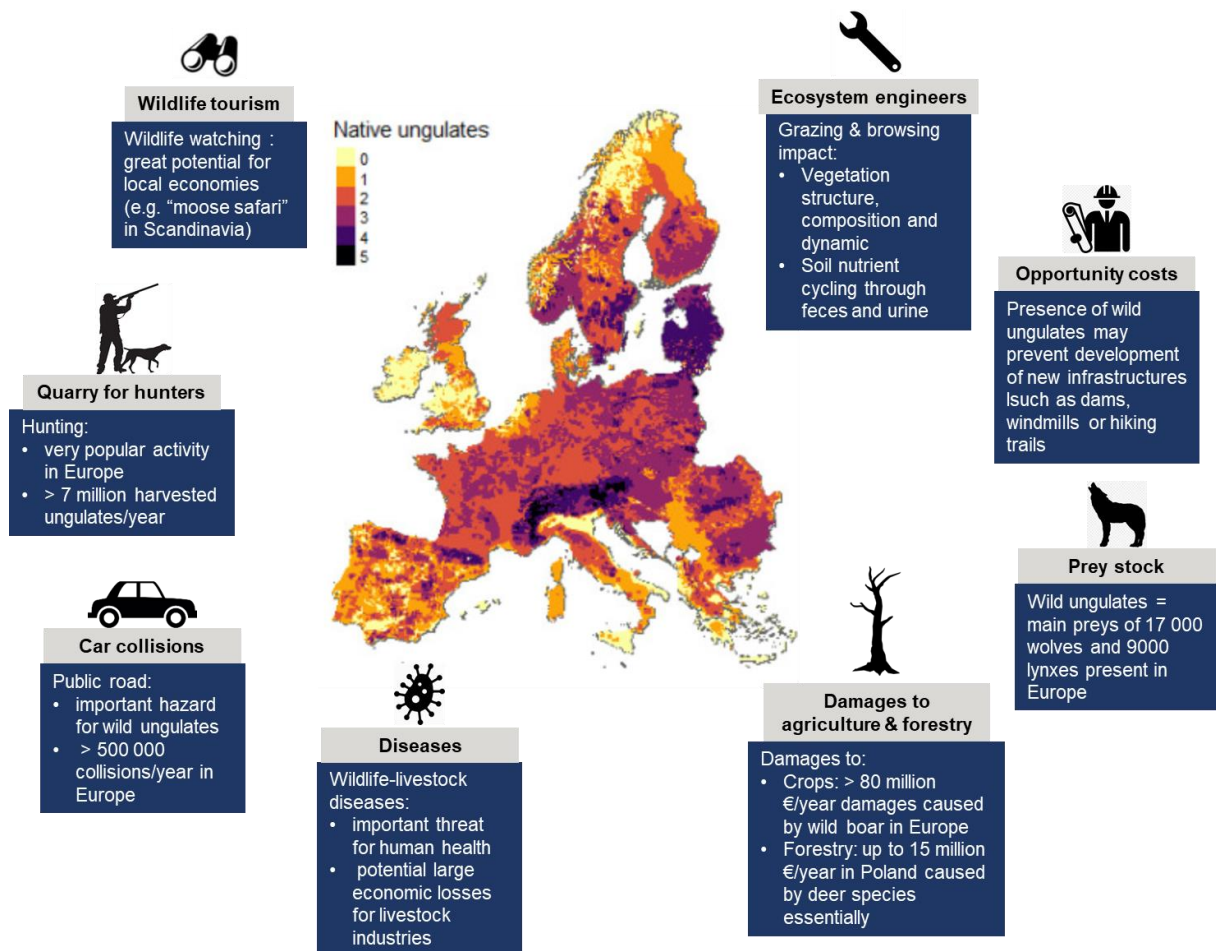


Figure 3: Graphical abstract of the different services and disservices offered by wild ungulates in Europe. Reproduction from Linnell et al. (2020)

Given the expected increase in human-wildlife conflicts due to the ongoing expansion and intensification of human activities (e.g. tourism, agriculture, urbanisation, outdoor sports), developing wildlife management policies promoting sustainable coexistence is urgently needed (Linnell et al., 2020; Valente et al., 2020). Investigating the main drivers of ungulates population dynamics and their responses to global changes (i.e. climate change and landscape anthropization), is then crucial if we aim to infer efficient management practices. Thus, as population dynamics and distribution are often the results of fine-scaled individual behavioural decisions, we propose through this thesis work, to focus on the link between spatial behaviours and environmental constraints. In this regard, I will first introduce the theoretical and methodological background of our study, before investigating the environmental and individual-level drivers of movements and space use in three alpine ungulate species.

Chapter 2:

Theoretical context

1. Living in a heterogeneous landscape: being at the right place at the right time

a. The evolutionary implications of behaviour and the movement ecology paradigm

Behavioural ecology aims to understand how behaviour evolves in relation to ecological conditions, including both the physical and the social environments (intra-specific and inter-specific competitors, predators and parasites, Davies et al., 2012). Considered as a fusion between ethology and ecology (hence sometimes the synonym eco-ethology is used, although less preferred), it is often said to have emerged during the 1960's when Niko Tinbergen (1963) outlined the four questions to consider when studying a particular behaviour (or any other biological trait in general). For example, if we ask the question “Why are roe deer males periodically territorial?”, we may answer the question as follows:

- *Causation or mechanisms*: the individual shows this behaviour because external stimuli trigger internal mechanisms like hormonal changes, or the activation of certain parts of the nervous system. In roe deer, the increase of daylength triggers hormonal changes in plasma testosterone levels, which play an important role in male territory establishment and defence behaviours (Sempéré & Lacroix, 1982)
- *Development or ontogeny*: The onset of the observed behaviour is influenced by genetic or developmental mechanisms. In roe deer, testosterone levels are correlated with testis, and territoriality thus emerges only when males have reached sexual maturity, i.e. when testis are fully developed, which explains also why territoriality is absent in fawns (Sempéré & Lacroix, 1982).
- *Adaptive value or function*: The observed behaviour provides an adaptive advantage in terms of survival or reproductive success for the individual and should be therefore favoured by natural selection if it is hereditary. Roe deer males defend a territory to attract females and their reproductive success is directly influenced by the ability of individuals to successfully hold a territory (Vanpé et al., 2009)

- *Evolutionary history or phylogeny*: The observed behaviour has evolved in response to both past and present selective pressures. Rutting period in roe deer is only occurring during July and August, yet males are territorial from March to August. This may be explained by the fact that roe deer males that initiate territoriality earlier may be more successful in holding and defending their territory and hence successfully breed with visiting females. Thus, the extension of the territorial season is thought to be the outcome of an evolutionary arms race, where the initiation of territoriality has been pushed as far back as is energetically possible, i.e. at the start of the vegetation period (Wahlström, 2013)

Causation and ontogeny are referred as the proximate causes of behaviours (i.e. how behaviours are expressed during the individuals' lifespan) while adaptive value and evolutionary history are referred to as ultimate causes (i.e. how and why behaviours emerged and evolved within populations or species). Behavioural ecologists have been investigating the proximate and ultimate causes of key fitness-related behaviours such as foraging (Perry & Pianka, 1997), mating strategies and tactics (Bowyer et al., 2020), predation avoidance (Laundre et al., 2010), territoriality and parental care (Gross, 2005), cooperation (T. Clutton-Brock, 2009), or communication (Hebets et al., 2016). Movement however may represent one of the most crucial behaviours for individual fitness, as it often is through movement that animals can perform many activities crucial for their survival and reproduction, such as foraging movements between and within food patches (Owen-Smith et al., 2010), escaping predators (Stankowich, 2008), or search for a mate (Foley et al., 2015), and track changing environmental conditions during migration (Fudickar et al., 2021) or search for better conditions (e.g. increased food availability or decreased competition) via dispersal (Bowler & Benton, 2005). Yet, research on movement behaviour has long been hampered by technical limitations in monitoring animals in the wild while concomitantly obtaining field estimates of individual demographic performance (Gaillard et al., 2010). Thanks to ongoing technological and methodological developments to track animals (GPS and biologgers, Wilson et al., 2014) and process and model the data (Demšar et al., 2015), researchers are increasingly able to collect and model animal movement and demographic data (i.e. survival and reproductive success). Work in movement studies has also been unified under the conceptual framework of movement ecology, which unifies several areas of enquiry in the broader field (Nathan et al., 2008). Under the Movement Ecology paradigm, animal movement behaviour is the result of the influence of four components: three

component intrinsic to the individual, the internal state (why move?, e.g. because of hunger, fear, fatigue, etc), motion (how to move?, e.g. swim, walk, crawl, fly), and navigation capacities (when and where to move? e.g. sensory abilities such as echolocation or magnetoreception, Whiley & Day, 2019), and cognitive abilities such as memorization and mental maps, (e.g. Trapanese et al., 2019), and one extrinsic component, environmental conditions. This conceptual framework, in combination with in the ongoing development in wildlife tracking technologies and associated analysis methods, allows to improve our understanding of the drivers of individual movement decisions, how these influence demographic parameters and ultimately translate into higher scales patterns of population dynamics and distribution (Morales et al., 2010). Movement ecology is especially relevant within the context of global change and human-dominated landscape, as for example mammals in areas with higher human impact ('human footprint') have reduced mobility globally, i.e. on average one-half to one-third the extent of their movements in areas with a low human footprint (Tucker et al., 2018). The authors argued that this was likely due to behavioural changes and physical limitations to movement, with impacts not only on individual performance and population persistence, but also other key ecosystem process such as nutrient cycling, predator-prey interactions or diseases transmission.

b. The case of food acquisition and optimal foraging theory

Foraging is a fundamental activity for animals, as it directly concerns the ability of individuals to locate and acquire food resources, and thus energy, which in return affects their survival or reproduction. For this reason, foraging studies represent one of the oldest and most investigated fields in behavioural ecology (Pyke, 2019). Of importance within this field is Optimal Foraging Theory (OFT), as it strongly influenced the development of foraging ecology. OFT is based on the key assumption that individual animals maximise their fitness by minimising the time and energy costs of foraging and maximising food intake. A key question addressed is hence how much time a forager should spend on any food patch, before moving to another; key predictions made by OFT thus concern habitat and diet choice and movements. (Schoener, 1971). MacArthur & Pianka (1966) and Emlen (1966) first formulated the idea that if animals use optimally their time and energy budgets, they should maximize the net energy gains per unit of time, by maximizing gross energy intake rate while minimizing the costs of energy acquisition. Animals may achieve this either by visiting patches with abundant resources (reducing

acquisition time) or which are spatially clustered between each other (reducing patch searching and traveling time), and select food items which are the most nutritious (i.e. through better or faster assimilation, shorter handling times and overall higher energetic value). Schoener (1971) further developed the theory by describing animal foraging behaviours as a continuum between two strategies, time minimizers or energy maximisers, which may be favoured differently by natural selection, depending on how net energy gains may ultimately translate into reproductive success. If for example reproductive function is a continuous function of net energy rate, then individuals which act as “energy maximizers” should be selected, whereas individuals with fixed reproductive outputs should be time-minimizers, i.e. they should minimize time spent acquiring the minimum resources necessary to their maintenance and reproduction (Boutin, 1990; Schoener, 1971). Importantly, whilst earlier studies on foraging strategies tried to estimate whether a species may be regarded more as an energy maximizer or a time minimizer, recent work suggest that in reality, the place of an individual on this continuum is likely to vary through time and space, depending on the individual internal state (e.g. high vs low energy reserves and/or high vs low energy requirements), but also on the temporal and spatial heterogeneity of resource distributions and the temporal scale at which foraging is studied (i.e. short vs long-term energy intake rate). For example, Bergman et al. (2001) demonstrated that bison behaved as time minimizers on the longest temporal scale (i.e. 4 days), by selecting patches with intermediate forage quantity and quality, rather than choosing patches with the highest forage quantity but lowest digestibility (as expected in an energy-maximizing strategy). However, over shorter time scales such as the 2h time scale used to record bison behaviour continuously, implicitly behaved as energy maximizers by foraging in the same patches at maximum instantaneous rates.

In addition to foraging strategies, an additional complexity comes from environmental heterogeneity, as the distribution of resources is often patchy and individuals must therefore dedicate an important part of their time and energy to locate and travel between food patches. Moreover, the exploitation of a given patch by an individual leads to a progressive decrease in the patch profitability, to the point where energetic costs linked to exploitation (e.g. hunting or handling time) may equal or even outweigh energetic gains. Therefore, the “marginal value theorem” (Charnov, 1976), one of the most broadly used optimality model, predicts that the optimal use of a patchy habitats should consist in individuals departing from the patch they are exploiting when their net rate of energy gain in the patch is inferior to the average rate of the habitat (i.e. across all other habitat patches). In addition, time spent within a given patch may

also depend of the amount of resources available in it and the travelling time between patches. In general, individuals may for example stay longer in a patch if it contains lower resources or if the time spent travelling is higher.

Despite some discrepancies between predictions and observations, which earned OFT some critics in its earlier development (G. H. Pyke, 1984), including at times heated debates (e.g. the “Eight Reasons Why Optimal Foraging Theory Is a Complete Waste of Time”, by Pierce & Ollason, 1987), OFT still laid the conceptual foundations for the study of foraging behaviour and lead to several important evolutionary insights which “should not be wasted” (Stearns & Schmid-Hempel, 1987). More than 50 years after its foundation, the conceptual and heuristic legacy of OFT is in fact now well-established, as the theory has developed considerably and demonstrated to be successful in terms of predictions (although more qualitatively than quantitatively) and thus proved to be a strong and useful theory in behavioural ecology (Pyke, 2019). The original OFT has been considerably expanded through the inclusion of several constraints on foraging behaviour linked either to external factors (e.g. risk avoidance, climatic and weather conditions), and internal factors (e.g. internal state like body reserves, health, reproductive state, or individual characteristics like sex or age). In the following paragraphs, I will review how some of these factors and their interactions may influence individual foraging activities and their resulting patterns in movement, habitat use and activity budgets.

c. The landscape of risk and the food/cover trade-off

One of the earliest criticism of OFT in its original form was that fitness may not depend only on foraging, but also on other activities linked to survival or reproduction, which may greatly constrain individual foraging behaviour (Hixon, 1982). Similar to the landscape of resources (the foodscape, Duparc et al., 2020), the spatiotemporal distribution of actual risk (i.e. “the landscape of risk” linked to direct predation, hunting, collisions with traffic), and perceived risk (i.e. the “landscape of fear”, Laundré et al., 2010) caused by the presence of predators and human disturbances, greatly influences the spatial behaviour and activity budgets of animals. This constraint was one of the first to be included in expanded models of OFT (Brown, 1988, 1992) to take into account that foraging may be a dangerous activity for prey species, as they might visit places where predators are more abundant, more able to detect them or to capture them, while also being less vigilant while they are eating (Sirot et al., 2021). Consequently, many species should adopt behavioural strategies that allow them to both maximize their energy acquisition and minimize the time spent at risk, if they are to maximize their fitness (Brown, 1992). How animals resolve this behavioural trade-off between foraging and risk avoidance has been one of the most studied questions in behavioural ecology (Verdolin, 2006). Lima & Dill (1990) for instance outlined four components in the way animals make behavioural decisions under predation risk constraints, i.e. where, when, what and how to feed, and at which spatial and temporal scales, i.e. from the choice of the location of the home range in the landscape (“second order of selection”) to the selection of patches (“third order selection”) and of food items within the latter (“fourth order selection”, Johnson, 1980, Figure 1). As “how” and “what to feed on” are beyond the scope of this thesis, we will not detail them and rather focus on the “when” and “where to feed” components of the food-risk avoidance trade-off.

First, “where to feed?” concerns decisions made by individuals regarding the spatial dimension of the food-risk avoidance trade-off, i.e. movement and habitat selection. Indeed, sometimes the best patches in terms of forage profitability may also present a higher probability of encounter with a predator (e.g. Hebblewhite & Merrill, 2009). Risk avoidance may then cause foraging opportunity loss for individuals, as it may for instance constrain individuals to either migrate, or establish their home range, select patches within them, or even places within patches, where foraging conditions may be suboptimal but offering lesser predation risk (Hebblewhite & Merrill, 2009; Smolko et al., 2018) or human disturbance, (e.g. tourism, recreational activities or hunting, Kolk et al., 2022; Pęksa & Ciach, 2015; Tolon et al., 2009).

These patches may also be selected by animals if they offer greater cover (i.e. decreased probability to be detected by predators, Loggins et al., 2019) or visibility (i.e. better ability to detect stalking predators, e.g. (Balme et al., 2007; Cowlshaw, 1997)), or escape opportunities (e.g. distance to refuge, Iribarren & Kotler, 2012), or increased group size (i.e. higher probability to detect or escape predators through shared vigilance and dilution effects, although at the potential cost of increased competition for food, Beauchamp, 2019; Creel et al., 2014; Polyakov et al., 2022).

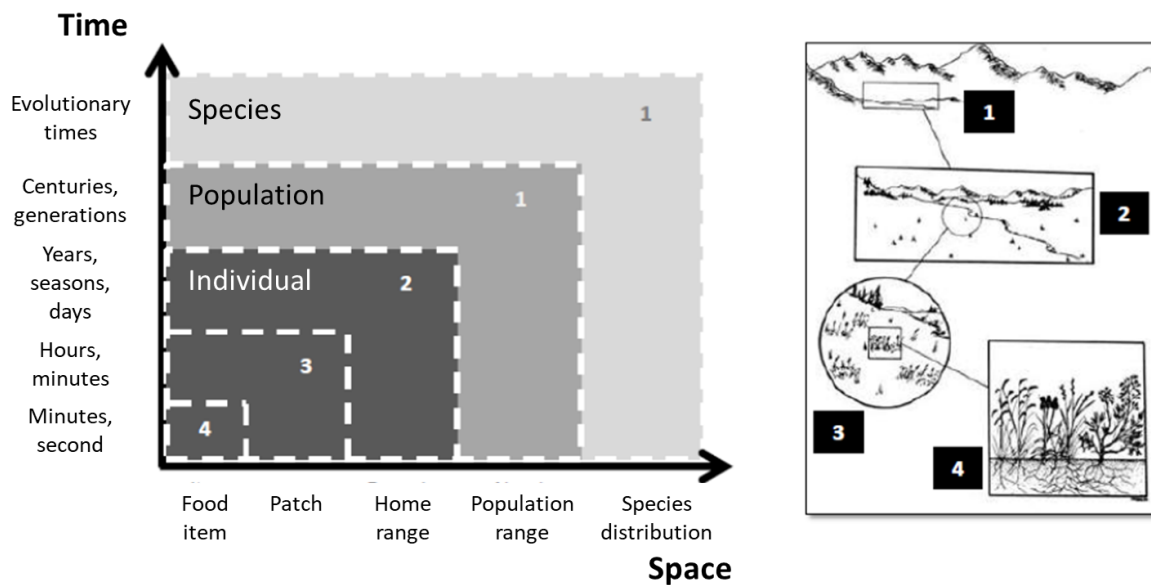


Figure 1: Diagram representing the multi-level (individual, population and species) and the spatio-temporal continuum of habitat selection scales, discretized in 4 main orders, from the species and population distribution ranges (1st order of selection) to the individual home range level (2nd order of selection), patches within the home range and food items within a patch (3rd and 4th order of selection, Johnson 1980). Adapted from Senft et al. (1987) and Gaillard et al.(2010).

On the other hand, “when to feed?” concerns decisions made by individuals regarding the temporal dimension of the food-risk avoidance trade-off, i.e. their activity budgets. Indeed, due to predator or human activity patterns occurring at various temporal scales, the perception of risk by animals may in return also show annual, seasonal and daily variations. In response, in periods of high perceived risk, individuals may increase the time spent in a refuge (Martín et al., 2003) and decrease the time spent foraging (Pęksa & Ciach, 2018). This may result in opportunity costs that individuals may compensate for or mitigate by shifting the use of risky yet profitable areas to times of lower perceived risk. The resulting alteration of activity budgets under risk avoidance constraints may then occur at various temporal scales, i.e. either during specific years, seasons (e.g. tourism or hunting season for example, Jayakody et al., 2008; Kolk

et al., 2022), days (e.g. week-end, Dorrance et al., 1975) or specific times of the day (i.e. daytime vs nighttime, Bonnot et al., 2015).

Moreover, the relative importance of food and risk avoidance constraints on individual space use and activity budgets may greatly differ between species (Figure 2). In ungulates small species are for example mostly regulated by predation and therefore expected to dedicate an important part of their time to risk avoidance. Inversely, intermediate and large size species may be less exposed to predation and are then primarily constrained by food quality and quantity respectively (Hopcraft et al., 2010).

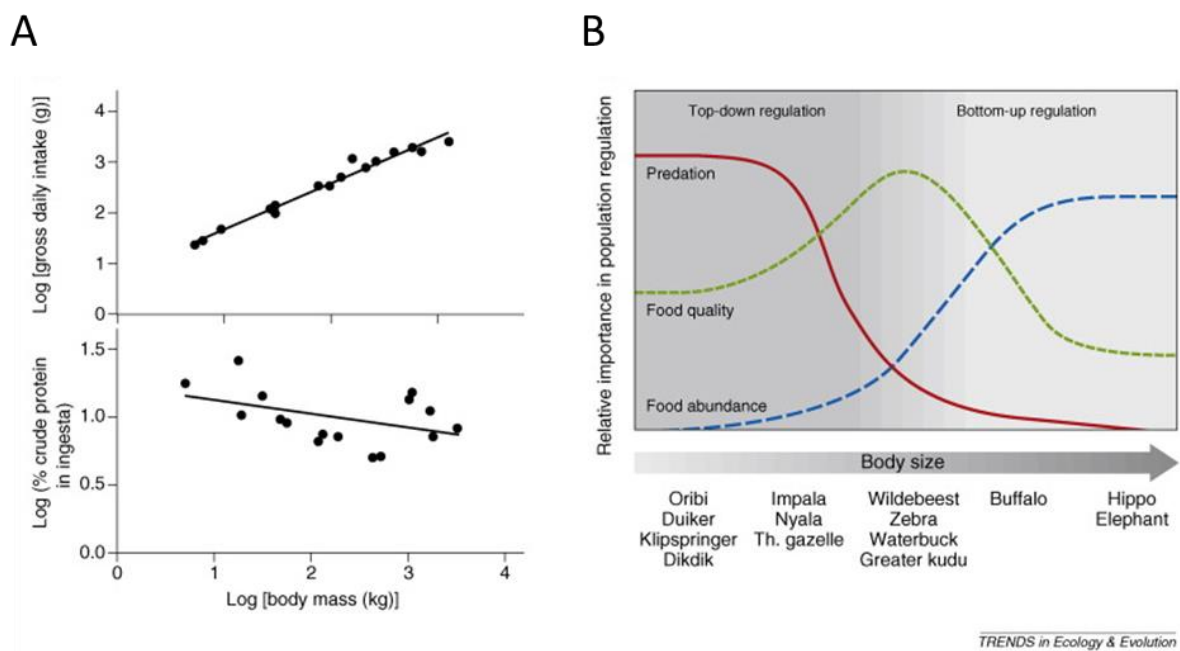


Figure 2: Regulation of large versus small herbivores predation, food quality and abundance (A) Large herbivores consume greater quantities of lower quality food, whereas small herbivores consume less food of higher quality because they are constrained by their high metabolism and limited digestive capacity (Jarman-Bell principle, see also section 2a.). Therefore, (B) large herbivores, such as elephants, tend to be regulated by food abundance (dashed blue line), whereas smaller herbivores, such as wildebeest, are regulated by food quality (dotted green line). The smallest herbivores, such as oribi, are mainly predator regulated (solid red line). From Hopcraft et al. (2010).

As individuals may occupy different sub-units of the same population range, the spatial and temporal heterogeneity of the population's foodscape and landscape of fear should generate interindividual variability in the resolution of the food-risk avoidance trade-off. However, environmental heterogeneity is not the only source of variability in the way individuals may address this behavioural trade-off. Individuals may also differ in their perception of risk and resources as well as their locomotor abilities and energetic requirements depending on their internal characteristics like sex, age or reproductive state (Harel et al., 2016; Laundré et al.,

2001; Searle et al., 2007). In the following paragraphs, we will then explain how these internal factors may, in combination with external factors like foraging and risk avoidance constraints, influence the spatial behaviour of individuals.

2. The influence of internal factors on the food-risk avoidance trade-offs

a. Sex-related differences and the importance of reproductive constraints

Sexual dimorphism, i.e. the presence of phenotypical (i.e. morphology, physiology, or behaviour) differences between males and females, has intrigued biologists for long time, including Darwin who mentioned it in the *Origin of Species* (1859). He later brought some responses to the causes of this phenomenon in “*The descent of Man*” (1871), where he explained in depth the concept of “sexual selection”. Sexual selection may take two forms: either males compete for access to females *via* direct and generally agonistic interactions such as fighting, leading to the evolution of weapons, or they compete to attract females which leads to the development of ornaments. Both of these characters are referred to as secondary sexual traits and their emergence may further accentuate sexual dimorphism.

The origin of sexual selection has often been attributed to anisogamy, i.e. the presence of size differences between the gametes of the two sexes (Trivers, 1972). Under the classical view males produce a large quantity of small and energetically low-cost gametes, the spermatozoids, which allow them to fertilise a very large number of females and should hence attempt to maximise individual fitness by mating with the maximum number of females. Conversely, females produce a limited number of large and energetically costly gametes, i.e. eggs, and they are also constrained by the temporal scales of production of these gametes. Female fitness may then not be maximized by additional matings but is instead dependent on the quality and viability of their offsprings, which may depend on the phenotypic quality of both females and males. Males with higher fighting capacity may also be the ones in better shape, healthy and with good quality genes which may sire offsprings of similar body condition. On the other side, in mating systems where attraction of females is more important than fighting for them, the handicap principle (Grafen, 1990; Penn & Számadó, 2020; Zahavi, 1975) suggests that females may select males based on morphological or behavioural traits bearing high costs in terms of energy expenditure and exposure to risk (e.g. the peacock’s tail making them easier to

be spotted or caught by predators), but which may be appealing for females and which turn out to be associated with greater phenotypic quality (i.e. honest signals). The reasoning behind this principle is that better quality males are generally the ones that are also the most capable to invest energy in sexual secondary traits and bear their costs, thus being both in better shape and more appealing to females than lower quality males that may have lesser energy to allocate to both their maintenance and to sexual secondary traits.

Nonetheless, even if anisogamy may partly explain the presence of sexual selection in polygynous species (i.e. species where males mate with several females), it may not hold for other mating systems like polyandry (i.e. females mating with several males). In fact, parental investment, i.e. the allocation of time and energy spent by both parents into the procreation and rearing of their offspring, may be also a decisive factor. Parental investment theory (Trivers, 1972) explains that the sex which invests the most energy and time in offsprings should be the one which exerts sexual selection on the other sex. This may result in sex differences in reproductive strategy, here defined as the way individuals invest time and energy in the production of viable offsprings. In polygynous species for example, females bear most of the costs linked to parental care and therefore allocate time and energy to their survival and those of their offspring. Males on the other side will mostly adopt strategies that will allow them to maximize their investment into their growth and the development of sexual secondary characters that will allow them to monopolize or attract females (e.g. high body mass, weapons such as horns or antlers, ornaments such as colourful feathers, (Loison et al., 1999; Owens & Hartley, 1998).

Thereby, sex-related differences in reproductive strategy have also been seen as one of the primary causes of sexual segregation, i.e. when sexes live separated from each other outside of the reproductive season. Indeed, the sex-specific requirements in energetic needs and risk avoidance may first lead to the use and selection of different habitats by males and females, i.e. spatial segregation (Ruckstuhl & Neuhaus, 2006; Wearmouth & Sims, 2008). In herbivore species the Jarman-Bell principle has for example been cited as one of the potential sources of sexual segregation, notably in ungulates: in brief, this principle states that the quality (i.e. its digestibility and nutrient content) of the food an herbivore consumes is inversely proportional to its size. This relies on the differences in allometric scaling with body mass of two physiological parameters: gut size/fill or intake capacity, which is proportional to body size (i.e. exponent of 1), and the energy requirements of the animals which increases more slowly with body size (i.e. exponent of 0.75, Kleiber, 1947). As a result, larger species or larger individuals

within a species, can tolerate lower-quality diets because their intake capacity scales faster with their body mass than their energy requirements, which allows them to ingest high quantities of food when its quality is lower, while smaller species or individuals are constrained to ingest smaller quantities of food and thus are highly dependent on its quality (Bell, 1971; Geist, 1974; Jarman, 1974; Müller et al., 2013). In the case of ungulates, more especially species with a marked sexual size dimorphism, females, which are smaller than males, may select habitats and patches with high forage quality, while males, whose foraging strategies should be more oriented toward growth maximization, should then select for areas with higher forage quantity (“forage selection” or “sexual dimorphism-body size” hypothesis, Ruckstuhl & Neuhaus, 2002). In addition, most ungulates are polygynous and females carry out most of the parental investment. As their reproductive success directly depends on their survival and those of their offspring, females should preferentially use habitats offering lesser exposure to predation or human disturbance, while males which are free from the constraint linked to offspring rearing, may be more prone to spend time in risky habitats, especially if those offer greater foraging opportunities (“predation risk hypothesis”, (K. E. Ruckstuhl & Neuhaus, 2002; Wearmouth & Sims, 2008).

Spatial segregation may also arise from the different sensitivities of males and females to harsh weather conditions such as low temperature and high wind in winter or high temperatures and no or little wind in summer (“weather sensitivity hypothesis”, Conradt et al., 2000; Jackes, 1973). This may be especially expected in species where sexual size dimorphism is important, as the larger size of males compared to females may make them more sensitive to cold, as heat loss increases faster with body weight than energy intake (Conradt et al., 2000; Jackes, 1973), or to heat through a higher thermal inertia and lower conductance (Porter & Kearney, 2009). As a result, under stressful weather conditions, males may be more prone than females to select habitats that buffer them against challenging weather conditions, even if those habitats sometimes offer decreased foraging conditions (Alonso et al., 2016; Bourgoïn et al., 2018; Loe et al., 2006; Mason et al., 2017).

Sexual spatial segregation may not be the only type of sexual segregation found in sexually dimorphic species. In reality, many species also exhibit only social segregation, i.e. when males and females live separated but in the same habitats. Due to their lower size, females may have a lower intake capacity than males, and thus need to forage during shorter but more frequent bouts, while males may forage for longer but less frequent bouts and spend more time in other activities such as lying or moving (Neuhaus & Ruckstuhl, 2002; Pęksa & Ciach, 2018). This

could then result in lack of synchronicity between male and female activity rhythms, which may then cause males and females to use the same areas but not at the same time or frequency, leading to social segregation (“activity budgets hypothesis”, (Ruckstuhl & Neuhaus, 2002; Wearmouth & Sims, 2008).

Alternatively, social constraints may also represent an important driver of sexual segregation as behavioural incompatibilities between males and females may lead individuals to preferentially interact and group with conspecifics of the same sex. Females for example typically tend to avoid agonistic interactions and male harassment (the “female avoidance of males hypothesis”, (Galezo et al., 2018; Peterson & Weckerly, 2017; Wearmouth et al., 2012), while males tend to interact with peers of similar age classes, where they may develop their fighting skills, evaluate their rivals and establish hierarchical relationships between them (“males social affinity hypothesis”, Bon et al., 2001; Bon & Campan, 1996; Le Pendu et al., 2000; MacFarlane & Coulson, 2009). Finally, the female affinity hypothesis suggests that females may also prefer to interact with other females and form same-sex groups where they can more efficiently develop skills associated with the rearing of offspring, including locating foraging and birth areas (Wearmouth & Sims, 2008).

It is important to note that depending on the species that is examined, sexual segregation may be explained by different hypotheses. For example, Bourgoin et al. (2018) showed partial or even full support for the five hypotheses presented to explain the presence of sexual segregation in Mediterranean mouflon, while other studies showed support for only one or some of the hypotheses (e.g. Loe et al., 2006; Whiteside et al., 2017). While this may indicate that sexual segregation is a complex phenomenon with many potential causes, these studies highlight the need to account for the influence of sex-related nutritional, reproductive, thermoregulatory and social constraints when investigating animal’ spatial behaviour and activity patterns.

b. Age-related differences and the importance of life history

Reproductive constraints may not only differ between the sexes but also within., as individuals of different ages and life stages may experience different constraints. In numerous taxa, individual investment in reproduction varies markedly with age or life stage (Clutton-Brock, 1984; Forslund & Pärt, 1995; Lemaître et al., 2015; McBride et al., 2015). In large herbivores, reproductive females are for instance constrained to select habitats that best compensate for the increased energetic requirements linked to pregnancy and lactation, while minimizing predation risk for their offspring (Bongi et al., 2008; Ciuti et al., 2009; Viejou et al., 2018). In contrast, immature and nonreproductive females are unconstrained by the presence of dependent young, resulting in age- and/or stage-specific space use patterns (Marchand et al., 2015; Oehlers et al., 2011; Viejou et al., 2018; Villaret et al., 1997).

On the other hand, the inability of immature males, which are still growing, to successfully compete with prime age males, often leads to the emergence of alternative reproductive tactics, which in turn result in age-related differences in spatial behaviours (Cederlund & Sand, 1994; Foley et al., 2015; Malagnino et al., 2021; Taylor et al., 2020). Patrolling behaviours during the territoriality period in roe deer result in higher movement rates in adult males compared to sub-adults, which are mostly unable to hold a territory and adopt alternative mating tactics (i.e. “peripheral” or “satellite” tactics, Liberg et al., 1998; Malagnino et al., 2021). In male white-tailed deer (*Odocoileus virginianus*), growing yearlings (i.e. one year old males) invested lower effort in mate search, resulting in lower movement rates during the rutting period compared to older males (Foley et al., 2015). From two years of age, males shared similar high movement rates due to their search for females, but adults (3 years and older) adopted Brownian walk-like patterns, suggesting that females locations were predictable for them, whereas subadults (2 year old males) adopted a Lévy walk, i.e. a type of movement strategy that may be optimal to locate new resources (under rather specific assumptions though, Foley et al., 2015). According to the authors, these results suggested that sub-adults may in fact have difficulty to locate reproductive females, potentially because of their lack of experience.

Younger individuals may be less familiar with their environment, and thus generally show a greater propensity to explore and get acquainted with it (“explore and exploit strategy”, Franks & Thorogood, 2018). Familiarity and memory have indeed been found as key drivers of individual mobility and home range formation (Gehr et al., 2020; Marchand et al., 2017; Piper,

2011). Consequently, older individuals are expected to have an increased knowledge of the distribution of resources and risk within their environment and therefore to show a higher foraging efficiency than younger individuals. They may for instance be more capable to locate and select habitats and patches with greater resource quality and/or lower predation risk (Franks & Thorogood, 2018; Pärt, 2001a, 2001b; Weimerskirch et al., 2014), and spend less time travelling to locate resources (Frankish et al., 2020), resulting eventually in decreased movement rates and smaller home ranges (Froy et al., 2018; Malagnino et al., 2021).

In addition, while age may be correlated positively with experience, it may also be correlated with senescence in old animals, i.e. the deterioration in muscular and physiological condition of the individual with age, which generally translates into decreased locomotor, cognitive and sensory capabilities (Nussey et al., 2013; Soulsbury & Halsey, 2018). Thereby, the influence of experience and senescence on age-related differences in movement and space use may sometimes be confounded, as reduced movement rates and smaller home ranges may be both correlated with individual knowledge of the shortest paths linking patches, or simply their decreased locomotor mobility with age (Froy et al., 2018; Malagnino et al., 2021).

Surprisingly, the influence of age on animal spatial behaviour is still overlooked in not few animal movement and space use studies, probably because of the difficulty to assess accurately individual age in the wild (Malagnino et al., 2021). Long-term monitoring studies, and experiments where individuals of known age are translocated into novel environments, could for instance help us disentangle the respective influences of age-specific reproductive constraints, experience and senescence on individual spatial behaviours and improve our understanding of the role played by age in animal movements and space use (Festa-Bianchet et al., 2017; Froy et al., 2018; Malagnino et al., 2021; Weimerskirch, 2018).

3. Thermoregulation: the physiological constraints of animal movement

Earlier in this thesis (section 2a.), we briefly mentioned the role exerted by weather conditions on individual habitat selection, stating that the larger individuals are expected to be the most sensitive to harsh climatic conditions. We propose in the following sections to explain in more details the physiological constraints posed by thermoregulation on the energetics of endothermic species, and how these influence individual differences in habitat selection and activity patterns.

a. The thermoneutral zone and the heat dissipation theory

Every species has an optimal range of body temperatures at which their cellular and metabolic processes are energetically optimized. As body temperature may first be correlated with the operative temperature (i.e. an indicator of ambient temperature taking into account the effects of both convection and radiation), most organisms attempt first to remain in areas where the operative temperature is within a range of favourable values (Boyles et al., 2011; Norris & Kunz, 2012). In endothermic species, which are mostly homeotherms (i.e. individuals which are able to maintain their body temperature within a narrow range of values, independently from external conditions), the thermoneutral zone (hereafter TNZ) refers to the range of operative temperatures where no regulatory changes in metabolic heat production, nor evaporative heat loss, is needed to maintain homeothermy (Kingma et al., 2012). Within this range, which is bounded by a lower and an upper critical temperature (LCT and UCT), metabolic rate is minimal, i.e. the basal rate of heat production is equal to the rate of heat loss to the environment. In contrast, any deviation of the operative temperature from the TNZ generally triggers autonomic thermoregulatory responses, like non-shivering or shivering thermogenesis when temperature is under the LCT, or panting and sweating when above the UCT, which allow individuals to avoid the deleterious effects of hypo- and hyperthermia. This however incurs costs in terms of increased metabolic rate linked to heat production or evaporative heat loss (Terrien, 2011).

Consequently, homeothermic species are expected to dedicate an important part of their energy budget to thermoregulation and the TNZ has then often been cited in the literature as the optimal

range of temperatures which promotes long term health and performance in animals, with energy costs above BMR often seen as unsustainable (Mitchell et al., 2018). However, this is a misconception, as the LCT and UCT are not thermal tolerance limits and most animals often live outside their TNZ without impairing their long-term energy balance and subsequent survival or reproduction (Figure 3, Mitchell et al., 2018).

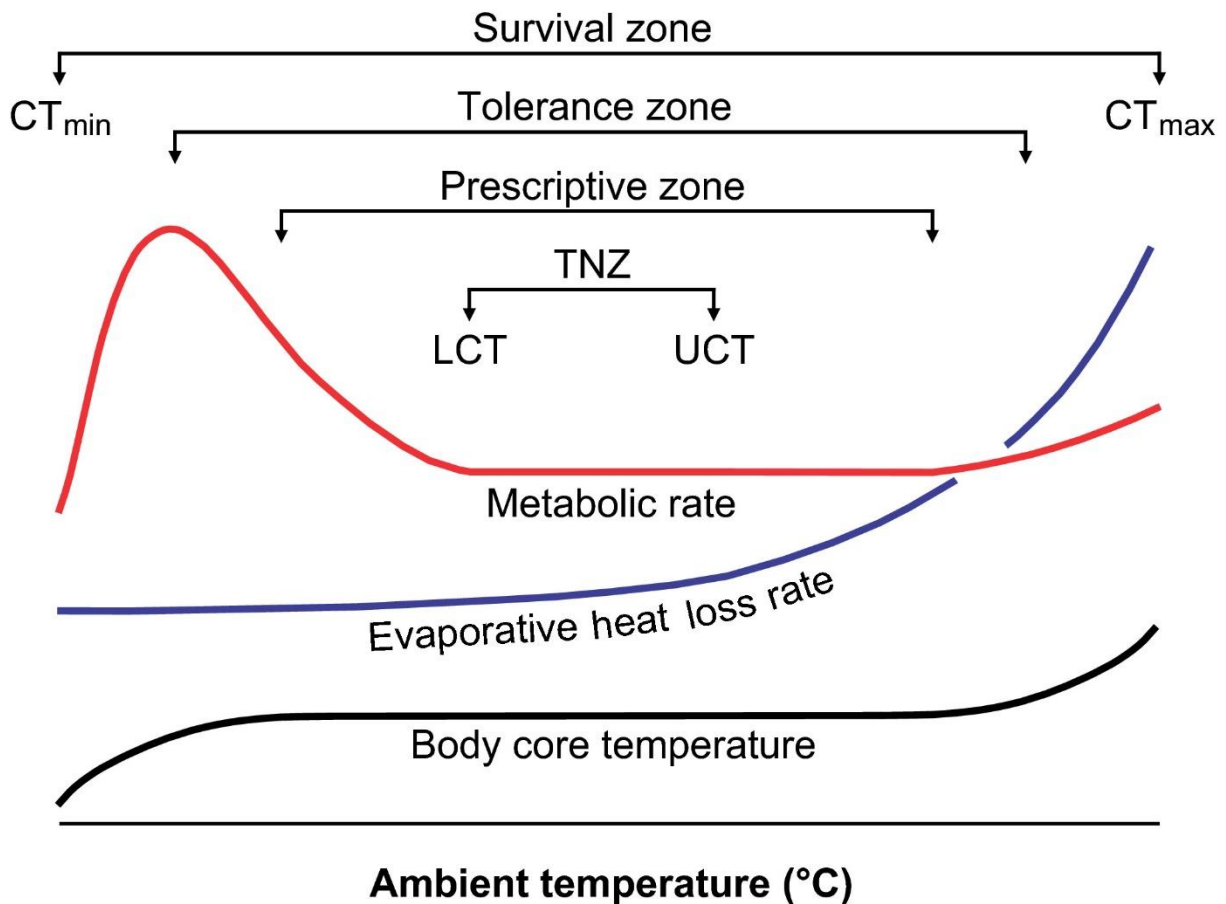


Figure 3: Steady-state relationships between the ambient temperature and the body core temperature, evaporative heat loss rate, and metabolic rate of mammals. Also shown is the thermoneutral zone (TNZ), as well as three zones of thermal safety. In the prescriptive zone, mammals are homeothermic and fully functional, with sustainable increased metabolic rate and evaporative heat loss (water loss) outside the TNZ. In the tolerance zone, but outside the prescriptive zone, individual lives are not threatened but physiological malfunction occurs (e.g. animals may be unable to reproduce), so individuals can survive but populations may decline if the conditions persist. In the survival zone but outside the tolerance zone, individual lives are at risk (e.g. from heatstroke or cold injury). LCT is the lower critical temperature, UCT is the upper critical temperature, CT_{min} is the critical thermal minimum, and CT_{max} is the critical thermal maximum. The three zones of thermal safety are not necessarily centred on the TNZ as we have drawn them: UCT is likely closer to CT_{max} than LCT is to CT_{min} . From Mitchell et al. (2018)

In fact, the heat dissipation limit theory (Speakman & Król, 2010) suggests that the energetic balance of animals should be mostly constrained by the capacity of individuals to expend energy

rather than acquiring it and that the maximum energy expenditure is then constrained by the heat dissipation capacity of the individual. Indeed, while mild hypothermia may sometimes have beneficial effects on individual survival (e.g. Conti et al., 2006), or reproduction, allowing individuals to expend more energy in highly costly energetic activities such as lactation (Król et al., 2007), mild hyperthermia on the other side induces many adverse effects such as damage to DNA, proteins, somatic or germ cells, as well as embryonic malformation and birth defects in pregnant females and numerous other malfunctions (Graham Jr, 2020; Roti Roti, 2008). Thus, heat dissipation capacity and the avoidance of hyperthermia are expected to be important drivers of energy allocation in endotherms, which in return is likely to influence various trade-offs such as future versus current reproduction and quality versus quantity of progeny, ultimately affecting individual performance and life-history strategies (Boyles et al., 2011; Nilsson & Nord, 2018, Figure 4).

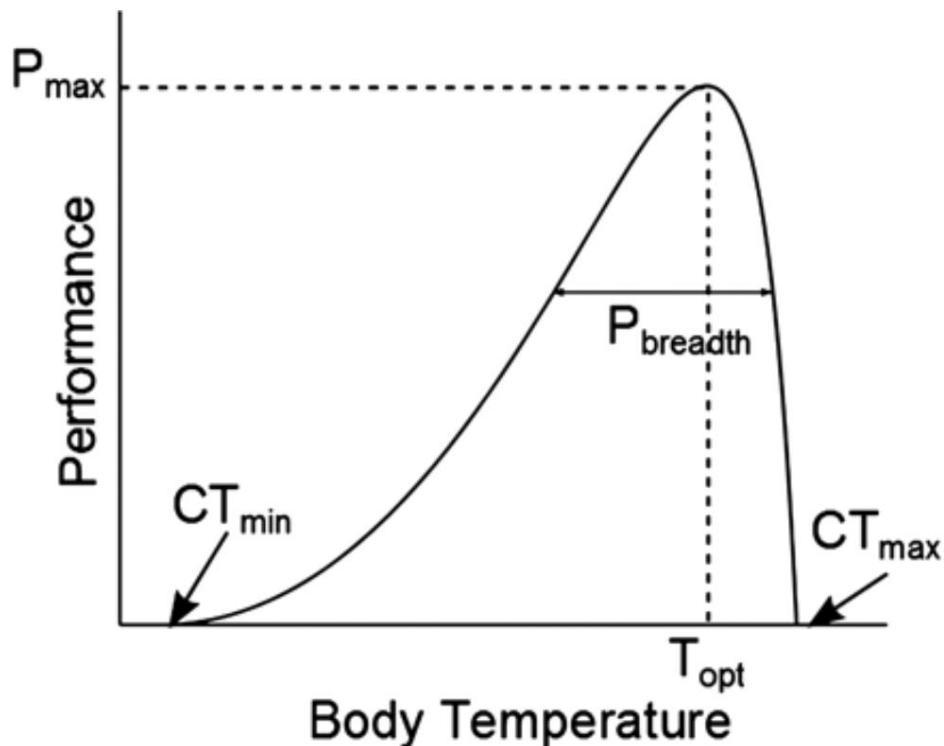


Figure 4: Relationship between body temperature and individual performance – shown are the thermal optimum (T_{opt}), performance breadth ($P_{breadth}$), and maximal performance (P_{max}). All animals have a range of body temperatures ($P_{breadth}$) over which performance is maximized (T_{opt} : optimum body temperature). CT_{min} is the critical thermal minimum and CT_{max} is the critical thermal maximum, respectively the lower and upper limits of the survival zone (Figure 3, Mitchell et al., 2018) As the consequences of hyperthermia are more detrimental than those of hypothermia, physiological performance declines more precipitously above optimum temperatures than below them, creating a “thermal cliff”. From Boyles et al. 2011.

b. Implications for species living in temperate and cold environments

Hyperthermia avoidance may be a particularly important constraint for endothermic species living in temperate and arctic environment, where the energetic balance of individuals is expected to be mostly constrained by their capacity to efficiently dissipate heat during seasons when resources are abundant but where thermal conditions are challenging, i.e. typically summer. While physiological autonomic responses like sweating or panting may prevent animals from hyperthermia, they are often transient and may be quite costly in terms of energy or water loss (Mitchell et al., 2018; Terrien, 2011). In contrast, behavioural responses are generally cheaper and much faster to implement. They usually fall into two categories, i.e. either animals seek thermal refuges like shade, or migrate at higher elevations, to buffer themselves from challenging temperatures (Aublet et al., 2009; Semenzato et al., 2021 in Alpine ibex; Marchand et al., 2015 in mouflon; van Beest et al., 2012), or they alter their activity budgets, typically by reducing activity levels during hot hours (Pipia et al., 2008; Bourgoïn et al., 2011 in mouflon; Brivio et al., 2016; Grignolio et al., 2018 in chamois; Semenzato et al., 2021 in Alpine ibex).

Even though behavioural thermoregulation may represent an efficient way for individuals to mitigate the deleterious effects of hyperthermia (which sometimes culminate in mass mortality events McKechnie & Wolf, 2010), a growing body of literature suggests behavioural thermoregulation may incur pervasive costs, too (Cunningham et al., 2021). These costs are often associated with missed opportunities to perform other key activities, such as foraging, territory defence or offspring provisioning (Cook et al., 2020; Mason et al., 2017; Santee & Bakken, 1987; Wiley & Ridley, 2016). While not being lethal *per se*, the accumulation of these costs due to chronic exposure to extreme temperatures (i.e. prolonged droughts and heat waves), may have a detrimental influence on the survival and reproductive output of individuals (e.g. body mass loss, reduce offspring growth, increased breeding failure, Conradie et al., 2019). Consequently, predicting the vulnerability of species to climate change may not only consist in assessing the potential of behavioural thermoregulation to buffer individuals from heat stress (e.g. Ciuti et al., 2009; Marchand et al., 2015; Mason et al., 2014; Semenzato et al., 2021), but also its potential opportunity costs. Whilst these costs have been investigated in some studies (Cook et al., 2020; Mason et al., 2017; Santee & Bakken, 1987; Wiley & Ridley, 2016), opportunity costs have in contrast rarely integrated in a formalized framework to predict the response of species to climate change (but see Veldhuis et al., 2019).

4. Thesis plan and objectives

In the first chapter of this thesis we explained the importance of the study of animal behaviour under the current context of rapid global environmental changes, as the ability of individuals to adjust their behaviours to different environmental context directly influences their performance (i.e. survival & reproductive success). We then explained further the fitness implications of individual behaviours in chapter 2 by discussing the case of food acquisition and optimal foraging theory and the resulting classical compromise between energy acquisition and risk avoidance most individuals must face in order to efficiently survive and reproduce. Yet, we also argued that, while the spatial and temporal distribution of food and risk may represent primary drivers of individual behavioural responses, individual characteristics such as sex and age, and other environmental drivers such as temperature and related behavioural thermoregulation, may also exert a great influence. The main objective of this thesis is to disentangle the roles of these different intrinsic and extrinsic factors on animal behaviour, by tackling three main questions (Figure 5):

- **Chapter 4: Do reproductive constraints or experience drive age-dependent space use in two large herbivores?**

In this article, we explore the relative influence of sex and age on the movements and space use of two ungulates species, the roe deer (*Capreolus capreolus*) and the Mediterranean mouflon (*Ovis gmelini musimon x Ovis sp.*). We discuss in particular the relative influence of reproductive constraints, linked to life stage and experience, on the daily distances travelled and monthly home range size of individuals.

- **Chapter 5: Thermal refuges availability shapes individual behavioural tactics in a heat stress sensitive species.**

In this second article we explore how behavioural thermoregulation may alter individual habitat use and activity budgets. Using GPS data from female chamois (*Rupicapra rupicapra*), we assess in detail how individuals may conciliate energy acquisition and behavioural thermoregulation by adjusting their time spent in thermal refuges and in their different activities in response to varying conditions of air temperature and access

to thermal refuges (i.e. percent of forest and north-oriented slopes in individual home ranges).

- **Chapter 6: Being cool ain't free: age and access to open areas drive opportunity costs in an alpine ungulate**

In relation to the second article, we then assess the potential energetic costs of behavioural thermoregulation for chamois, either in terms of opportunity costs (i.e. less time spent in forage-rich but thermally challenging areas), or in terms of movement costs. We also assessed how the influence of age through experience may induce inter-individual variability in the way individuals tackle this apparent behavioural trade-off between food acquisition and behavioural thermoregulation.

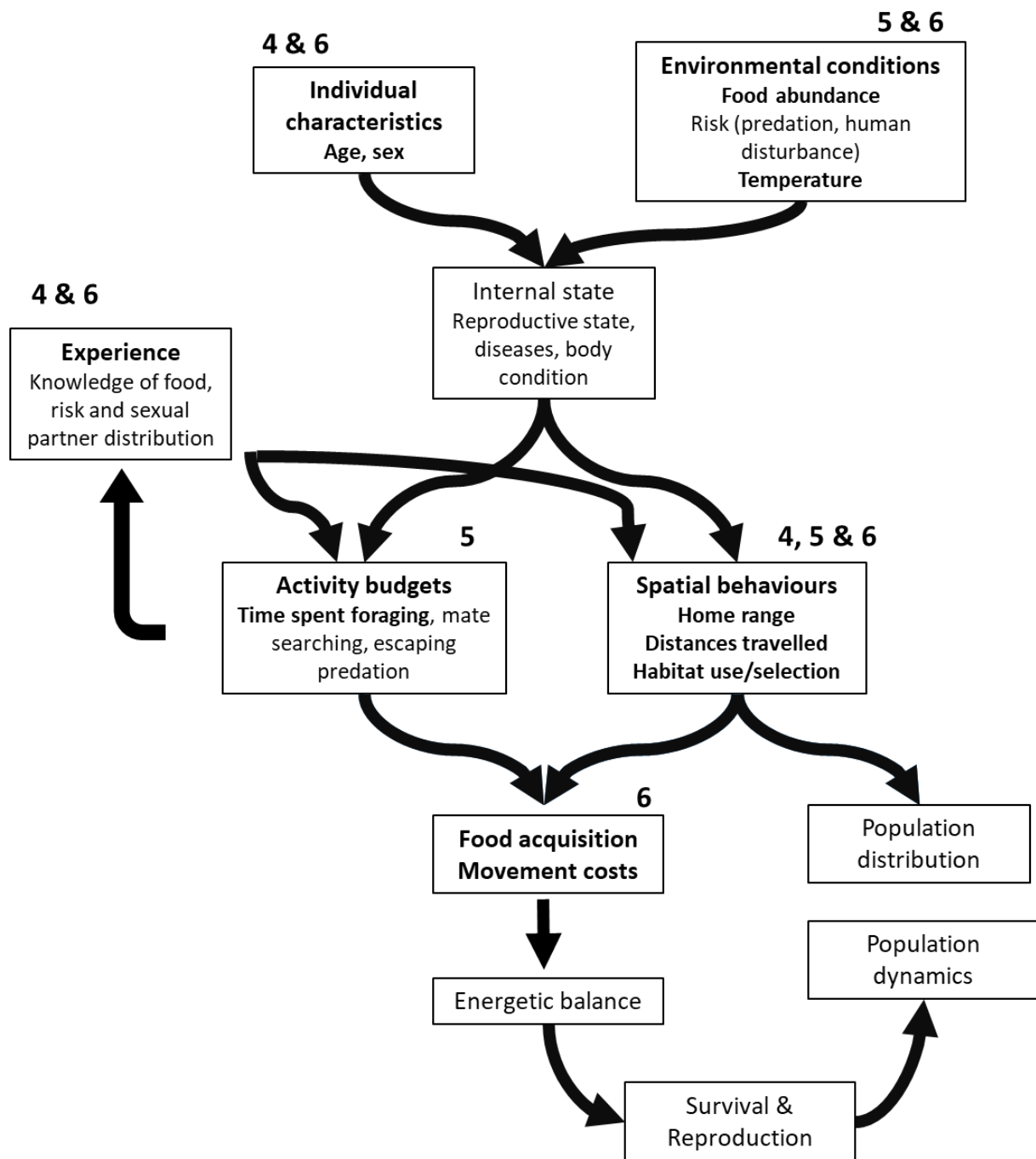


Figure 5: Outline of the theoretical context and plan of the thesis. Items in bold represent the different factors and their influence on related response variables investigated in each chapter (numbers in bold). Arrows indicate the direct influence of an item on another.

Chapter 3:

Methods

1. Study species

a. Taxonomy and distribution

Chamois (*Rupicapra rupicapra*), mouflon (*Ovis gmelini musimon*) and roe deer (*Capreolus capreolus*) are ungulates belonging to the *Cetartiodactyla* order, which regroups species with an even number of digits (2 or 4). They belong to the *Ruminantia* suborder, which, in contrast with monogastric herbivore species, is represented by polygastric species, i.e. the stomach consists of one true stomach (abomasum) and three pre-stomachs (rumen, reticulum and omasum). More particularly, ruminants owe their name to rumination, a predigestion process where ingested food is first fermented by microbial actions before being regurgitated and rechewed to break it further and facilitates digestion (Gordon, 1968). Chamois and mouflon are *Caprinae* species belonging to the *Bovidae* family, which is characterized by the presence of permanent non-ramified horns, i.e. two-part structure consisting of a bone interior encapsulated in a keratin sheath, while roe deer is a *Capreolinae* species belonging to the *Cervidae* family, characterized by the presence in males of antlers, i.e. entirely bony structures which are shed and regrown each year, contrary to horns.

While roe deer refers to a unique species, mouflon is a vernacular and ambiguous term which designates certain species of sheep of the *Ovis* genus. In its most common acceptance, it refers *stricto sensu* to all the descendants of the *Ovis gmelini* species (also known as *Ovis orientalis*) which originates from the mountainous regions of Middle East including Central Turkey, Armenia, Azerbaïdjan, Iran and Irak. Genetic studies also indicate the domestic sheep *Ovis aries* to be result of the domestication of this species between 11000 and 9000 BC (Ryder, 1984). Classically, *Ovis gmelini* is categorized into 5 subspecies being the Armenian mouflon (*O. g. orientalis*), the Esfahan mouflon (*O. g. isphahanica*), the Laristan mouflon (*O. g. laristanica*), the Cyprian mouflon (*O. g. ophion*) and the Mediterranean, or European mouflon (*O. g. musimon*), which is one of our study species. Still, the taxonomy of this subspecies

remains debated as genetic evidence suggests it originates from primitive domestic sheep populations introduced into Corsica and Sardinia which later became feral (Poplin, 1979). Moreover, the later crossbreeding of this subspecies with modern sheep in some populations even lead some authors to encourage the use of *Ovis gmelini musimon x Ovis sp* to refer to this species (J. M. Cugnasse, 1994). Nonetheless, by commodity, we will refer to the Mediterranean or European mouflon as “mouflon” later in this manuscript.

Finally, chamois is represented by two main species of the genus *Rupicapra* (Corlatti et al., 2022):

- the northern chamois *Rupicapra rupicapra*, which is categorized in seven subspecies mostly present in the Alpine arc (alpine chamois, *R.r.rupicapra*, the most abundant subspecies), as well as other mountains of Southern and Central Europe (*R.r.cartusiana* in Chartreuse massif, *R.r.balcanica* in the Balkans, *R.r.tatrica* in the Tatra, *R.r.carpathica* in the Carpathians), as well as in Anatolia (*R.r.asiatica*) and in the Caucasus (*caucasica*).
- the southern chamois *Rupicapra pyrenaica*. which is categorized in three subspecies mostly present in the Pyrenean (*R.p.pyrenaica*), the Cantabrian (*R.p.parva*), and the Apennine mountains (*R.p.ornata*)

Until the end of the 1970's, ungulates populations in France and in the rest of Europe, occurred at rather low densities, mostly because of the important hunting pressure they were facing (Apollonio et al., 2010; Maillard et al., 2010). Afterwards, this situation drastically changed, as ungulates population saw a very strong and continuous increase in their numbers, mostly due to changes in management measures (Maillard et al., 2010). In France in 1979, the limitation of harvest quotas was acted in the law for deer species and extended to mountain ungulates in 1990. In the same time, the limitation of adult females shooting through selective shooting of calves instead, and the systematic and repeated translocations of individuals from high density to low density areas, largely participated to the increase of population density (Maillard et al., 2010). Other factors have also contributed to this phenomenon, such as the decreased severity of winters due to warmer climate (Myrsterud & Sæther, 2010) and the increase of resource availability, linked to the joint renaturalisation of habitats following the abandonment of agriculture in rural areas (especially mountains), and the intensification of agriculture in remaining cultivated land (Apollonio et al., 2010). Roe deer (*Capreolus capreolus*) may be considered as the species which benefited the most of these changes in socio-ecological factors

in Europe, with an estimated population size of more than 6.2 million individuals going up to more than 9.5 million individuals in the 2000's. (Burbaiteè & Csányi, 2009). Authors argue however that these numbers are likely to be underestimated, and that the actual population size of roe deer in Europe may be 1.5 times higher, the central European population being estimated to 15 million individuals. During the same period, 1.7 million individuals were harvested in 1984 up to 2.7 million in the early 2000's (Burbaiteè & Csányi, 2009). The size of the harvested bag then increased much more slowly, reaching 3 million individuals in 2017, while roe deer range covered 74% of Europe surface (Linnell et al., 2020), being the most widespread ungulate of the continent (from the Mediterranean to Scandinavia and from Western Europe to the beginning of East European Plain, Figure 1). In France, roe deer has been ceaselessly colonizing new habitats such as agrosystems, Mediterranean and mountain areas, to such extent that the species is now present on 90% of the total land area of metropolitan France (Maillard et al., 2010).

Mountain ungulates population also saw their numbers rising in the last decades, although in a lesser manner than roe deer, mostly thanks to translocations and management measures. Mouflon for example, was first reintroduced in Europe at the beginning of the 20th century, but most of current European mouflon populations derived from naturalisation program in the second half of the century. In France for example, mouflon was reintroduced for the first time in 1949 in the Mercantour massif (Cugnasse, 2001). Most of individuals used in translocations were a mixed breed of Corsican or Sardinian mouflon with domestic sheep. In 2010, the total French continental mouflon population was estimated to be at around 20 000 individuals (Corti et al., 2010). In 2016, mouflons were present in 5100 km² (0.9% of metropolitan France territory), with 60% of their distribution occurring in the Alps (Figure 1), the rest being shared between the Central Massif, as well as the Pyrenees, and northern France (Ardennes, Somme and Oise departments, Barboiron et al., 2018). If mouflon distribution increased during the last decade, the bag of hunted individuals decreased by around 30%, with more than 3500 individuals hunted in 2010 against less than 2500 in 2020, suggesting a potential recent decline in some populations, which however needs to be confirmed with further research.

Originating from Asia, chamois arrived in Europe during Mindel glaciation around 400 000 to 350 000 BC, but only colonized the major part of the continent during the second half of the Würm period (50 000 to 10 000 BC). Endemic to France, the northern chamois (*Rupicapra rupicapra*) was still present in 10 000 BC in the Alps, Jura, Provence and the Central Massif (Barboiron et al., 2018). The species then disappeared from these massifs, except in the Alps

where it remained until nowadays. By the end of the 19th century, chamois had already began to reappear in Jura, and during the second half of the 20th century, it was successfully reintroduced into the Vosges and the Central massif. Currently, the distribution area of the chamois covers more than 24 000 km², i.e. 4.4% of metropolitan France, with 84% of the distribution range being in the Alps (Figure 1), the rest being shared between the Jura, Vosges and Central massif (Barboiron et al., 2018). In 2016, the bag of hunted individuals was around 12 500 alpine chamois (Barboiron et al., 2018).

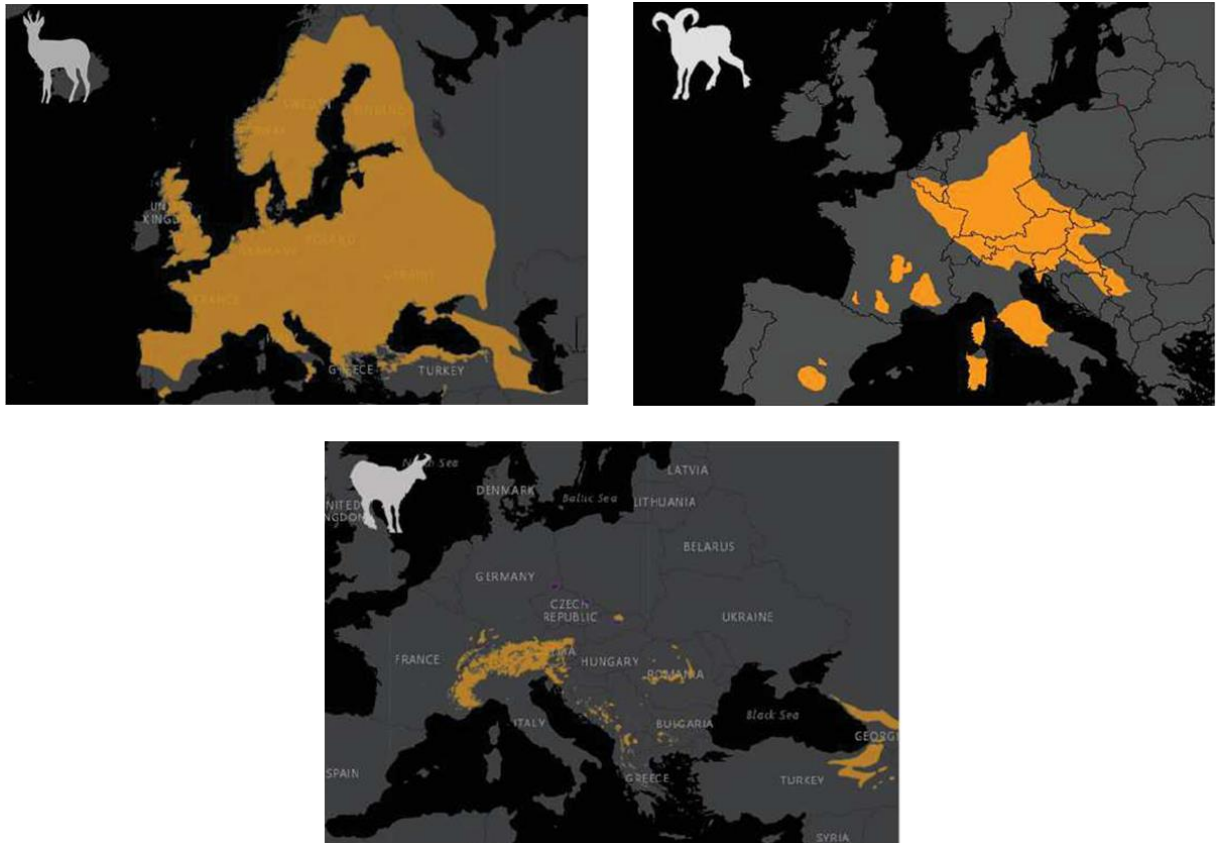


Figure 1: Distribution maps of roe deer (*Capreolus capreolus*), Mediteranean mouflon (*Ovis gmelini musimon x Ovis sp*) and Northern chamois (*Rupicapra rupicapra*) in Europe. Adapted from Seigle-Ferrand (2021)

b. Morphology

Roe deer is the smallest cervid in Europe, weighing between 20 and 25 with a maximum of 49 kg (Andersen et al., 1998). The species is slightly dimorphic as males only weight 10% more than females and grow a pair of antlers between December and March and cast them near mid-October (Sempéré & Lacroix, 1982, Figure 2A). Chamois and mouflon are both medium size ungulates, with a marked sexual size dimorphism. Adult chamois and mouflon males weigh

between 30-50 kg (80% confidence interval: 30-42 kg in chamois and 48-49kg in mouflon, Movit database Seigle-Ferrand, 2021) and are on average 30% heavier than females (80% confidence interval: 25-34 kg in chamois and 21-30 kg in mouflon, Movit database Seigle-Ferrand, 2021). Despite a significant sexual size dimorphism, male and female chamois are very similar looking, as both have straight permanent horns with a characteristic hook at their tip, making them difficult for the untrained eye to tell apart males from females (Figure 2C). Inversely, sexual dimorphism is much more marked in mouflon, as males have large horns that can reach 90 cm, whereas females do not have any or just little ones (Corti et al., 1994, Figure B).

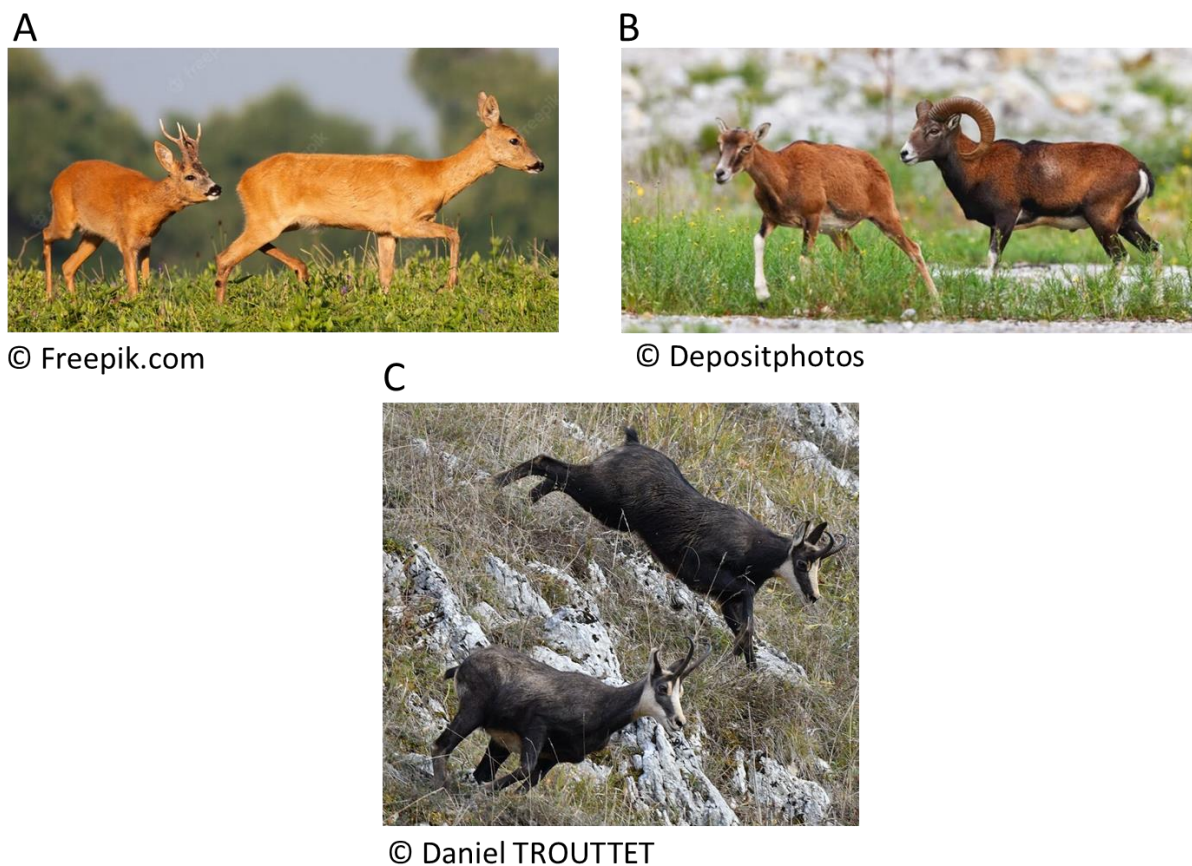


Figure 2: Males and females of A) roe deer (male on the left, female on the right), B) Mediterranean mouflon (female on the left, male on the right), and C) chamois (female at the bottom, male on the top of the picture). While roe deer show little size dimorphism, the presence of antlers in males allow to easily distinguish them from females (except during the fall of antlers between October and December). Inversely, while size dimorphism is significant in chamois, they look very similar although females may have thinner horns and neck size than males. The tips of females' horns may also be more distant from each other and their curve less obtuse than those of males.

c. Diet and habitats

Thanks to their compartmented stomach, ruminants are able to predigest ingested forage items via foregut fermentation, a process performed by the microbial flora present in the rumen, allowing them to make use of the plant cell wall by digesting fiber structures such as cellulose and hemicellulose, into volatile fatty acids (Clauss et al., 2010). Yet, digestive capacities quite differ among member species (Clauss et al., 2010), and various feeding types have been documented in this group (Hofmann, 1989). Roe deer for example are typically classified as a browser species, i.e. they preferentially feed on browse, leaves, shoots, generally from woody plants (e.g. shrubs, trees). On the other side, mouflon used to be classified as a grazer species, i.e. preferentially feeding on grasses, although recent work showed forbs and shrubs also represented a major part of their diet depending on forage availability (Marchand et al., 2013). Mouflon, like chamois, may then also be considered as an intermediate feeder, i.e. feeding either on grasses or browse depending on forage availability.

Due to their browsing feeding type, forest is a major component of roe deer living ranges. Not only providing resource, forest also constitute a refuge against predation and perceived risk, as well as challenging weather conditions (Myserud, 1996). Yet, the high plasticity of this species, allowed roe deer to expand and colonize a vast variety of habitats (Andersen et al., 1998), including low mountain areas, fragmented landscape or open agricultural plains (Morellet et al., 2011; Torres et al., 2015). Chamois and mouflon are mostly found into mountain areas, although they may also be spotted at lower altitudes. Mouflon in Central Europe for example are now mostly observed in deciduous and mixed forest. Chamois on the other side, maybe observed at altitudes exceeding 2000m as well as under 400m, the ruggedness of the terrain being more important than actual altitude, due to the extensive use of steep slopes and cliffs by chamois as a refuge against predation (Baruzzi et al., 2017; Pérez-Barberia & Nores, 1994). When it comes to foraging activities, in contrast with roe deer, open meadows and pastures are preferentially selected by mouflon and chamois, although they do use forest as a refuge against predation and challenging thermal conditions. (Marchand et al., 2015).

d. Social organisation and reproduction

Through their evolution, ungulates have developed a vast and diverse range of social organisations and mating systems, although most member species tend to be more or less gregarious and polygynous. Roe deer is considered a solitary species mostly because of males which, from March to August, form an exclusive territory and actively patrol within it to prevent any intrusion by other males (Liberg et al., 1998). This patrolling behaviour is even more marked during the rutting period in July-August, where males also patrol in search for reproductive females that cross their territories and with which they will attempt mating. Although considered solitary, roe deer remain an exception among large herbivores, as they actually form mixed-sex groups out of the rutting period, notably in winter (Pays et al., 2007), while sexual segregation is commonly observed in most species (Rückstuhl & Neuhaus, 2002). Chamois males for example may be solitary or living in small groups of 2 or 3 individuals, while females form larger groups, mostly of related individuals due to their high philopatry (Loison et al., 2008). Mouflon also form monosex groups, with groups of adult females and their offspring living separately from groups of adult males. Sexual segregation is yet relaxed during the rutting period in November-December, when both chamois and mouflon males visit then females' groups to attempt mating (Bon et al., 1992). Roe deer males are sexually mature at the age of one, but most males successfully reproduce for the first time when they have reached full physical maturity and are able to successfully hold a territory (in general at 3 years old; Vanpé et al., 2009). Similarly, chamois and mouflon reach sexual maturity when age around 1.5 years old but successfully reproduce for the first time around 4.5 years of age in chamois (Garel et al., 2009) and around the same for mouflon males (Bon et al., 1992). In mouflon, older males generally adopt a tending tactic, following receptive females and impeding attempts of other males to mate, while young subordinate males often adopt a coursing tactic, attempting to breach the defence of the tending males (Bon et al., 1992)

Roe deer females reach sexual maturity at the age of one and give birth from the end of April to the very beginning of June with most of birth events occurring in May (Linnell, 1994; Plard et al., 2014). Females most of the time give birth to two fawns, and in rare cases to three (Andersen et al., 2001). During the first two months of their life, fawns show a hiding behavior during the first two months of their life, i.e. fawns remain lying and hidden typically in tall grasses or shrubs, while their mother goes on foraging trips (Linnell, 1994; Tull et al., 2001; Van Moorter et al., 2009). In chamois and mouflon, the age of first reproduction of females is

around 1.5 years old (Garel et al., 2005, 2009) and give birth in May-June for chamois, and in April-May for mouflon (Bon et al., 1993). In contrast to roe deer, chamois and mouflon's lambs follow their mothers very early after their birth (Langbein et al., 1998; Lent, 1974).

2. Study sites

a. Aurignac

The study on roe deer was carried out at Vallons et Coteaux de Gascogne (Zone Atelier PyGar), near Aurignac in the southwest of France (43°16'N, 0°52'E, 260-395 m above sea level; Figure 3) in a 19 000 ha rural region. It is a hilly area composed of two large forests (672 and 463 ha, 6.0% of the study area), numerous small woodland patches (mean \pm SD $\frac{1}{4}$ 2.4 \pm 11.5 ha, 18.8%), meadows (37.2%), crops (cereals, oilseed and fodder crops, 31.6%) and hedgerows (3.6%). The study area is typical of a modern agricultural landscape with human presence scattered throughout in small villages, farms and isolated houses, and connected via secondary roads. The climate is oceanic, with an average annual temperature of 11–12°C and 800 mm precipitation (Morellet et al., 2011). Other ungulates like wild boar *Sus scrofa* and red deer *Cervus elaphus* are also present. No natural predators are present on the study site, although free-ranging dog and red foxes *Vulpes vulpes* may occasionally predate adults and young fawns respectively. Hunting represents now the main source of regulation for roe deer, and occurs regularly from the mid-September to the end of January (until 2008) or February (since 2009), mostly using dogs for drive hunting. During summer, that is from 1 June to the 2nd Sunday of September, male roe deer can also be hunted by stalking.

b. Massif of Caroux-Espinouse

The study on mouflon was carried out in the Caroux-Espinouse massif in southern France (43°38'N, 2°58'E, 150-1124 m above sea level; Figure 3) in a 17 000 ha low elevation mountain range, which is part of the Parc Natural Régional du Haut-Languedoc (306 000 ha). This area is characterized by deep valleys interspersed between plateaux which are mainly exploited for the timber of conifers (*Pinus sylvestris*, *Pinus nigra* and *Picea abies*). Slopes are covered by

broadleaved trees (mainly beech, *Fagus sylvatica*, chestnut, *Castanea sativa*, and evergreen oak, *Quercus ilex*) or rocky areas and open moorlands (either grass-rich heather, *Erica cinerea* and *Calluna vulgaris*, or broom, *Cytisus oromediterraneus* and *Cytisus scoparius*). The massif is subject to three types of climatic conditions. In its north-western part, oceanic and mountain climate exert an important influence, while the south of the massif is under a Mediterranean climate. This results in generally warm annual temperatures and high annual precipitations (average of 9.1°C & 1356 mm between 2002 and 2022 at the Murat-sur-Vèbre station, Météo France, 1022m a.s.l.), more than half of precipitations principally occurring during autumn and winter while summers are generally hot and dry. Snowfalls however are generally rare (12±4 days/year at 900m a.s.l.) and only remain on the highest plateaux (Marchand, 2013).

The area has a low human presence (39 inhabitants/km²) with generally limited human activities, particularly in the central National Hunting and Wildlife Reserve (1658 ha) where the hunting of mouflon is forbidden and activities are strictly regulated (see Marchand et al., 2015 for more details). Inversely, unprotected areas outside the wildlife reserve are subject to high disturbance pressures related to tourism (i.e. hiking) and hunting from March to August and from September to February respectively (Marchand et al., 2014; Martinetto et al., 1998). Free-ranging dogs, red foxes and golden eagles *Aquila chrysaetos* are also present and may occasionally predate on young or diseased individuals. Since 2014, the presence of a wolf has been detected as well, and some related predation events have also been documented (Pascal Marchand, personal communication). Still, hunting remains the main source of regulation of mouflon in the massif, and is performed either via driven hunts with hounds (as for wild boar *Sus scrofa* and roe deer inhabiting the area), or by stalking (maximum of 4 hunting guides each accompanying one or two hunters in the whole harvesting area, Marchand et al., 2014)

c. Massif des Bauges

The study on chamois was carried out in the Massif des Bauges, which is located in the French Prealps cornered by the cities of Chambéry, Annecy and Albertville (Figure 3). In total, the massif covers an area of 165 km² and its elevation ranges between 250m and 2217m above sea-level for its highest peak (i.e. the Arcalod, one of the 14 peaks of the massif exceeding 2000m a.s.l.). Due to its peculiar geological history, linked to the Alps' orogeny, the massif is characterized by a remarkable series of calcar folds and perched anticlinal and synclinal

features, resulting in steep slopes and many cliffs, which are ideal refuges for chamois. By its location in the prealps, the massif constitutes a first wall against oceanic depressions, and is there subject to high annual precipitations, i.e. around 2000 mm/year (annual mean recorded by Meteo France station in Les Aillons, 900m a.s.l. between 1985 & 2013) and rather cool temperatures, around 8.9°C (annual mean recorded by Meteo France station in Lescheraines, 590m a.s.l Duparc, 2016), which allows snow cover to persist in the massif during 5 months (November-April) at more than 1000m a.s.l.

Thanks to its climatic, geologic and topographic situation, the massif owns an important floristic and faunistic diversity (more than 1600 listed plant species representing 25% of the flora diversity of France, 50 % of listed French nesting birds also present in the massif), and is notably home to 5 species of wild ungulates, i.e. red deer, roe deer, wild boar, mouflon and chamois. This natural heritage has been attracted an increasing number of tourists and residents and thus lead to the creation of the Parc Naturel Regional du Massif des Bauges, which englobes 65 municipalities and covers 90 000 ha, in order to sustainably respond to this increasing socio-economic pressure. 22% of the park area notably are dedicated to the protection of wildlife via Natura2000 zones and the National Game and Wildlife Reserve of Bauges Massif (45°40' N, 6°14' E; 900 to 2200 m a.s.l., 5200 ha). All monitored individuals in our study were captured in the wildlife reserve, within two study sites, i.e. Charbonnet-Pleuven and Arménaz-Pécloz. The two study sites are approximately 7 km distant from each other, separated by deep valleys with no exchange of individuals between them. 18% and 25% of study sites' area in Charbonnet-Pleuven and in Arménaz-Pécloz respectively is covered by forests, mostly represented by beech (*Fagus sylvatica*) and fir (*Abies alba*) groves. The remainder of the study sites' area is covered by grasslands and by rocky areas (Lopez, 2001). Except for golden eagle and red foxes, which may occasionally predate newborn, and non resident wolf, chamois has no natural predators in the wildlife reserve and is mainly regulated by hunting (small parties of three to four hunters). Other ungulates such as mouflon (*Ovis gmelini musimon*, 20%), roe deer (*Capreolus capreolus*, 4%), wild boar (*Sus scrofa*, 4%) and red deer (*Cervus elaphus*, 2%) are also hunted within the reserve (Courbin et al., 2022).

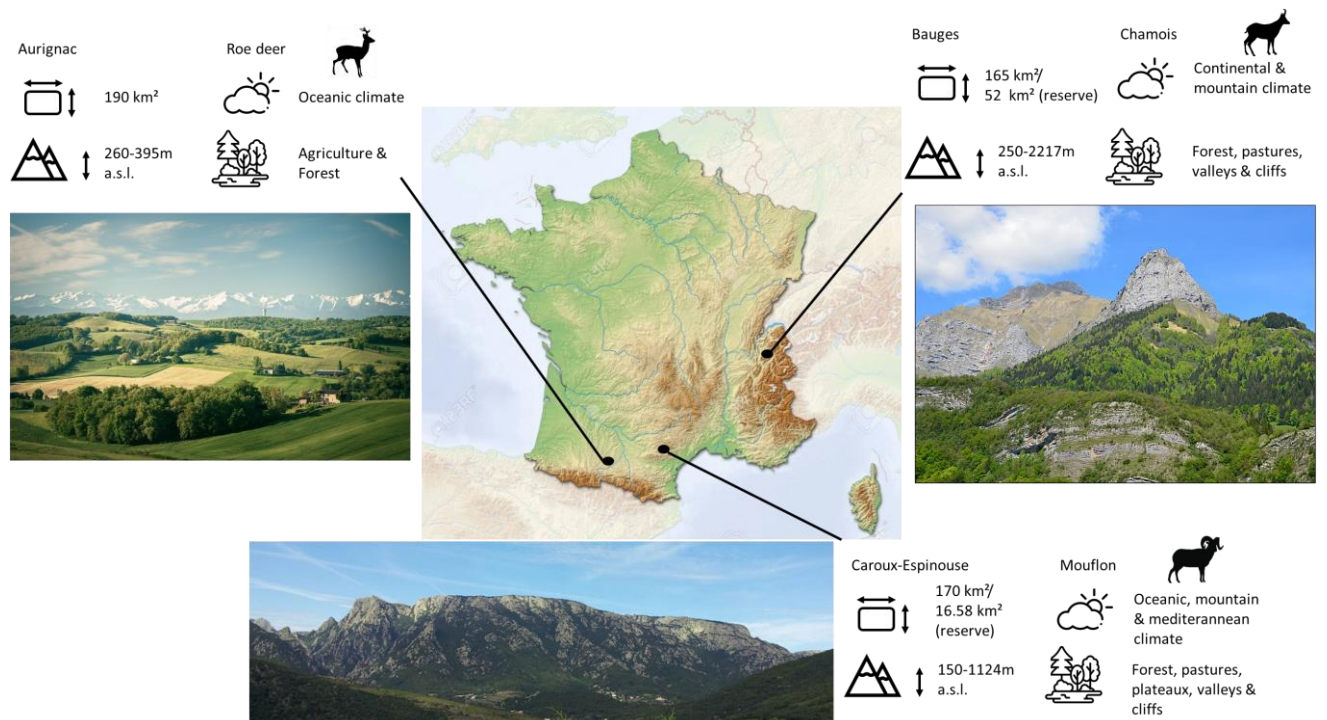


Figure 3: Location and characteristics of species' study sites

d. Long term monitoring of populations

Every year since the 1970-1990's until current days, animal captures have been performed on the different study sites by field technicians and researchers in order to monitor the inhabiting ungulates populations. Several measurements are performed in order to estimate the individuals' age, body condition and growth (i.e. body mass, metatarsus length, horns/antlers length), health, diet, reproductive status and genetics (sampling of feces, hair, ectoparasites such as ticks, blood). Captured animals are also marked and identified through subcutaneous transponders, ear tags or collars with coloured bands and letters, allowing field technicians to visually mark and recapture animals and estimate population densities. Since 2003, a subset of animals captured on each different study site have also been collared with GPS tracking device (see table 1 for name and brand details). All GPS collars weighed less than 3% of the individual body mass and were programmed with various scheduling (see Table 1). In the end, the combination of data about individuals' characteristics such as body condition, genetic information, diet, parasites and diseases and locations, enables researchers to investigate the link between the spatial behaviour of individuals, their performance in terms of survival and

reproduction and the resulting population genetic structure as well as its spatial and demographic dynamics.

Table 1: Procedure and type of data collected on animals during long term monitoring in each study site

	Aurignac	Caroux-Espinouse	Bauges
Institution/Laboratory	INRA/CEFS	OFB	OFB
Start of population monitoring	1993	1974	1985
Start of first GPS deployment	2003	2003	2003
Number of GPS monitored individuals	495	356	284
Period of captures	January-February	May-July	June-Early September
Type of capture	Drives with human beaters and long nets	"guillotine" traps and drop nets baited with salt licks	drop nets baited with salt licks
Type of measurements and sample collected on individuals	Age, body mass, metatarsus length, tick counts, blood, feces and hair samples	Age, body mass, metatarsus length, tick counts, blood, feces and hair samples	Age, body mass, metatarsus length, tick counts, blood, feces and hair samples
Type of marking procedure	ear tags, collars with coloured bands, subcutaneous transponders	ear tags, collar with coloured bands, subcutaneous transponders	ear tags, collars with coloured bands
Type of GPS tracking device	Lotek 3300 Revision 1, Lotek 3300 Revision 2, Lotek GSM Small WildCell, Vectronic PLUS-1C Store On Board Vectronic PLUS Mini-1C (GSM), Vectronic vertex plus (GPS), Vectronic vertex plus (GSM)	i-gotU GT-120, Lotek 3300S, Lotek 6000S, Lotek Litetrack, Milsar, Vectronic Vertex Lite	Lotek 3300 S, Lotek Litetrack, Vectronic GPS Plus, Vectronic Vertex Lite, Vectronic Vertex Plus
GPS scheduling	1 location/10 min to 6 hours	1 location/20 min to 24 hours	1 location/10 min to 24 hours

Chapter 4

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Do reproductive constraints or experience drive age-dependent space use in two large herbivores?



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Abstract

Life histories are strongly age dependent, notably linked to the onset of reproductive maturity and subsequent senescence. Consequently, ageing is predicted to impact behaviour, through the expression of either mating tactics in males or neonatal antipredator tactics in females. However, the influence of ageing, and the associated reproductive activity, on spatial behaviour remains poorly investigated. In this regard, we quantified age- and sex-specific intra-annual variation in movement rates and space use of two large herbivores with contrasting life histories: the roe deer, *Capreolus capreolus*, an asocial species with a territorial male mating strategy and a hider neonatal tactic, and the Mediterranean mouflon, *Ovis gmelini musimon* × *Ovis* sp., a gregarious species with a roaming male mating strategy and a follower neonatal tactic. We expected age-related differences to be mostly related to (1) age-specific mating tactics during the rut for males and the presence/absence of offspring for females, and (2) experience and/or locomotory senescence otherwise. During the rutting period, older roe deer males travelled greater daily distances than younger males due to patrolling behaviours for territory defence, whereas older mouflon males travelled less than younger males, which often adopted coursing tactics to mate with females. During the birth period, reproductive females had smaller home ranges than nonreproductive females in roe deer, whereas no marked differences were observed in mouflon females. The most marked age-related variation in space use of mouflon occurred outside the reproductive periods; specifically, the oldest individuals travelled less far and had a smaller home range (females only) than younger individuals. Our findings illustrate how space use tactics vary within and between populations of large herbivores, providing strong evidence that age and reproductive activity are major determinants of their spatial behaviour.

Introduction

Animals living in heterogeneous and/or seasonal environments must cope with marked spatial and/or temporal variation in resource availability and predation risk, resulting in seasonal variation in space use (Nicholson, Bowyer, & Kie, 1997; Mysterud & Ims, 1998; Gunnarsson et al., 2005; Godvik et al., 2009; Gillies & Clair, 2010; Tucker et al., 2018). However, not all individuals respond in the same way to changes in environmental conditions. Indeed, individuals differ in their perception of resources and risks, their locomotor abilities and their energetic requirements (Harel, Horvitz, & Nathan, 2016; Laundré, Hernández, & Altendorf, 2001; Searle, Hobbs, & Gordon, 2007). For example, in dimorphic and polygynous vertebrates, sexual size dimorphism is associated with sex differences in resource requirements, activity patterns, sensitivity to adverse weather conditions and social preferences, often leading to sex-specific patterns of movement and space use (Bourgoin, Marchand, Hewison, Ruckstuhl, & Garel, 2018; Catry, Phillips, Croxall, Ruckstuhl, & Neuhaus, 2006; Ruckstuhl & Neuhaus, 2002, 2006).

In an analogous way to other life history traits, the sex-specific spatial ecology of a given species (Ruckstuhl & Neuhaus, 2006) is also expected to be strongly structured by age and life stage (Charlesworth, 1980; Stearns, 1992; Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toïgo, 2000). For instance, old individuals are reported to move less and use restricted home ranges compared to younger individuals, as a result of a decline in locomotor performance and/or greater experience, presumably through a better knowledge of the distribution of resources and predation risk in the local environment (birds: Catry et al., 2006; Harel et al., 2016; fish: Magnhagen et al., 2008; large herbivores: Froy et al., 2018; Montgomery, Vucetich, Peterson, Roloff, & Millenbah, 2013; Thurfjell, Ciuti, & Boyce, 2017; carnivores: MacNulty et al., 2009). Furthermore, allocation to reproduction varies markedly with age and/or life stage in numerous vertebrate taxa (Clutton-Brock, 1984; Forslund & Pärt, 1995; Lemaître et al., 2015; McBride et al., 2015). In most species, for instance, young males that are still growing are unable to compete for mates with older fully grown males and so often adopt alternative reproductive tactics, resulting in age-specific patterns of movement and space use during the rutting period (Cederlund & Hakan, 1994; Foley et al., 2015; Taylor et al., 2020). Likewise, during the critical perinatal period, female large herbivores are constrained to select those habitats that best compensate for the increased energetic requirements linked to pregnancy and lactation, while minimizing predation risk for their offspring (Bongi et al., 2008; Ciuti et al., 2006, 2009; Viejou et al., 2018). In contrast, immature and nonreproductive females are unconstrained by the presence of dependent young, resulting in age- and/or stage-specific space use patterns (Kie & Bowyer, 1999; Marchand et al., 2015; Oehlers, Bowyer, Huettmann, Person, & Kessler, 2011; Viejou et al., 2018; Villaret, Bon, & Rivet, 1997).

Surprisingly, age dependence is still often largely overlooked in studies of spatial behaviour, mostly because of the difficulty of accurately assessing the age of individuals in the field. The increasing number of long-term monitoring studies (Festa-Bianchet, Douhard, Gaillard, & Pelletier, 2017), in combination with the development of tracking technologies (e.g. GPS, Kays, Crofoot, Jetz, & Wikelski, 2015), offers new opportunities to assess the crucial role that age may play in determining an animal's movement behaviours. A better understanding of which individual attributes shape patterns of movement and, more specifically, locomotion, is of fundamental importance as locomotion makes up a substantial part of an animal's daily energy budget (Halsey, 2016). Moreover, the amount of energy that an animal expends while moving can significantly constrain the amount of energy available for growth and reproduction, resulting in long-term implications for individual fitness (Grémillet et al., 2018). Recent work on large herbivores has highlighted the importance of age-related differences in movements and space use (e.g. Eggeman, Hebblewhite, Bohm, Whittington, & Merrill, 2016), investigated the relative importance of locomotor senescence and experience (e.g. Froy et al., 2018; Thurfjell et al., 2017) and inferred relationships between these behavioural modifications and survival/reproduction (e.g. Froy et al., 2018; Taylor et al., 2020). However, there is a need to delve deeper into the effect of age on movement in both males and females in a larger number of species that differ in sexual dimorphism (which affects senescence patterns in ungulates) and sociality level.

In this study, we investigated the influence of sex and age on fine-scale movements and home range size over the annual cycle in two large herbivore species, the roe deer, *Capreolus capreolus*, and the Mediterranean mouflon, *Ovis gmelini musimon* × *Ovis* sp. Home range size results from the different components of individual movements such as speed, sinuosity or recursion (Börger, Dalziel, & Fryxell, 2008; Péron, 2019; Van Moorter, Rolandsen, Basille, & Gaillard, 2016). Hence, differences in small-scale movements, when measured with simple statistics such as cumulated distance travelled in a day, do not always translate to a similar extent at a larger scale (Tablado et al., 2016). Therefore, we analysed two proxies of space use, the daily distance travelled (DDT) and the resulting monthly home range size (monthly HRS). We also accounted for the established influence of habitat type on the extent of individual movements, using species-specific proxies (i.e. % woodland for roe deer, Morellet et al., 2011; % grass-rich areas for mouflon, Garel et al., 2007; Marchand et al., 2014; see Methods and the Appendix), and evaluated the following hypotheses.

During the rutting period (July–August in roe deer, mid-October–December in mouflon), we expected reproductive males of both species to show a marked difference in DDT and monthly

HRS compared to nonreproductive males, but with a species-specific signal related to their contrasting mating tactics. In the territorial roe deer, most males successfully reproduce for the first time when they have reached full physical maturity and are able to successfully hold a territory (in general at 3 years old; Vanpé et al., 2009). During the territorial period, and particularly during the rut, we predicted that adult bucks would have higher DDT due to patrolling behaviours within their territories (H1a), but should also have smaller monthly HRS (H1b) compared to younger nonreproductive males, most of which are expected to be nonterritorial, with less constrained movements. In the roaming mouflon, while males generally do not reproduce before 4 years old, alternative mating tactics have been reported. Whereas older males generally adopt a tending tactic, following receptive females and impeding attempts of other males to mate, young subordinate males often adopt a coursing tactic, attempting to breach the defence of the tending males (Bon, Gonzales, Bosch, & Cugnasse, 1992). We therefore predicted that young subordinate males would have both higher DDT (H2a) and larger monthly HRS (H2b) during the rut than old dominant males and nonreproductive males.

Following parturition, the movements and home ranges of reproductive females should be constrained by the presence of offspring compared with nonreproductive females (Bongi et al., 2008; Ciuti, Bongi, Vassale, & Apollonio, 2006). This should be particularly apparent in the roe deer which adopts a hider antipredator tactic (Linnell, Nijhuis, Teurlings, & Andersen, 1999), but much less so in mouflon where offspring are capable of following their mother shortly after birth (Langbein, Scheibe, & Eichhorn, 1998; Langbein, Streich, & Scheibe, 1998). Females give birth for the first time at 2 years old in roe deer, and 2 or 3 years old in mouflon, while the vast majority of females of both species subsequently reproduce every year (Gaillard et al., 2000; Garel et al., 2005). We therefore predicted that during parturition adult roe deer females (≥ 2 years old) would have lower DDT (H3a) and smaller monthly HRS (H3b) than younger females (<2 years old), while no age-related differences in DDT (H4a) or monthly HRS (H4b) were expected for female mouflon.

Outside of the reproduction periods, we expected age-specific variation in movement to be driven by experience, which is assumed to be higher in older individuals, and/or locomotor performance, which should decrease in senescent individuals (Froy et al., 2018). We therefore predicted that old individuals of both sexes and both species (H5: roe deer males; H6: mouflon males; H7: roe deer females; H8: mouflon females) would have (1) lower DDT and (2) smaller monthly HRS than young individuals outside the reproductive periods.

Methods

Study areas

The study on roe deer was carried out at Vallons et Coteaux de Gascogne (Zone Atelier PyGar) in the southwest of France (43°16'N, 0°52'E, 260–395 m above sea level; Fig. 1) in a 19 000 ha rural region. It is a hilly area composed of two large forests (672 and 463 ha, 6.0% of the study area), numerous small woodland patches (mean \pm SD = 2.4 \pm 11.5 ha, 18.8%), meadows (37.2%), crops (cereals, oilseed and fodder crops, 31.6%) and hedgerows (3.6%). The study area is typical of a modern agricultural landscape with human presence scattered throughout in small villages, farms and isolated houses. The roe deer is hunted by drive hunting from the second Sunday in September to the end of January (until 2008) or February (since 2009), mostly using dogs, and by stalking of males only from 1 June to the second Sunday in September.

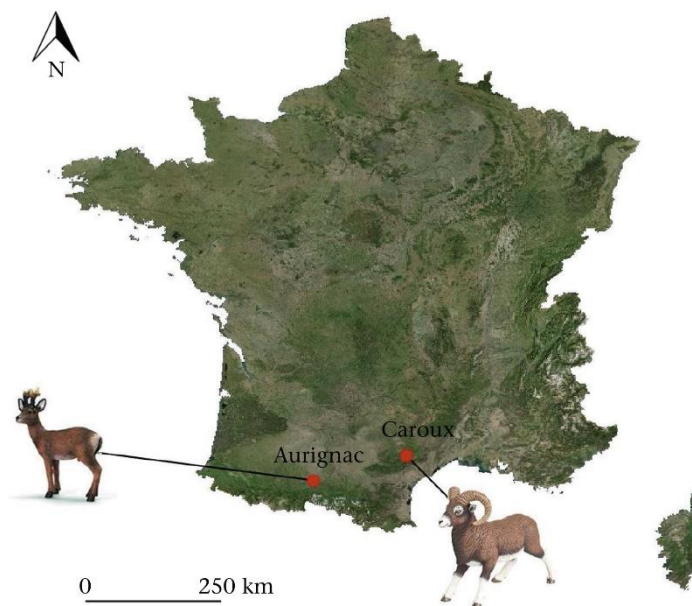


Figure 1: Study sites in France. The study on roe deer was carried out at Vallons et Coteaux de Gascogne (here named Aurignac, i.e. the closest town to the study site) and the study on mouflon was carried out in the Caroux-Espinouse massif.

The study on mouflon was carried out in the Caroux-Espinouse massif in southern France (43°38'N, 2°58'E, 150–1124 m above sea level; Fig. 1) in a 17 000 ha low elevation mountain range. This area is characterized by deep valleys interspersed between plateaux which are mainly exploited for the timber of conifers (*Pinus sylvestris*, *Pinus nigra* and *Picea abies*). Slopes are covered by broadleaved trees (mainly beech, *Fagus sylvatica*, chestnut, *Castanea sativa*, and evergreen oak, *Quercus ilex*) or rocky areas and open moorlands (either grass-rich heather, *Erica cinerea* and *Calluna vulgaris*, or broom, *Cytisus oromediterraneus* and *Cytisus*

scoparius). The area has a low human presence (39 inhabitants/km²) with limited human activities, particularly in the central National Hunting and Wildlife Reserve (1658 ha) where the hunting of mouflon is forbidden and activities are strictly regulated (see Marchand et al., 2015 for more details).

Capture and marking

Roe deer were caught in winter (from 16 November to 27 March) from 2005 to 2016 using drives with human beaters and 4 km of long-nets. Drives were carried out without dogs to reduce stress. When an animal was captured, it was immediately tranquilized with an intramuscular injection of acepromazine by a person licensed to do so (Federation of European Laboratory Animal Science Associations category C accreditation). The animal remained conscious between capture and release, but this short-acting neuroleptic quickly attenuates the response to stress and prevents any adverse effects in deer (Montané et al., 2003). The drug dose (1.65 mg/injection) was calculated following Montané et al. (2003). To reduce stress and risk of injury, each tranquilized animal was then transferred to a wooden retention box until the end of catching operations. Then, it was removed from the box by three highly experienced animal handlers, with the eyes covered to minimize stress during handling procedures. We marked each individual with ear tags, weighed and sexed them. We classified the individuals into three age classes: juveniles (6–10 months old), yearlings (18–22 months old) and adults (more than 2.5 years of age). Juvenile roe deer were identified by the presence of a tricuspid third premolar milk tooth (Ratcliffe & Mayle, 1992), while we used tooth wear to distinguish yearlings from adults (Hewison et al., 1999). Finally, we equipped some of the animals (N = 287, Table 1) with a GPS collar (Lotek 3300 or Vectronic GPS PLUS-1C Store On Board). GPS collars weighed 400 g corresponding to no more than 3.5% and less than 2% of the lowest and highest individual body mass, respectively. For juveniles, which have not completed body growth (neck circumference about 2.5 cm less than that of yearlings), we accounted for a projected growth of about 10% by fitting the collar slightly looser. After 11 months of GPS monitoring, we used the preprogrammed remote drop-off system to retrieve the collars and download the recorded data. The animal capture and handling protocol was carried out in accordance with local and European animal welfare laws (prefectural order from the Toulouse Administrative Authority to capture and monitor wild roe deer and agreement no. A31113001 approved by the Departmental Authority of Population Protection).

Mediterranean mouflon were caught during spring and summer (from May to July), from 2010 to 2018, using collective or individual traps (enclosure with mesh walls and a guillotine door triggered when the animal pulls a wire while entering the trap) and 40×40 m or 5×5 m drop nets baited with salt licks. For fixed traps, to reduce the time between capture and handling and so avoid stress, as captures mostly occurred at night, traps were checked early every morning during the capture period. In addition, to further limit the risk of heat stress, traps were generally positioned under tree cover. Mouflon caught with drop nets triggered manually were processed immediately after the capture. These catch procedures do not require specific bedding, food or water. The capture and handling of mouflon were carried out by highly experienced animal handlers from the Office Français de la Biodiversité. As soon as an animal was handled, it was restrained with the eyes covered to reduce stress. We sexed each individual and determined age by tooth eruption patterns in females, with individuals classified as one of lamb, 1, 2, 3, ≥ 4 years old, and by horn growth annuli in males, with individuals classified as one of lamb, 1, 2, 3, 4, 5, 6, ≥ 7 years old (Garel, Cugnasse, Hewison, & Maillard, 2006). A random sample of individuals at least 2 years old was fitted with GPS collars (Lotek 3300). We only included GPS-collared individuals of known age ($N = 90$, i.e. first captured as lamb, 1, 2, 3 years old for females, or as lamb, 1, 2, 3, 4, 5, 6 years old for males) in the analyses, grouping them into four age classes (i.e. 2–3, 4–6, 7–8 and > 8 years old, Table 1) to obtain balanced sample sizes. All efforts were made to minimize the handling time used to take measurements and adjust the collar, to release individuals on site as soon as possible. Mouflon were equipped with GPS collars weighing 400 g, a weight never exceeding 2.5% and less than 1% of the body mass of the smallest and largest individual, respectively. To allow for possible seasonal variation in neck circumference, we left a gap of 3 cm between the GPS collar and the animal's neck while making sure that the collar would not rotate. After 1 year of GPS monitoring (depending on the batteries' life), we retrieved the collar using a remote drop-off system (triggered manually) and downloaded the recorded data. The mouflon capture and handling protocol was carried out in accordance with local and European animal welfare laws (prefectural decree no. 2009-014 delivered to the Office National de la Chasse et de la Faune Sauvage by the Préfecture de Paris, in accordance with the French environmental code—Art. R421-15 to 421-31 and R422-92 to 422-94-1).

From repeated observations of GPS-collared individuals throughout the year as part of long-term capture–mark–recapture monitoring of both populations, we were able to ascertain that the GPS collars did not cause changes in behaviour (foraging, social behaviour) compared to other unmarked individuals in the population. In addition, we did not detect any adverse effects linked to the wearing of the collars in terms of injury or reproductive activity.

Table 1: Number of roe deer and mouflon per sex and age class at capture for the analyses of daily distance travelled (DDT) and monthly home range size (HRS)

Response variable	Sex	Roe deer			Mediterranean mouflon			
		Juveniles	Yearlings	Adults	2–3	4–6	7–8	>8
DDT	Females	25	24	93	9	17	8	3
	Males	20	17	65	25	17	12	6
HRS	Females	56	25	93	9	17	8	3
	Males	51	17	64	25	17	12	6

GPS monitoring

We scheduled GPS collars to record locations of roe deer every 10 min over a 24 h period, once or twice each month, and every 6 h all year round otherwise. As the days sampled at 10 min intervals were selected randomly within the month, irrespective of environmental conditions, and the total monitoring period spanned 12 years (2005–2016), we can assume that these data provide a reliable representation of age-specific monthly space use at the population level. We scheduled GPS collars to record locations of mouflon every 2 h all year round, alternating between even hours on one day and odd hours on the following day.

To improve the accuracy of GPS locations for roe deer, we used differential correction (Adrados, Girard, Gendner, & Janeau, 2002). Moreover, in case capture and handling of roe deer temporarily altered their behaviour, we removed all locations recorded during the first 7 days after the release date of the animal (Morellet et al., 2009). For mouflon, GPS monitoring was programmed to begin only after a predetermined date which was several days or weeks after animal handling. A large percentage of juvenile roe deer dispersed during the monitoring period, around their first birthday (34%; Debeffe et al., 2012). Hence, we removed locations recorded during the dispersal period for individual roe deer classified as dispersers, following Ducros et al. (2020), to ensure that we only analysed habitual ranging behaviour. Note that no juvenile mouflon were monitored. Finally, we screened GPS locations of both species for erroneous locations (i.e. fixes that would imply an unfeasible movement speed given the distance from/to the previous/next location) using a method inspired by Bjørneraas, Van Moorter, Rolandsen, and Herfindal (2010), but adapted to our specific study models' behaviour. We removed 85 fixes (0.02% of all locations) and 165 fixes (0.04% of all locations),

respectively, from the 10 min and 6 h schedules in roe deer, and 1760 fixes (i.e. 0.03% of all locations) in mouflon.

Statistical analyses

We analysed two proxies of space use: DDT and monthly HRS. Depending on species and sex, the correlation between average monthly DDT and monthly HRS ranged between 0.03 and 0.59, suggesting the two variables were partially related (as expected from the link between movements and home range emergence; e.g. Van Moorter et al., 2016), but also that they provided a degree of independent complementary biological information.

DDT

We used data from the 10 min GPS schedule for roe deer and the 2 h GPS schedule for mouflon to compute the DDT for each individual as the sum of the step lengths between each pair of consecutive locations over 24 h. As some scheduled locations were missing, we restricted our analyses to 24 h periods for which a minimum of 130 (>90% for roe deer) and 10 (>83% for mouflon) scheduled locations were available, generating 2151 DDT for roe deer and 20 549 DDT in mouflon. Then, to ensure that DDT was comparable among individuals despite a few missing fixes, we averaged observed values of DDT based on the 10 min or 2 h steps for each individual-day, and multiplied this by the number of steps scheduled per day (i.e. 143 10 min steps in roe deer; 11 2 h steps in mouflon). We used linear mixed models (LMMs) to investigate variation in log-transformed DDT in relation to age and month, including individual identity as a random effect on the intercept. We included the main effects and two-way interaction between age and month. As we were interested in investigating age-related differences in space use, rather than the differences between species and sexes, and because of marked a priori differences in both life history and GPS monitoring schedule, we ran separate models for each species and sex. Moreover, to control for the known influences of habitat type on ranging behaviour (roe deer: Morellet et al., 2011; mouflon: Garel et al., 2007; Marchand et al., 2014; Appendix), we included in all models the percentage of woodland (roe deer) or of grassland (mouflon) within the monthly HRS of each individual.

Monthly HRS

We estimated monthly HRS for each individual using data from the 6 h GPS schedule in roe deer (> 110 scheduled fixes per month) and the 2 h GPS schedule in mouflon (> 330 scheduled fixes per month). Only individual-months with data available on all days of a focal month were included in the analyses (N = 2403 and 937 monthly HRS in roe deer and mouflon, respectively). We used the fixed-kernel method to estimate monthly HRS. Although other methods are available and may be more suited when fixes are collected at very frequent time intervals, the fixed-kernel method is the most commonly used method in the literature (Kie et al., 2010), and is well suited for comparing home range size among age classes and months (the shape and location of the home ranges are not under scrutiny here). As differences in smoothing parameter may result in differences in monthly HRS (Pellerin, Saïd, & Gaillard, 2008), we set the smoothing parameter h to the median value obtained for each species to recalculate monthly HRS for each individual. We estimated monthly HRS at the 90% isopleth, as recommended by Börger et al. (2006), to obtain an unbiased estimate. To investigate age-related variation in log-transformed monthly HRS, we fitted the same model structure as for DDT (see details above).

Model selection

We fitted models using maximum likelihood and used Akaike's information criterion (AIC, Burnham & Anderson, 2002) and Akaike weights to select the model with the most support. When ΔAIC was < 2 between competing models, we retained and interpreted the model with the fewest parameters following the rule of parsimony. We also calculated the marginal and conditional R^2 of the models, which can be interpreted as the proportion of variance explained by the fixed effects alone, or by both fixed and random effects, respectively (Nakagawa & Schielzeth, 2013). We performed all statistical analyses using R software version 3.6.1 (R Core Team, 2019) and 'lme4', 'adehabitatHR' and 'adehabitatLT' packages (Bates et al., 2015; Calenge, 2011). We performed the selection process on a model subset including the null model and all models that included the percentage of woodland (roe deer) or of grassland (mouflon).

Results

Male age-specific space use during the mating season

In both species, the best models for explaining variation in DDT among males included the two-way interaction between age and month (Table 2), while the best model for explaining variation in monthly HRS included an additive age effect only in roe deer, and no age effect in mouflon (Table 2).

Table 2: Candidate linear mixed models to investigate variation in log-transformed daily distance travelled (DDT) and monthly home range size (HRS) in roe deer and mouflon males, with individual identity as a random effect on the intercept.

Response variable	Species	Models	K	Δ AIC	AIC weight	R ² m	R ² c
DDT	Roe deer	Month + Age +% Woodlands + Month*Age	38	0.00	0.974	0.26	0.37
		Month + Age +% Woodlands	17	7.25	0.026	0.22	0.33
		Month +% Woodlands	15	22.17	0.000	0.19	0.32
		% Woodlands	4	174.85	0.000	0.03	0.15
		Null model	3	184.91	0.000	0.00	0.14
	Mouflon	Month + Age +% Grasslands + Month*Age	51	0.00	1.000	0.20	0.48
		Month + Age +% Grasslands	18	157.95	0.000	0.18	0.46
		Month +% Grasslands	15	241.21	0.000	0.08	0.34
		% Grasslands	4	1421.48	0.000	0.0	0.21
		Null model	3	1423.74	0.000	0.00	0.20
HRS	Roe deer	Month + Age +% Woodlands	17	0.00	0.606	0.35	0.64
		Month + Age +% Woodlands + Month*Age	39	0.79	0.393	0.36	0.66
		Month +% Woodlands	15	14.99	0.001	0.33	0.63
		% Woodlands	4	163.05	0.000	0.23	0.53
		Null model	3	251.27	0.000	0.00	0.53
	Mouflon	Month +% Grasslands	15	0.00	0.635	0.45	0.74
		Month + Age +% Grasslands	18	1.08	0.365	0.47	0.73
		Month + Age +% Grasslands + Month*Age	51	22.86	0.000	0.49	0.75
		% Grasslands	4	403.95	0.000	0.24	0.64
		Null model	3	480.44	0.000	0.00	0.16

Models were ranked according to AIC selection criteria using the difference in AIC values (Δ AIC), the number of estimated parameters (K) and the AIC weight of each model. The three best ranked models are presented followed by the habitat type model and the null model. The best supported model is in bold. R²m and R²c are marginal and conditional R², respectively (see Nakagawa & Schielzeth, 2013).

In roe deer, in agreement with H1a, differences in DDT between age classes were detected during the territorial period, and more particularly during the rutting period: adult DDT was 8.55 ± 0.40 km/day in July and 7.54 ± 0.29 km/day in August, i.e. 51.5% and 44.1%, respectively, greater than juvenile DDT (July: 5.64 ± 0.48 km/day; August: 5.24 ± 0.41 km/day), and 33.9% and 9.4%, respectively, greater than yearling DDT (July: 6.39 ± 0.60 km/day; August: 6.90 ± 0.60 km/day; Fig. 2a). In contrast, the monthly HRS of adult males was consistently smaller than that of younger individuals throughout the year (average monthly HRS

for adult males 14.7% and 18.4% smaller than juveniles and yearlings, respectively; Fig. 2c), providing only partial support for H1b.

In mouflon, during the rutting period, we observed higher DDT in nonreproductive males (2–3 years old: 1.69 ± 0.09 km/day and 1.44 ± 0.08 km/day in November and December, respectively; Fig. 2b) and younger adult males (4–6 years old: 1.59 ± 0.1 km/day and 1.25 ± 0.07 km/day in November and December, respectively) compared to older adult males (7–8 years old: 1.27 ± 0.07 km/day and 0.93 ± 0.05 km/day, 19.9–24.9% and 25.5–35.0% less in November and December, respectively; >8 years old: 1.26 ± 0.11 km/day and 0.85 ± 0.07 km/day, 20.8–25.8% and 31.7–40.4% less in November and December, respectively; Fig. 2b), in agreement with H2a. However, contrary to our prediction H2b, these age-related differences were not observed at the home range scale (Fig. 2d).

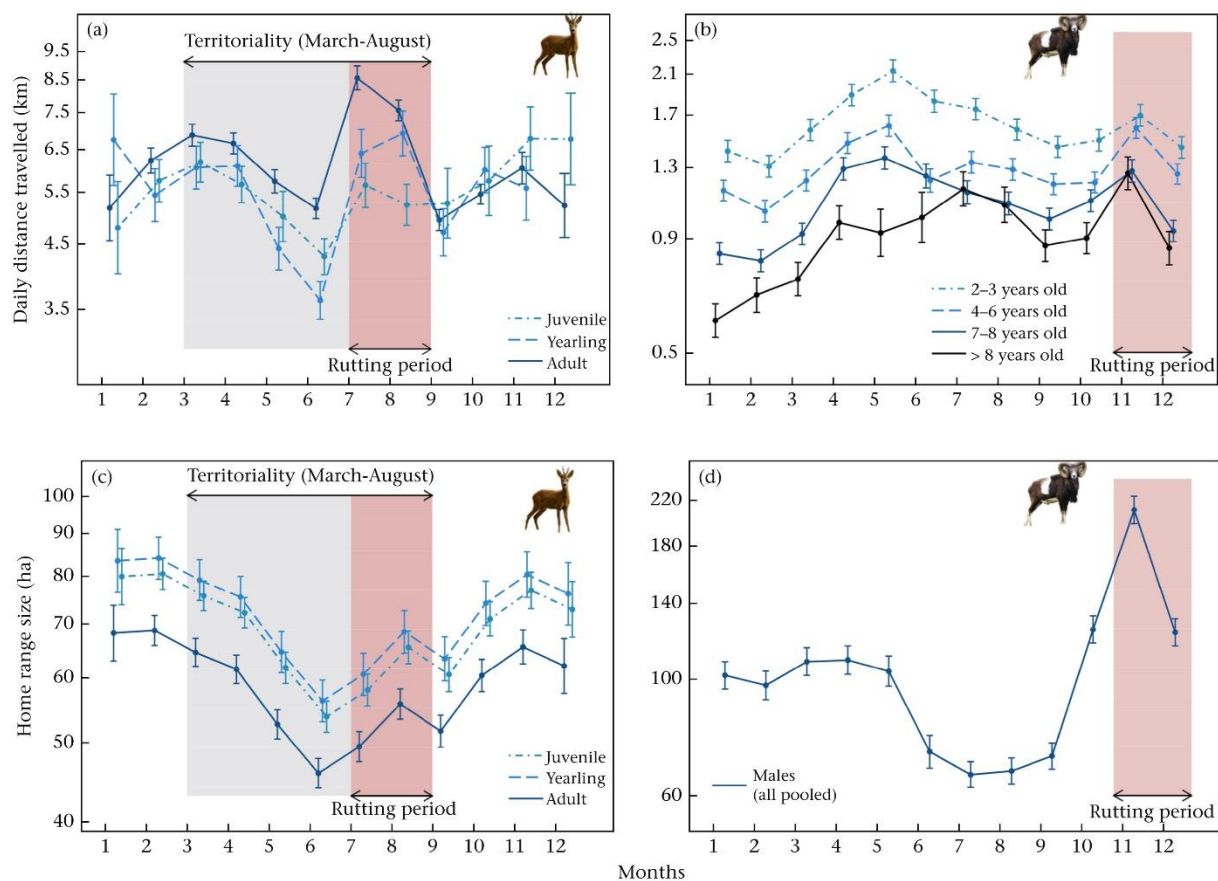


Figure 2: Predicted daily distance travelled of (a) roe deer males and (b) mouflon males, and monthly home range size in (c) roe deer males and (d) mouflon males over the year (1 = January) for different age classes. We used a logarithmic scale on the y axis. Points and bars represent the predicted estimates and associated standard errors derived from the selected model.

Female age-specific space use following parturition

In roe deer females, the best model for explaining variation in DDT included month only, whereas for monthly HRS the best model included the two-way interaction between age and month (Table 3). These results did not support our prediction H3a that, following parturition, reproductive females should have lower DDT, but supported our prediction H3b that reproductive females should have lower monthly HRS than nonreproductive females (Fig. 3a, c). Indeed, during the peak of parturition in May, the monthly HRS of nonreproductive females was 51.20 ± 2.47 ha, whereas it was 39.62 ± 2.66 ha for yearlings and 37.27 ± 1.25 ha for adults, i.e. 22.7% and 27.2% smaller, respectively. These differences persisted to the following month in June, when nonreproductive females had a monthly HRS of 42.29 ± 2.11 ha, whereas those of yearling and adult females were 35.87 ± 2.51 ha and 34.70 ± 1.18 ha, respectively, i.e. 15.2% and 17.9% smaller.

Table 3: Candidate linear mixed models to investigate variation in log-transformed daily distance travelled (DDT) and monthly home range size (HRS) in roe deer and mouflon females, with individual identity as a random effect on the intercept

Response variable	Species	Models	K	Δ AIC	AIC weight	R^2_m	R^2_c
DDT	Roe deer	Month + % Woodlands	15	0.00	0.846	0.24	0.42
		Month + Age + % Woodlands	17	3.59	0.141	0.24	0.43
		Month + Age + % Woodlands + Month*Age	39	8.35	0.013	0.26	0.45
		% Woodlands	4	247.90	0.000	0.11	0.28
		Null model	3	322.33	0.000	0.00	0.25
	Mouflon	Month + Age + Month*Age	50	0.00	0.654	0.13	0.26
		Month + Age + % Grasslands + Month*Age	51	1.27	0.346	0.13	0.26
		Month + Age + % Grasslands	18	85.32	0.000	0.11	0.26
		Month + % Grasslands	15	154.36	0.000	0.09	0.25
		% Grasslands	4	967.70	0.000	0.00	0.16
		Null model	3	976.14	0.000	0.00	0.13
HRS	Roe deer	Month + Age + % Woodlands + Month*Age	39	0.00	0.99	0.41	0.62
		Month + Age + % Woodlands	17	5.34	0.01	0.39	0.61
		Month + % Woodlands	15	11.06	0.00	0.38	0.61
		% Woodlands	4	814.87	0.00	0.04	0.25
		Null model	3	839.96	0.000	0.00	0.27
	Mouflon	Month + Age + % Grasslands	18	0.00	0.947	0.18	0.64
		Month + % Grasslands	15	5.78	0.053	0.16	0.64
		Month + Age + % Grasslands + Month*Age	51	23.82	0.000	0.23	0.68
		Null model	3	77.02	0.000	0.00	0.40
		% Grasslands	4	78.69	0.000	0.00	0.42

Models were ranked according to AIC selection criteria using the difference in AIC values (Δ AIC), the number of estimated parameters (K) and the AIC weight of each model. The three best ranked models are presented followed by the habitat type model and the null model. The best supported model is in

bold. R2m and R2c are marginal and conditional R², respectively (see Nakagawa & Schielzeth, 2013). For DDT in mouflon females, we included the best ranked model without age (Month+Grasslands) to facilitate comparison of R²m and R²c values with the best selected model.

In mouflon females, the best model for explaining variation in DDT included the two-way interaction between age and month (Table 3). Our prediction H4a, that there would be no age-related variation in movement rates during the birth period linked to the lamb follower tactic, was partially supported as, although 2–3-year-old females had a DDT of 1.15 ± 0.08 km/day in March, i.e. 2.5% higher than that of 4–6-year-old females (March: 1.12 ± 0.05 km/day), 17.8% higher than that of 7–8-year-old females (March: 0.97 ± 0.05 km/day) and 14.0% higher than that of >8-year-old females (March: 1.00 ± 0.7 km/day); these differences disappeared the following month, in April, when most birth events occur (Fig. 3b). Concerning prediction H4b, the monthly HRS of old females was consistently 14.2–20.3% smaller than that of younger females throughout the year (Fig. 3d), making it difficult to conclude whether the presence of a lamb generated age-related differences in space use during the birth period.

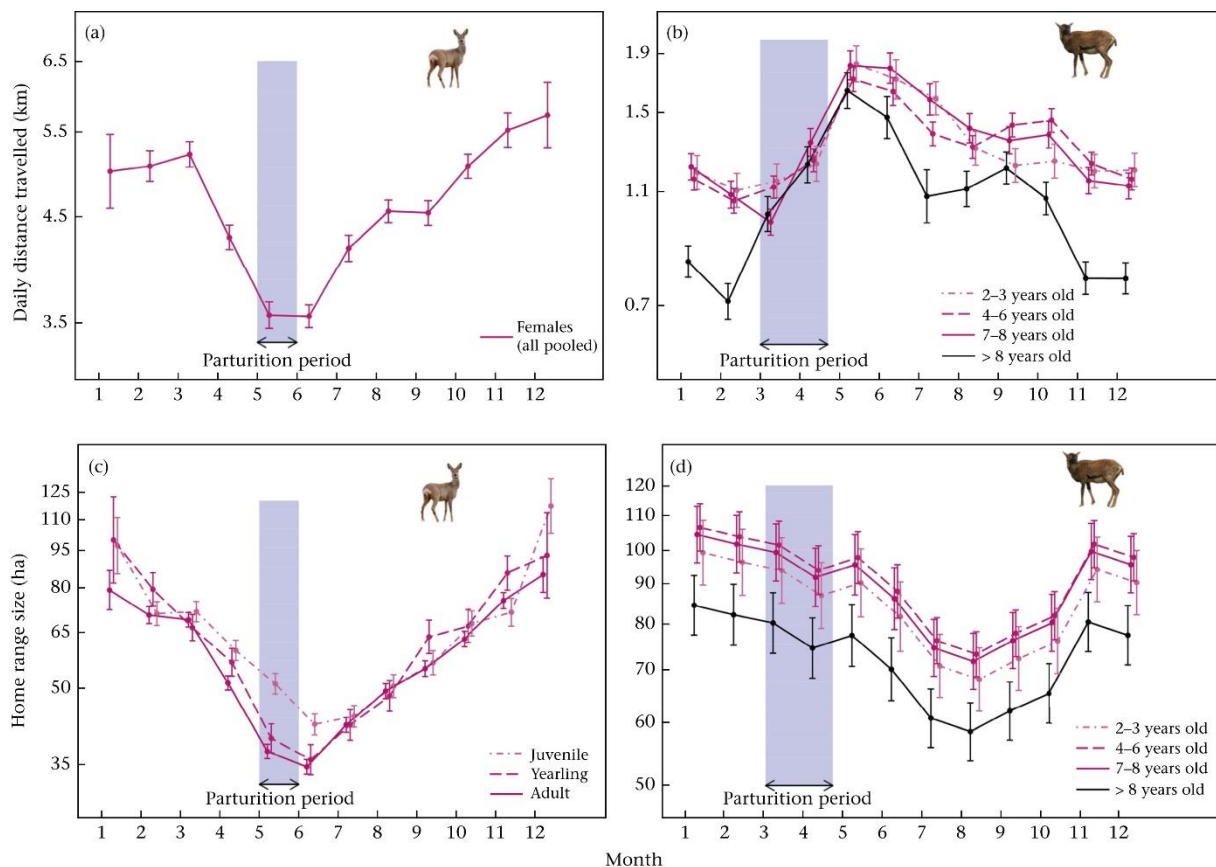


Figure 3: Predicted daily distance travelled for (a) roe deer females and (b) mouflon females, and monthly home range size in (c) roe deer females and (d) mouflon females over the year (1 = January) for different age classes. We used a logarithmic scale on the y axis. Points and bars represent the predicted estimates and associated standard errors derived from the selected model.

Age-specific space use outside reproduction periods

In roe deer, outside of the territorial and rut periods for males and the parturition period for females, there was some age-related variation in monthly HRS only. Monthly HRS of adults of both sexes was generally lower than that of younger individuals. Specifically, monthly HRS of adult males was, on average, 14.7% and 18.4% lower than those of juveniles and yearlings, respectively. No clear pattern of age-related differences in space use were observed in roe deer females. These results do not support our predictions H5a and H7a that older individuals should have lower movement rates than younger individuals, but do support our prediction H5b (but not H7b) that they should have smaller home ranges linked to increased experience and/or lower locomotor capacity.

In mouflon, the DDT of the oldest males were systematically smaller than those of younger males (except for 7–8-year-old males in July and August), as the oldest individuals (>8 years old) travelled between 0.59 ± 0.05 km/day (January) and 1.16 ± 0.10 km/day (July) per day, which was 13.6–32.0%, 12.8–48.8% and 32.1–58.2% lower than the DDT of 7–8, 4–6 and 2–3-year-old males, respectively (Fig. 2b). The oldest mouflon females (>8 years old) also had a lower DDT, mainly from June to February, compared to the other female age classes, i.e. between 0.71 ± 0.1 km/day (February) and 1.4 ± 0.12 km/day (June) per day, that is, 10.3–34.5%, 9.7–36.4% and 0.1–35.6% lower than 7–8, 4–6 and 2–3-year-old females, respectively (Fig. 3b). Second, monthly HRS was also markedly lower in the oldest females (>8 years old) across the entire year (Fig. 3d; 14.2–20.3% smaller than all other age classes), while no such age-related effect was observed for males. This supports our predictions H6a, H8a,b that old mouflon, particularly females, have lower movement rates and smaller ranges than younger individuals (see Table 4).

Overall, when included in the selected model, the percentage of variance attributed to age-related variation in space use (obtained by comparing the conditional R² of the best model and the marginal R² of the same model with no age-related effect) ranged between 2 and 12%, representing between 0.001 and 14% of the total variance explained by the selected models (Table 2, Table 3). The variance explained by the random effect of individual identity ranged between 11% and 46% of the total explained variance.

Table 4: Summary of predictions and results

Sex	Species	Breeding period		Outside breeding period	
		DDT	HRS	DDT	HRS
		Age-related differences linked to reproductive constraints, i.e. rutting (and territoriality in roe deer) in males, parturition in females		Age-related differences linked to increased experience and lower locomotor capacity in older individuals	
		H1a: Adults > younger males due to adult patrolling behaviours	H1b: Adults < younger males due to adult territorial behaviours		
Males	Roe deer	Supported	Partially supported	H5a: not supported	H5b: supported
		H2a: younger subordinates > older dominant males	H2b: younger subordinates > older dominant males		
Males	Mouflon	Supported	Not supported	H6a: supported	H6b: not supported
		H3a: Older females < younger females due to the hider tactic of fawns.	H3b: Older females < younger females due to the hider tactic of fawns.		
Females	Roe deer	Not supported	Supported	H7a: not supported	H7b: not supported
		H4a: No age-related differences expected as lambs adopt a follower tactic	H4b: No age-related differences expected as lambs adopt a follower tactic		
Females	Mouflon	Partially supported	Not supported	H8a: supported	H8b: supported

Discussion

Investigating the age-specific impact of reproduction (rutting for males, parturition and care for females) on movements and home ranges in two contrasting ungulate species allowed us to infer (1) that male spatial behaviour varied with age, reflecting the contrasting mating tactics of the two species, and (2) that females of all ages modified their movement patterns and/or home range size during parturition, but, particularly, the extent of these modifications differed markedly between reproductive and nonreproductive females in roe deer. In addition, we clearly demonstrated that (3) throughout the year, the oldest individuals tended to move the least and/or occupy the smallest ranges, particularly in mouflon. Age-specific alternative male mating tactics have previously been reported (Dominey, 1984; Hogg, 1984), while certain authors have suggested that individuals may modify their ranging behaviour as a result of experience and

ageing (Daugherty & Sheldon, 1982; Wunderle, 1991). However, empirical studies of the extent of age-specific spatial behaviour, particularly in relation to reproduction, have until recently been limited to a few situations where direct observation of known-aged individuals was possible (e.g. Corlatti et al., 2012; Foley et al., 2015; Taylor et al., 2020). Our findings, based on a large GPS data set of aged individuals, therefore, illustrate the range of variation in space use tactics, both within and between populations of large herbivores, and provides strong evidence that age is a major determinant of spatial behaviour.

In large herbivores, the time and energy males invest in reproduction depend strongly on their age, and the mating tactics that they adopt to access reproductive females during the breeding period (Corlatti et al., 2012; Foley et al., 2015; Hogg, 1984; Liberg, Johansson, Andersen, & Linnell, 1998; Willisch & Neuhaus, 2009). However, these findings were mostly based on observational studies of male–male and male–female interactions and territoriality. From a comprehensive investigation of movement behaviour throughout the year, we found age-specific patterns of mobility in two species of large herbivores for which direct observations are seldom feasible. Furthermore, the pattern of age dependence in movement behaviour differed markedly between species, strongly suggesting that life histories may have an important influence on spatial behaviour. For example, we found that adult roe deer males, which are territorial from March to August (Vanpé et al., 2009), had high levels of mobility, but smaller home ranges, than younger males. This is probably due to the patrolling behaviour required to successfully delimit a territory and to exclude other males (Liberg et al., 1998). In contrast, most 1- and 2-year-old males are unable to defend a territory (Vanpé et al., 2009). Despite this, mobility of males of both younger age classes also increased during the rut, although to a lesser extent than for older males, possibly related to attempted courting of receptive females (Melis, Hoem, Linnell, & Andersen, 2005). Indeed, subadults may attempt to mate with a female within an adult male's territory ('satellite' tactic), or through use of buffer zones between adult territories, allowing them to perform short raids towards unattended females ('peripheral' tactic, Liberg et al., 1998). Alternatively, young males may be more mobile due to harassment by territorial adults (Wahlström, 1994).

Age-specific movements during the rutting period were less pronounced in male mouflon than in roe deer. In contrast to roe deer, young male mouflon travelled relatively more during the peak of the rutting period compared to older animals. Subordinate/young males (4–6 years old) generally reproduce by courting females (i.e. breaching the defence of a dominant male to chase after the female, Bon et al., 1992; Hogg, 1984), whereas dominant old males (i.e. 7–8 and >8 years old) generally tend receptive females (i.e. directly or indirectly impeding attempts by

other males to mate). However, the higher mobility of young males did not translate to relatively larger home ranges during the rutting period. Instead, the range of males of all ages increased markedly at that time (Fig. 2d), probably linked to excursions outside their usual home range (Bon et al., 1992; Portanier et al., 2017). Courting is probably a behaviour that occurs at a very local scale, that is, the rutting area, and is thus not detectable at the home range scale. Further work to better understand the link between spatial behaviour and mating tactics should investigate fine-scale movements and habitat selection of males versus females and their interactions (Bourgoin et al., 2018; Marchand et al., 2015).

Because habitat use of female large herbivores is constrained by the presence of dependent young (Bongi et al., 2008; Ciuti et al., 2006, 2009), we expected marked stage-specific variation in mobility and home range size during the critical perinatal period depending on maternal care tactics. While no age-related differences were expected in mouflon, a gregarious species, with young that are able to follow their mother within 24 h after birth (Langbein, Scheibe, & Eichhorn, 1998), we particularly expected a postnatal reduction in mobility and space use in roe deer which express a hider tactic for the first 2–3 months of life. During the birth period, all mouflon females travelled longer distances, indicating that the presence of a lamb did not impede their mobility. In contrast, roe deer females of all ages, including those that did not reproduce, decreased their daily mobility and home range size during late spring. However, reproductive females had smaller monthly home ranges than nonreproductive females (i.e. juveniles) during the last month of pregnancy, and during parturition and lactation, but maintained a similar level of mobility, compared to nonreproductive females. Owing to the hider tactic of their offspring, lactating roe deer females must frequently commute between their hidden fawn(s) and the richest foraging patches to offset the energetic costs of lactation, which are particularly high in this income breeder. This may explain why the mobility of reproductive roe deer females was not markedly lower than that of nonreproductive does, while their monthly home range size was lower during the parturition period (see Bongi et al., 2008, for similar results). Previous studies reported that movements and space use of females in both species were strongly influenced by food availability and quality during this period of resource flush (Morellet et al., 2013; Marchand et al., 2015; see Appendix). Further research is hence needed to disentangle the relative influence of offspring presence and behaviour from resource distribution and quality on female mobility during the parturition period.

Outside the reproduction periods, we expected age-related differences in space use related to increased experience with age and/or senescence in locomotor performance in the oldest individuals (Catry et al., 2006; Froy et al., 2018; MacNulty et al., 2009; Montgomery et al.,

2013). We found strong support for our predictions in both sexes and both species, but at different spatial scales (Table 4). In roe deer, adults tended to use smaller monthly home ranges than younger individuals all year round, and this pattern was more pronounced in males than in females (see also Saïd et al., 2009). This was also observed in mouflon females, but, interestingly, not in mouflon males. In contrast, no clear age-related differences in distance travelled were detected in roe deer, whereas in mouflon this was much lower in older animals of both sexes for most of the year. Older individuals may have a more accurate cognitive map of the distribution of resources and risks within their environment, and so may be more efficient at locating and navigating between resource patches, resulting in lower distances travelled and smaller range sizes (Froy et al., 2018; Morellet et al., 2013). Indeed, memory and familiarity have been revealed as key components involved in mobility and home range emergence in both theoretical and empirical studies (Gehr et al., 2020; Marchand et al., 2017; Piper, 2011; Wolf, Frair, Merrill, & Turchin, 2009). In addition, decreasing locomotor performance with age could also lead to lower daily mobility and range size (Froy et al., 2018). As animals get older, a complex process of physiological and physical deterioration (i.e. functional senescence, Nussey, Froy, Lemaitre, Gaillard, & Austad, 2013; Soulsbury & Halsey, 2018) has been observed in laboratory research (Kirkwood, 2005; Niccoli & Partridge, 2012; López-Otín, Blasco, Partridge, Serrano, & Kroemer, 2013), altering locomotor performance, space use and foraging behaviour in later life (Catry et al., 2006; Froy et al., 2018; MacNulty et al., 2009), and underpinning demographic senescence in survival and reproduction (Jones et al., 2014; Nussey et al., 2013). Our results indicate that this may occur in one of our study species as we found that, outside the reproduction periods, the mobility of both sexes and the monthly home range size of females were lowest among the oldest mouflon. We were unable to quantify age-related senescence in the mobility of roe deer due to the absence of an adequate sample of old known-aged individuals. Indeed, lack of accurate information about an animal's age in most studies probably explains why the relative contribution of experience and locomotor performance to age-dependent patterns of movement and space use remains poorly understood. Further research should aim to clarify this issue by taking advantage of the long-term monitoring of individual space use provided by technological improvements in biologgers (Froy et al., 2018). Experiments whereby individuals of known age are translocated to novel environments would also allow us to tease apart the role of experience and physiological ageing on mobility and range use.

Finally, while we have demonstrated marked age-related variation in space use in two large herbivores, many other intrinsic and extrinsic factors that are difficult to control for in the wild may drive individual movement decisions. For example, large herbivores must adjust their

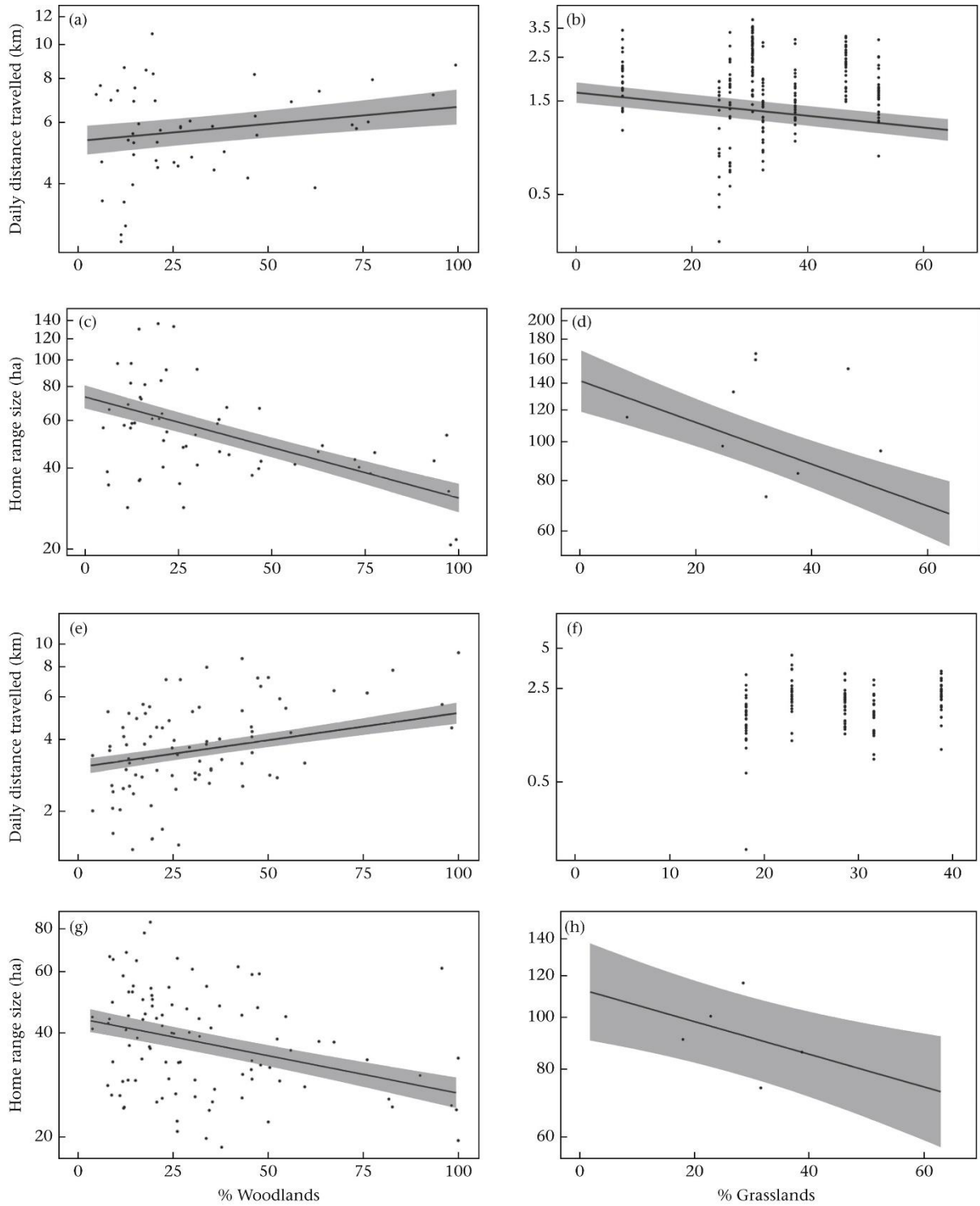
behaviour in response to the spatiotemporal dynamics of both resource availability (green-up in spring, senescence in autumn, Morellet et al., 2013) and risk (hunters and natural predators, Benhaiem et al., 2008; Bonnot et al., 2013). By analysing relative variation in space use among age classes over the same monitoring period and landscape, we assumed that individuals of each age class had, on average, experienced roughly the same environmental conditions so that the resulting patterns are a fair representation of age-dependent space use at the population level. However, our modelling approach also revealed that a large proportion of intraindividual variation in space use was not related to age and remained unexplained. Consistent between-individual differences in movement behaviours have been increasingly reported (Bonnot et al., 2015; Gervais et al., 2020; see Hertel, Niemelä, Dingemans, & Mueller, 2020 for a review), with consequences for life histories (Bonnot et al., 2018). To better evaluate the consequences of global change for the mobility of wild populations, further research should aim to disentangle the intrinsic drivers of interindividual variability in space use, such as personality (Dingemans, Kazem, Reale, & Wright, 2010; Jolles, King, & Killen, 2019; Réale, Gallant, Leblanc, & Festa-Bianchet, 2000), from extrinsic factors such as adverse environmental conditions (Marchand et al., 2015) and habitat fragmentation (Marchand et al., 2017).

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Appendix

As habitat composition of the home range has the potential to markedly influence individual movements and space use (Myserud et al., 1998; see Gaudry et al., 2018 for a recent example), we considered the percentage of woodlands and of grass areas in individual ranges to index habitat composition/landscape configuration for roe deer and mouflon, respectively. Indeed, these habitat types have been revealed as major drivers of habitat selection in the studied populations of roe deer and mouflon (Garel et al., 2007; Marchand et al., 2014; Morellet et al., 2011). Indeed, the habitat productivity hypothesis (Harestad & Bunnell, 1979) suggests that individuals should adjust their home range size to resource availability in order to minimize the area used for sustaining their energy requirements, while limiting energy expenditure during foraging movements (see e.g. Naidoo et al., 2012; Tufto, Andersen, & Linnell, 1996; Van Beest, Rivrud, Loe, Milner, & Myserud, 2011 for empirical support of this hypothesis in large herbivores). For the Aurignac study site, the land cover map was based on aerial photographs (BD Ortho from the Institut Géographique National, <http://professionnels.ign.fr/bdortho-50cm>) for which homogeneous habitat polygons (in ArcView GIS 3.3, Esri, Redlands, CA, U.S.A.) were manually digitized and assigned to a habitat type that was determined annually by field observations during summer. For the Caroux-Espinouse study area, we derived habitat types from the processing (k-means unsupervised classification) of a SPOT satellite image taken in July 2005 and field validation in a 25 × 25 m grid (Tronchot, 2008) and classified habitat types following Marchand et al. (2015).



Appendix A1: Data points and predicted daily distance travelled (DDT) in (a) roe deer males and (b) mouflon males, and monthly home range size (HRS) in (c) roe deer males and (d) mouflon males in relation to habitat composition of the home range (i.e. % of woodlands or grasslands in the monthly HRS in May in adult roe deer males, and in 7–8-year-old mouflon males). Data points and predicted DDT for (e) roe deer females and (f) mouflon females (data points only), and monthly HRS for (g) roe deer females and (h) mouflon females in relation to habitat composition of the home range (i.e. % of woodlands in the monthly HRS in May in adult roe deer females, and in 7–8-year-old mouflon females). We used a logarithmic scale on the y axis and the line represents the estimated slope derived from the selected model and its 95% confidence interval.

Habitat type was selected in the best supported model describing variation in DDT and in monthly HRS for both sexes and for both species (Table 2, Table 3), except for DDT in mouflon females (see Table 3, Fig. A1f). In roe deer males DDT increased by 0.64 km/day (from 5.63 ± 0.25 to 6.28 ± 0.32 km/day, an 11.3% increase; Fig. A1a) between the first quartile (27.6%) and the third quartile (75.6%) of the percentage of woodlands in the monthly HRS for adult males in May, while in mouflon males, DDT decreased by 0.29 km/day (i.e. a 19.6% decrease, from 1.48 ± 0.11 to 1.19 ± 0.12 km/day; Fig. A1b) from the first quartile (16.3%) to the third quartile (48.3%) of the percentage of grass areas in the monthly HRS for males 7–8 years old in May. The monthly HRS of roe deer males decreased by 20.45 ha (from 58.63 ± 2.48 ha to 38.18 ± 1.87 ha, i.e. a 34.9% decrease; Fig. A1c) between the first quartile (25%) and the third quartile (75%) of the percentage of woodland, while in mouflon males, the monthly HRS decreased by 36.98 ha (from 117.45 ± 8.39 to 80.46 ± 6.01 ha, i.e. a 31.5% decrease; Fig. A1d) between the first quartile (16.3%) and the third quartile (48.3%) of the percentage of grass areas in the monthly HRS.

The DDT of roe deer females increased by 1.00 km/day (from 3.51 ± 0.11 to 4.50 ± 0.18 km/day, i.e. a 28.4% increase; Fig. A1e) between the first quartile (25.4%) and the third quartile (75.4%) of the percentage of woodlands in the monthly HRS in May. The monthly HRS of roe deer adult females decreased by 8.17 ha (from 38.38 ± 1.30 to 30.21 ± 1.26 ha, i.e. a 21.3% decrease; Fig. A1g) between the minimum first quartile (27.4%) and the third quartile (75.4%) of the percentage of woodlands in the monthly HRS, while in mouflon females, the monthly HRS decreased by 18.83 ha (from 99.34 ± 9.02 to 80.51 ± 8.10 ha, i.e. a 19.0% decrease; Fig. A1h) between the first (17.9%) and the third quartile (47.9%) of the percentage of grass areas in the monthly HRS.

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Chapter 5

The availability of thermal refuges shapes a functional response in the thermoregulatory behavioural tactic of a heat-sensitive species.

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Abstract (250 words)

With the ongoing rise in global average temperatures, animals are expected to increasingly dedicate their time and energy to thermoregulation. In response to extreme temperatures, animals typically either seek for and move into thermal refuges, or reduce their activity during the hottest hours of the day. Yet, resource availability in thermal refuges is often lower, which, in combination with the reduction of foraging activity, may force individuals to further adjust their behaviours to alleviate the indirect energetic costs of behavioural thermoregulation. We estimated individuals' time-budget and daily habitat use of chamois (*Rupicapra rupicapra*), using Hidden Markov Models built from GPS data from 26 collared females monitored during summer in the French Alps, and analysed how they varied in relation to both temperature and within-home range access to thermal refuges, i.e. forest and northern slopes. When facing heat stress, individuals increased their use of thermal refuges and reduced their time spent foraging or relocating during daytime, but individual responses markedly differed depending on their access to thermal refuges. Individuals that had access to forest increased their daily time spent foraging, while individuals with access to northern slopes increased the time spent relocating at the expense of foraging. Including local landscape context and jointly analyse individual behaviour, energetics and life-history is hence key for obtaining improved insights into the potential impacts of climate change on cold-adapted species.

Introduction

Global average surface temperature has increased by 0.95-1.20°C since the late 1800's and are predicted to increase further by 1.5°C to 4°C by 2100 (IPCC, 2021), with critical consequences on ecosystem dynamics (Hoegh-Guldberg et al., 2018). In alpine environments, global warming is even more severe (Schwager et al., 2019) with consequences on plant distribution and phenology, as increasing temperature induces altitudinal shifts, shorter winters and earlier green-up and senescence (Cremonese et al., 2017; Vitasse et al., 2021). Such changes in vegetation can have cascading effects on herbivore species distributions (Hamann et al., 2021; Brivio et al., 2019) and population dynamics (Lovari et al., 2020; Reiner et al., 2021). In addition, temperature rise may force individuals to dedicate an increasing part of their time and energy to thermoregulation (insects: Kellerman & Heerwarden, 2019; fish: Amat-Trigo et al., 2023; birds: Conradie et al., 2019; mammals: Conradt & Guinness, 1997; van Beest et al., 2012; Brivio et al., 2016) in order to prevent heat stress (Speakman & Król, 2010). To avoid costly and transient autonomic responses (i.e. involuntary thermo-effector responses such as sweating; Maloney et al., 2005; Terrien et al., 2010), animals can also buffer challenging thermal conditions through behavioural responses such as modification of space use, e.g. by relocating to thermal refuges (forests, northern slopes, higher elevations, or shaded areas; Aublet et al., 2009; Semenzato et al., 2021; Marchand et al., 2015; van Beest et al., 2012), or alteration of activity budgets, typically by reducing activity levels during hot hours (Pipia et al., 2008; Bourgoïn et al., 2011; Brivio et al., 2016; Grignolio et al., 2018; Semenzato et al., 2021). However, behavioural thermoregulatory responses may come at a cost for the individual, as it can potentially have cascading effects on individuals' resource acquisition and exposure to predation risk, with fitness consequences in the long term (Myserud & Østbye, 1999; Mason et al., 2017, Conradie et al., 2019). For example, when temperatures increase, animals may decrease the time allocated to foraging, in particular in food-rich but thermally challenging open habitats (e.g. meadows, grasslands) where predators' detection is yet high, and restrict their activity to resting in thermal refuges such as forests, where food is more scarce, and where predation risk may be higher due to limited visibility and low predators detectability. This may lead individuals to display mitigation mechanisms in return, typically by increasing their foraging activity at dawn and dusk (e.g. Borowik et al., 2020), or during night-time (Grignolio et al., 2018) in an attempt to compensate during the coolest hours for lost foraging opportunities during hottest ones. But those compensatory mechanisms can also come with detrimental consequences (e.g. higher exposure to nocturnal predators, Gehr et al. 2017). Understanding how species cope with high temperatures then requires to go beyond the classical food acquisition/predation risk avoidance trade-off (Mason et al., 2017) and investigate the

additional thermoregulatory constraints individuals have to cope with (Herfindal et al., 2020 in ibex). This is of crucial importance to evaluate the effects of global warming on population dynamics, as behavioural thermoregulatory tactics (changing habitat use, modifying their allocation to different activities during hot hours, shifting to night-time activity) may directly impact energetic balance and *in fine*, fitness (e.g. van Beest & Milner, 2013).

The two major components of the behavioural tactic to challenging thermal conditions (space use and activity budgets) may however be balanced differently among individuals living in contrasting landscapes. For instance, alpine environments are characterized by a high degree of landscape heterogeneity (e.g. in terms of topography), leading individuals to experience different biotic and abiotic conditions in their individual home ranges which can consequently drive individual differences in habitat selection (Duparc et al., 2019; Herfindal et al., 2020). Depending on the relative availability of suitable habitats for foraging, thermoregulating and escaping predation, individuals may indeed adjust their behaviour differently to environmental constraints, displaying context-dependent habitat use or selection. Such functional responses in habitat selection (Myrsterud & Ims, 1998; Holbrook et al., 2019) have been widely documented in large herbivores, particularly regarding the influence of food resources or predation refuges (“foodscape” and “landscape of fear”; Herfindal et al., 2009; Morellet et al., 2011; van Beest et al., 2016; Duparc et al., 2019). Similar responses could be expected according to the availability of thermal refuges but still remain unexplored. Investigating inter-individual variability in behavioural thermoregulatory responses is yet essential, not only to identify thermal refuges that may need conservation efforts in various contexts, but also to better grasp the ability of individuals and populations with contrasted thermal landscapes to overcome the challenges posed by global warming.

Accordingly, we examined here the inter-individual variability in the behavioural responses (activity budget and habitat selection) of GPS-tagged chamois *Rupicapra rupicapra* to summer temperature, accounting for the differences in their access to thermal refuges (i.e. thermal landscape) in their home ranges. During summer, female chamois require huge amount of resources and energy to lactate (>80% of adult females give birth few weeks before) and must at the same time accumulate fat reserves for overwintering, while avoiding challenging thermal conditions during daytime. Our goal in this study was then to determine how behavioural decisions made by individuals at fine temporal scale (i.e. the 20-min location scale) in response to current temperature and habitat conditions, will influence resulting individual’s activity budget (i.e. total daytime & night-time budget). Based on movement metrics, we identified three behavioural states (assumed as foraging, resting and relocating, Beumer et al., 2020), and

assessed the extent to which temperature constrained the temporal distribution of those behaviours in individuals with contrasted access to thermal refuges. At the fine scale and during the hot hours of the day, we predicted that all animals should favour resting at the expense of heat-producing activities (foraging and relocating) with increasing temperature, especially when individuals are in habitats with thermally challenging conditions, i.e. open areas (P1a). Inversely, when animals are in thermal refuges such as forest or northern slopes during hot hours, the thermal buffer provided by those habitats should allow individuals to maintain their activity level whatever the temperature (P1b). We also predicted that individuals should decrease their resting activities during the dusk and night following hot-daytime temperatures in favour of foraging and relocating (P1c). In a second time, we expected that the differences in access to thermal refuges will result into individual differences in daily habitat use (set of predictions P2), which combined with differences in behaviour probabilities between habitats, would result in individual differences in activity budgets (set of predictions P3). We therefore predicted that individuals with low access to thermal refuges will remain mostly in open areas when daily mean temperature increased (P2a), and would therefore be constrained to increase their total time spent resting during daytime (P3a). Inversely, we predicted that individuals with higher access to thermal refuges would spend more time in these latter when temperature increased during daytime (P2b) and that their total time spent foraging and relocating during daytime should therefore remain constant (P3b). Finally, we predicted for individuals with low access to thermal refuges, that total time spent resting would decrease during dusk, night and dawn following hot-daytime temperatures, in favour of foraging and relocating to compensate for the decreased time spent in these behaviours during daytime (P3c). Inversely, we expected no significant changes in night-time activity budgets for females which had access to thermal refuges, as they would have been able to maintain their activity level during daytime and thus would have no need to compensate (P3d).

Methods

Study sites

We conducted our study in the Réserve Nationale de Chasse et de Faune Sauvage of Les Bauges massif, in the northern French Alps (45°40' N, 6°14' E; 900 to 2200 m a.s.l., 5200 ha). We focused on two alpine , i.e. Charbonnet-Pleuven and Arménaz-Pécloz, 7 km distant from each other and separated by deep valleys with no exchange of individuals between them. Both areas were mostly covered with grasslands and rocky open areas, and were comparable in terms of forest cover (mostly beech *Fagus sylvatica* and fir *Abies alba*, 18% and 25% of study sites'

areas, respectively), and north-oriented slopes (i.e. north and north east orientation, see the “Environmental characteristics” section; 11% and 17%, respectively; Lopez 2001).

The Reserve is inhabited by a chamois population of approximately a thousand individuals (Maillard et al., 2014). In this population, births occur from the end of April until the end of June, with 80% of births occurring before 15 June (Loison, 1995). Most adult females give birth each year (>80% of ≥ 2 year-old females; Pioz et al., 2008). In summer, most adult female chamois require huge amount of resources to bear the high energetic costs of lactation and to accumulate fat reserves for overwintering at the same time (Morin et al., 2016). Hence, females are expected to dedicate a very important part of their time to foraging activities in thermally challenging open grasslands.

GPS data

Data collection

Between 2014 to 2016, during July and August, 26 chamois adult females were trapped with drop nets baited with artificial salt lick and equipped with GPS collars (Vectronics GPS Plus or Vectronics Vertex Plus) scheduled to record one location every 20 min from mid-July to mid-August (12th July-18th August in 2014; 11th July-17th August in 2015; 09th July-15th August in 2016) and one location every 4h during the rest of the year. Captures were performed by the Office Français de la Biodiversité (previously Office National de la Chasse et de la Faune Sauvage) according to the ethical conditions detailed in the specific accreditations delivered by the Préfecture de Paris (prefectorial decree n°2009-014) and in agreement with the French environmental code (Art. R421-15 to 421-31 and R422-92 to 422-94). As collar deployment and recovery occurred during summer, the total number of summer days with 20-min locations available per individual ranged between 6 and 38 days (median/mean = 16/19). We filtered out erroneous GPS locations (<0.3% for both 20-min and 4h schedules) based on unlikely movement characteristics (Bjørneraas et al., 2010; $\Delta = 1500$ m, $\mu = 1000$ m, $\alpha = 80\%$ quantile of movement speeds from a focal individual, $\theta = -0.95$).

Environmental characteristics

Characterization of thermal refuges

We distinguished three distinct habitat types offering contrasted thermal conditions, i.e. forests and north-oriented slopes (i.e. north and north east orientation, hereafter referred as “northern slopes”; between 337.5-360° and 0-67.5°; Bačkor, 2010), both considered as thermal refuges, and open habitats, i.e. areas without protection/shelter from high temperatures. Indeed, during the hottest hours (between 12:00 to 16:00 UTC) of the hottest days (i.e. daily mean temperature

>17°C, see appendix S1 & S2), the temperature (as estimated from the collar sensors) in forest was on average -1.2°C lower than in open habitats (range: -3.7 to 1.3°C, median: -1.5°C, see also Appendix S1). Similarly, the temperature in northern slopes was on average -2.2°C lower than in open habitats (range: -6 to 0.8°C, median: -1.6°C). Habitat classification was based on the combination of a habitat map with a 25-m resolution (Institut National de l'Information Géographique et Forestière) and an aspect map derived from a digital elevation model with a 25-m resolution (Institut National de l'Information Géographique et Forestière).

Thermal refuges and open habitats also contrasted in terms of availability of food resources for chamois. In July and August, the mean edible biomass in open areas (July: 34g.m⁻²; August: 32g.m⁻²) was close to three times higher than in forest (July: 12g.m⁻²; August: 11g.m⁻²) and about one and a half times higher than in northern slopes (18g.m⁻²; August: 22 g.m⁻²; Duparc et al. 2020).

Access to thermal refuge in summer home ranges and habitat under locations

We used 4h locations over the July-August period to estimate individuals' summer utilization distribution, using the fixed-kernel method (Worton, 1989) with a smoothing parameter h set to the median value of individual smoothing parameters ($h_{\text{individual}}=h_{\text{ref}}$). We determined the summer home range at the 90% isopleth of utilization distribution, to obtain an unbiased estimate (Börger et al. 2006). We then determined the proportion of thermal refuges within individual summer home ranges and habitat types at chamois locations.

Temperature data

Local temperatures were recorded every 15 min at the Phenoclim weather station (CREA Mont-Blanc) located in Chérel mountain pastures (45°40'54.6"N, 6°12'26.0"E, 1380 m above sea level, i.e. 2-6 km distant from the areas used by chamois). The temperature records were matched with corresponding GPS locations of chamois recorded at the same time, whereas the mean temperature of the two closest records was associated with the GPS location recorded at the 20th (matched with the mean temperature between records at the 15th minute and the 30th minute) or 40th minutes of each hour (matched with the mean temperature between records at the 30th minute and the 45th minute). Daily mean temperatures ranged between 6 and 23°C, with a mean and median of 15°C.

Statistical analyses

P1. Identifying behavioural states and modelling behavioural responses at the location scale

Following Beumer et al. (2020), we fitted Hidden Markov Models (HMMs) to the movement data of chamois derived from the 20 min-scheduled GPS locations (only location bursts with gaps <6 consecutive locations; McClintock & Michelot, 2018), to identify the main behavioural states of chamois. We used smoothed speed (speed smoothed over the previous two steps and the next two steps for each location) and spatial angle (i.e. turning angle calculated at a constant step length, see details in Patin et al., 2018), to characterize the three latent behavioural states that we assumed as approximating resting-ruminating (i.e. very low speed, high spatial angles [low directional persistence]), foraging (i.e. intermediate speed and angles), and relocating (i.e. high speed, low spatial angle [directional persistence], Beumer et al., 2020; see also Appendices S3 & S4). We modelled smoothed speed and spatial angle with a gamma and a von Mises distribution, respectively. To determine whether individuals would adjust their behaviours at the location scale in response to current environmental conditions, we fitted HMMs including temperature at the weather station, the habitat at the individual's current location (i.e. open habitat, forest or northern slopes), and the time of the location (20 min scale accounted as a circular variable) as covariates on the state distribution probabilities. Starting values of HMM were initialized by fitting 30 times a simple HMM without environmental covariates on state transitions probabilities, each time using a set of random starting values within a biologically relevant range based on observed chamois step length and turning angle distributions. We fitted all HMMs using *momentuhmm* R CRAN package (version 1.5.3, McClintock & Michelot, 2018). We selected the most parsimonious HMM, i.e. the one with a $\Delta AIC < 2$ and the minimum number of transition probability coefficients, following a similar approach (based on the number of model parameters) adopted by Clay et al. (2020). Finally, each GPS location was assigned to one of the three behavioural states using the Viterbi algorithm ("viterbi" function from "momentuhmm" package), and predicted values of stationary state probabilities (i.e. probability of being in a given state for each location depending on environmental covariates) were derived from state transition probabilities using an adhoc function described by Clay et al. (2020).

P2. Modelling of daily habitat use

To test whether individuals adjust their use of thermal refuges during hot days, we assessed how the proportions of total time spent in each of the three relevant habitat types (three response

variables: open areas, forests and northern slopes) varied with daily mean temperature recorded at the weather station, the percentage of forest and the percentage of northern slopes available in the individuals' home range, as well as the two-way interactions between temperature and percentage of forest and temperature and percentage of northern slopes. We separated models for hottest (7 to 18 UTC, hereafter simplified as "daytime") versus coolest hours of the day (18 to 7 UTC, hereafter simplified as "nighttime" although including twilight hours, Appendix S1 & S2), as we expected habitat use to be more affected by thermal refuges in home ranges during the hottest times of the day. We retained only days where 72 locations were recorded (median/mean = 12/17 days per individual). We used a mixed baseline-category logit model ("mblogit" function from R CRAN package "mclgfit", version 1.1-27.1, Bates et al., 2015) and included the identity of the individual as a random intercept. We then selected the most parsimonious model based on AIC criterion (Burnham & Anderson, 2002), retaining the one within a $\Delta AIC < 2$ and with the smallest number of degrees of freedom.

P3. Modelling of daytime and night-time behavioural budgets

We estimated the daytime and night-time proportions of time spent in the three behavioural states identified by HMMs (assumed as resting/ruminating, foraging and relocating). Then, we modelled these proportions with multinomial models, according to the daily mean temperature recorded at the weather station, the period of the day (hot daytime vs cool nighttime) and the percentage of forest and northern slopes available in the individuals' home range. We followed the same model selection procedure as we described in section "P1: Modelling of daily habitat use".

Contrasting individual chamois with variable thermal landscapes

We used a hierarchical clustering analysis (HCA) based on home ranges' topographical variables (i.e. % forest, % northern slopes) to identify clusters of individuals sharing similar thermal landscapes. The number of optimal categories was chosen so that differences between chamois in terms of thermal landscape were maximised, i.e. contrasting individuals that had low access to thermal refuges (category 1 in Table 1 & Figure 1), access to northern slopes mostly (category 2), access to forest mostly (category 3), or access to both northern slopes and forest (category 4).

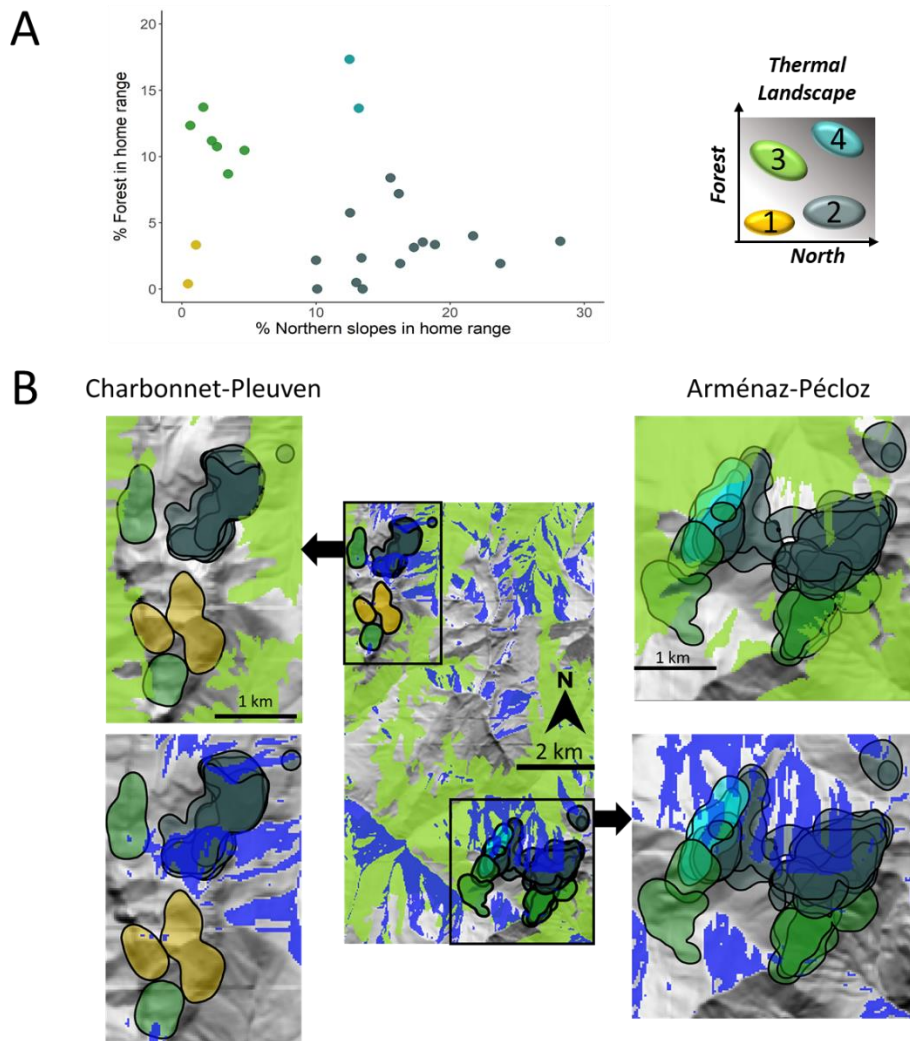


Figure 1: A) Types of individual thermal landscapes found in the Hierarchical Clustering Analysis, and B) associated individual summer home ranges (coloured by types of thermal landscape). Green areas represent forest habitats and blue areas represent northern slopes.

This classification allowed us to specify appropriate values of % forest and northern slopes when testing our predictions. Based on mean values of each cluster (Table 1), we considered that a value of 2.5% for a given thermal refuge, will represent a low individual's access to this latter, whereas a value of 15% will represent a high access. Thereby, when computing and plotting our models' predicted values, we specified values of 2.5% and 2.5% northern slopes to predict the response of individuals living essentially in open areas and with low access to both thermal refuges. Inversely, we used either a combination of 2.5% forest and 15% northern slopes for predictions concerning individuals which had mostly access to northern slopes, and 15% forest and 2.5% northern slopes for individuals which had access mostly to forest. As very few individuals had access to both thermal refuges in their home range, and as we were more interested in comparing individuals with low access vs individuals with access to thermal

refuges, and also in potential differences between individuals with access to forest vs access to northern slopes, we did not use a set of 15% forest and 15% northern slopes in our predictions.

Table 1: Means and standard deviations (SD) of categories from the hierarchical clustering analysis.

Type of thermal landscape	Number of individuals	Mean % forest [min-max] in home range	Mean % north [min-max] in home range
1: low access to forest & northern slopes	2	1.9 [0.4-3.3]	0.8 [0.5-1.1]
2: access to northern slopes mostly	15	3.2 [0.0-8.4]	16.6 [10.0-28.2]
3: access to forest mostly	7	14.2 [8.7-32.6]	2.18 [0.1-4.7]
4: access to forest & northern slopes	2	15.5 [13.6-17.3]	12.8 [12.5-13.2]

Results

P1. Behavioural adjustments to increasing temperature in relation to the habitat at each location

At the location scale, the probabilities to forage, rest or relocate varied with temperature, time of the day and the habitat the individual was currently in (model selection results in Table 2). The two-way interaction between temperature and time of the day was retained in the selected model. Accordingly, chamois differentially adjusted their behaviour to increasing temperature depending on the time of the day, notably the probabilities to relocate or rest/ruminate and to a lesser extent, the probability to forage (Figure 2). When temperature increased during the hottest hours of daytime, i.e. at 12:00 UTC, chamois decreased their heat-producing activities: the probability to relocate decreased by 9% while the probability of resting increased by 7% when temperature increased from 10°C to 20°C (Figure 2), thus partially supporting prediction P1a. However, contrary to our prediction P1a, the probability to forage remained quite constant with increasing temperatures during daytime.

Table 2: Candidate Hidden Markov Models to investigate variation in states probabilities in chamois in response to environmental covariates. The top five best ranked models and the null model are presented. The best selected model is in bold. Time of the day: the time of the location (20 min scale) modelled as a circular variable); Habitat: the habitat under the current location, i.e. open habitat, forest or northern slopes.

Models	N.coefficients	AIC	Δ AIC
Temperature* Time of the day + Habitat	48	487390.7	0.0
Temperature* Time of the day * Habitat	108	487399.1	8.5
Temperature* Time of the day	36	487459.8	69.2
Temperature + Time of the day + Habitat	36	487546.0	155.3
Temperature + Time of the day	24	487608.7	218.0
Temperature	12	487951.5	719.7
Null model	6	488047.5	815.6

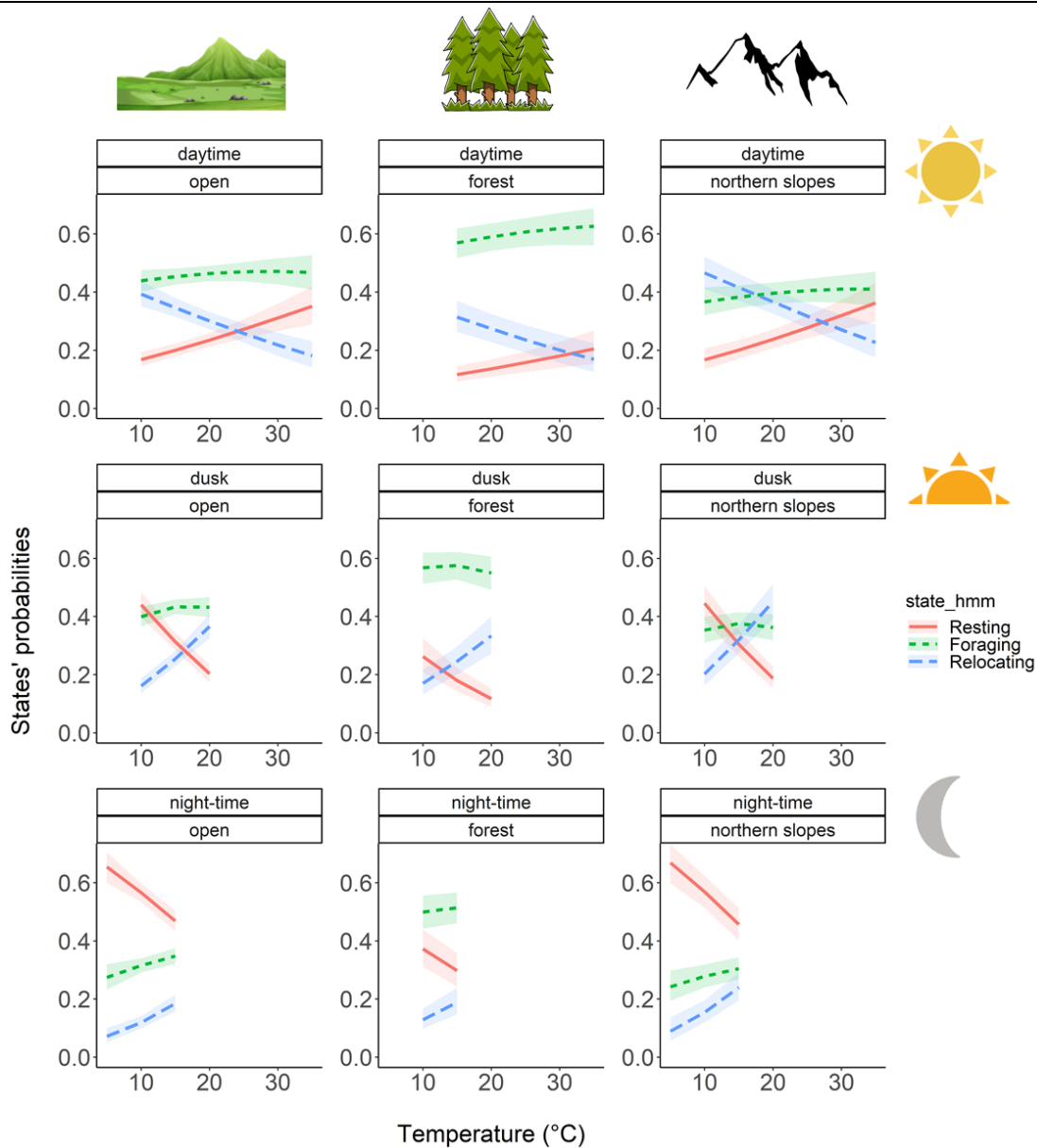


Figure 2: Stationary state probabilities from the Hidden Markov Model as a function of current temperature and current habitat under each location, during daytime (12:00 UTC), dusk (18:00 UTC), and night-time (00:00 UTC). Ribbons and error bars correspond to the 95% CI.

P2. Daily variation in habitat use in response to daily mean temperature and the available thermal refuges

Both during daytime and during night-time, the percentage of time spent in each habitat type varied with the daily mean temperature and the availability of thermal refuges in the home range (Table 3). Both two-way interactions between temperature and availability of forest and northern slopes were retained in the best selected model for daytime, whereas only the two-way interaction between temperature and the availability of forest was retained for night-time (Table 3). As predicted, female chamois which had low access to thermal refuges remained mainly in open areas during both daytime and night-time (Figure 3 A&D, support to P2a). Inversely, female chamois which had access to thermal refuges, decreased their use of open areas and increased their use of thermal refuges (i.e. forests or northern slopes) when daily mean temperature increased during daytime (support to P2b), but also to a lesser extent during cooler hours of the day (Figure 3). During daytime, when daily mean temperature increased from 10 (temperature below the threshold triggering behavioural thermoregulation) to 20°C (above this threshold, see Appendix S1 & S2), individuals that had access to forests in their home range increased their daily time spent in forests by 27% during daytime (Figure 3B), and by 9% during cool hours of the day (Figure 3E). Similarly, chamois with access to northern slopes increased their time spent in this thermal refuge by 22% between 10 and 20°C during daytime (Figure 3C), and by 7% during cool hours of the day (Figure 3F).

Table 2: Candidate mixed baseline-category logit model to investigate variation in daily habitat use (% of time spent in each habitat) in chamois, with individual identity as a random effect on the intercept. The best selected model is in bold. Temp=daily mean temperature; Forest = % of forest in home range; North.slop = % of northern slopes in home range.

<i>Daytime models</i>	<i>df</i>	<i>AIC</i>	<i>delta</i>	<i>weight</i>
Temp + Forest + North.slop + Forest:Temp + North.slop:Temp	15	17293.5	0	1
Temp + Forest + North.slop + North.slop:Temp	13	17316.4	22.85	0
Temp + Forest + North.slop + Forest:Temp	13	17321.4	27.89	0
Temp + North.slop + North.slop:Temp	11	17324.6	31.06	0
Temp + Forest + Forest:Temp	11	17336.4	42.9	0
Temp + Forest + North.slop	11	17379.8	86.21	0
Temp + Forest	9	17390.6	97.06	0
Temp + North.slop	9	17391.7	98.16	0
Temp	7	17402.9	109.37	0
Forest + North.slop	9	18046.4	752.81	0
Forest	7	18061.2	767.65	0
North.slop	7	18063.5	770	0
Null model	5	18072.2	778.65	0
<i>Night-time models</i>	<i>df</i>	<i>AIC</i>	<i>delta</i>	<i>weight</i>
Temp + Forest + North.slop + Forest:Temp	13	19957.1	0	0.671
Temp + Forest + North.slop + Forest:Temp + North.slop:Temp	15	19958.5	1.43	0.328
Temp + Forest + Forest:Temp	11	19970.9	13.84	0.001
Temp + Forest + North.slop + North.slop:Temp	13	20099	141.91	0
Temp + North.slop + North.slop:Temp	11	20101.7	144.59	0
Temp + North.slop	9	20206	248.93	0
Temp + Forest + North.slop	11	20206.3	249.27	0
Temp	7	20216.5	259.48	0
Temp + Forest	9	20219.8	262.78	0
Forest+North.slop	9	20581.8	624.72	0
North.slop	7	20583	625.97	0
Forest	7	20593.6	636.51	0
Null model	5	20594.4	637.3	0

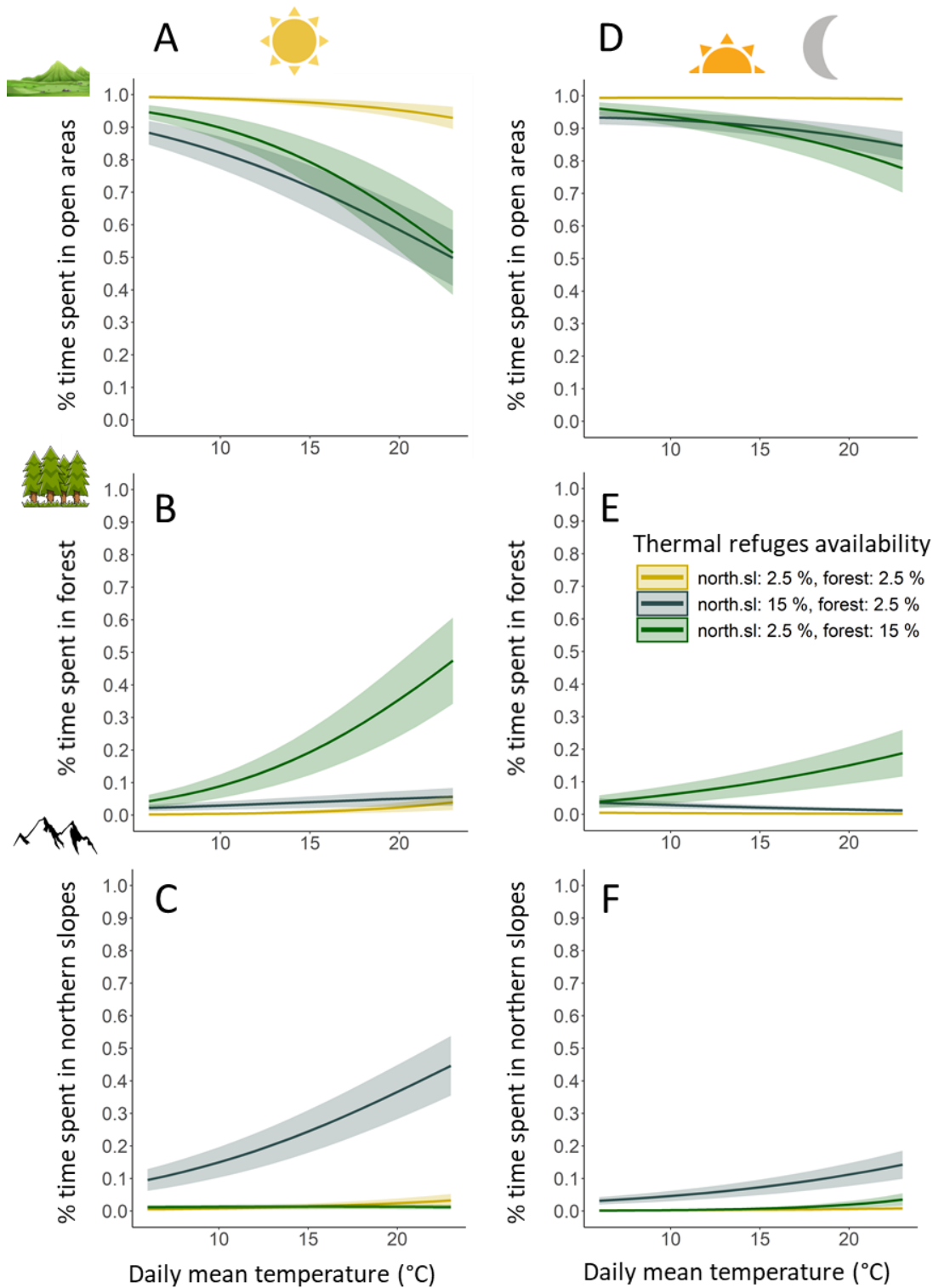


Figure 3: Variations in the predicted daytime (left panels) and night-time (including dawn and dusk, right panels) percentage of time spent in open areas, forests or northern slopes depending on the daily mean temperature, and the thermal refuges available in the individuals' home range. Ribbons represent standard errors. Individuals with low access to thermal refuges = 2.5% northern slopes & 2.5% forest. Individuals with mostly access to northern slopes: 15% northern slopes & 2.5% forest. Individuals with mostly access to forest=2.5% northern slopes, 15% forest.

P3. Adjustments in daytime and night-time behavioural budgets to increasing daily mean temperature in relation to the availability of thermal refuges

During daytime, the proportion of time devoted to the three behavioural states varied with temperature, the availability of forest and the availability of northern slopes in individuals' home range, in an interactive way (Table 4). Contrary to our predictions P3a and P3b, during daytime, time spent resting decreased for most individuals, particularly in individuals with a large proportion of forests in their home range (i.e. 15%, Figure 4A). Hence, when daily mean temperature increased from 10 to 20°C, chamois with low access to thermal refuges (i.e. 2.5 % of their home range covered by either forest or northern slopes) or mainly access to northern slopes (i.e. 15 % of their home range), decreased their time spent resting by 7%, and 5% respectively, while chamois with access to forest decreased it by 15%. On the other side, time spent relocating increased with daily mean temperature for all individuals, i.e. by 7% in chamois with low access to thermal refuges, by 12% in those with access to northern slopes mostly, and by 10% in those with access to forest mostly (Figure 4C). The variation in the proportion of daily time spent foraging with increasing temperature was more complex, as it increased by 6% for individuals with forest in their home range while it remained constant for individuals with low access to thermal refuge, and decreased by 7%, for individuals with access to northern slopes (Figure 4B).

During night-time, the proportion of time devoted to the three behavioural states varied with temperature, the availability of forest and the availability of northern slopes in individuals' home range, in an interactive way (Table 4). In accordance with our prediction P3c, during night-time following hot daytime temperatures, time spent resting decreased individuals with low access to thermal refuges. However, contrary to our prediction P3d, time spent resting also decreased in individuals with access to thermal refuges, and in particular in individuals with access to forest (Figure 4D). When daily mean temperature increased from 10 to 20°C, chamois with low access to thermal refuges or mainly access to northern slopes, decreased their time spent resting by 3%, and 7% respectively, while chamois with access to forest decreased it by 15%. Inversely and as expected, time spent relocating increased by 3% and 2% in individuals with low access to thermal refuges or access to forest, and up to 7% for individuals with access to northern slopes (Figure 4F). The variation in the proportion of time spent foraging with increasing temperature was the same as the daytime response, as it increased by 12% for individuals with forest in their home range, while it remained constant for individuals with low access to thermal refuge and with access to northern slopes mostly (Figure 4E).

Table 3: Candidate mixed baseline-category logit models to investigate variation in activity budgets (% of time spent in each state) in chamois, with individual identity as a random effect on the intercept. The best selected model is in bold. Temp=daily mean temperature; Forest = % of forest in home range; North.slop = % of northern slopes in home range.

<i>Models</i>	<i>df</i>	<i>AIC</i>	<i>ΔAIC</i>	<i>weight</i>
Temp + Forest + North.slop + Forest:Temp + North.slop:Temp	15	33125.8	0	0.912
Temp + Forest + North.slop + Forest:Temp	13	33130.7	4.92	0.078
Temp +Forest + Forest:Temp	11	33135.6	9.83	0.007
Temp + North.slop + North.slop:Temp	11	33137.5	11.74	0.003
Temp + Forest + North.slop + North.slop:Temp	13	33139.8	13.99	0.001
Temp + North.slop	9	33156.7	30.95	0
Temp + Forest	9	33158.6	32.83	0
Temp +Forest + North.slop	11	33159	33.19	0
Temp	7	33163.3	37.57	0
North.slop	7	33301.1	175.31	0
Forest+North.slop	9	33304.1	178.37	0
Forest	7	33304.7	178.92	0
Null model	5	33307.9	182.15	0
<hr/>				
<i>Night-time models</i>	<i>df</i>	<i>AIC</i>	<i>ΔAIC</i>	<i>weight</i>
Temp + Forest + North.slop + Forest:Temp + North.slop:Temp	15	60904	0	0.996
Temp + Forest + Forest:Temp	11	60915.4	11.36	0.003
Temp + Forest + North.slop + Forest:Temp	13	60919.8	15.76	0
Temp + North.slop + North.slop:Temp	11	60936.8	32.79	0
Temp + Forest + North.slop + North.slop:Temp	13	60939.8	35.75	0
Temp	7	60953.6	49.57	0
Temp + Forest	9	60957.1	53.05	0
Temp + North.slop	9	60958.4	54.38	0
Temp + Forest + North.slop	11	60961.5	57.41	0
Null model	5	61114.2	210.16	0
Forest	7	61115.6	211.52	0
North.slop	7	61117.2	213.18	0
Forest + North.slop	9	61123.6	219.55	0

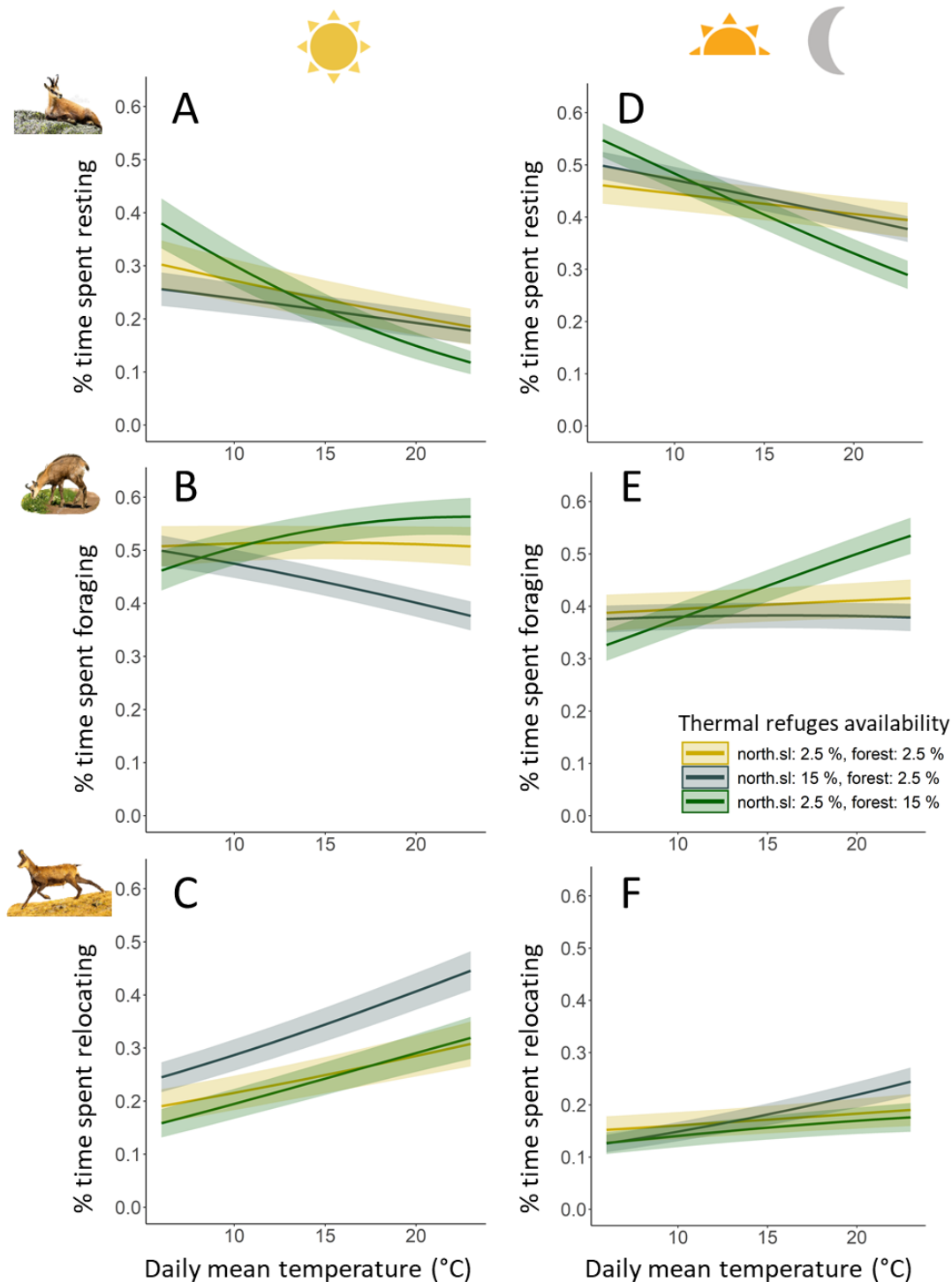


Figure 4: Variations in the predicted daytime (left panels) and night-time (including dawn and dusk, right panels) percentage of time spent resting, foraging or relocating depending on the daily mean temperature, and the thermal refuges available in the individuals' home range. Ribbons represent standard errors. Individuals with low access to thermal refuges = 2.5% northern slopes & 2.5% forest. Individuals with mostly access to northern slopes: 15% northern slopes & 2.5% forest. Individuals with mostly access to forest=2.5% northern slopes, 15% forest.

Discussion

We assessed how individuals fine-tuned their response to hot summer temperatures. More particularly, we demonstrated how habitat use and activity budget may not only vary with temperature, but also with the foodscape and thermal landscape, providing a functional response. This provided a novel and markedly refined understanding of how chamois in different landscapes may cope with challenging temperatures during summer. Below we discuss in detail how individuals' access to thermal refuge generates inter-individual variability in their behavioural responses to increasing temperatures and the implications of how this could impact the energy budget, demography and spatial distribution of this endotherm mountain herbivore.

Relocating into thermal refuges under high summer temperatures is a commonly documented behaviour in large herbivores (moose: van Beest et al., 2012; ibex: Semenzato et al., 2021; mouflon: Marchand et al., 2015). These responses may however incur costs in terms of energy acquisition and behavioural budgets, as behavioural thermoregulation often trades-off against foraging (e.g. see Cunningham et al., 2021 for a review in mammals and birds). In cold-adapted ungulate species for example, relocating in thermal refuges may typically provide decreased foraging conditions (e.g. Alston et al., 2020; Street et al., 2016; van Beest et al., 2012 in moose, Mason et al., 2017; Semenzato et al., 2021 in ibex). Likewise, chamois decreased their daily time spent in open habitats in favour of thermal refuges, i.e. forest and northern slopes, when daily mean temperatures increased, while forage quality and quantity are up to three times higher in open habitats than in forest or northern slopes (Duparc et al., 2020). Thus, moving into thermal refuges may incur indirect energetic costs due to reduced foraging conditions, if no behavioural adjustments are made by individuals to alleviate the latter.

Chamois showed such behavioural adjustments by increasing their relocating activity and exhibiting a more contrasted response in foraging activity. Importantly, we showed that the availability of thermal refuges in individuals' home range, had an important influence on individual responses to high temperatures. Thermal refuges availability indeed first shaped a functional, i.e. a context-dependant, response in habitat use in chamois females (i.e. individuals increased their use of thermal refuges when those were more abundant). Even more importantly, we also showed a functional response in behavioural budgets adjustments, i.e. depending on the type and availability of thermal refuges, individuals allocate time differently to each behaviour. The increase in time spent relocating during the cooled hours of the day when daytime temperature increased, especially for chamois with access to forest, was unexpected, but could be a consequence of the reduced time spent in rich open habitats during daytime.

Compensation mechanisms have been observed in other large herbivore species, typically by shifting a part of their daytime activity to night-time (Grignolio et al., 2018; Borowik et al., 2020; Semenzato et al., 2021). Here, increased activity during night-time may correspond to individuals travelling back from thermal refuges to open areas, where they may then spend more time looking for food items inside of patches, i.e. foraging activity, or visiting more food patches i.e. relocating activity, in order to mitigate the opportunity costs (i.e. missed foraging opportunities linked to decreased forage quantity, Cunningham et al. 2021) of moving into thermal refuges during daytime.

However, in addition to shifting their daytime activity to night-time, it is more likely that individuals did also try to mitigate opportunity costs once they were in thermal refuges during daytime. The reduced quantity of forage in forests for example may explain the increased propensity of chamois to forage when in this habitat, which lead individuals to increase their time spent foraging during the hottest days, especially during daytime (Figure 4). Similarly, chamois in areas with northern slopes showed an increased propensity to relocate during the hottest days, in accordance with the hypothesis that the reduced forage availability and quality in northern slopes (Duparc et al., 2020) requires chamois to spend more time searching for and visiting food patches. Analyses of residency times and patch revisitation rates could allow to test whether the increased time spent foraging and relocating is related to increased time spent searching and visiting food patches or moving into thermal refuges. Moreover, this could also allow us to identify sites of interest which may offer the best compromise in terms of forage availability, quality and thermal cover (Bracis et al., 2018), especially by collecting high-frequency movement data (Munden et al., 2019).

Behavioural thermoregulation may induce direct energetic costs for individuals, as increased time spent relocating towards and within thermal refuges, may lead to increased distances travelled and cumulated elevation change, which in return is likely to yield increased movement costs (Wilson et al., 2020). This will also need to be investigated in further studies as behavioural responses may indeed differ between individuals, and yield a potentially important variability in individual seasonal variation in body mass, with important repercussions on individual fitness. The energetic consequences of these behavioural alterations could be determined then by combining a quantification of the foodscape (Duparc et al., 2020) with field-based estimates of the costs of movement (e.g. Chimienti et al., 2020 in muskoxen; see also Klappstein et al., 2022). This is now possible using new energy-selection functions models, applied to high-frequency biologging data, which allow to quantify the energetic consequences of both movement and resource selection (Klappstein et al., 2022). Crucially, an additional

complexity comes from human disturbance - as the hottest day may correspond to the sunniest days and thus the days with the highest site frequentation by hikers, the influence of human disturbance should also be accounted for in further studies (Enggist-Düblin & Ingold, 2003; Pęksa & Ciach, 2018), especially to disentangle the role of forest and northern slopes as refuges against either hot temperatures or human disturbance. For example, Courbin et al. (2022) showed that chamois flexibly respond to the presence of hikers through diel migrations to/from trails.

To conclude, we showed in this study that behavioural thermoregulation incurs opportunity costs for chamois during summer, and that these costs may be modulated by the local constraints experienced by individuals. In a context of more frequent heat waves and droughts due to global warming (IPCC, 2021), it is then more than likely that these costs will keep increasing, and this might constitute quite an important issue for the conservation of cold-adapted species. As other capital breeders (Arnold, 2020), chamois rely indeed on fat reserves accumulated during spring and summer to face winter food scarcity and the energetic costs of gestation and lactation. Changes in foraging efficiency linked to behavioural thermoregulation may then lead to potential changes in energy acquisition and related offsprings' maternal care (e.g. Scornavacca et al., 2016). Consequently, further work will be needed to determine whether the diverse costs of behavioural thermoregulation (i.e. decreased forage quality and quantity, lost foraging opportunities, increase in costly movements for relocations), may outweigh or not its benefits (i.e. preventing hyperthermia), if we aim to assess the vulnerability of chamois population to climate change.

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Supplementary material

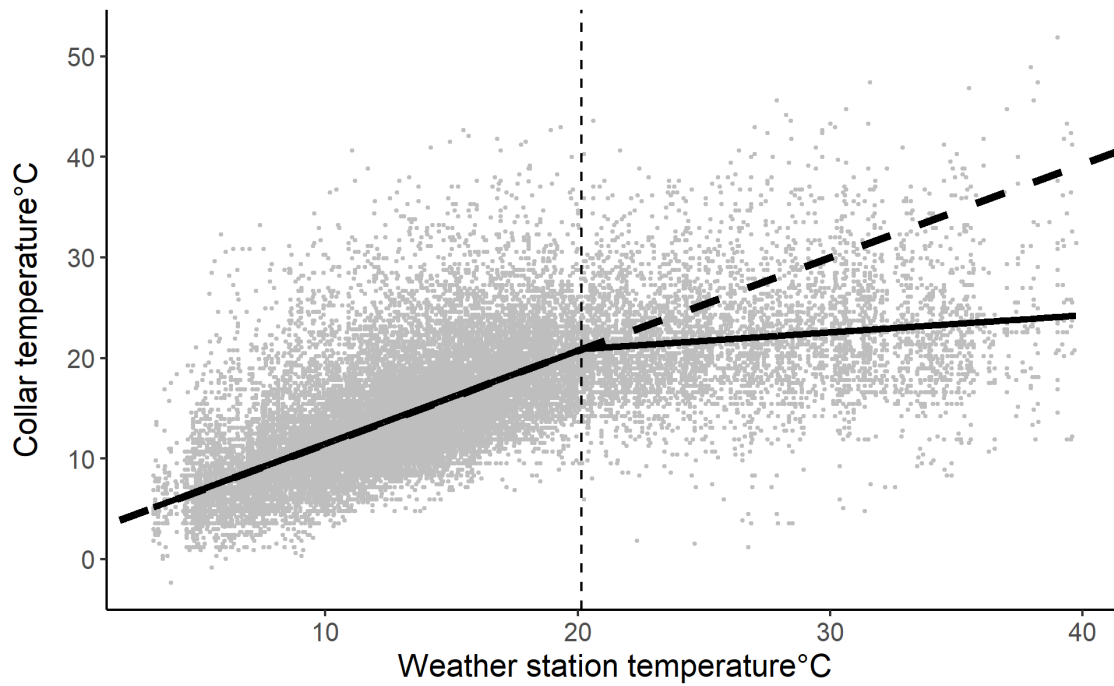
Appendix S1: Determination of heat stress threshold

GPS collars were embedded with a sensor which recorded temperature at the same time as GPS locations. The ambient temperature experienced by chamois was derived from the temperature recorded by such sensors using the correction from Jiang et al. (2012):

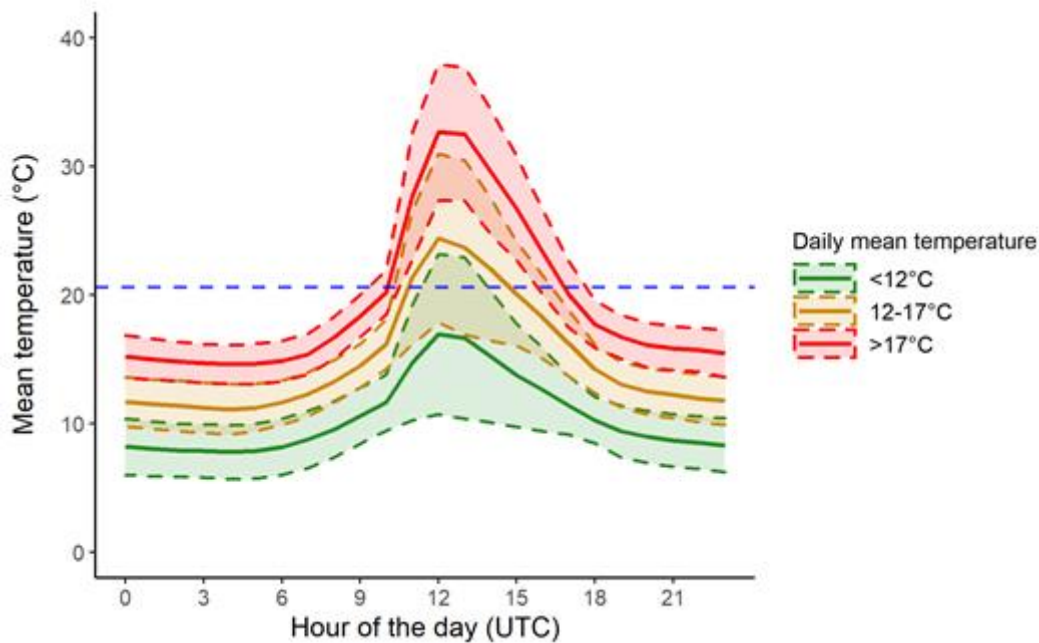
$$T_{\text{ambient}} = (T_{\text{sensor}} - 0.156 \times T_{\text{animal}} - 0.128) / (1 - 0.156)$$

where T_{ambient} = ambient temperature, T_{sensor} = temperature recorded by sensors embedded in GPS collars fitted on chamois, and T_{animal} = body temperature of animals, here 39°C (Dematteis et al., 2008).

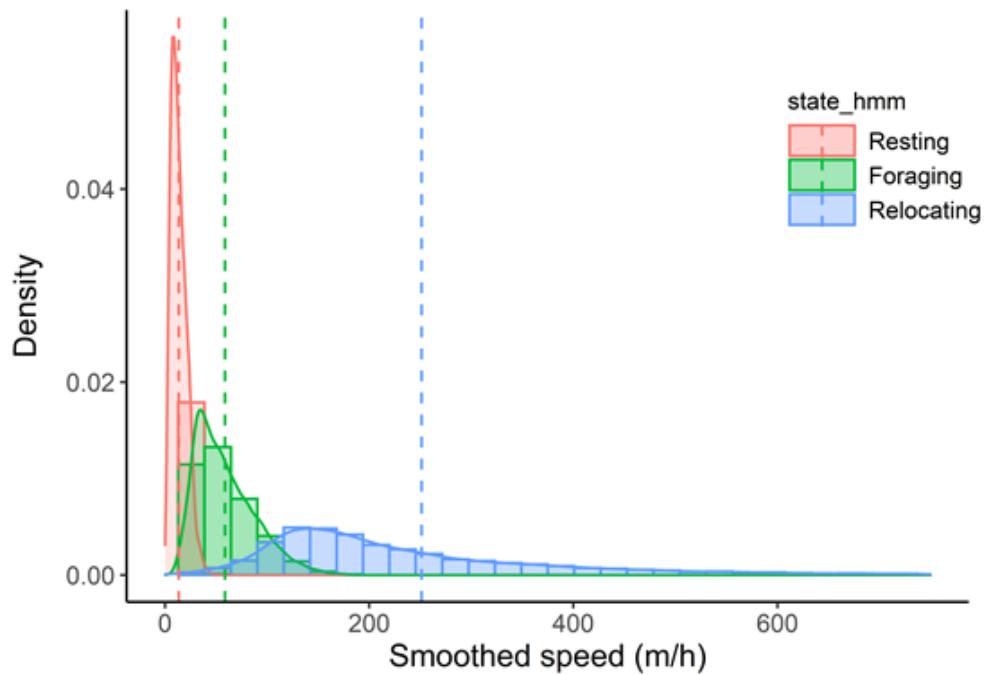
Considering that chamois may experience thermal discomfort when the ambient temperature increases above a certain threshold, and hence start to show a thermoregulatory behaviour, we estimated this temperature threshold using a segmented regression of ambient temperature experienced by the animal against the temperature recorded at the weather station. We found a marked threshold-dependent relationship between ambient temperatures and temperatures recorded at the weather station. Below 20.6 °C (95% CI = 20.3–20.9) at the weather station, ambient temperatures increased between 0.86 and 1.06°C per 1 °C rise at the weather station, and between 0.16 and 0.36 when temperature was above 20.6°C at the weather station. In addition, it is worth noting that when daily mean temperature did not exceed 12°C, hourly temperature averages did not exceed 20.6°C during daytime while it did when daily mean temperature exceeded 12°C, and especially when temperatures exceeded 17°C (Appendix S2). We may then consider in what follows, that animals may have experienced moderate heat stress when daily mean temperature was between 12 and 17°C, and strong heat stress when temperature exceeded 17°C.



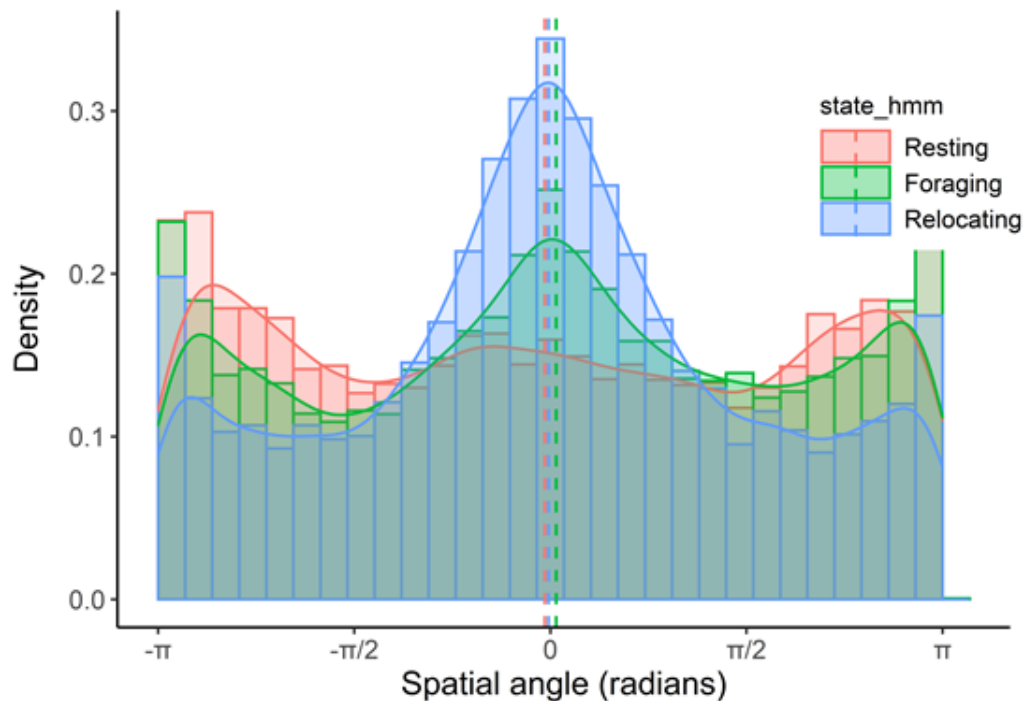
Appendix S1: Segmented regression of ambient temperature against temperature recorded at the weather station. The solid line represents predicted values of the model, the vertical dashed line the temperature value recorded at the weather station for which the slopes' breaks appear.



Appendix S2: Hourly temperature averages at the weather station, aggregated by daily mean temperature. Ribbons represent standard deviation of observed data. The blue dashed horizontal line represent the 20.6°C temperature threshold unveiled in the segmented regression of ambient temperature against station temperature.



Appendix S3: Density plots of observed Smoothed speed for each state specified in the Hidden Markov Model. Dashed vertical lines represent the mean smoothed speed value for each state (Resting: 13.6 ± 7.6 m/h; Foraging: 58.8 ± 29.4 m/h; Relocating: 251.3 ± 185.8 m/h).



Appendix S4: Density plots of observed spatial angle for each state specified in the Hidden Markov Model. Dashed vertical lines represent the mean smoothed speed value for each state (Resting: -0.04 ± 1.94 ; Foraging: 0.05 ± 1.84 ; Relocating: 0.02 ± 1.62).

Chapter 6

Being cool ain't free: age and access to open areas drive opportunity costs in an alpine ungulate.

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Target journal : Behavioural Ecology

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Abstract

Relocating into thermal refuges under high summer temperatures is a commonly documented behaviour in large herbivores. These responses may however incur costs in terms of energy acquisition, as individuals may typically allocate time and energy to visit places where they can efficiently achieve thermoregulation, but where foraging conditions may be suboptimal. In a context of climate change, these opportunity costs are then expected to be increasingly frequent, yet they have still been rarely assessed. In addition, how individuals' trade-off escaping heat stress, moving and foraging in good quality patches may depend on animals' conditions and age, another aspect that has also rarely been explored so far. Using chamois (*Rupicapra rupicapra*) as a case study, in a population where the distribution of resources (the "foodscape") has been evaluated previously, we investigated whether temperature modified daily movement costs, and the ability of individuals to exploit the most beneficial resource patches (lost opportunities). We then assessed whether individual behavioural and spatial responses differed according to the habitat features in their home range and their age. Our results uncovered the existence of such opportunity costs related to behavioural thermoregulation in chamois, as individuals visited places with worse foraging conditions when temperature increased. Moreover, older females, i.e. individuals aged 10 or more, had generally access to higher forage quantity, and were the ablest to keep on visiting locations with high forage availability compared to younger females when exposed to increasing temperatures. The relative success of older females to keep visiting places with high forage quantity could possibly be due to their increased experience that may allow them to better exploit their environment. Further work will be needed to assess whether age-related differences in opportunity costs linked to behavioural thermoregulation, may potentially lead to age-related differences in survival or reproductive success and impact population demographics.

Introduction

Global warming is expected to have marked consequences on ecosystems dynamics, especially in alpine environments (Schwager & Berg, 2019). Indeed, the increase of annual temperatures may induce altitudinal shifts in plant distributions, as well as earlier vegetation green-up and senescence (Cremonese et al., 2017; Vitasse et al., 2021), which may influence large herbivore species distribution (Brivio et al., 2019) and population dynamics (Garel et al., 2004; Lovari et al., 2020). In addition to these indirect effects, the increasing occurrence of extreme temperatures, heat waves and drought events (Hov et al., 2013) may also strongly impact individuals' behaviour. Particularly, cold-adapted species are expected to dedicate an important part of their time and energy to thermoregulation when facing heat stress situations, typically by travelling into thermal refuges, or reducing their level of activity (Borowik et al., 2020; Grignolio et al., 2018). While these responses enable individuals to remain in their thermo-neutral zone and avoid the deleterious effects of hyperthermia on metabolism and water loss (Terrien, 2011), adjustments in habitat selection and activity budgets may however come at a cost for the individual. For example, if closed-canopy forests may constitute an ideal thermal refuge (Borowik et al., 2020; Elmore et al., 2017), they may nonetheless offer decreased forage availability for an ungulate compared to other more open habitats, due to the less-developed forest understory (Lashley et al., 2011; McCann et al., 2016). On the long-term, behavioural thermoregulation may induce potential fitness costs to individual because of lost opportunities (Cunningham et al., 2021), underlying decreased energetic gain it might induce. In response, large herbivores have been shown to display mitigatory mechanisms such as increasing their foraging activity during the coolest hours of the day, i.e. dusk and night-time, to palliate the costs of daytime behavioural thermoregulation (Grignolio et al., 2018). Studying how individuals' behavioural tactics may allow them to cope with heat stress while meeting their energetic requirements, is then of crucial importance if we aim to assess the consequences of global warming on population dynamics.

In this regard, age may be an important driver of individual's space use. Indeed, individuals' experience, i.e. their knowledge of the distribution of resources and risk in their environment, increases while their locomotor abilities decrease as they get older, both of these phenomenon leading animals to use restricted movement and home ranges (Froy et al., 2018; Malagnino et al., 2021). In addition, abilities to physiologically thermoregulate get worse as animals age, by compromising both thermogenesis or the capacity to conserve or dissipate heat (Grosiak et al., 2020), increasing the sensitivity of aged individuals to thermal stress (i.e. hypo- and hyperthermia), which may then have a greater need to buffer themselves from stressful conditions, and display different behavioural thermoregulation tactics than younger individuals

(e.g. in salmon Morita et al., 2010). Still, studies investigating the influence of age on individuals' spatial tactics remain scarce, essentially because of the difficulty of getting accurate estimates of individuals' age in the field (but see Froy et al., 2018; Malagnino et al., 2021).

Mountain ungulates may be particularly affected by temperature increase, both because temperature is expected to increase in mountain areas more rapidly than elsewhere in Europe, and because species like chamois (*Rupicapra rupicapra*) or ibex (*Capra ibex*), for the European species, occupy partly or mostly (depending on populations) open areas above treeline. Individuals living above treeline may therefore be particularly exposed to direct sun radiation, which should lead to behavioural and spatial mitigation. Such behavioural and spatial responses have been uncovered in an increasing number of species recently (e.g. ibex Mason et al., 2017; Semenzato et al., 2021; chamois Brivio et al., 2016; Grignolio et al., 2018), and reveal that responses are complex, depending on local habitat features experienced by individuals, and can be counterintuitive. For instance, rather than resting more, some individuals may have to “commute” more often between shady and foraging areas (as suggested in chamois in Malagnino et al. submitted). The costs incurred by the range of behavioural responses to increasing temperature in terms of increasing energetic expenditure or lost opportunities for foraging has however rarely been assessed. In addition, how individuals trade-off escaping heat stress, moving and foraging in good quality patches may depend on animals conditions and age, another aspect that has rarely been explored so far. Using chamois, which age can be determined on adults, as a case study, in a population where the foodscape has been evaluated previously (Duparc et al., 2019, 2020), we investigated whether temperature modified daily energy expenditure (movement patterns across the landscape) and the ability of individuals to exploit the most beneficial resource patches (lost opportunities), and whether individual behavioural and spatial responses differed according to the habitat features in their home range and their age.

Our main hypothesis was that age, temperature and access to open areas will interact to influence individuals' resource acquisition and energy expenditure. First, we predicted that 1a) with increasing daily mean temperature, individuals would relocate into thermal refuges with decreased foraging conditions, and thus would have access to decreased daily mean resources quantity and quality. We also predicted that 1b) older individuals should be more experienced and hence should have access to higher resources quantity and quality on a daily basis than younger individuals, i.e. they should visit locations with higher forage availability and quality. We then made the prediction that, in return, individuals will use their environment more intensely by 2a) increasing their daily total space use, i.e. the total surface area they exploit

daily, to visit more food patches and mitigate the energetic costs of decreased access to forage quantity and quality. Due to experience and/or decreased locomotor abilities related to senescence, we also expected that 2b) older individuals would show a lower space use than younger individuals. Finally, we predicted that 3a) increased space use, due to time spent travelling to thermal refuges and between patches, should also lead to increased energetic costs linked to movement. Again, in relation to experience and senescence, 3b) lower space use in older individuals should then be translated into lower energetic movement costs compared to younger individuals

Methods

Study sites

We conducted our study in the Reserve Nationale de Chasse et de Faune Sauvage of Les Bauges massif, in the northern French Alps (45°40' N, 6°14' E; 900 to 2200 m a.s.l., 5200 ha), within two study sites, i.e. Charbonnet-Pleuven and Arménaz-Pécloz. Study sites are approximately 7km distant from each other, separated by deep valleys with no exchange of individuals between them. Eighteen percent and twenty-five percent of study sites' area in Charbonnet-Pleuven and in Arménaz-Pécloz respectively is covered by forests mostly represented by beech (*Fagus sylvatica*) and fir (*Abies alba*) groves. The remainder of the study sites' area is covered by grasslands and by rocky areas (Lopez, 2001). Finally, north-oriented slopes (i.e. north and north east orientation, see the “Environmental characteristics” section), also represent eleven and seventeen percent of the area of Charbonnet-Pleuven and Arménaz-Pécloz study sites respectively.

The Reserve is inhabited by a chamois population of approximately a thousand of individuals (Maillard et al., 2014). In this population, births occur from the end of April until the end of June, with 80% of births occurring before 15 June (Loison, 1995). Most females give birth each year when they are aged two and more, as more than 80% of them are observed lactating (Pioz et al., 2008). In summer, female chamois requires large resources to bear the high energetic costs of lactation, and to accumulate fat reserves for the winter at the same time. Hence, females are expected to dedicate a very important part of their time to foraging activities to meet their high energetic demands.

Data collection

Between 2014 to 2016, during July and August, 26 chamois adult females were trapped with drop nets baited with artificial salt lick and equipped with GPS collars (Vectronics GPS Plus or Vectronics Vertex Plus) scheduled to record 1 location every 20 min from mid-July to mid-August (12th July-18th August in 2014; 11th July-17th August in 2015; 09th July-15th August in 2016) and 1 location every 4h during the rest of the year. Captures were performed by Office Français de la Biodiversité (previously Office National de la Chasse et de la Faune Sauvage) according to the ethical conditions detailed in the specific accreditations delivered by the Préfecture de Paris (prefectorial decree n°2009-014) and in agreement with the French environmental code (Art. R421-15 to 421-31 and R422-92 to 422-94). As collar deployment and recovery occurred during summer, the total number of summer days with 20-min locations available per individual ranged between 6 and 38 days (median/mean = 16/19.9). We filtered out erroneous GPS locations (<0.3% for both 20-min and 4h schedules) based on Bjørneraas et al. (2010).

Environmental characteristics

The foodscape: map of resources quality and quantity

We used the 25x25m foodscape raster map computed by Duparc et al. (2020) to determine resources quantity and quality. The mean edible biomass available in each raster cells (in g/m²) was used as a proxy of forage quantity. We used the phenology of plants in each raster cells, as a proxy of forage quality. More precisely, four phenological stages were identified in Duparc et al. (2020), being growth, flowering, appearance (fruiting) and loss of fruit (senescence), and coded into four phenology scores between 1–4, respectively. We then used the community weighted mean (CWM) of the plant phenology scores i.e. the mean of the species' phenology scores, weighted by the relative abundance of each species in the community, as a proxy of plant development over time and quality in each raster cells. As Duparc et al. (2020) showed that the flowering stage was the most selected by chamois during summer, potentially for its high nutrient content, we considered that quality will be increasing when phenological scores would get closer to 2, and decreasing when becoming inferior or superior to 2.

Resources availability in individual's home range

We used 4h locations over the July-August period to estimate individuals' summer utilization distribution, using the fixed-kernel method (Worton, 1989) with a smoothing parameter h set to the median value of individual smoothing parameters ($h_{\text{individual}}=h_{\text{ref}}$). We determined the summer home range at the 90% isopleth of utilization distribution, as recommended by Börger et al. (2006) to obtain an unbiased estimate.

As behavioural thermoregulation may allow individuals to buffer themselves from heat stress but at the same time, induce energetic costs linked to lost opportunities (Cunningham et al., 2021), we characterized three exclusive habitat types offering variable thermal and foraging conditions, i.e. forests and north-oriented slopes (i.e. north and north east orientation, hereafter referred as “northern slopes”; between 337.5-360° and 0-67.5°; Bačkor, 2010). Habitat classification was based on the combination of a habitat map with a 25-m resolution (Institut National de l’Information Géographique et Forestière) and an aspect map derived from a digital elevation model with a 25-m resolution (Institut National de l’Information Géographique et Forestière). Then, based on the analyses of a raster map of the distribution edible biomass computed by Duparc et al., (2020), and the temperature data recorded by each individual’s GPS collar, we quantified the mean amount of resources available in each habitat type and temperature differences between them. Thereby, we confirmed through this method that open areas were susceptible to offer the best conditions in terms of forage availability (resources quantity 1.5 up to almost 3 times higher than in thermal refuges), but at the cost of challenging temperatures, open areas being on average 1.2°C and 2.2°C higher than respectively, forest and northern slopes between 12:00 to 16:00 UTC during the hottest days (i.e. daily mean temperature >17°C, see appendix S1 & S2). Finally, depending on the relative availability of suitable habitats, individuals may adjust their behaviour differently to environmental constraints, displaying context-dependent habitat use or selection (Myserud & Ims, 1998; Holbrook et al., 2019). In this regard, as available conditions may sometimes strongly vary between individuals, we decided to compute the proportion of open areas in individuals’ home ranges, and use it as an integrative proxy of both forage (positive correlation) and thermal refuges availability (negative correlation), allowing us to account for these variables while keeping our statistical analyses simple.

Temperature data

Current temperatures were recorded every 15 min at the Phenoclim weather station (CREA Mont-Blanc) located in Chérel mountain pastures (45°40'54.6"N, 6°12'26.0"E, 1380 m above sea level, i.e. 2-6 km far from the area used by chamois). Each temperature recorded at plain hours were matched with corresponding GPS locations of chamois recorded at the same time, whereas the mean temperature of the two closest records was associated with the GPS location recorded at the 20th or 40th minutes of each hour. Daily mean temperatures ranged between 6 and 23°C, with a mean and a median of 15°C.

Statistical analyses

P1: Variation of forage quantity and quality of visited locations

To investigate how forage quantity and quality of locations visited by individuals would vary in response to temperature, access to open areas and age, we calculated, for each individual-day, the daily mean of edible biomass and mean phenology score under locations. As some locations were missing we restricted our analyses to 24h period with an exact number of 72 locations, i.e. no missing locations (n=446 individual-days). We then used linear mixed models (LMMs) to first investigate variation in the daily mean edible biomass of visited cells and in the daily mean phenology score in relation to daily mean temperature and access to open areas, by including their two-way interaction and individual identity as a random effect on the intercept. Both response variables were log-transformed to achieve normality in model's residuals. Concerning daily variations of forage quality, as mean phenology scores were very different between July (<2) and August (>3), and given our models already included a three-way interaction, we split our dataset and ran one model for each month separately. We then selected the most parsimonious model based on AIC criterion (Burnham & Anderson, 2004), retaining the one within a delta AIC <2 and with the smallest number of degrees of freedom.

P2: Daily space use

We quantified space use for each individual, i.e. the total number of raster pixels visited by the individual during 24h. We then used generalized linear mixed models (LMMs) with a Poisson error distribution, to investigate variations in the daily total number of visited raster pixels in relation to daily mean temperature and access to open areas by including, in each model type, their two-way interaction and individual identity as a random effect on the intercept.

P3: Energetic landscapes and variations of daily costs of transport (DCoT)

We computed energy landscapes within individuals' home range using a 25x25m digitalized elevation model (DEM) and the function *enerscape()* from the R CRAN package "enerscape" (Berti et al., 2022). This function allowed us to compute the mean energetic costs of moving into each pixels of our DEM. We then calculated daily costs of transport for each individual as the sum of energetic costs linked to each visit of a raster pixel over 24h. We defined a visit as every step where an individual would leave its current raster pixel to go into another pixel. Finally, we used linear mixed models (LMMs) to investigate variation in log-transformed DCoT in relation to daily mean temperature and access to thermal refuges, by including, their

two-way interaction between these two covariates, and the individual identity as a random effect on the intercept.

For all modelling procedure, we selected the most parsimonious model based on AIC criterion (Burnham & Anderson, 2004), retaining the one within a delta AIC <2 and with the smallest number of degrees of freedom.

Results

P1: Variations of used forage quantity & quality in response to hot temperatures, age and access to open areas

Forage quantity, i.e. daily mean edible biomass of the raster pixels visited by chamois (72 fixes), varied with age, temperature, percentage of open areas and the two-way interaction between age and temperature (Table 1). In accordance with our prediction 1a), forage quantity decreased when temperature increased, with a steeper slope for females aged between 5 to 9 years old. Indeed, when the percentage of open areas available in the individual home range was set at 85%, and when daily mean temperature increased from 10°C to 20°C, daily mean biomass under locations decreased by 20%, 42% & 14% for individuals aged between 2 to 4 years old, 5 to 9 years old & 10 to 17 years old respectively (Figure 1A). Older individuals also seemed to use areas with higher forage quantity than younger individuals at both low and high temperatures (support to prediction 1b). For individuals with 85% of open areas in their home range, daily mean biomass under locations was 44% & 17% higher for chamois aged between 10 to 17 years old compared to individuals aged between 2 to 4 years old & 5 to 9 years old respectively when daily mean temperature was equal to 10°C, and 47% & 43% higher when temperature was at 20°C (Figure 1A). Individuals with higher availability of open areas in their home range visited areas with higher forage quantity than individuals with a lower access to open areas. Daily mean edible biomass under locations was indeed 60% higher for individuals with 95% of their home range covered by open areas compared to individuals with only 75% of their home range covered by open areas.

Table 1: Candidate generalized linear mixed models performed to investigate daily variations of proxies of forage quantity and quality in chamois, with individual identity as a random effect on the intercept. The top 3 best ranked models are presented followed by the model with only additive effects of all predictors (i.e. Age+Temperature+%open areas) or just Temperature, and the null model. The best selected model is in bold.

Forage quantity: log(daily mean biomass under location)				
Predictors	df	AIC	delta	weight
Age + Temperature + % Open areas + Age:Temperature	9	375.4	0	0.476
Age + Temperature + % Open areas + Age:Temperature + Temperature:% Open areas	10	377	1.61	0.213
Age + Temperature + % Open areas + Age:Temperature + Age:% Open areas	11	377.8	2.41	0.142
Age + Temperature + % Open areas	7	383.6	8.22	0.008
Temperature	4	394.5	19.16	0
Null model	3	424.6	49.26	0

Forage quality: log(daily mean phenology score under location) in July				
Predictors	df	AIC	delta	weight
Age + Temperature + % Open areas + Age:Temperature + Temperature:% Open areas	10	-638.2	0	0.363
Age + Temperature + % Open areas + Age:Temperature	9	-637.1	1.11	0.208
Age + Temperature + % Open areas + Temperature:% Open areas	8	-636.3	1.92	0.139
Age + Temperature + % Open areas	7	-634.9	3.26	0.071
Temperature	4	-630.1	8.15	0.006
Null model	3	-592.7	45.49	0

Forage quality: log(daily mean phenology score under location) in August				
Predictors	df	AIC	delta	weight
Temperature + % Open areas	5	-1448.5	0	0.535
Temperature + % Open areas + Temperature:% Open areas	6	-1446.5	1.98	0.198
Age + Temperature + % Open areas	7	-1445.6	2.94	0.123
Temperature	4	-1440.7	7.82	0.011
Null model	3	-1419.7	28.82	0

In July, forage quality, i.e. daily mean phenology score, varied with age, temperature, percentage of open areas and the two-way interaction between temperature and percentage of open areas (Table1). Forage quality decreased (i.e. phenology score getting further away from 2) with increasing temperature, with a steeper slope for individuals with a lower availability of open areas in their home range (support to 1a). Indeed, when daily mean temperature increased from 10°C to 20°C, daily mean phenology score, decreased by 6%, 4% & 3% for individuals where 75%, 85 & 95% of their home range was covered by open areas respectively (Figure 1B). Older individuals aged between 2 to 4 years old and between 10 to 17 years old, also used areas with higher forage quality (i.e. phenology score closer to 2) than individuals aged between 5-9 years old. Daily mean phenology under locations was indeed 4% higher for chamois aged

between 2 to 4 & 10 to 17 years old compared to individuals aged between 5 to 9 years old (Figure 1B).

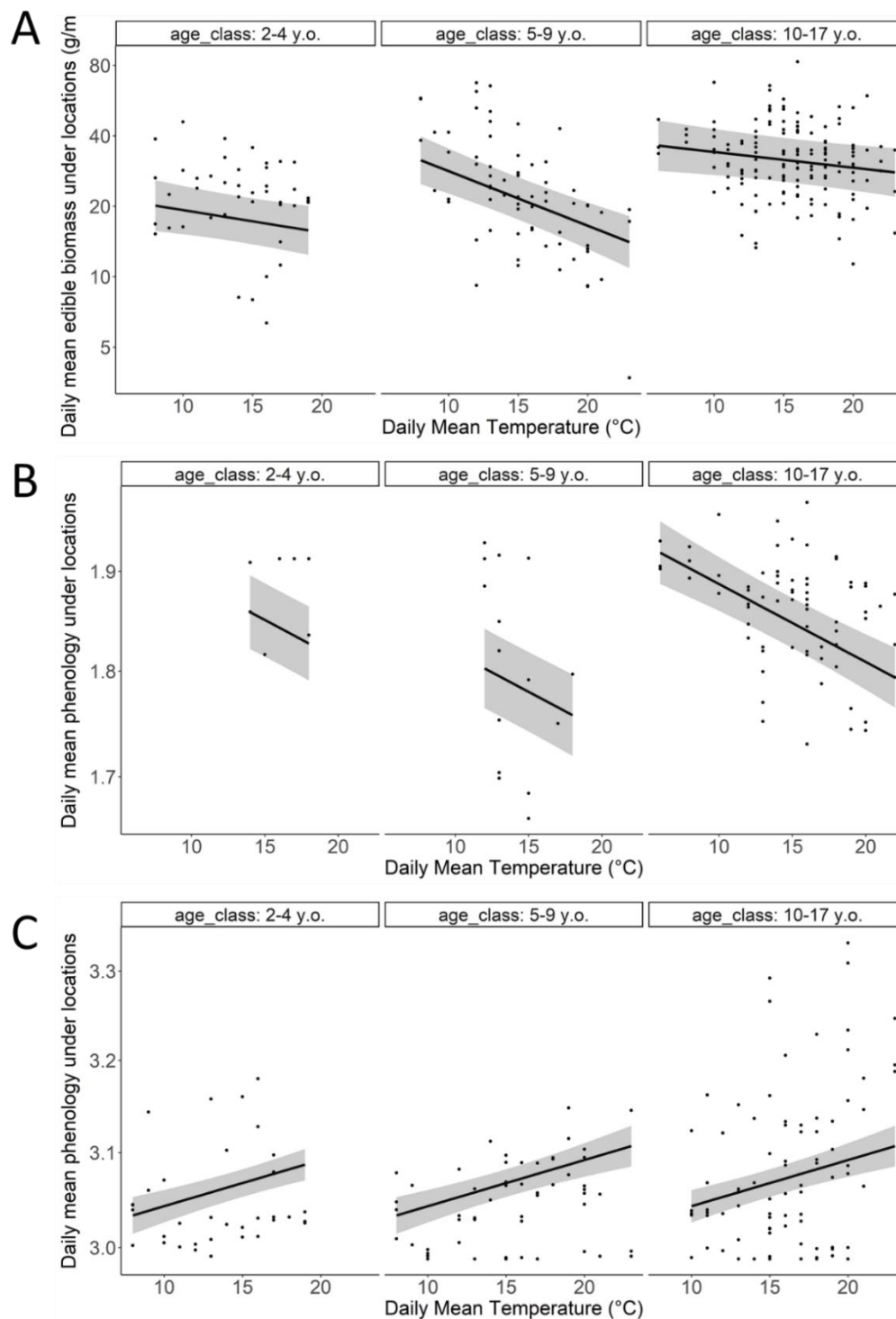


Figure 1: Variations in the predicted (line) and observed (points) daily mean edible biomass under locations (A) and in phenology in July (B), August (C), depending on the daily mean temperature and age class for individuals with 85% of their home range covered by open areas. As Duparc et al. (2020) showed that the flowering stage was the most selected by chamois during summer, potentially for its high nutrient content, we considered that quality will be increasing when phenological scores would get closer to 2, and decreasing when becoming inferior or superior to 2. As a consequence, negative slopes in July and positive slopes in August, both represent a decrease in forage quality, as the mean phenology score in both cases is getting further away from 2 when daily temperature increases. Ribbons represent standard errors.

In August, forage quality varied with mean temperature and the availability of open areas in the individual home range (Table 1). Forage quality decreased with daily mean temperature, i.e. mean phenology score under locations increased and went further away from 2. For individuals with 85% of open areas available in their home range, daily mean phenology score under locations increased by 2% when daily mean temperature increased between 10 to 20°C (Figure 1C). The more individuals had access to open areas, the higher food quality was, i.e. here the lower phenology score was (i.e. closer to 2). At 10°C, daily mean phenology score under locations was 2% lower, i.e. resource quality was 2% higher, for individuals with 95% of open areas compared to individuals with 75% of open areas in their home range (Figure 1C).

P2: Variations of space use in response to temperature, age and access to open areas

The best model explaining variations in daily number of unique visited cells (UVC) included age, temperature, percentage of open areas, and the two-way interactions between temperature and percentage of open areas, and between age and percentage of open areas (Table 2).

Table 2: Candidate generalized linear mixed models used to investigate daily variations of proxies of space use and movement costs in chamois, with individual identity as a random effect on the intercept. The top 3 best ranked models are presented followed by the model with only additive effects of all predictors (i.e. Age+Temperature+% open areas) or just Temperature, and the null model. The best selected model is in bold.

Space use: Daily number of unique visited cells

Predictors	df	AIC	delta	weight
Age+Temperature+% Open areas+Age:Temperature+Age:% Open areas+Temperature:% Open areas+Age:Temperature:% Open areas	13	2871.4	0	0.464
Age+Temperature+% Open areas+Age:% Open areas+Temperature:% Open areas	9	2872.8	1.41	0.229
Age+Temperature+% Open areas+Age:Temperature+Age:% Open areas+Temperature:% Open areas	11	2873.6	2.27	0.149
Temperature	3	2878.1	6.69	0.016
Age+Temperature+% Open areas	6	2882.6	11.2	0.002
Null model	2	2898.2	26.81	0

Movement costs: Daily cost of transport

Predictors	df	AIC	delta	weight
Age+Temperature	6	118.1	0	0.196
Age+Temperature+% Open areas+Age:% Open areas	9	118.5	0.32	0.167
Age+Temperature+% Open areas+Age:% Open areas+Temperature:% Open areas	10	119.3	1.22	0.107
Temperature	4	119.6	1.43	0.096
Age+Temperature+% Open areas	7	119.9	1.81	0.079
Null model	3	143.5	25.33	0

UVC increased when temperature increased, with a steeper slope for females with less access to open areas. Indeed, when daily mean temperature increased from 10°C to 20°C, UVC increased by 21%, 11% & 1% for individuals aged between 5 to 9 years old with 75, 85 & 95% of their home range covered by open areas respectively (Figure 2). Older individuals also visited more cells than younger individuals when they had low access to open areas. Inversely, they visited less cells than younger individuals when they had higher access to open areas. Individuals aged between 10 to 17 years visited 14% & 2% more cells than individuals between 2 to 4 & 5 to 9 years when 75% of their home range was covered by open areas (Figure 2). On the other side, individuals aged between 10 to 17 years old visited 11% & 5 less cells than individuals between 2 to 4 and 5 to 9 years old respectively when 85% of their home range was covered by open areas. (Figure 2).

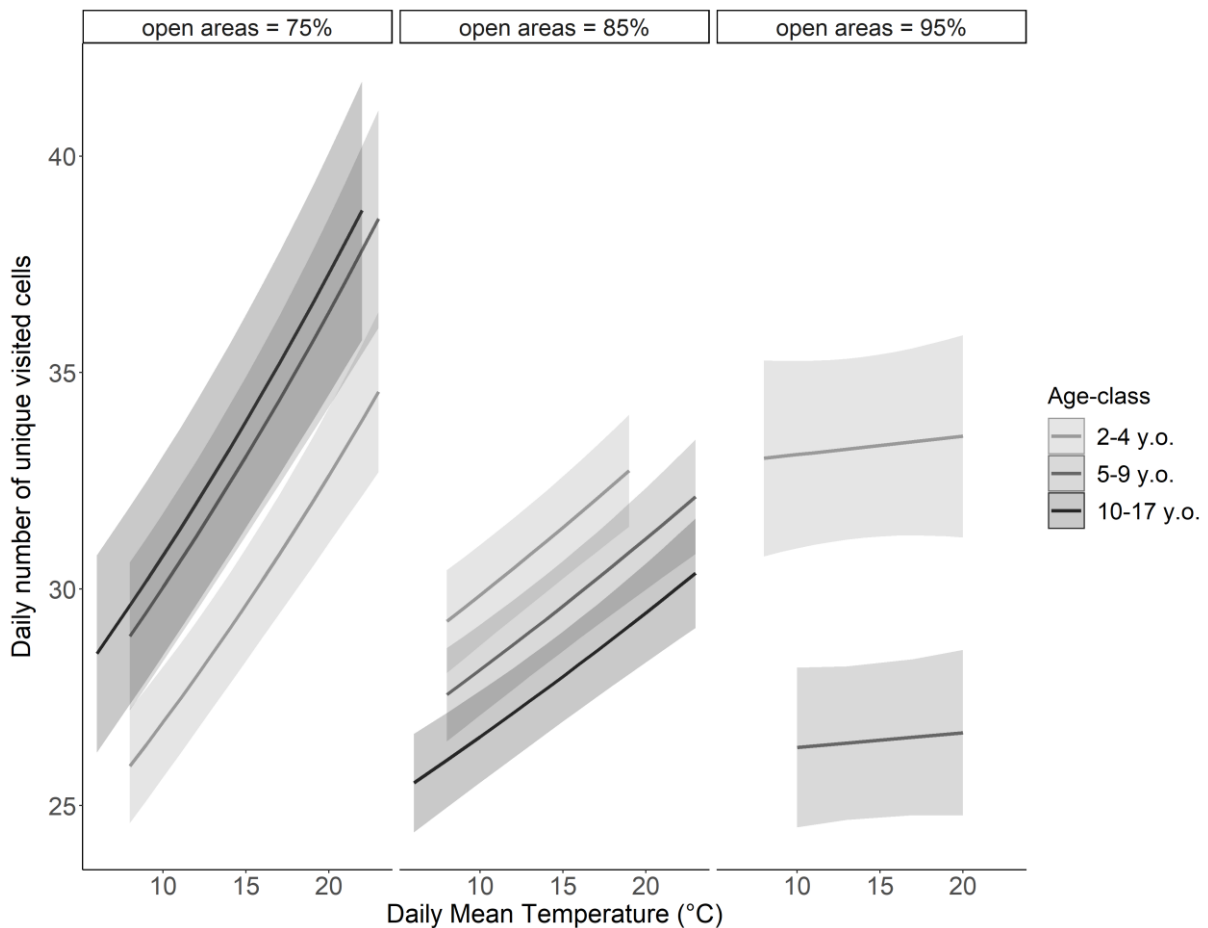


Figure 2: Variations in the predicted (line) daily number of unique visited cells depending on the daily mean temperature, the availability of open areas in the home range, and the age-class of the individual. Ribbons represent standard errors.

P3: Variations of daily costs of transport in response to temperature, age and access to open areas

The best models for explaining variations in daily costs of transport (DCOT) included only the effect of daily mean temperature (Table 2). DCOT increased when temperature increased, i.e. by 31% respectively when daily mean temperature increased from 10°C to 20°C (support to 3a but no support to 3b, Figure 3).

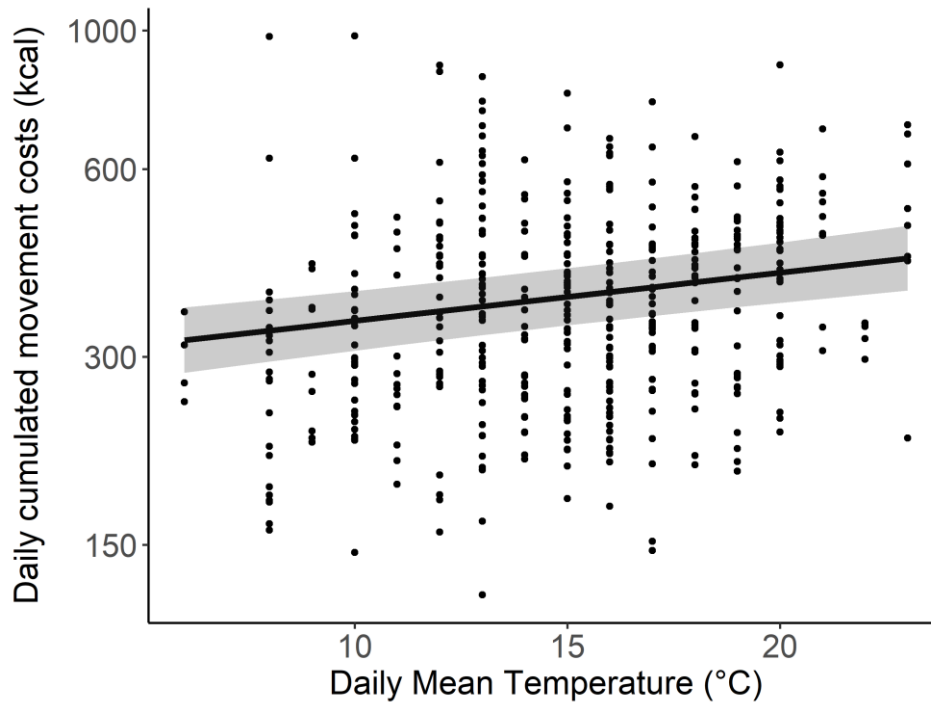


Figure 3: Variations in the predicted (line) and observed (points) DCT depending on the daily mean emperature. We used a logarithmic scale one the y axis. Ribbons represent 95% CI.

Discussion

By quantifying daily variations in forage availability and cost of transport, we assessed how behavioural thermoregulation may be associated with non-negligible energetic costs for an individual, via missed opportunities and increased movement and space use. Moreover, we emphasized the important influence of local constraints given by different thermal and food landscapes (i.e. thermal refuges/open areas availability), and internal factors, i.e. age, on individual responses to hot summer temperatures in terms of forage acquisition and space use. Thermal landscapes (Elmore et al., 2017) and age have long been mentioned as possible factors influencing animals' spatial behaviour, but studies exploring them in the wild are relatively recent (e.g. thermal landscape: Allred et al., 2013; Alston et al., 2020; Williamsen et al., 2019;

age: Foley et al., 2015; Froy et al., 2018; Malagnino et al., 2021). Our study provides further insights about how their interaction may yield consequent among-individual heterogeneity in the behavioural response of chamois to increasing temperatures. Below, we discuss in details how the different impacts of summer hot temperatures on chamois forage acquisition and movement costs, are modulated by individuals' age and thermal landscapes, and their possible implications for the energy budget and demography of this endotherm mountain herbivore.

Many studies have demonstrated the existence of thermoregulatory behaviours such as activity shifts or seeking shade in large herbivores (Borowik et al., 2020; Grignolio et al., 2018; Semenzato et al., 2021; Williamsen et al., 2019). Yet, while behavioural thermoregulation may carry pervasive costs on its own (Cunningham et al., 2021), the energetic consequences of behavioural adjustments for individuals have rarely been investigated. Often these manifest as opportunity costs. Indeed, the engagement of individuals into thermoregulatory behaviours is made at the detriment of foraging, providing for offspring or mating (Conradie et al., 2019; Darnell et al., 2020), which are crucial activities for individual survival and reproductive success. In a context of climate change, missed opportunities are expected to be increasingly frequent, especially if the costs of missed opportunities outweigh the benefits of behavioural thermoregulation (e.g. Conradie et al., 2019 in birds). Our results uncovered the existence of such opportunity costs related to behavioural thermoregulation in chamois, as individuals visited places with worse foraging conditions when temperature increased. Especially, while the decrease in forage quality was relatively small, forage quantity was drastically lower for all individuals, up to 42%. Such a decrease in resource quantity in patches visited during hot days could have consequent effects on individuals' energy budget, especially during July and August where energetic needs of females linked to lactation are increased. Decreased forage conditions might indeed lead to decreased milk production and maternal investment (e.g. through successful suckling events) which may in turn result in lower weaning success for females (Scornavacca et al., 2016). Of course, females might also compensate these costs by spending more time visiting food patches and foraging, as observed in mountain goats for example (Hamel & Côté, 2008). In our study alike, the increased space use, i.e. the increased surface area (daily number of unique visited cells) used by chamois during the hottest days suggest that females may roam within their home range to acquire sufficient resource. On another side, this may also be linked to the increased time spent by individuals relocating from open areas to thermal refuges. In any case, increased space use may also yield additional movement costs, as cost of transport increased by 30% during the hottest days.

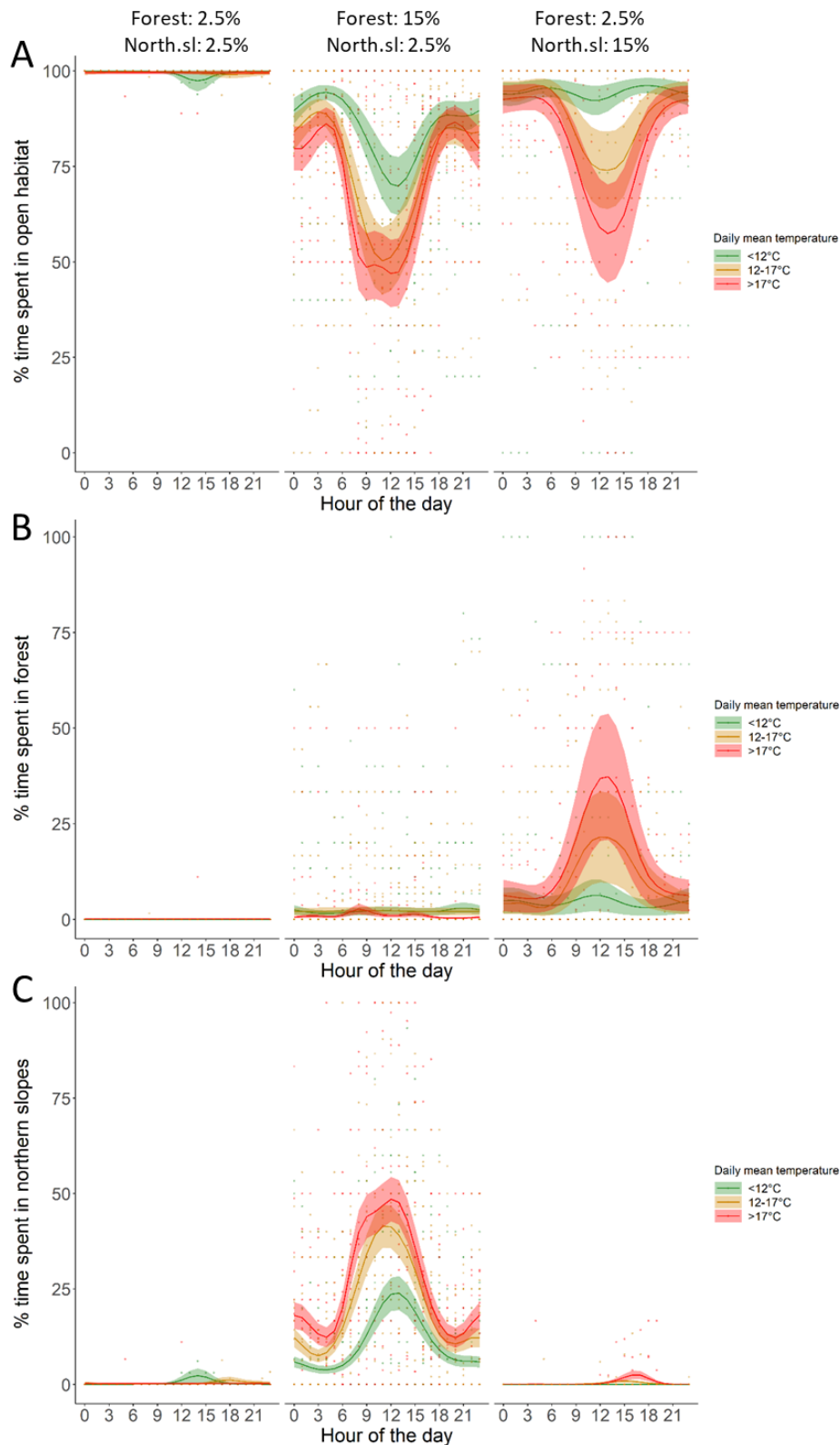
More importantly, local thermal landscape within an individual's home range, as well as its age, both play an important role in individual responses to heat stress, especially in terms of

forage acquisition and space use. Individuals that had access to more thermal refuges (hence less to open areas), visited locations where forage quantity was on average lower than individuals with greater access to open areas. As we expected, they also showed a greater increase of space use when daily mean temperature increased, certainly as a result of a greater time spent foraging and visiting food patches to compensate for the decreased forage quantity once they relocated in thermal refuges during daytime (see Appendix S1 & S2). The landscape characteristics of home ranges may therefore constrain the responses of individuals at lower scales. In brief, while individuals might live in landscapes where they can easily access thermal refuges, they may do it at the detriment of increased access to resource, while individuals living in more open landscapes may on the contrary have enhanced access to forage but with less access to thermal refuges. Further work should attempt to assess the energetic consequences of the variable tactics deployed by individuals to acquire resource while coping with summer extreme temperatures, as it may lead to among individual heterogeneity in energy budgets.

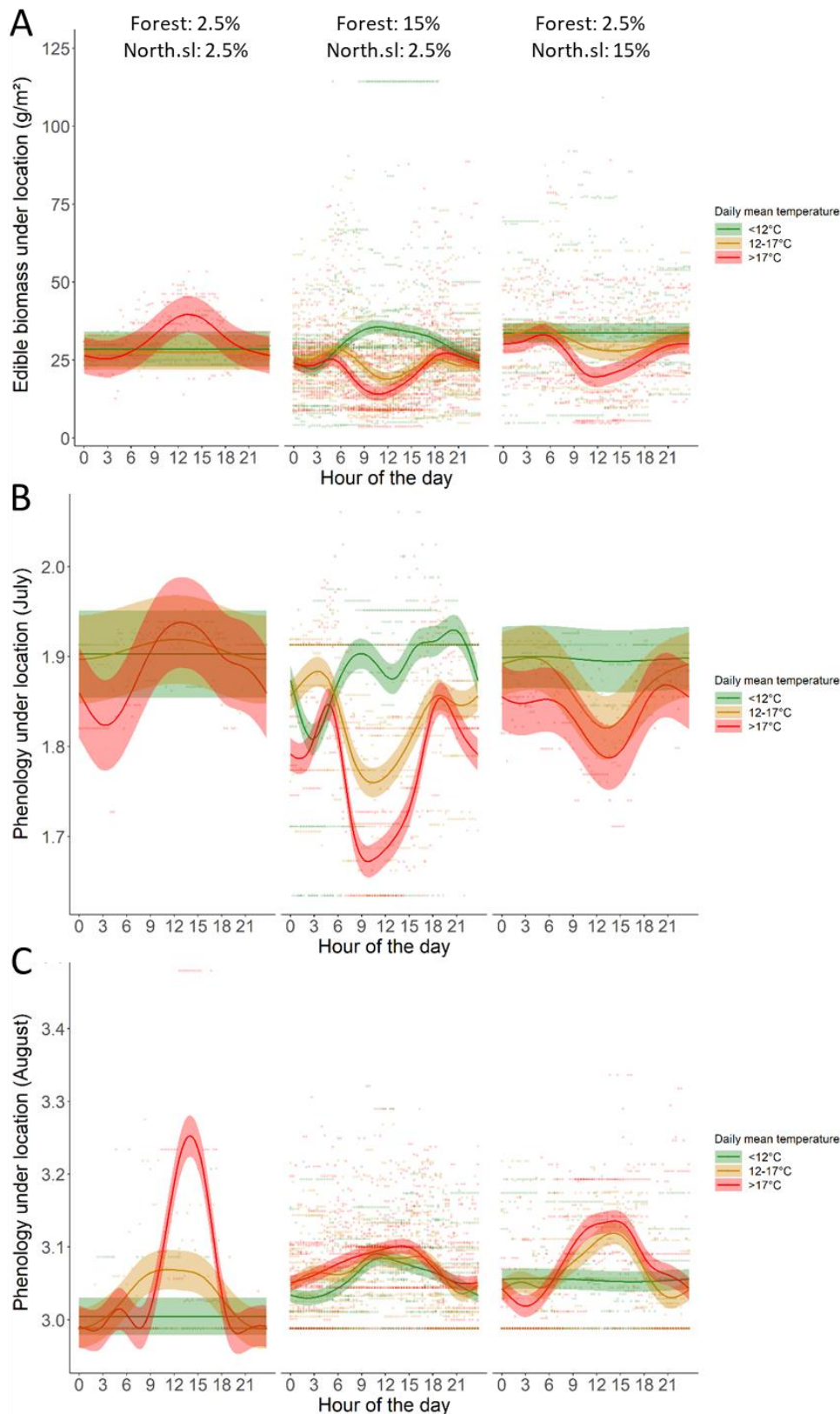
Older females, i.e. individuals aged 10 or more, had generally access to higher forage quantity and when exposed to increasing temperatures, were the ablest to keep on visiting locations with high forage availability compared to younger females. A first explanation could be that older females are the most experienced ones, i.e. they have a better knowledge of their environment, and thus an enhanced ability to better exploit it, by establishing for example their home ranges in areas with advantageous features (e.g. typically resource quantity, see Froy et al., 2018). Alternatively, social effects related to hierarchy and dominance behaviours may also be at play in our study. Fattorini et al. (2018) showed indeed in Apennine chamois females (*Rupicapra pyrenaica ornata*) that during the lactation period, aggression, vigilance, and stress peaked, despite abundant food resources. In particular, dominance was positively correlated with age, and while prime-aged females (4-8 years in Fattorini et al. (2018), Locati & Lovari,(1991), 5-9 years old in our study) were found to be more often involved into aggressions than other females, they would nonetheless be less prone to emerge victorious from an altercation with older, more dominant females. We may consequently argue here, that the greater decrease in forage quantity observed in prime-aged females during the hottest days, might be due to dominance behaviours displayed by older females, which might monopolise patches offering the best compromise between forage availability and thermal conditions, and prevent younger females from exploiting these latter. Further work investigating how females' spatial behaviours are related to their age but also to the presence of conspecifics with various age, is then needed to disentangle the respective influence of experience and dominance on chamois spatial ecology and energy acquisition.

To sum up, we first showed that individuals' thermoregulatory behaviours induced energetic costs not only related to movement, but also to opportunity loss, which may have critical impacts on individual performance. As other capital breeders (Arnold, 2020), chamois indeed rely on fat reserves accumulated during spring and summer to face winter food scarcity, as well as the increased energetic costs linked to gestation and lactation for females. In a context of more frequent heat waves and droughts due to global warming (IPCC, 2021), we can assume that time and energetic costs allocated to behavioural thermoregulation during summer will keep increasing. Further work will then be needed to first determine whether the costs of behavioural thermoregulation (i.e. decreased forage quality and quantity, lost foraging opportunities, increase in costly movements for relocations) will outweigh the costs of acute exposure to heat stress (Conradie et al., 2019). Importantly, we also showed that opportunity loss related to behavioural thermoregulation were modulated by both individuals' local thermal/food landscapes, and their age. Further consequences on individual performance will need to be determined, by for example assessing how differences in opportunity loss related to thermal landscape and age, may potentially induce important individual variability in seasonal variations in females' body mass, or other fitness-related traits such as e.g. weaning success, which may have important repercussions on individual fitness, and *in fine* on population dynamics (Gaillard et al., 2000). Finally, it is important to note that an additional complexity may come from human disturbance - as the hottest day may correspond to the sunniest days and thus the days with the highest site frequentation by hikers. In this regard, the influence of human disturbance should also be accounted for in further studies (Enggist-Diiblin & Ingold, 2003; Pęksa & Ciach, 2018). In conclusion, our results highlight the need for combined studies investigating how individual behaviour, energetics and life-history may respond to increasing temperatures, within the constraints imposed by individuals' local landscape context and internal factors (e.g. sex, age, reproductive status), which should allow to better predict the individual and population-level responses of cold-adapted species to climate change.

Supplementary material



Appendix S1: Predicted (lines) and observed (points) of A) daily percentage of time spent in open areas, B) forest and c) northern slopes, depending on the hour of the day. General Additive Mixed Model was used to predict how the use of each habitat varied with the hour of the day, daily mean temperature and the type of thermal refuge available to the individual in its home range, as well as their interaction. Ribbons represent standard errors.



Appendix S2: Predicted (lines) and observed (points) of A) mean edible biomass under location, B) mean phenology score in July and c) in August under location, depending on the hour of the day. General Additive Mixed Model was used to predict how mean edible biomass or phenology score, varied with the hour of the day, daily mean temperature and the type of thermal refuge available to the individual in its home range, as well as their interaction. Ribbons represent standard errors.

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Chapter 7:

Synthesis, discussion and perspectives

1. Synthesis & Discussion

a. **Through reproductive constraints, experience, senescence or dominance, age is a major driver of spatial behaviour**

In chapter 4 and 6, we investigated how internal factors may constrain the spatial behaviour of individuals. More precisely, we showed that age is an important driver of individual space use and movements in three ungulates species with contrasted life history traits, i.e. the roe deer, the Mediterranean mouflon and the chamois. While it has long been suggested that individuals may modify their spatial behaviour as a result of different life stage constraints or experience and senescence (Daugherty & Sheldon, 1982; Wunderle, 1991), empirical studies investigating age-specific space use and movements have until recently been limited to a few situations where direct observation of known-aged individuals was possible (Corlatti et al., 2012; Foley et al., 2015; Taylor et al., 2020). Our findings, based on a large GPS data set of aged individuals, therefore, illustrate the range of variation in space use tactics, both within and between populations of large herbivores, and provide strong evidence that age is a major determinant of spatial behaviour.

Indeed, we first demonstrated in chapter 4 that reproductive constraints related to life stage had a major influence on age- and sex-specific intra-annual variation in movement rates, i.e. daily distances travelled, and space use, i.e. home range size. This was especially the case in roe deer during the rutting period, where older males travelled greater daily distances than younger males due to patrolling behaviours for territory defence, whereas older mouflon males travelled less than younger males, which often adopted coursing tactics to mate with females. During parturition, age-related differences between roe deer females were also detected, as reproductive females had smaller home ranges than non-reproductive ones, whereas no marked differences were observed in mouflon females. Our results confirmed that the age-dependency of life histories such as mating tactics and reproductive status is likely to induce important inter-individual variability in spatial behaviour.

In addition to reproductive constraints, we also clearly demonstrated that throughout the year the oldest individuals tended to move the least and/or occupy the smallest ranges. We indeed found strong support for our predictions in both species and sexes, although at various scales. In roe deer, adults, and more particularly adult males, generally used smaller monthly home ranges than younger individuals all year round. This was also observed in mouflon females, but, interestingly, not in mouflon males. In contrast, no clear age-related differences in movement rates were detected in roe deer, whereas in mouflon, older individuals travelled much shorter distances than younger individuals. In chapter 6 we also showed that age strongly influenced chamois forage acquisition, particularly concerning forage quantity. Compared to younger females, older females, i.e. individuals aged 10 or more, had generally access to higher forage quantity and were able to continue visiting locations with high forage availability when exposed to increasing temperatures. The influence of experience may then provide a first explanation, as older individuals may have a more accurate cognitive map of the distribution of resources and risks within their environment. They may then be more efficient at locating and navigating between resource patches, resulting in lower distances travelled in mouflon and smaller daily and monthly range sizes in chamois and roe deer. Alternatively, decreasing locomotor capacities linked with the onset of senescence could also explain these age-related differences. As animals get older a process of physiological and physical deterioration generally takes place (Nussey et al., 2013), which can lead to altered locomotion, space use and foraging in later life (Froy et al., 2018; MacNulty et al., 2009). Finally, social effects related to hierarchy and dominance behaviour may also be at play and remain to be explored. The greater decrease in forage quantity observed in prime-aged chamois females during the hottest days might be due for example to dominance behaviours displayed by older females. The latter may indeed be more dominant and might monopolise patches offering the best compromise between forage availability and thermal conditions and prevent younger females from exploiting them (Fattorini et al., 2018). Further research should now aim to clarify the respective influence of experience, senescence and dominance on age-related differences in spatial behaviour. Experiments whereby individuals of known age are translocated to novel environments could for example allow us to tease apart the role of experience and physiological ageing on mobility and range use. On the other hand, mapping the contacts and potential agonistic interactions between conspecifics could help us understand how social effects related to hierarchy and dominance may also shape the spatial behaviour of animals, notably concerning forage acquisition.

Finally, whilst we have demonstrated the marked influence of age on space use in three large herbivores, many other intrinsic and extrinsic factors may also shape individual movement

decisions. Factors like the spatiotemporal dynamics of both resource availability (green-up in spring, senescence in autumn, Morellet et al., 2013) and risk (hunters and natural predators, Benhaiem et al., 2008; Bonnot et al., 2013) have for example also been reported as major drivers of the spatial behaviour of ungulates. By analysing relative variation in space use among age classes over the same monitoring period and landscape, we assumed that individuals of each age class had, on average, experienced roughly the same environmental conditions so that the resulting patterns are a fair representation of age-dependent space use at the population level. However, our modelling approach also revealed that a large proportion of intra-individual variation in space use was not related to age and remained unexplained. Consistent between-individual differences in movement behaviour have been for instance increasingly reported (Bonnot et al., 2015; Gervais et al., 2020; Hertel et al., 2020), with consequences for life histories (Bonnot et al., 2018). To better evaluate the consequences of global change for the mobility of wild populations, further research should aim to disentangle the intrinsic drivers of interindividual variability in space use, such as personality (Dingemanse et al., 2010; Jolles et al., 2020; Réale et al., 2000), from extrinsic factors such as adverse environmental conditions (Marchand et al., 2015) and habitat fragmentation (Marchand et al., 2017).

b. In addition to age, local landscape constraints also shape behavioural responses of animals to environmental factors

In addition to demonstrating the existence of energetic costs related to behavioural thermoregulation, we also showed in chapter 6 that opportunity costs in chamois may be modulated by local landscapes constraints in addition to internal factors. Indeed, depending on their age, and depending on the availability of thermal refuges/open areas in their home ranges, chamois responded to hot summer temperatures differently in terms of forage acquisition and space use. Even though the effects of thermal conditions and age on animal spatial behaviour have long been mentioned, surprisingly they have been mostly overlooked, even if nowadays a growing number of studies tend to take these factors into account (e.g. thermal landscape: Allred et al., 2013; Alston et al., 2020; Williamsen et al., 2019), age: Foley et al., 2015; Froy et al., 2018; Malagnino et al., 2021). In this regard, our study, to the best of our knowledge, may be one of the few to account for both of these external and internal factors at the same time and provides novel and interesting insights about how the interactions between these drivers may cause among-individual heterogeneity.

The availability of thermal refuges/open areas within individual home ranges played an important role in chamois responses to heat stress, especially in terms of forage acquisition and space use. When experiencing high temperatures, individuals visited thermal refuges during the day, where forage quantity was between 1.5 up to 3 times lower than in “sunnier” open areas. To mitigate these opportunity costs, individuals then increased the surface area they used during the day, to acquire sufficient resources. As we discussed in chapter 5, it is in fact highly probable that the increased daily space use by chamois may be related to the greater time spent foraging within and relocating between food patches. This may indeed have allowed individuals to compensate for the decreased forage quantity available in thermal refuges.

Importantly, we showed in chapter 5 that the local constraints posed by individual home range composition, had also an important influence on individual responses to hot temperatures, especially on adjustments in behavioural budgets. Particularly, individuals that had within home range access to forest increased their time spent foraging when daily mean temperature increased, whereas other individuals decreased their time spent foraging and increased their time spent relocating. These differences might be explained by the different constraints related to resource distribution and the different permeability to movement of these two habitats. For instance, forests in our study sites are mostly dominated by beech (*Fagus sylvatica*) and fir (*Abies alba*), where the herbaceous strata may be poorly developed (Figure 1). Chamois may then adopt a browsing behaviour, i.e. performing many small-scale movements rather than the usual grazing behaviour they would display in open grass meadows (Tablado et al., 2016). The potentially reduced permeability of forests to chamois movement, as well as the limited size of forest patches, are also susceptible to play a role in individual decisions to favour small-scale displacements in this habitat. On the other side, northern slopes in our study area are typically characterized by alpine meadows interspersed with scree and rocky areas (Figure 1). As a result, chamois may perform larger-scale movement when travelling from one meadow to another in northern slopes.

As other capital breeders (Arnold, 2020), chamois indeed rely on fat reserves accumulated during spring and summer to face winter food scarcity and the increased energetic costs linked to gestation and lactation for females. In a context of more frequent heat waves and droughts due to global warming (IPCC, 2021), we can assume that time and energy costs allocated to behavioural thermoregulation during summer will keep increasing. Further work will now be needed to first determine whether the costs of behavioural thermoregulation (i.e. decreased forage quality and quantity, lost foraging opportunities, increase in costly relocation movements) may or may not outweigh the costs of acute exposure to heat stress (Conradie et al., 2019).

Importantly, we showed that opportunity loss related to behavioural thermoregulation was modulated by both differences in the local thermal/food landscapes, and individual age. Whilst individuals with higher access to thermal refuges may be able to more easily achieve thermoregulation, they may however have less access to forage than individuals living in home ranges with more open areas. Moreover, older individuals were the ones who experienced the lower opportunity costs related to behavioural thermoregulation, potentially due to their higher experience or their higher dominance rank. The energetic consequences of the variable tactics deployed by individuals to acquire resource while coping with high summer temperatures should thus also be explored, as they may lead to among individual heterogeneity in energy budgets, which could potentially translate into interindividual variability in survival or reproductive success.

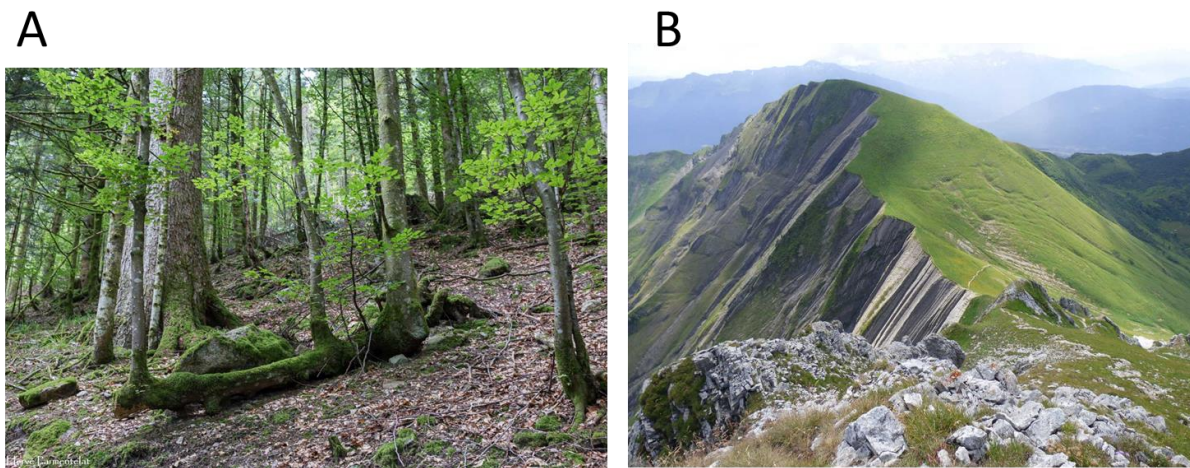


Figure 1: A) Fir-beech forest typically encountered on the lower elevations in our study sites. Note how the understory is poorly developed due to the important cover of fallen leaves. B) Northern (left) and southern (right) slopes of the Armenaz mountain. While southern slopes mostly consist in alpine meadows, these latter are interspersed with scree and rocky areas in the northern slopes.

2. Perspectives

Our results highlighted the need for combined studies investigating how individual behaviour, energetics and life-history may respond to increasing temperatures, within the constraints imposed by the local landscape context within individual home ranges and internal factors (e.g. sex, age, reproductive status). In the following paragraphs, we will discuss more exactly how these studies should allow to better predict individual and population-level responses of cold-adapted species to climate change.

a. Investigating the response of wild ungulates to climate change by more accurately describing individual thermal landscapes

Whilst the major threats to biodiversity are overexploitation, habitat loss and invasive species, climate change, interacting with these drivers, may become one of the principle causes of future species extinctions. Especially larger mammalian species may be among the most vulnerable to warming climate, mostly due to their difficulty or even inability to access thermal refuges (McCain & King, 2014). Consequently, many efforts have been made recently by researchers to predict the survival, range and abundance of species under different scenarios of future climate conditions (Rondinini & Visconti, 2015). More particularly, mechanistic models have been increasingly favoured by scientists due to their predictive power (Pacifci et al., 2015). To be successful however, these types of model require that the variables are included and parameterised properly (Mitchell et al., 2018).

Indeed, understanding how heat is exchanged between an individual and its environment, as well as how body temperature and other thermoregulatory variables respond to challenging thermal conditions, is necessary to accurately predict species responses to climate change. However, as stated by Mitchell et al. (2018) in their thorough review revisiting concepts of thermal physiology, the proper integration of principles of heat transfer and thermoregulation is “not always evident”. The authors indeed pointed out that predictive models often present diverse misconceptions related to concepts of thermal physiology in large mammals, such as heat exchange, evaporative loss, the thermal neutral zone, homeothermy or the role of size and shape. For instance, similarly to many other studies, we used in chapter 5 and 6 of this thesis, the ambient temperature and the availability of thermal refuges to investigate the influence of thermal conditions on the behavioural responses of our monitored chamois individuals. However, this approach may be biased as, for example, dry heat exchange between an individual and its environment is not primarily driven by air temperature, but mostly by radiation (Mitchell et al., 2018, Figure 2).

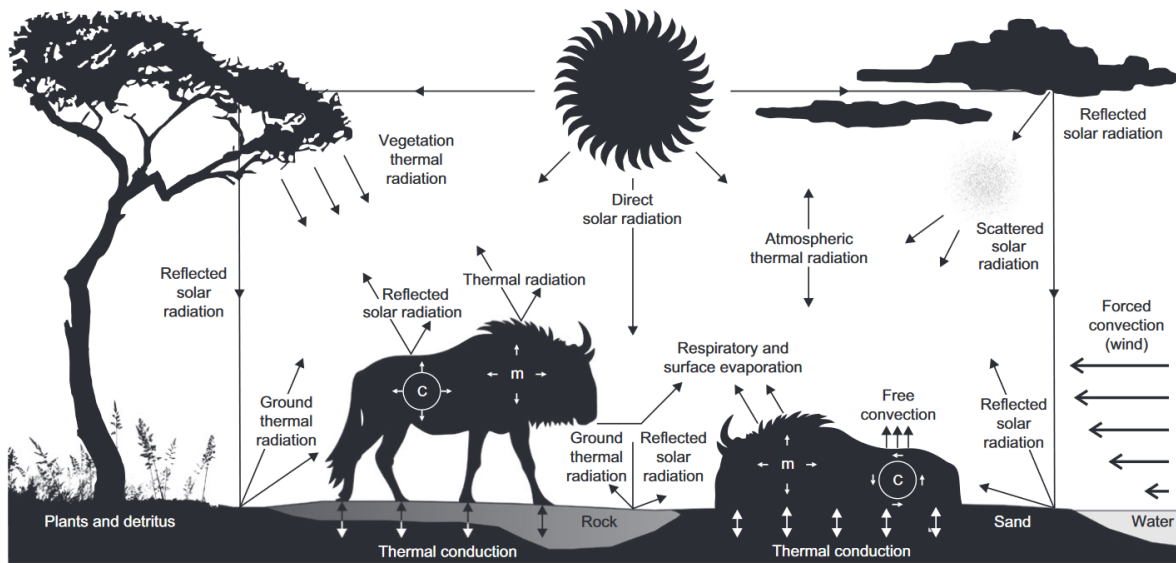


Figure 2: Avenues of heat transfer between mammals and their environment. The thermal status of a large mammal in its natural habitat usually is influenced by radiant heat exchange much more than by conductive and convective heat exchange. Entering the shade only partly removes a major component of radiant heat transfer because radiation penetrates the shade from multiple sources. Convection is the only heat exchange mechanism that depends directly on air temperature, but air temperature is the climate metric used almost ubiquitously in predictive models. Evaporative cooling is a powerful mechanism for dissipating metabolic heat and dry heat load, and is sustainable as long as water is available. Within a mammal, significant heat is produced by metabolism (m) and is transferred throughout the body by convection and a small conduction component (c). From Mitchell et al. (2018).

Other common misconceptions concern the role and sustainability of evaporative cooling and the overestimation of its energetic costs, the misinterpretation of the thermoneutral zone as a zone of thermal tolerance or sustainable energetics, or the failure to appreciate the potentially disadvantageous role of current animals' size and shape under future climate conditions. Consequently, while some predictive models may still be valid and valuable under inappropriate assumptions, future research needs to include appropriately the principles of thermal physiology to more accurately investigate the behavioural, spatial, survival and reproductive responses of large mammals under changing climate (Mitchell et al., 2018).

Particularly, accurately describing thermal environments is of prime importance, as it should allow us to quantify the spatial and temporal heterogeneity of thermal conditions. Indeed, the operative temperatures perceived by organisms may sensibly vary depending on landscape features, as thermal environments are highly influenced by topo-edaphic factors (e.g. soil, slopes, aspect, surface rock) and vegetation structure and cover (Elmore et al., 2017). As a consequence, individuals living in different parts of a given landscape may experience very different thermal landscapes and thus different thermal options, which are very likely to dictate the amount of suitable habitats for organisms (Rakowski et al., 2019; Tanner et al., 2017). In addition to spatial heterogeneity, thermal landscapes may also be temporally dynamic, as what

may constitute a thermal refuge at a given point in time may cease to be one at another time. Open areas for example may constitute thermal hotspots in summer during the hottest hours of the day, due to the high radiation load, whereas forests may be considered as thermal refuges (Olson et al., 2014). However, during night-time, open areas but may be used as a thermal refuge and forests a thermal hotspot as radiative heat may be more efficiently dispersed under an open sky than a canopy (McCann et al., 2016). A first avenue for improvement in our study could then be for instance the inclusion of solar radiation and wind conditions measured in different habitats at different period of the day and year, to obtain a more accurate estimation of the spatial and temporal variability of thermal conditions available to our monitored animals. In the end, this could provide use with a better understanding of the influence of thermal conditions on population demographic performance, as thermal landscape heterogeneity is likely to induce important variability in individual spatial and behavioural responses, eventually leading to individual fitness variations. We may for example first assess whether behavioural thermoregulation always carries opportunity costs in ungulates species. For example, it may likely be the case in populations of mountain ungulates like chamois or mouflon, which highly rely on grasslands for foraging but may depart and leave these habitats for shade when exposed to high temperatures. Inversely, as a browser species, roe deer heavily rely on forest to find food and they may be less impacted by opportunity costs linked to behavioural thermoregulation. Similarly, chamois and mouflon populations living in more heterogeneous thermal landscapes may for example be better able to achieve behavioural thermoregulation, as they may have access to more diverse thermal refuges than populations living exclusively in open areas, which on the other side may have access to better foraging conditions. We could then assess if the differences of thermal landscapes experienced by individuals and populations may lead to differences in behavioural tactics and eventually to variability in individuals' fitness and in population dynamics.

Finally, while investigating the role of spatial and temporal heterogeneity of thermal conditions is therefore critical to understand how changing climate will influence population demographics and distribution, an additional complexity comes from animals' thermal physiology. Indeed, each species and individuals present different shape, size, morphology, integument (e.g. skin, fur, feathers), metabolic heat production and thermoregulatory responses (e.g. evapotranspiration like sweating and panting), which also drives heat exchanges between animals and their environment (Elmore et al., 2017; Fuller et al., 2016). These are likely to induce additional inter- and intra-species variability in susceptibility to climate change. Indeed, as each species and individuals also display different metabolic requirements, the strategies they may deploy, to address the increasingly important challenge of acquiring food, escaping

predation and being thermally balanced at the same time (Veldhuis et al., 2019), might be quite diverse, which could potentially result in individual-level variations in performance and population-level variations in demographic parameters and distribution. In this regard, mechanistic niche models may represent promising avenues, as they rely on functional traits (e.g. morphology, physiology, behaviour) and spatial habitat data (e.g. climate, vegetation cover, topography) to assess individual fitness (Pacifci et al., 2015). As a result, they are considered to give a better approximation of climatic niche in which an organism can exist, revealing thereby areas and habitats which are or will become suitable or not for them (Pacifci et al., 2015). The modelling tools developed in the *NicheMapR* package for example, allow to tackle this challenge by calculating at the same time species and individuals' microclimate, heat and water exchange as well as their dynamic energy budget (Kearney et al., 2021). However, the important amount of detailed data on species' functional traits and spatial habitat required to run these models, and the fact that most of them do not account for biotic interactions, may preclude their extensive application and call for the use of combined methods (see the review of Pacifci et al., 2015).

b. Accessing animals fine-scale behavioural and energy budgets to predict individuals' responses to climate change

Along with morphology, physiology, or phenology, behaviour is a key functional trait, i.e. an “attribute of an organism that influences fitness, their responses to the environment and ecosystem processes” (García-Llamas et al., 2019). Investigating the link between behaviour and individual performance has therefore been one of the main priorities for behavioural ecologists. However, studying animal behaviour in the wild has long been a human and technical challenge. The main hurdle so far has been the possibility to observe animals and monitor physiological proxies across contrasted environmental situations in the wild on extended period of times. However, the combination of recent innovative technologies to track animals (GPS and biologgers, Wilmers et al., 2015), powerful computer capability to process big data, and novel statistical methods (Demšar et al., 2015), are now allowing tackling questions linking small scale behaviours, physiological proxies, and movement to spatial population processes that were previously beyond our capacity to investigate in the wild (Kays et al., 2015).

Various methods of behavioural classification using data derived from remote sensing technologies (typically GPS trajectories and associated activity data) can be found in the literature (e.g. decision trees, linear discriminant analysis or template-matching), each with various advantages and disadvantages (Resheff et al. 2014). Many of these methods however failed to take in account the temporal sequencing of data (Wilson et al. 2018), treating each data points as if it is independent from previous and next points, which could result in a biased classification, as time-series data like GPS locations and activity measures are known to show strong spatio-temporal autocorrelation. Besides, many studies have for example been using activity data to classify animals' behavioural states into solely being active or inactive. While this has proved efficient to study animals' daily, seasonal and annual activity rhythms (Bourgoin et al., 2008; Carnevali et al., 2016; Marchand et al., 2015), this however gives a rather coarse approximation of individuals' behavioural states.

On another side, state-space models (Beyer et al., 2013; Morales et al., 2004), and notably Hidden Markov Models, have been gaining an important popularity among movement ecologists (McClintock et al., 2020), for their ability to adequately model animal movement as a state-dependent process, i.e. a time series of states, where each of them may be defined by a set of movement parameters extracted from trajectory-derived metrics (e.g. step lengths and angle concentration typically). This modelling techniques allowed us for instance to go beyond the “classic” dichotomous inactive/active behavioural classification, by inferring movement modes of individuals, that we assumed constituted proxies of biologically relevant behavioural states, i.e. resting/ruminating, foraging and relocating (eg. Beumer et al., 2020). We remain aware that caution is needed when interpreting our results, as states found using the HMM approach on telemetry data, are only proxies of animals underlying true behaviours. Due to the 20 min resolution of our data, it is very likely that a lot of animals' behaviours may go “under the radar” and this is why the inclusion of fine-scaled data from biologging technologies represent exciting opportunities to access and study refined version of animals' behavioural budgets.

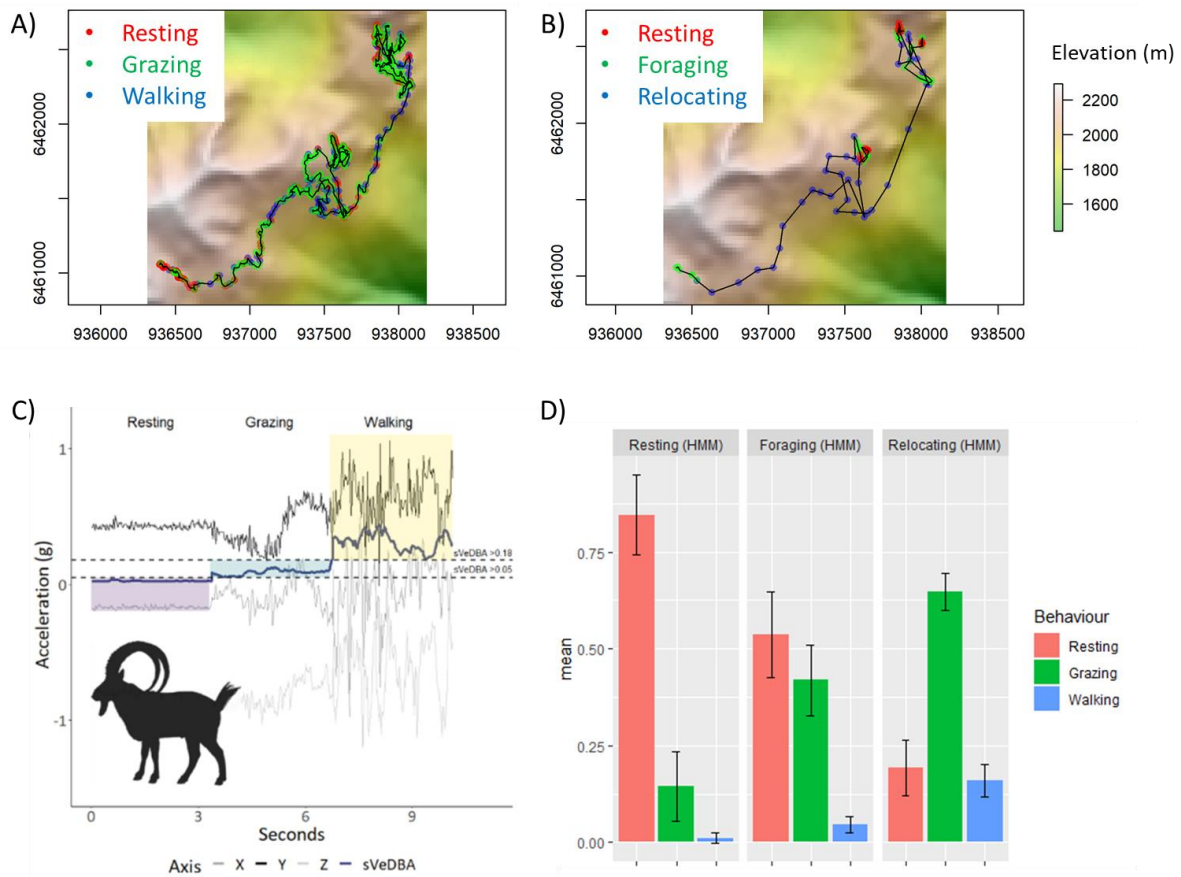


Figure 3: (A) A dead-reckoned path (here subsampled at 1 location/min, courtesy of James Redcliffe) of an ibex path monitored in the Massif de Belledonne in summer 2017 (from June 2nd 03:40 UTC to June 3th 12:40). Dead-reckoning between GPS fixes was achieved using accelerometers (20 Hz recording frequency) and magnetometer (8 Hz recording frequency) to derive animal Vectorial Dynamic Body Acceleration (VeDBA) and heading with respect to magnetic North (subsequently corrected to true North). From Redcliffe (2021). (B) The same path subsampled at 1 location/20 min to which we apply a Hidden Markov Model with 3 latent states supposed to be proxies of Resting, Foraging and Relocating Behaviour. (C) Smoothed VeDBA (sVeDBA, VeDBA smoothed over 40 events, i.e. 2s of recording) was also used to derive ibex behaviours via a classification method using 2 sVeDBA thresholds (appearing in dashline, resting: $\leq 0.05g$, grazing: $>0.05g \ \& \ \leq 0.18g$, walking: $> 0.18g$). (D) Comparison between classification using sVeDBA and Hidden Markov Models (HMM). Results show for each movement mode found in the HMM, its mean relative composition in terms of behaviours found in the classification using sVeDBA for 6 monitored ibexes in summer 2017. For instance, we can observe that on average, 84.6% of the resting mode in our HMM classification is represented by the resting mode in the sVeDBA classification, 14.4% by the grazing mode and 1% by the walking mode. Interestingly, the foraging mode in our HMM classification is, in addition to grazing behaviour, also highly represented by resting behaviours from the sVeDBA classification. On another side, the relocating mode in our HMM classification mainly consisted in grazing, while also being the mode where walking was the most important. A potential interpretation of these results could be that animals may have in reality two foraging modes: an intensive one (foraging in our HMM classification) where animals spent more time within each patch and less time travelling between them, similar to what is often called area-restricted search in the literature (Dorfman et al., 2022), and an extensive foraging mode, where they spent less time within each patch and more time travelling between them and searching food items while on the go.

Indeed, during the last decade, the ceaseless increase in the use animal-borne sensors recording simultaneously multiple data streams on individuals' movement path (e.g. accelerometry,

magnetometry, pressure, ambient temperature), paired with fine-scale environmental data (e.g. vegetation composition, phenology and structure, topography, climatic conditions), have proved efficient into answering new questions about the foraging, migration, habitat selection, physiological performance, energetics, and sociality of wild animals (Wilmers et al., 2015). The use of tri-axial acceleration data for instance, in combination with classification models has been shown to be very valuable for behavioural ecologists and ecophysiologicals, because of its ability to provide accurate description of animals' behaviours (Shepard et al., 2008; Tatler et al., 2018; Wilson et al., 2018, Figure 3) and associated energy expenditure (i.e. the "energy landscape", Shepard et al., 2013). When applied to our monitored ungulates' populations, these methods could provide more accurate estimates of the total spent by individuals eating and ruminating, as well as their total daily costs of transport (e.g. measures of Vectorial or Overall Dynamic Body Acceleration, Gleiss et al., 2011). Coupled with fine-scale maps of resources quality and quantity, as well as topography and vegetation structure and composition, we would then be able to investigate how these environmental factors may influence individuals' energy acquisition and expenditure.

In the end, all of the information about individuals' energy dynamics may be highly valuable as it should allow us to implement dynamic energy budget individual-based models (DEB-IBMs). Briefly said, DEB-IBM offers a theoretical framework that link all together individuals' performance to their spatial behaviour, energy dynamics and habitat heterogeneity, using information about individuals' movements, habitat use, behavioural budget, energy acquisition and expenditure and individuals' survival and reproductive success (Figure 4). As a result, DEB-IBM has been increasingly used by behavioural and ecophysiologicals, as it offers a powerful approach to predict how individuals and population would perform in changing environments, via linking behaviour and physiology (Chimienti et al., 2020). The implementation of these models may however still be quite challenging, as it requires to recapture individuals several times to monitor their lifetime variations of spatial behaviours, body condition, fecundity or reproductive success, which is very rare in our chamois population but more frequent in our roe deer and mouflon populations.

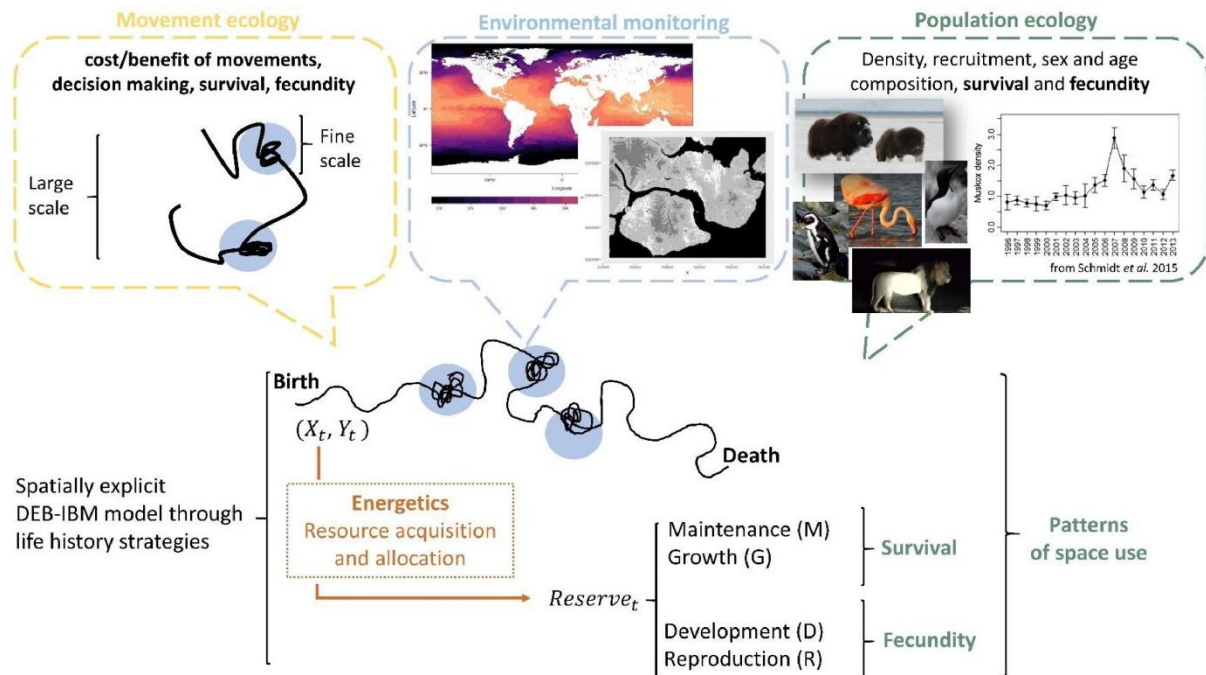


Figure 4: General framework linking individual processes to population dynamics. Input data (dashed boxes): movement data collected with bio-logging technology, providing high resolution information on individuals' movements, cost/benefits of different activities, animal decision making, information on survival and fecundity, environmental data and knowledge of the status and the dynamic of the population. By parameterizing spatially explicit Dynamic Energy Budget (DEB) – Individual Based Models (IBM), the theoretical framework integrates movements, habitat heterogeneity as well as energy acquisition and allocation throughout the life time of individuals constituting populations. The DEB part of the model, allocates reserves (core of the model, dotted box) for maintenance (M), Growth (G), Development (D) and Reproduction (R) estimating individual survival and fecundity (outputs). Together with the IBM part, the framework also estimates patterns of space use of individuals that can be validated against data collected during population monitoring programs. The framework is applicable to any species for which such data are available. From Chimienti et al. (2020)

c. Taking in account the landscapes of interactions: predation, disturbance and competition

While individuals may roam more or less freely in their environment to address their different needs, they also have to share their landscape with conspecifics and other species, which may represent for them competitors or predators. Escaping predation or human disturbance for instance, represents a major constraint for small and medium-sized ungulates species, directly influencing their behaviour (Laundre et al., 2010). Depending on species and the local context (e.g. predator abundance, availability of escape routes and refuges), individuals may for example shift their activity during periods where predator or human activity may be minimal, or select habitats which offer a lower perceived risk of predation (Bonnot et al., 2013; Hebblewhite & Merrill, 2009). In the case of our studies on chamois habitat use and behavioural

budgets, it is for instance very likely that the hottest days also represented the sunniest ones and thus the days with the most human frequentation. Hence, chamois' departure from open areas to thermal refuges may then also represent chamois escaping human hiking disturbance (e.g. Courbin et al., 2022). As a result, we might wonder if chamois uses forests and northern slopes more as refuges against challenging thermal conditions, human disturbance or both. Recent work by Thel et al. (in prep), suggested that chamois activity may be driven by both of these variables, while the authors yet also highlighted that individuals responded more extensively to temperature than human disturbance. In any case, these results advocate for the inclusion of accurate estimates of human disturbances in future studies, in order to tell apart any confounding effects with thermal conditions. Equipping hikers with GPS trackers could for instance represent an effective avenue to quantify the spatial and temporal disturbance they may exert (e.g. Marion et al., 2021).

In addition to predation or human disturbance, individuals may also face an additional pressure from competition with other conspecifics or species which uses the same resources (Corlatti et al., 2019; Ferretti et al., 2015; Latham, 1999). Competition between organism may either occur indirectly via the depletion of patches' resources limiting the personal forage acquisition of both competitors (exploitative competition), or via direct interactions such as the display of aggressive behaviours typically (interference competition, Latham, 1999). In chapter 6, we for instance showed important differences between older and younger female chamois in terms of access to forage. Older females may first be more experienced and thus be abler or "competitive" than younger females, at locating food patches, or during the hottest days, thermal refuges which offer greater forage availability. Alternatively, the greater reduction in forage quantity seen in prime-aged females on the hottest days may be related to older females' dominance behaviours, which may prevent younger females from taking advantage of patches that offer the best balance of forage availability and thermal conditions, which could constitute a case of interference competition. (Fattorini et al., 2018). Further research investigating how females' spatial behaviours are related to their age, as well as the presence of conspecifics of varying ages, is thus required to disentangle the influence of experience, and dominance (Figure 5, the "landscape of rage", Redcliffe, 2021)., on chamois spatial ecology and energy acquisition, especially in a context of global warming where the earlier green-up and senescence of vegetation may accentuate the effects of competition. This is all the more important given that the age-related differences in energy acquisition, either related to experience or dominance, may lead to age-structured heterogeneity in survival and reproductive success (Weladji et al., 2006), with potentially cascading consequences on population dynamics (Gaillard et al., 2000).

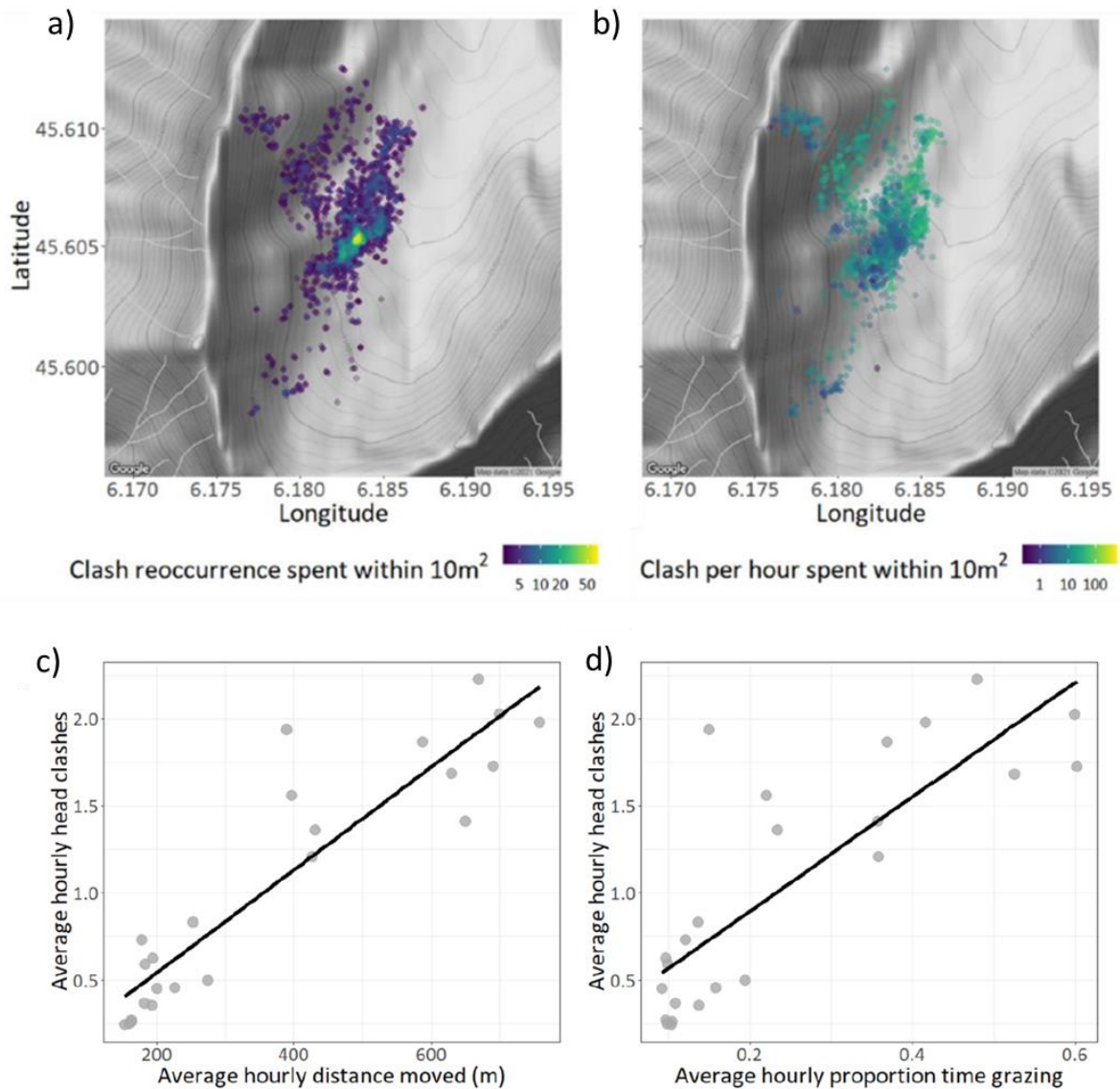


Figure 5: Mapped head clash behaviours of domestic goats, with each behaviour location coloured by (a) the number of reoccurrences to show density (with reoccurrences being defined as two or more incidences of head-clashing within 10 m² of one another) and (b) clashes per hour spent per location (with time spent being defined from 1 Hz location data within 10 m² of one another). (c) Scatter-plot of mean hourly head-clashes across all individuals against average hourly distance moved across all individuals (calculated from the dead-reckoned path); (d)- Scatter-plot of average hourly head-clashes across all individuals against the average hourly proportion of time spent grazing across all individuals. Data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within les Bauges, France. While the majority of head clashes occurred in the goat pen during the whole study (a), at the hourly scale (b), most clashes occurred at the edges of the goats foraging range, where the vegetation quality may also be highest, being least grazed. As head clashes frequency also increased with distance moved (c) and time spent grazing by goats (d), the author argues that head clashes in the edges of goat ranges may indeed likely be related to interference competition for higher resources. From Redcliffe (2021).

3. Conclusion

Our understanding of animal movement is grounded in optimal foraging theory and has long been driven by the food-risk avoidance trade-off: if they are to maximize their fitness, animals should maximise their energy acquisition while minimizing the time they spent at risk. This is of course an oversimplification, as animal movement is a complex process happening at various scales and constrained by numerous internal and external factors, such as the distribution of resources and risk, but also the distribution of conspecifics, weather conditions, movement costs or life history traits. While it is difficult to take all of these factors into account, the study of their potential interactions and relative influence on animal spatial behaviours, may provide us with valuable insights. This is what we attempted in this thesis work, notably by investigating how constraints related to age and to thermal conditions impacted animal spatial behaviours and behavioural budgets. Our study demonstrated that age and local thermal landscape constraints are major determinants of individual spatial behaviour, and their relative influence needs to be further explored. Future studies should aim to determine how individuals from different populations and living in different landscapes context may adopt different behavioural tactics in response to extreme temperatures, and how these tactics may impact individual fitness. A fine-scale description of the foodscape, the thermal landscape, the social landscape, as well as of behavioural and energetic budgets, could allow us to tackle questions like: What is the relative influence of each internal (e.g. sex, age) and external constraint on individual behavioural tactics? Are certain individuals, populations or even species, more constrained by forage availability, thermal refuge availability, predation or human disturbance? What is the range of tactics deployed by individuals, populations or species, to conciliate energy acquisition, avoidance of risk and competition and behavioural thermoregulation? What are the energetic consequences of these tactics, in terms of opportunity or movement costs for example, and what is their influence on individual fitness and population dynamics?

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Appendix

Research

Past, present and future of chamois science

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The chamois *Rupicapra* spp. is the most abundant mountain ungulate of Europe and the Near East, where it occurs as two species, the northern chamois *R. rupicapra* and the southern chamois *R. pyrenaica*. Here, we provide a state-of-the-art overview of research trends and the most challenging issues in chamois research and conservation, focusing on taxonomy and systematics, genetics, life history, ecology and behavior, physiology and disease, management and conservation. Research on *Rupicapra* has a longstanding history and has contributed substantially to the biological and ecological knowledge of mountain ungulates. Although the number of publications on this genus has markedly increased over the past two decades, major differences persist with respect to knowledge of species and subspecies, with research mostly focusing on the Alpine chamois *R. r. rupicapra* and, to a lesser extent, the Pyrenean chamois *R. p. pyrenaica*. In addition, a scarcity of replicate studies of populations of different subspecies and/or geographic areas limits the advancement of chamois science. Since environmental heterogeneity impacts behavioral, physiological and life history traits, understanding the underlying processes would be of great value from both an evolutionary and conservation/management standpoint, especially in the light of ongoing climatic change. Substantial contributions to this challenge may derive from a quantitative assessment of reproductive success, investigation of fine-scale foraging patterns, and a mechanistic understanding of disease outbreak and resilience. For improving conservation status, resolving taxonomic disputes, identifying subspecies hybridization, assessing the impact of hunting and establishing reliable methods of abundance estimation are of primary concern. Despite being one of the most well-known mountain ungulates, substantial field efforts to collect paleontological, behavioral, ecological, morphological, physiological and genetic data on different populations and subspecies are still needed to ensure a successful future for chamois research and conservation.

Keywords: behavior, conservation, ecology, genetics, life history, *Rupicapra*, taxonomy, wildlife diseases

Background

The chamois *Rupicapra* spp. is a member of the family Bovidae, subfamily Caprinae, which includes species adapted to mountainous environments. The subfamily may be further divided into different tribes, depending on the classification system (cf. Simpson 1945, Hassanin et al. 2009); however, the taxonomy of mountain ungulates remains largely unsolved. Irrespective of classification subtleties, mountain ungulates inhabit areas that make them particularly susceptible to environmental variations due to, e.g. land use and climate change. Among the Caprinae species, however, the chamois possibly shows the highest behavioral plasticity, which has allowed the genus to occupy a vast area, making it one of the most iconic mammals inhabiting the mountainous regions of Europe and the Near East, as well as an intriguing species for ecological investigations.

Currently, the most accepted classification, based on a combination of morphometric, genetic and behavioral characteristics, considers two species: the northern chamois *R. rupicapra* and the southern chamois *R. pyrenaica* that are further subdivided into seven (*cartusiana*, *rupicapra*, *balcanica*, *tatica*, *carpatica*, *caucasica* and *asiatica*) and three (*ornata*, *parva* and *pyrenaica*) subspecies, respectively (cf. Masini and Lovari 1988, Corlatti et al. 2011). The most abundant subspecies, the Alpine chamois *R. r. rupicapra*, is distributed throughout the Alps and is assessed as least concern by the IUCN. Most other subspecies are only present in limited areas where they face several threats, including poaching, overhunting, human disturbance, competition with livestock, habitat loss and degradation, infectious diseases, hybridization with introduced individuals of other subspecies, and climate change. Addressing these conservation issues relies not only on available knowledge of chamois biology, but also on the identification of future research priorities. A recent review of chamois biology is available in Corlatti et al. (2022a), while

conservation status of both species has been recently assessed by Herrero et al. (2020) and Anderwald et al. (2021); however, to date, the literature lacks compelling insights into future research challenges. In this paper, experts from across Europe outline the state of chamois science, as discussed at the 3rd *Rupicapra* Symposium held online from Makarska (Croatia) in 16–18 June 2021, focusing on research trends and on key aspects of taxonomy and systematics, genetics, life history, ecology and behavior, physiology and disease, management and conservation. The goal of this communication is to provide a state-of-the-art overview of research trends, as well as the most challenging issues in chamois research and conservation.

Research trends

The study of chamois has a longstanding history. Much of our current knowledge is owed to the pioneering work of Camerano (1914), Couturier (1938), Krämer (1969) and Schröder (1971), among others. Since then, research activity has flourished, greatly increasing our understanding of the biology of chamois species and subspecies. Research contributions, however, are not evenly distributed over time and across taxa. As Fig. 1 shows, the number of peer-reviewed scientific articles focusing on chamois has increased markedly over the past 40 years, with a 273% increase after the year 2000 and has stabilized since 2010, for a total of 756 publications (see Supporting information for the list of publications, and for a description of the methodological approach to data collection and analysis).

With respect to the trend in the number of chamois publications in proportion to those on Caprinae, publications increased more rapidly for chamois than for mountain ungulates as a whole, and chamois publications accounted for 16% of all Caprinae publications in the study period (Fig. 2).

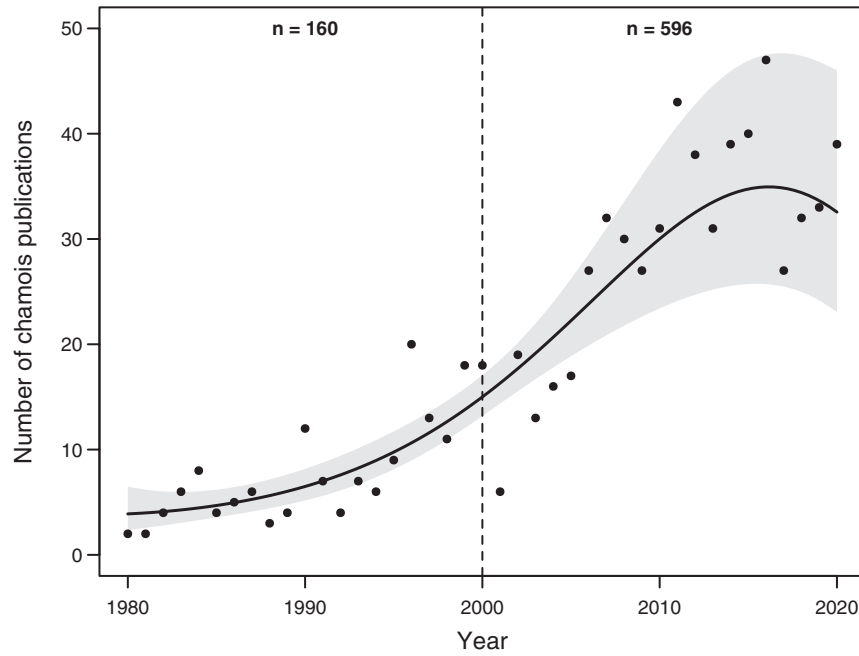


Figure 1. Number of peer-reviewed publications on chamois *Rupicapra* spp., between 1980 and 2020. The fitted line shows the expected response of a 3rd level polynomial autoregressive Poisson model; the shaded area indicates the 95% confidence level. The dashed line separates the first from the last two decades (midyear 2000 used as midpoint).

Major biases emerged in the number of publications when species and subspecies were taken into account, although these broadly reflect the relative abundance of each species/subspecies (cf. abundance data in Corlatti et al. 2022a). About 80% of all chamois publications between 1980 and 2020

mentioned the northern chamois *R. rupicapra* (n=608), while the southern chamois *R. pyrenaica* was mentioned in only 28% (n=208). Differences were even more evident when considering subspecies. For the same time frame, only 8.2% (n=50) of the publications on the northern

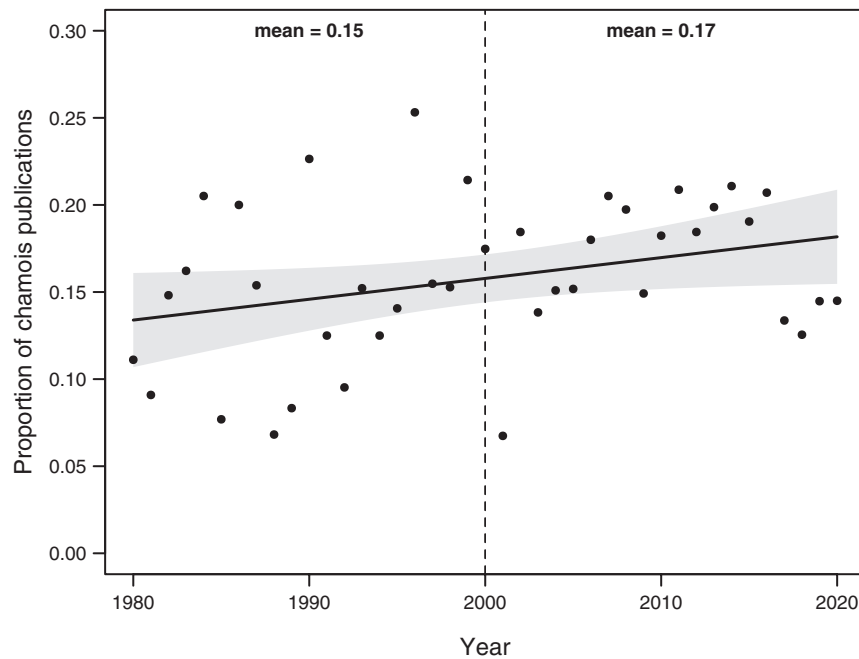


Figure 2. Proportion of publications on chamois with respect to publications on all Caprinae species, between 1980 and 2020. The fitted line shows the expected response of a Gaussian linear model; the shaded area shows the 95% confidence level. The dashed line separates the first from the last two decades.

chamois considered subspecies other than the Alpine one, i.e. *R. r. cartusiana* = 0.5% (n = 3), *R. r. tatrica* = 3.6% (n = 22), *R. r. carpatica* = 0.2% (n = 1), *R. r. balcanica* = 2.3% (n = 14), *R. r. asiatica* = 0.3% (n = 2), *R. r. caucasica* = 1.3% (n = 8). The situation appears more balanced for the southern chamois subspecies, with *R. p. parva* and *R. p. ornata* accounting for 27.9% (n = 58) of all *pyrenaica* publications, or 12.0% (n = 25) and 15.9% (n = 33), respectively).

When analyzed by topic, we found that veterinary sciences have clearly dominated chamois research in the last four decades, involving about one third of all publications (Table 1). Genetics, behavior and life history also accounted for a large proportion (in total, over 50%) of the *Rupicapra* literature. Taxonomy and systematics were the least studied (ca 4%), although the low percentages for movement ecology and population dynamics (ca 9 and 6%, respectively) were perhaps even more surprising, given the importance of these disciplines for management and conservation (a topic mentioned explicitly in 17% of publications). However, in the recent *Rupicapra* symposium, these values were much different: of the 49 contributions, only about 10% concerned genetics, taxonomy and systematics (n = 5), while life history, ecology and behavior had the highest number of contributions (39% (n = 19)); physiology and disease covered 24% (n = 12), and management and conservation, 27% (n = 13).

The state-of-the-art knowledge and knowledge gaps for each topic illustrated in Table 1 are described in greater detail in the following sections. Emphasis is on the main challenges for the future of chamois research and conservation, and only the most recent and/or relevant articles are cited.

Taxonomy and systematics

Chamois taxonomy and systematics have been continuously revised since the beginning of the 20th century. Over the years, authorities such as Neumann, Lydekker, Camerano and Couturier expressed different views about the taxonomic status of *Rupicapra*, supporting classifications based on morphology for one, two or even three distinct species (cf.

Corlati et al. 2022a). Much of the current taxonomy is owed to the works of Lovari and Scala (1980) and Nascetti et al. (1985), that, based on morphometric and electrophoretic data, support a subdivision into two species: the southern chamois *R. pyrenaica*, and the more recent northern chamois *R. rupicapra*. These species colonized Europe in successive waves, possibly from eastern Europe (Masini and Lovari 1988). The debate was reignited with the advent of molecular methods: initial phylogenies based on mitochondrial DNA revealed not two, but three very old clades (from the early Pleistocene, 1.9 Mya) with a clear geographic signal (Crestanello et al. 2009, Rodríguez et al. 2009), one for each of the morphological species. Nuclear markers (e.g. microsatellites, melanocortin-1 receptor gene, introns) also clustered populations into three groups, but these groups did not align in a simple way with mitochondrial lineages. Pérez et al. (2017) suggested that the patterns of differentiation for various molecular markers in chamois are best explained as reticulate evolution. Recent analyses of complete mitochondrial genomes (Iacolina et al. 2021) supported the subdivision into three clades: two corresponding to the classical species *R. pyrenaica* and *R. rupicapra*, and a third including the subspecies *R. p. ornata* and *R. r. cartusiana*.

This long-lasting controversy raises the question of whether chamois taxonomy will ever be resolved. Although most of the recent literature relies on the use of molecular tools, the inconsistencies in the molecular systematics outlined above suggest that analysis of a limited number of markers will not suffice to solve this issue in chamois. Phylogeny and phylogeography derived from a single marker gene, protein sequence and non-coding regions reflect only the evolution of that particular DNA segment. Consequently, the use of a single or several markers has led to problems of interpretation, since other chamois genes may have different rates of evolution, and different genes accumulate mutations at different rates. Phylogenetic analysis comparing results from modern and ancient specimens could help to map the complex evolutionary history of chamois by better estimating mutation rates for different markers; in addition, genomic analyses of a representative number of individuals from each subspecies will likely improve our understanding (see next

Table 1. Chamois publications by topic from 1980 to 2020. The search statement used for each topic and the percentage (with absolute number in parentheses) of publications by topic with respect to the total number of *Rupicapra* publications (n = 756) are indicated. Percentages sum to > 100% and numbers to > 756 because the same publications may be tagged under multiple topics.

Topic	Search statement	% of all chamois publications
Taxonomy and systematics	'rupicapra' AND 'taxonomy' OR 'systematics'	4.1 (n = 31)
Genetics	'rupicapra' AND 'genetic' OR 'DNA'	20.5 (n = 155)
Life history	'rupicapra' AND 'growth' OR 'reproduction' OR 'survival'	13.4 (n = 101)
Ecology and behavior	'rupicapra' AND 'population dynamics'	6.0 (n = 45)
	'rupicapra' AND 'predation' OR 'competition'	10.1 (n = 76)
	'rupicapra' AND 'behavior' OR 'mating' OR 'social'	18.0 (n = 136)
	'rupicapra' AND 'diet' OR 'foraging'	9.9 (n = 75)
	'rupicapra' AND 'home range' OR 'movement' OR 'dispersal' OR 'habitat selection'	9.4 (n = 71)
Physiology and disease	'rupicapra' AND 'physiology' OR 'disease' OR 'parasites'	36.5 (n = 276)
Conservation and management	'rupicapra' AND 'conservation' OR 'protection' OR 'management'	16.8 (n = 127)

section). To support taxonomics below the species level, however, a clearer understanding of chamois evolutionary history is needed, but this will require contributions from other fields of research such as paleontology, morphology and behavior.

Notably, despite its importance for elucidating the evolutionary history of chamois, no paleontological research was presented or discussed during the third chamois meeting, although ancient DNA studies are ongoing. The earliest fossil of chamois dates back to some 800 000 years ago, in eastern Europe, but the species remains unidentified (Fernandez and Crégut 2007); therefore, it is likely that the chamois has been present in eastern Europe from the end of the Early Pleistocene. Instead, the oldest fossil associated with *R. pyrenaica*, from the southern French Pyrenees, is 440 000 years old (Rivals 2004). Therefore, although the two extant species were both in Europe at the beginning of the Würm glaciations, the northern chamois failed to colonize the southernmost areas, making them a refuge for the southern species (Masini and Lovari 1988). More paleontological material is needed to clarify the evolutionary history of the chamois, and of mountain ungulates in general, a challenging task limited by the scarcity of fossil records in mountains (Schaller 1977).

In conclusion, although taxonomy is often considered particularly relevant to chamois population management, and large-scale decision making would undoubtedly benefit from a well-defined taxonomic classification, we caution against relying on interpretations drawn from individual tools, either behavioral, morphological, paleontological or genetic/genomic, as results are intrinsically probabilistic, and partial at best. Furthermore, regardless of the taxonomic status assigned, we suggest the value of single chamois populations should be also assessed at the historical and conservation levels (Corlatti et al. 2011).

Genetics

Various neutral molecular markers (mitochondrial genes, microsatellite markers, sex-determining Y genes) have been

used to study phylogeny, population genetic structure, hybridization, demographic history and local adaptation in chamois. Traditional neutral markers (such as microsatellites) indicate that the Alpine chamois *R. r. rupicapra* has high values of genetic diversity for almost all markers analyzed, while the Apennine chamois *R. p. ornata* shows an extremely low level of genetic diversity; most other chamois subspecies show intermediate values. More recently, coding regions (e.g. major histocompatibility complex, MHC) and the simultaneous analysis of a large number of genomic markers (single nucleotide polymorphisms, SNPs) have been used to gain more detailed insight into the adaptive genetic diversity and evolutionary potential of the species (Pérez et al. 2014).

Application of recent advances in genomic technologies could provide even more valuable information. For example, given the ongoing taxonomic controversies mentioned in the previous section, combining available data with the analysis of whole genomes could give us a better understanding of the evolutionary relationships within the genus *Rupicapra* (Fig. 3). In addition, non-invasive genetic monitoring of chamois using environmental DNA (eDNA, e.g. feces, urine, hair, etc.) could be used to establish and monitor management and conservation units and to provide the basis for decisions concerning the maintenance of chamois evolutionary potential. Finally, the genetic analysis of ancient samples (e.g. whole mtDNA sequencing) would enable the evaluation of genetic loss and changes over time associated with population dynamics and evolutionary processes.

Genetic and genomic methods should also be applied to determine the impact of human-induced changes in climate and land use on chamois populations, as these are likely to be complex and involve multiple biotic and abiotic factors (Vitasse et al. 2021). For example, adaptation to shifts in vegetation and changing interspecific interactions can be studied through diet, traditionally analyzed from field observation or through microscopical analysis of fecal pellets or stomach contents. However, the simultaneous taxonomic identification of all dietary items can now be performed using DNA extracted from fresh fecal pellets (through ‘metabarcoding’ or ‘metataxonomics’). Similarly, the effect of dietary, behavioral or environmental changes on health can be implied through

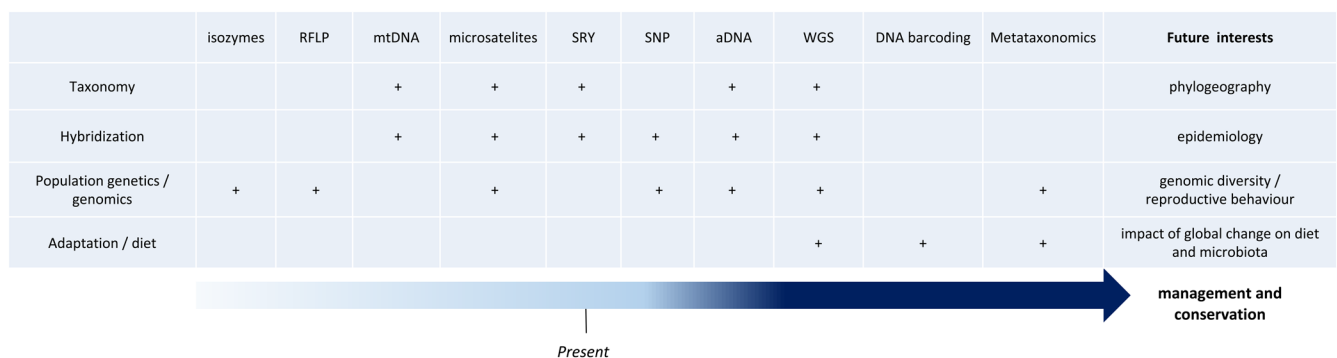


Figure 3. Flowchart linking management and conservation issues relevant to chamois that can be addressed using molecular markers and approaches (currently available or under development) and their potential future applications.

the study of the gut microbiota (e.g. helminths) and microbiota composition (bacteria, fungi and viruses). Changes in the microbiota are known to influence an individual's ability to adapt to alterations in the environment with consequent implications on health, survival and possibly fitness (Hauffe and Barelli 2019).

Technological advances in conservation genomics now make it possible to answer new and relevant questions, such as 'Which genes are under selection?', 'What are the genes associated with specific traits?', 'Are these changes associated with adaptation or other natural processes?'. In fact, high quality genome-scale data could increase the precision of traditional parameters such as genetic diversity, mutation rate and effective population size, provide better understanding of the mechanisms that allow chamois to adapt to a changing environment, as well as improve species conservation efforts.

In addition, whole genome technologies could clarify the impact of hybridization on conservation status, since hybridization between species or subspecies, resulting from legal and illegal translocations of chamois, could lead to the loss of local adaptation to particular niches. Despite awareness of this risk for over a decade (Crestanello et al. 2009), evidence of recent hybridization has only been reported between different subspecies of *R. rupicapra* in regions where chamois have been introduced for hunting purposes (reviewed by Iacolina et al. 2019), even though hybridization between other chamois taxa is suspected. Therefore, cases of hybridization in chamois should be identified and their consequences monitored, possibly using whole genome studies to distinguish gene introgression from hybridization.

Genetic and genomic markers are powerful tools for answering many management questions, and may be more cost effective and rapid than intensive field work. Wildlife practitioners should be made aware of the availability of different markers and approaches, the questions that can be answered, and the type and number of samples required for their application, as well as costs, so that these tools can be applied effectively, keeping in mind that for some management questions traditional markers/approaches will still be more efficient.

Life history

Research on chamois life history traits is mainly limited to the Alpine subspecies *R. r. rupicapra* and, to a lesser extent, the Pyrenean chamois *R. p. pyrenaica*. Further efforts are needed to answer several open questions on growth, reproduction and survival. Chamois of all subspecies are nearly monomorphic, with the notable exception of a seasonal sexual dimorphism in body mass just before the rut in late autumn, when males are notably heavier than females (Rughetti and Festa-Bianchet 2011). The evolutionary meaning of this dimorphism is unclear, but it may indicate a high investment in male–male mating competition, allowing adult males to lose more than 15% of their body mass during the rut, while maximizing their probability of overwinter survival

(cf. Ferretti et al. 2014, Apollonio et al. 2020). Interestingly, the extent of mass loss during the rut is age- and site-specific (Mason et al. 2011); therefore, it would be worth investigating how environmental heterogeneity influences sex- and age-specific patterns of body mass, and how mass is associated with the opportunity for sexual selection (below) and the probability of survival. Increasing evidence for ecological plasticity in chamois (Reiner et al. 2021) also raises the question of species-specific resilience towards climate and other environmental changes. While a decline in body mass with increasing summer temperature has been reported, the response may be conditional on the possibility of choosing habitats where it may be possible to overcome the negative effects of increasing temperatures, as in the case of open alpine areas versus forests (Reiner et al. 2021). Alongside the opportunity to investigate site-specific variations in compensatory growth (Rughetti and Festa-Bianchet 2010) and its possible trade-off with reproductive success and survival, the effects of body mass variations is one of the most promising research areas, as it has obvious evolutionary relevance, and should be analyzed from morphological, behavioral and physiological perspectives.

The intense competition among males during the rut, and their significant loss in body mass, would suggest a high level of polygyny, yet there appears to be a low level of this reproductive strategy (Corlatti et al. 2015a). Thus far, however, no conclusive data have been collected; as for most other Caprinae, variance in male reproductive success is unknown and consequently, the level of polygyny of chamois is still debated. The degree of polygyny can be quantified through the intensity of sexual selection on males, I_m , the variance in male reproductive success divided by the square of the mean reproductive success (Arnold and Wade 1984). As shown in other ungulate species, behavioral and genetic I_m often differ from each other, and this may be particularly true for bovids, where copulations can be repeated, and ejaculations are not obvious. Consequently, future studies should combine the collection of observational data from marked populations with genetically determined paternity data (even though sampling most kid-mother dyads and all potential fathers may be difficult) since the usefulness of I_m is critical both from an evolutionary and applied perspective, as knowledge of this parameter could improve management of hunted populations, where the age–sex structure is often skewed towards younger individuals and females. Variation occurs not only between, but also within mating systems: alternative male mating tactics in chamois – territorial and non-territorial – have been widely studied (von Hardenberg et al. 2000, Corlatti et al. 2012a), but some fundamental questions remain. For example, while other mountain ungulates may switch tactics in adverse environmental and climatic conditions, e.g. with deep snow cover (Alpine ibex *Capra ibex*: Apollonio et al. 2013), in chamois the adoption of a given tactic appears less flexible, though its benefits and costs can change with weather stochasticity (Corlatti et al. 2020). The mechanisms allowing the coexistence of alternative tactics, however, are still largely unknown. For example, it is unclear

whether such tactics are frequency-dependent or, as shown in other mountain ungulates, condition-dependent and if so, whether they reflect individual characteristics, or specific exogenous conditions. More generally, a more comprehensive evaluation of the role of environmental factors on the chamois mating system is needed, including the influence of the environment (e.g. open alpine areas versus forests), as observed in other ungulate species with mating system polymorphism, such as fallow deer *Dama dama* (Thirgood 1991).

Although there is increasing evidence of unbiased sex-specific survival (Gonzalez and Crampe 2001, Bocci et al. 2010, Corlatti et al. 2012b), for many subspecies this information is completely unknown. Furthermore, the pattern of age-specific survival in both sexes (Loison et al. 1999), how this changes with environmental heterogeneity, and the trade-off between survival and other traits such as body mass, horn size or reproductive success are not fully understood (Tettamanti et al. 2015, Corlatti et al. 2017). The determinants of the survival of specific sex- and age classes and how their impact may change with different environments and demographic conditions also require investigation, yet are key to chamois management. For example, high survival of kids is crucial in driving the demographic trend of chamois populations in face of climatic changes (Lovari et al. 2020, Chirichella et al. 2021). Given the scarcity of data on this topic, and on the survival of all demographic classes in general, a comparative analysis of data from different populations and possibly different Caprinae species, is urgently needed to enable proactive and sustainable population management, as well as to interpret data linked to the benefits and costs of different reproductive tactics.

Ecology and behavior

Published accounts of some aspects of chamois ecology and behavior are surprisingly scarce, yet are key to chamois conservation. For example, environmental change, interspecific competition, the return of predators and increased human disturbance may interact to create a dynamic scenario affecting the behavior and ecology of chamois, and still need to be fully elucidated.

Chamois feeding ecology is well known, at least at the local scale. Chamois have been previously classified as intermediate feeders (Hofmann 1989), and more recently as cattle-type feeders on the basis of their intraruminal papillation (Clauss et al. 2009). Grasses are key dietary components, especially in summer (Espunyes et al. 2019a), but woody species could also be important. Their importance for chamois survival is expected to be spatially heterogeneous: woody plants are only consumed during periods of fasting (e.g. winter) in some areas, but are core components of chamois diet in others (e.g. common heather *Calluna vulgaris* in eastern Pyrenees: Espunyes et al. 2019a). Consequently, as the ongoing shrubification of secondary grasslands is expected to reduce grass availability in open mountainous landscapes (Espunyes et al. 2019b), the potential for colonizing

woody plants to compensate for reduced nutritional intake requires investigation. Habitat modifications such as wood encroachment and successional changes in secondary meadows may also interact with climatic changes and impact chamois life history traits by, e.g. improving feeding conditions in spring (Espunyes et al. 2021). However, the effects of such changes on chamois feeding ecology are complex, and may be critical to recruitment. For example, early onset of vegetation green-up may mismatch with weaning, which is when juveniles depend on fresh nutritious vegetation, impacting their survival (Lovari et al. 2020). At the same time, climate change may significantly alter forest dynamics, by increasing the frequency and magnitude of natural disturbances (Senf and Seidl 2021), possibly leading to improved foraging opportunities in forested areas due to reduced tree cover (Vavra and Riggs 2010).

Feeding ecology is tightly related to spatial ecology; therefore, collecting high-quality environmental and vegetational data using satellite telemetry will help to disclose fine-scale patterns of forage selection (cf. Duparc et al. 2020). More generally, the chamois is a potential candidate for mapping environmental changes, since in this species, altitudinal shifts, changes in habitat use or behavior (e.g. in circadian and circannual activity rhythms: Brivio et al. 2016), are expected in response to climate and land use changes. Recent studies suggest site-specific responses to environmental changes, likely mediated by local conditions (cf. Ciach and Pęksa 2019). Unfortunately, however, information on chamois spatio-temporal behavior is limited and the scarcity of replicates often makes it difficult to extrapolate the results of local studies to other populations. Chamois social behavior, including grouping patterns, intra-sexual aggression or mother-offspring relationships, has been quite extensively investigated but mostly in the Alpine, Pyrenean and Apennine subspecies (Corlatti et al. 2022a). One of the best-known aspects of chamois behavior is male mating behavior, where alternative reproductive tactics have been locally reported, although the suggested ecological mechanisms of their long-term co-occurrence (Lovari et al. 2006, Corlatti et al. 2015a, 2020, cf. 'Life History') require support from studies conducted in different areas. On the other hand, there is an urgent need for information on key aspects of female behavior, including habitat selection, ranging movements, dispersal and reproductive behavior. More generally, investigating differences in behavioral patterns at specific and subspecific levels may improve understanding of the impact of local environmental conditions on chamois social behavior (cf. Kavčič et al. 2021a) and, more broadly, the eco-evolutionary patterns leading to the morphological and behavioral variation typical of the Caprinae subfamily (cf. Schaller 1977).

Future management decisions will also depend on a better understanding of the relationships between chamois and other species. For example, while the potential effects of interspecific competition between chamois and red deer *Cervus elaphus* (Ferretti et al. 2015) or European mouflon *Ovis aries musimon* (Chirichella et al. 2013), as well as interactions

with livestock (Mason et al. 2014) have been assessed for some populations, they may vary substantially among sites (Corlatti et al. 2022a). As prey species, the contribution of chamois to the diet of gray wolf *Canis lupus* (Mori et al. 2017) or Eurasian lynx *Lynx lynx* (Molinari-Jobin et al. 2007) has been evaluated locally, but the demographic impact of predators on chamois populations at large remains unknown.

Finally, given the impact of global change on mountain ecosystems, future chamois research should focus on the effects of environmental changes on a number of ecological and behavioral aspects. Information gaps on chamois ecology and behavior especially concern taxa other than *R. r. rupicapra*, *R. p. pyrenaica* and *R. p. ornata*. For example, most information on life history consequences of climate change derives from Alpine or Apennine studies (cf. Lovari et al. 2020, Corlatti et al. 2022a). Furthermore, the mechanistic link between increasing temperature and chamois responses is unclear, and chamois may be influenced directly (i.e. through effects on behavior) or indirectly (i.e. through effects on resources) (Lovari et al. 2020, Reiner et al. 2021).

Physiology and diseases

The interest in chamois health and parasitology is longstanding, with contributions dating to the 19th century. However, it was only in the 1960s and 1970s that academic groups (namely in Bern, Vienna, Ljubljana, Turin and Lyon) focused with greater continuity on the diversity and quantitative characterization of the helminth communities of *R. rupicapra*. Several decades later, the etiological, physio-pathological and epidemiological investigation of keratoconjunctivitis (IKC) (Grattarola et al. 1999, Degiorgis et al. 2000, Arnal et al. 2013) and sarcoptic mange outbreaks in chamois (Rossi et al. 1995, Fernández-Morán et al. 1997) were investigated. In the early 1990s, the onset of pestivirus by genotype 4 of the border disease virus (BDV-4) (Alzieu et al. 2004, Arnal et al. 2004, Hurtado et al. 2004), a novel outbreak disease in *R. p. pyrenaica*, promoted a more integrative approach for health assessments of chamois populations.

In the 2000s, research on chamois disease benefitted from the increasing availability of advanced fit-to-purpose diagnostic and analytical tools, to explore the intraspecific variability of major chamois pathogens and their molecular-based epidemiology, including cross-transmission opportunities at the interface with livestock or sympatric wildlife (Luzzago et al. 2016, Fernández-Aguilar et al. 2017). In parallel, passive and active disease surveillance was fruitfully integrated into long-term studies of chamois ecology using marked populations, which allowed the development of population models to address conservation-oriented debates and disease mitigation measures (Serrano et al. 2015). An example of this integrative approach was the demonstration of the spontaneous extinction, approximately two decades from onset, of the much-feared BDV-4 pestivirus in the intensively monitored chamois population of Orlu, in the French Pyrenees (Gilot-Fromont et al. 2018). Equally

interesting was the description of the link between IKC spread and the herd-specific social behavior of females (Gelormini et al. 2017). These results suggested the need for multidisciplinary research to understand outbreak dynamics in the notoriously susceptible wild *Rupicapra* populations.

Despite these remarkable advances in chamois health research, many other questions are waiting to be explored. With few exceptions, there is a lack of descriptive and experimental trials to explore the underlying mechanisms responsible for differences in immune responses (e.g. genetic background, coinfections, resource availability and quality, geology, population density or social stress among others), which could explain why some social units or populations are more resilient to the effects of outbreak diseases than others, despite sharing the same or neighboring mountain ranges. In addition, factors explaining the shift from the epidemic to the endemic status of persisting pathogens (e.g. sarcoptic mange) are unknown for chamois. Both knowledge gaps negatively impact the adoption of research-based chamois-pathogen(s) coexistence strategies by wildlife managers. The bias towards a limited number of *Rupicapra* subspecies (namely *R. r. rupicapra*, *R. p. pyrenaica* and, to a lesser extent, *R. r. tatraica*, *R. p. ornata* and *R. p. parva*) is also notable and should be addressed. In fact, very recently, tick vectors, tick-borne diseases and endoparasites have been studied in *R. r. rupicapra* but also the poorly investigated *R. r. balcanica*; this research provided new insights into chamois parasitological status and tick infestation of the Balkan chamois (Yankov et al. 2021). By combining parasitological and infectious disease studies, other authors also reported an unexpectedly high prevalence of tick-borne *A. phagocytophilum*, including zoonotic strains, in Alpine chamois of the eastern Italian Alps (Grassi et al. 2021). These two examples illustrate that chamois throughout Europe may harbor and suffer from known parasitological and viral diseases as well as those caused by emerging pathogens, such as tick-borne pathogens; thus, increased and standardized screening is recommended wherever possible.

Finally, more effort should be devoted to exploring the relationships between climate/environmental changes and the dynamics of chamois pathogens, with respect to current/expected hosts, pathogen and vector shifts and related conservation threats.

Conservation and management

The conservation status of the genus *Rupicapra* is favorable: both the northern and the southern species are abundant and have been increasing in number and range (particularly towards low altitudes) from the second half of the 20th century. However, five of the 10 subspecies are threatened, three are decreasing in population size or range, and even some populations of the most abundant subspecies (e.g. *R. r. rupicapra*, *P. p. parva* and *R. p. pyrenaica*) have started to decline (Herrero et al. 2020, Anderwald et al. 2021). Overall, more detailed and up-to-date information on abundance and

Table 2. Status of chamois throughout its distribution range. Conservation threats are scale- and context-dependent – CB: lack of cross border coordinated management; CC: climate change; CL: competition with livestock; CW: competition with wild ungulates; D: diseases; G: interbreeding with Alpine chamois *R. r. rupicapra*; HL: habitat loss; OH: over harvesting; P: poaching; PS: small population size (Shackleton et al. 1997, Herrero et al. 2020, Anderwald et al. 2021). ¹ This includes ~100 chamois hybridized with Alpine chamois living in the Low Tatras. ² Proposal by Anderwald et al. (2021). ³ Indicates that translocations have occurred for the relevant species and subspecies.

	Number	Trend	Threats	CITES appendix	Habitat directive annexes	Bern convention appendix	IUCN 2020–2021	Translocations
Northern chamois <i>R. rupicapra</i>	~550 000	Stable (?)	CL, CW, D, G, HL, OH, P, PS		V	III		+ ³
Chartreuse chamois <i>R. r. cartusiana</i>	1500	?	CL, G, HL, OH, P				VU, D1+2	
Alpine chamois (Alps) <i>R. r. rupicapra</i>	~ 500 000	Stable (?)	CC, CW, D, HL, OH					+
Balkan chamois <i>R. r. balcanica</i>	< 10 000	?	CB, CL, G, HL, P		II, IV			+
Tatra chamois <i>R. r. tatrica</i>	1100 ¹	↑	D, P, PS		II, IV		EN, B1+2ab	+
Carpathian chamois <i>R. r. carpatica</i>	8000	?	CL, P					
Caucasian chamois <i>R. r. caucasica</i>	> 9000	?	CL, CW, P				VU, C1	
Anatolian chamois <i>R. r. asiatica</i>	800	?	CL, CW, HL, P				EN, C1+2a(i) ²	
Alpine chamois (New Zealand) <i>R. r. rupicapra</i>	> 18 500	↑						
Southern chamois <i>R. pyrenaica</i>	71 500	?	CC, CL, CW, D, HL		V	III	LC	+
Apennine chamois <i>R. p. ornata</i>	2500	↑	CC, CL, CW, HL	II	II, IV	II	VU	+
Cantabrian chamois <i>R. p. parva</i>	16 000	?	CC, D, HL					+
Pyrenean chamois <i>R. p. pyrenaica</i>	53 000	?	CC, D, HL					+
Total	~ 620 000	?	CC, CL, CW, D, G, HL, OH, P, PS					+

distribution is required, especially for the least-known subspecies (cf. ‘Research trends’).

The main conservation challenges are summarized in Table 2. To address these, action plans with concrete conservation measures, mainly involving the implementation of hunting regimes with respect to age- and social structure, establishment of protected areas and game reserves, and regular population monitoring (e.g. using traditional count or molecular methods) have been partially implemented, but are still lacking for several subspecies and regions. Regardless of geographical scale and taxonomic status, effective conservation and management of chamois principally benefits from the collection of rigorous periodic data on population size, age-sex structure and distribution. Currently, this information is mainly obtained using block counts which, despite underestimating true size and presence, particularly in forested habitats (Corlatti et al. 2015b), may provide useful trend data if conducted over several years in a standardized manner and environmental conditions affecting detection remain stable (cf. Reiner et al. 2020). However, other monitoring methods could be used to provide estimates of population size and/or distribution, including, e.g. distance sampling, density-dependent biometric indices, population reconstruction,

camera traps and GPS-tracking (Kavčić et al. 2021b). The use of non-invasive molecular approaches using eDNA from fecal samples combined with classical or spatially-explicit capture–mark–recapture methods are particularly promising, especially in areas where direct observations of chamois are difficult, such as forests. However, the reliability of a given method (that is, the ability to meet the underlying assumptions) may vary depending on local conditions; therefore, future studies should seek to investigate the robustness of different estimators of absolute population size and distribution under different environmental conditions. Furthermore, studies are urgently needed to assess the reliability of relative abundance indices (e.g. block counts, camera trapping rate) to track spatio-temporal variations in population size and allow for the adoption of sustainable field work effort in the long term.

Information on population size and distribution is particularly relevant to active management, as the chamois is hunted throughout most of its distribution range with a variety of hunting regimes that should be based on reliable knowledge of these two parameters. Harvesting plans generally adopt simplified age classes or more sophisticated grouping systems; however, for any given population, conservative harvest

quotas should be decided according to current demographic structure, with the aim of avoiding strong skews in sex- and age-ratios to ensure long-term viability and persistence (cf. Skonhofs et al. 2002), but also to avoid a biased selection of different behavioral traits. Although information on harvest rate is still fragmentary for many subspecies (Damm and Franco 2014), in some populations overharvesting of certain sex- and age-classes, especially adult males, still persists, possibly due to trophy hunting. We caution against these practices which, besides representing a conservation threat, might lead to unintentional artificial selection and disruption of natural evolutionary trajectories. More generally, information on the effects of hunting on chamois is lacking, including the short- and long-term consequences of different hunting regimes on space use, mating behavior, physiology, population structure and demography.

The future of chamois conservation and management will further depend on a number of different factors, with impacts on demography and life history traits that still need to be fully clarified. These include, for example, hybridization among species and subspecies (cf. 'Genetics'), climate change (cf. 'Life history'), land use changes and recent ecological changes, mainly with respect to competition with other wild ungulates, predation by carnivores (cf. 'Ecology and behavior'), and impact of parasites and pathogens (cf. 'Physiology and disease'). With carefully collected life history data, predictions of future distributions and the sustainability of management interventions could be modeled. It is worth mentioning the importance of translocations, including introductions and reintroductions, which, irrespective of their purpose (including hunting – e.g. New Zealand, Slovakia, Czech Republic or conservation – e.g. Apennines), have played a key role in the recovery of chamois. Translocations are still used to restock and rewild, but should carefully consider the genetic origin of source and host populations, while taking into account the challenges of taxonomic classification (cf. 'Taxonomy and systematics'). Finally, conflicts between chamois and human-related activities such as forestry should also be addressed. Overall, the browsing impact of the species appears limited, but local and species-specific negative effects have been reported (Kupferschmid et al. 2014). It seems likely that the impact of chamois on forest ecosystems will vary depending on site conditions, population density and hunting regimes, suggesting that a more extensive assessment over multiple populations of subspecies living in different ecological conditions is needed. More generally, a deeper understanding of the impact of chamois and other wild Caprinae species on vegetation, i.e. on forest/grassland ecosystems, will require long-term assessment using appropriate community-based metrics (cf. Nopp-Mayr et al. 2020).

Conclusions

The Caprinae subfamily consists of species with a great diversity of forms and behaviors, the result of complex

eco-evolutionary scenarios favored by radiation towards very different ecological conditions (cf. Schaller 1977). In many respects, the chamois occupies an intermediate position in the evolutionary pathways between forest-dweller, monogamous and monomorphic goat antelopes such as the serow *Capricornis* spp. and highly dimorphic, highly polygynous wild sheep *Ovis* spp. inhabiting open habitats (Geist 1987). Accordingly, the chamois is a very interesting target for ecological investigations, but at the same time a great effort is needed to collect data over large geographical areas to enable the extrapolation of results to other populations.

Research on the genus *Rupicapra* has markedly increased over the last decades, contributing substantially to our knowledge of the biology and ecology of mountain ungulates. However, the majority of chamois publications are focused on populations inhabiting the Alps and, to a lesser extent, the Pyrenees and Apennines. While this bias may be partly explained by the greater abundance of the Alpine and Pyrenean subspecies compared to the others (cf. Herrero et al. 2020, Anderwald et al. 2021), we suggest that the scarcity of replicates from other subspecies and/or geographic areas is limiting the advancement of chamois science and its application to conservation. The importance of environmental heterogeneity in shaping behavioral and life history traits, especially in response to ongoing climatic change, is increasingly evident, and will be one of the biggest challenges for the future of chamois research and conservation. Substantial contributions to this challenge may derive from site-specific quantitative assessment of reproductive success, investigation of fine-scale foraging patterns and dietary variations, and a mechanistic understanding of disease outbreaks and site-specific resilience, which may help clarify the mechanisms of life history trade-offs. From a conservation perspective, the resolution of taxonomic disputes, the estimation of the degree and importance of subspecies hybridization, the assessment of the impact of different hunting regimes, and the adoption of reliable methods for estimating population abundance are issues of primary concern. Overall, substantial field efforts to collect paleontological, behavioral, ecological, morphological, genetic and physiological data on populations from different subspecies and geographic areas are needed to clarify several aspects of the evolutionary biology and ecology of chamois. Mobilization of research groups to expand their work on less-known subspecies, and broader collaboration among experts would greatly contribute to a better understanding of subspecies-specific biology and management, thereby ensuring a successful future for chamois conservation and research.

Author contributions

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Data availability statement

Data is available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.fbg79cnx2>> (Corlatti et al. 2022b).

Supporting information

The Supporting information associated with this article is available with the online version.

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Résumé

L'intensification des activités humaines depuis le milieu du 20^{ème} siècle, a induit d'importants changements dans la composition géochimique de l'atmosphère terrestre ainsi que dans la composition du paysage, entraînant d'importants changements dans la biosphère terrestre et aquatique. En effet, la biodiversité mondiale fait aujourd'hui face à une crise majeure, les taux d'extinctions pour la plupart des espèces animales et végétales atteignant désormais des valeurs 100 à 1000 fois supérieures aux taux « normaux » d'extinction. Les principales sources de ce déclin sont multiples, parmi elles se trouvent notamment la surexploitation, la dégradation et la fragmentation des habitats et les invasions biologiques. Si la plupart de ces causes sont responsables du déclin actuel de la biodiversité, le réchauffement climatique quant à lui, en altérant profondément le fonctionnement biogéochimique des écosystèmes, constitue la menace principale pour la persistance des espèces dans le futur. Il a été notamment démontré que le changement climatique est responsable de l'augmentation des températures globales, induisant des changements importants dans la phénologie et la distribution des communautés végétales, accélérant la perte d'habitats ou la diffusion des maladies, ou encore augmentant de manière dramatique la fréquence des événements climatiques extrêmes comme les cyclones, les inondations, les sécheresses et vagues de chaleur, tout cela pouvant conduire à terme à des extinctions locales voire globales des populations.

Dans ce contexte, une des questions primordiales pour les biologistes est aujourd'hui de savoir comment des espèces, qui se sont adaptées aux conditions locales de leur environnement sur des pas de temps de plusieurs milliers à millions d'années, peuvent-elles aujourd'hui faire face à des changements environnementaux beaucoup plus soudains, prenant place sur quelques décennies à centaines d'années. Parmi l'ensemble des pistes explorées, la plasticité phénotypique est alors souvent évoquée. Désignant l'ensemble des changements morphologiques, physiologiques, phénologiques et comportementaux induits par l'environnement sur les individus tout au long de leur vie (du développement embryonnaire à la mort de l'individu), la plasticité phénotypique est ainsi souvent considérée comme une voie potentielle pour les individus et les populations, pour faire face à court et moyen termes aux changements rapides des conditions environnementales, avant de s'adapter à plus long terme via le processus de sélection génétique.

Parmi les composantes de la plasticité phénotypique, la plasticité comportementale à récemment été plus particulièrement étudiée dans la littérature. Il est notamment suggéré que les individus et les espèces étant les plus flexibles dans leurs comportements, serait les plus aptes à faire face aux changements environnementaux rapides induits par l'homme. En disposant d'une plus grande palette de comportements innés permettant de faire face à différents contextes environnementaux (plasticité contextuelle), ou en ayant des capacités d'apprentissage supérieures permettant d'acquérir de nouveaux comportements (plasticité développementale), les espèces plus flexibles sont par exemple plus aptes à reconnaître et éviter de nouveaux prédateurs potentiels, à utiliser de nouvelles ressources et de nouveaux habitats, ou encore à faire face à de nouvelles conditions environnementales. De ce fait, la plasticité comportementale est ainsi notamment citée comme l'une des principales voies par lesquelles les populations animales pourront faire face aux changements climatiques. Les études reliant les réponses comportementales des individus face aux variations climatiques sont néanmoins encore récentes, et un important travail de recherche est désormais nécessaire pour déterminer comment ces réponses peuvent influencer la survie et la reproduction des individus et à terme la dynamique des populations.

L'étude du comportement animal est ainsi capitale pour comprendre quels sont les mécanismes qui régissent la dynamique spatiale et temporelle des populations et comment celles-ci répondront face au changement climatique. De nombreuses études ont ainsi montré que la distribution des populations est influencée par les comportements spatiaux des individus à fine échelle, concernant par exemple la recherche de nourriture ou de partenaires sexuels ou l'évitement de la prédation, ou la recherche de conditions environnementales plus favorables via la dispersion ou la migration. Les récents progrès des technologies de suivi individuel (GPS et biologgers) et des outils statistiques et méthodologiques associés, ainsi que le développement des études de populations à long terme, rendent désormais possible la collecte et le traitement d'informations capitales, permettant de relier les comportements spatiaux des individus avec leurs performances démographiques (survie et reproduction) et la dynamique des populations qui en découle.

Au sein des mammifères, les ongulés sont parmi les espèces les plus étudiées, ce qui peut s'expliquer par leur très grande importance d'un point de vue écologique, économique, social et culturelle. Les ongulés sont en effet considérés comme des espèces clés pour les écosystèmes, en premier du fait de leur position intermédiaire dans les réseaux trophiques, servant à la fois de proies pour les carnivores mais aussi pour certaines populations humaines ayant recours à la

chasse de subsistance. D'autre part, la plupart de ces espèces étant herbivores, les ongulés influencent aussi directement la composition et la structure de la végétation, et assurent par la même occasion plusieurs processus écosystémiques comme la dispersion des graines, le cycle des nutriments dans le sol, ou même les régimes d'incendie. L'influence de ces espèces sur les agrosystèmes et les écosystèmes cependant dépend principalement de leur abondance, qui quant à elle, est fortement influencée par les facteurs anthropiques. On estime ainsi que 58 % des plus grandes espèces sauvages connaissent des déclin de population et sont aujourd'hui menacées d'extinction, les principales causes étant la chasse et le braconnage, la compétition avec les troupeaux domestiques, et la perte d'habitat liée aux activités humaines (déforestation, agriculture, urbanisation). De ce fait et de par leur rôle écologique, économique et social, les ongulés sauvages font aujourd'hui l'objet d'importants enjeux de gestion et de conservation.

Alors que la majorité des espèces menacées se trouvent sur le continent africain ou asiatique, aucune espèce en Amérique du Nord, et seulement une seule espèce d'ongulés sauvage (le bison européen) est menacée d'extinction en Europe. Si cela est en premier dû au fait que la plupart des mégaherbivores nord-américains et européens ont disparu pendant l'extinction de la mégafaune du Quaternaire, il n'en reste pas moins que les populations d'ongulés sauvages restantes ont connu ces dernières décennies un véritable renouveau démographique. A la fin du 19^{ème} et au début du 20^{ème} siècle, les fortes pressions exercées par la chasse, la déforestation et la compétition avec les troupeaux domestiques, amènent les populations européennes d'ongulés sauvages à leur plus bas niveau historique, certaines espèces comme le chevreuil faisant pratiquement face à des extinctions locales notamment en Angleterre ou en Suède. C'est alors durant la seconde moitié du 20^{ème} siècle, sous les effets conjugués de nombreux programmes de réintroductions, de changements dans les pratiques de chasse et de gestion des populations, mais aussi de la renaturalisation de certains habitats en lien avec la déprise agricole ainsi que l'extirpation locale des grands prédateurs comme le loup ou l'ours, que les populations d'ongulés sauvages vont alors connaître un nouvel essor démographique. Les sangliers, les cervidés (cerfs, élans, rennes, chevreuil) et, bien que dans une mesure un peu moindre, les ongulés de montagne (chamois, bouquetins et mouflons), ont ainsi largement prospéré au cours des 40 dernières années, ce qui n'est pas sans poser de nouvelles problématiques de gestion et de conservation.

Les espèces de montagne par exemple font encore face à plusieurs menaces comme la chasse et le braconnage, la compétition avec les troupeaux domestiques, le changement climatique ou encore l'apparition de zoonoses, autant de cause qui sont parfois à l'origine du déclin actuel de

certaines populations. D'un autre côté, l'explosion démographique des sangliers ainsi que des cervidés comme les chevreuils et les cerfs, posent aujourd'hui plusieurs problèmes et conflits avec les activités humaines, surtout dans un contexte de paysage fortement anthropisé (routes, aires urbaines étalées, agriculture et foresterie). Chaque année par exemple, plus d'un demi-million de collisions de véhicules avec la faune sauvage sont recensées en Europe, 360 000 d'entre elles impliquant des chevreuils. Les dommages agricoles infligés par les sangliers quant à eux représentent plus de 80 millions d'euros chaque année, et les dégâts forestiers infligés par d'autres espèces d'ongulés peuvent varier de 150 000 euros en Suède jusqu'à 15 millions par an en Pologne.

Ainsi, dans un contexte où les conflits entre l'homme et la faune sauvage seront certainement plus fréquents en raison de l'expansion et de l'intensification des activités humaines (par exemple, le tourisme, l'agriculture, l'urbanisation, les sports de plein air), la mise en place de politiques de gestion de la faune sauvage favorisant une coexistence durable est plus nécessaire que jamais. L'étude des principaux moteurs de la dynamique des populations d'ongulés et de leurs réponses aux changements globaux (c'est-à-dire le changement climatique et l'anthropisation des paysages) est donc cruciale si nous voulons en déduire des pratiques de gestion efficaces. Dès lors et étant donné que la dynamique et la distribution des populations sont souvent le résultat de comportements à échelle fine réalisés par les individus, nous proposons à travers ce travail de thèse, d'explorer plus particulièrement le lien entre les comportements spatiaux et les contraintes environnementales.

Notre compréhension des mouvements et du comportement des animaux est largement fondée sur la théorie de l'approvisionnement optimal, qui vise à expliquer les différentes solutions au compromis entre l'acquisition des ressources et l'évitement des risques auxquelles sont confrontés tous les animaux. Les animaux sont effet susceptibles d'ajuster leur comportement différemment en fonction de la distribution spatiale des ressources ainsi que des risques (ex : dérangement humains, prédateurs) et zones de refuge. Ainsi, maximiser leur apport énergétique tout en minimisant le temps passé dans les zones à risque, a longtemps été vu par les écologistes comme le défi principal auquel sont confrontés les grands herbivores et dictant ainsi leurs comportements. Il s'agit cependant d'une simplification que l'on peut aujourd'hui qualifier d'excessive, car les contraintes qui influencent les choix comportementaux d'un individu à tout moment sont en réalité diverses. Six contraintes majeures sur les déplacements peuvent être identifiées, parmi lesquelles non seulement le paysage alimentaire et le paysage des risques, mais aussi les contraintes liées à l'histoire de vie (les besoins des individus variant en fonction,

par exemple, de leur âge, de leur sexe, de leur condition, de leur statut reproductif, influençant leurs comportements spatiaux en conséquence), le paysage énergétique (résultant des coûts de déplacement nécessaires pour se déplacer d'un endroit à l'autre), les contraintes météorologiques et climatiques, et les contraintes sociales (ex : interactions entre conspécifiques). Il n'y a donc pas une mais généralement plusieurs solutions, dans un paysage donné, qui résout le problème complexe de coût-bénéfice auquel est confronté un herbivore pour choisir où être, quoi faire, combien de temps rester, et où se déplacer ensuite.

Dans un premier temps, nous avons étudié comment les facteurs internes peuvent contraindre le comportement spatial des individus. Plus précisément, nous avons montré que l'âge est un facteur important de l'utilisation de l'espace et des mouvements des individus chez deux espèces d'ongulés ayant des traits d'histoire de vie contrastés, à savoir le chevreuil et le mouflon méditerranéen. En effet, bien qu'il ait été suggéré depuis longtemps que les individus peuvent modifier leur comportement spatial en raison des contraintes liées aux différentes étapes de leur vie, ou de l'expérience et de la sénescence les études empiriques sur l'utilisation de l'espace et les déplacements en fonction de l'âge se sont limitées jusqu'à récemment à quelques situations où l'observation directe d'individus d'âge connu était possible.

Nous nous attendions à ce que les différences liées à l'âge soient principalement liées aux tactiques d'accouplement spécifiques à l'âge pendant le rut pour les mâles et la présence/absence de progéniture pour les femelles, et l'expérience et/ou la sénescence locomotrice en dehors des périodes de reproduction. Pendant la période de rut, les chevreuils mâles plus âgés parcouraient de plus grandes distances journalières que les jeunes mâles en raison de comportements de patrouille pour la défense du territoire, tandis que les mouflons mâles plus âgés voyageaient moins que les jeunes mâles, qui adoptaient souvent des tactiques de course pour s'accoupler avec les femelles. Pendant la période de naissance, les femelles reproductrices avaient des domaines vitaux plus petits que les femelles non reproductrices chez les chevreuils, alors qu'aucune différence marquée n'a été observée chez les femelles mouflons. La variation la plus marquée liée à l'âge dans l'utilisation de l'espace chez le mouflon s'est produite en dehors des périodes de reproduction ; plus précisément, les individus les plus âgés se déplaçaient moins loin et avaient un domaine vital plus petit (uniquement chez les femelles) que les individus plus jeunes. Nos résultats, basés sur un large ensemble de données GPS d'individus d'âges divers, ont ainsi pu démontrer la variabilité des tactiques spatiales, à la fois au sein et entre les deux populations d'herbivores étudiées, et fournir des preuves solides que l'âge est un déterminant majeur des comportements spatiaux.

Dans un second temps, nous avons évalué comment les individus affinent leur utilisation de l'espace et leur budget d'activité en réponse aux températures estivales, en prenant notamment en compte les contraintes locales d'accès aux refuges thermiques. Face à l'augmentation continue de la température moyenne mondiale, les espèces de grands herbivores devraient en effet consacrer de plus en plus de temps et d'énergie à la thermorégulation, en particulier les espèces sensibles au stress thermique comme les ongulés de montagne. Sous l'effet de températures extrêmes, les animaux peuvent par exemple réduire leur activité pendant les heures les plus chaudes de la journée, ou se relocaliser dans les refuges thermiques. Cependant, ces réponses peuvent toutefois entraîner des coûts d'opportunités en termes d'acquisition d'énergie, les individus allouant alors plus de temps et d'énergie aux comportements thermorégulateurs qu'à d'autres activités cruciales pour leur survie et leur succès reproductif, comme la recherche de nourriture, ou de partenaire sexuel, ainsi que les soins parentaux. A partir de l'analyse de trajectoires GPS issues de femelles chamois suivies pendant l'été dans les Alpes françaises, nos résultats ont ainsi pu démontrer l'existence de coûts d'opportunité liés à la thermorégulation comportementale, les individus se rendant les jours de forte chaleur, dans les refuges thermiques comme la forêt ou les pentes nord, où la quantité de ressources était pourtant 1.5 à 2 fois moins élevée que dans les pelouses alpines, habitat majoritairement visité lorsque les températures étaient peu élevées. Dans le même temps, nous avons pu démontrer que, pour compenser les coûts d'opportunité induits par la thermorégulation le jour, les chamois ont alors augmenté leur activité de recherche alimentaire et de déplacement de jour comme de nuit. De manière nouvelle, nous avons notamment montré que suivant le type de refuges auxquels avaient accès les animaux à l'intérieur de leur domaine vital, les individus répondaient différemment. Ainsi, les individus ayant accès à la forêt ont augmenté leur temps quotidien consacré à la recherche de nourriture, tandis que les individus ayant accès aux pentes nord ont diminué leur temps de recherche de nourriture et augmenté le temps consacré à se déplacer sur de plus grandes distances, probablement pour pouvoir visiter plus de parcelles de nourriture.

Enfin, nos résultats ont permis de démontrer que les coûts d'opportunité liés à la thermorégulation comportementale étaient à leur tour fortement modulés par l'âge des individus. Comparées aux jeunes femelles, les femelles plus âgées, c'est-à-dire les individus âgés de 10 ans ou plus, généralement visitaient des endroits où la quantité de ressources étaient plus élevées. Les différences avec les femelles les plus âgées étaient notamment particulièrement exacerbées les jours de forte température, la quantité de ressource des localisations visitées par les femelles plus jeunes diminuant nettement plus fortement avec la

l'augmentation de la température, que chez les femelles les plus âgées. Une explication possible serait alors que les femelles plus âgées auraient plus d'expérience, ce qui signifierait qu'elles auraient une meilleure connaissance de leur environnement et donc une plus grande capacité à l'exploiter. Elles pourraient alors par exemple être plus efficaces que les jeunes femelles, pour localiser les patches de nourriture, ou pendant les jours les plus chauds, les refuges thermiques qui offrent une plus grande disponibilité de ressources. D'autre part, des effets sociaux liés aux comportements de hiérarchie et de dominance peuvent également être en jeu dans notre étude. La diminution plus importante de la quantité de fourrage observée chez les femelles d'âge mûr pendant les jours les plus chauds, pourrait être due aux comportements de dominance affichés par les femelles plus âgées, qui pourraient monopoliser les patches offrant le meilleur compromis entre disponibilité du fourrage et conditions thermiques, et empêcher les femelles plus jeunes de les exploiter.

En conclusion, ce travail de thèse a permis de mettre en évidence que la prise en compte du contexte paysager local et l'analyse conjointe du comportement individuel, de l'énergétique et de l'histoire de vie sont essentielles pour obtenir une meilleure compréhension des impacts potentiels du changement climatique sur les espèces adaptées au froid. Dans un contexte de changement climatique, les opportunités manquées devraient alors être de plus en plus fréquentes, les individus devant consacrer de plus en plus de temps aux comportements de thermorégulation, ce qui pourrait avoir des conséquences négatives sur les performances démographiques des individus et la dynamique des populations à plus long terme, notamment si les coûts des opportunités manquées sont supérieurs aux bénéfices de la thermorégulation comportementale. Une diminution des conditions d'alimentation pourrait par exemple conduire à une baisse de la production laitière et de l'investissement maternel, ce qui pourrait à son tour entraîner une baisse du succès du sevrage chez les femelles. Bien sûr, les femelles pourraient également compenser ces coûts en passant plus de temps à visiter les parcelles de nourriture et à chercher de la nourriture, comme cela a été observé chez d'autres espèces d'ongulés sauvages, et également suggéré ici dans le second et le troisième article. De plus amples études sont alors nécessaires pour évaluer les impacts énergétiques et démographiques du changement climatiques sur les populations d'ongulés sauvages. Une définition plus précise des paysages thermiques (prenant en compte notamment les effets de la radiation solaire sur la thermorégulation des individus), couplée à une définition plus fine des comportements et de la dépense énergétique des individus (via l'utilisation de biologgers), et des paramètres démographiques (ex : taux de survie ou succès reproducteur des individus), pourraient par

exemple permettre de déterminer avec plus de précision quelles sont les conséquences énergétiques et démographiques des tactiques comportementales déployées par les individus pour faire face aux fortes températures.

Résumé: Dans un contexte de conflits entre l'homme et la faune sauvage de plus en plus fréquents, en raison de l'expansion et de l'intensification des activités humaines (tourisme, agriculture, urbanisation, sports de plein air), la mise en place de politiques de gestion de la faune sauvage favorisant une coexistence durable, est plus nécessaire que jamais. Il est ainsi crucial d'étudier les principaux moteurs de la dynamique des populations d'ongulés et leurs réponses au changement climatique et l'anthropisation des paysages, si nous voulons en déduire des pratiques de gestion efficaces. Etant donné que la dynamique et la distribution des populations sont souvent le résultat de comportements à échelle fine effectués par les individus, nous avons par conséquent proposé à travers ce travail de thèse, d'explorer plus particulièrement le lien entre les comportements spatiaux, les facteurs internes et les contraintes environnementales. A partir des données issues du suivi de trois espèces d'ongulés sauvages, à savoir le chevreuil (*Capreolus capreolus*), le mouflon méditerranéen (*Ovis gmelini musimon x Ovis sp.*) et le chamois (*Rupicapra rupicapra*), nous avons d'abord montré que l'âge était un déterminant majeur des comportements spatiaux des animaux. Pendant la période de rut, les mâles âgés de chevreuil parcouraient de plus grandes distances quotidiennes que les jeunes mâles en raison de comportements de patrouille pour la défense du territoire, tandis que les mâles âgés de mouflon voyageaient moins que les jeunes mâles, qui adoptaient souvent des tactiques de coursing pour s'accoupler avec les femelles. Pendant la période de naissance, les femelles reproductrices avaient des domaines vitaux plus petits que les femelles non reproductrices chez les chevreuils, alors qu'aucune différence marquée n'a été observée chez les femelles mouflons. La variation la plus marquée liée à l'âge dans l'utilisation de l'espace chez le mouflon s'est produite en dehors des périodes de reproduction ; plus précisément, les individus les plus âgés se déplaçaient moins loin et avaient un domaine vital plus petit (femelles uniquement) que les individus plus jeunes. De même, dans une autre étude, nous avons également montré que les femelles chamois plus âgées visitaient des endroits où la quantité de fourrage était plus importante que les femelles plus jeunes, peut-être en raison de leur plus grande expérience ou de la sénescence locomotrice. Nous avons ensuite démontré que des facteurs externes, tels que la température et les contraintes du paysage local, peuvent également influencer les réponses comportementales des animaux. Les individus qui avaient accès à un plus grand nombre de refuges thermiques, tels que les forêts et les versants nord, avaient tendance à augmenter leur utilisation de ces habitats pendant les jours de températures élevées. Ceci était toutefois associé à des coûts d'opportunité, car les refuges thermiques offraient généralement des conditions de fourrage réduites, obligeant en retour ces mêmes individus à augmenter le temps passé en recherche alimentaire et à se déplacer afin de rassembler suffisamment de ressources. Dans l'ensemble, nos résultats ont démontré que la variabilité individuelle de l'âge et des contraintes paysagères locales, induit une hétérogénéité interindividuelle dans les tactiques comportementales, qui sont susceptibles de se traduire par des différences individuelles dans les budgets énergétiques qui restent maintenant à explorer dans des études ultérieures.

Mots-clés : âge, expérience, sénescence, contraintes reproductives, recherche alimentaire, thermorégulation comportementale, refuges thermiques, coûts d'opportunité, budgets d'activité

Abstract: In a context where human-wildlife conflicts are expected to be more frequent due to the expansion and intensification of human activities (e.g. tourism, agriculture, urbanisation, outdoor sports), instituting wildlife management policies promoting sustainable coexistence is more needed than ever. Investigating what are the main drivers of ungulates population dynamics and their responses to global changes (i.e. climate change and landscape anthropization), is then crucial if we aim to infer efficient management practices. Consequently, and as population dynamics and distribution are often the results of fine-scaled behaviours made by individual, we proposed through this thesis work, to more particularly explore the link between spatial behaviours, internal factors and environmental constraints. Based on the data from the monitoring of three wild ungulates species, i.e. roe deer *Capreolus capreolus*, mediterranean mouflon *Ovis gmelini musimon x Ovis sp.*, and chamois *Rupicapra rupicapra*, we first showed that age was a major determinant of animals' spatial behaviours. During the rutting period, older roe deer males travelled greater daily distances than younger males due to patrolling behaviours for territory defence, whereas older mouflon males travelled less than younger males, which often adopted coursing tactics to mate with females. During the birth period, reproductive females had smaller home ranges than non-reproductive females in roe deer, whereas no marked differences were observed in mouflon females. The most marked age-related variation in space use of mouflon occurred outside the reproductive periods; specifically, the oldest individuals travelled less far and had a smaller home range (females only) than younger individuals. Similarly, in another study, we also showed that older chamois females visited locations with higher forage quantity than younger females, possibly because of their higher experience or locomotor senescence. We then demonstrated that external factors such as temperature and local landscape constraints, may also shape animals' behavioural responses. Individuals which had access to more thermal refuges such as forests and northern slopes, tended to increase their use of these habitats during days of high temperatures. This however was associated with opportunity costs, as thermal refuges typically offered decreased forage conditions, forcing in return these same individuals to increase their time spent foraging and relocating in order to gather sufficient resources. Overall, our results demonstrated that individual variability in age and in local landscape constraints induces among-individual heterogeneity in behavioural tactics, which are likely to result into individual differences in energy budgets that remains now to be explored in further studies.

Keywords: age, experience, senescence, reproductive constraints, foraging, behavioural thermoregulation, thermal refuges, opportunity costs, activity budgets