Doctoral Dissertation

The impact of habitat characteristics on spatio-temporal behaviour of red deer (*Cervus elaphus*)

submitted by

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Affidavit

I hereby declare that I have authored this dissertation independently, and that I have not used any assistance other than that which is permitted. The work contained herein is my own except where explicitly stated otherwise. All ideas taken in wording or in basic content from unpublished sources or from published literature, as well as those which were generated using artificial intelligence tools, are duly identified and cited, and the precise references included. Any contribution from colleagues is explicitly stated in the authorship statement of the published papers.

I further declare that this dissertation has not been submitted, in whole or in part, in the same or a similar form, to any other educational institution as part of the requirements for an academic degree.

I hereby confirm that I am familiar with the standards of Scientific Integrity and with the guidelines of Good Scientific Practice, and that this work fully complies with these standards and guidelines.

Zernez, 18.09.2025 Thomas REMPFLER (manu propria)

The question is not what you look at, but what you see.

Henry David Thoreau

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Preface

In 2015, the Canton of Grisons' Hunting and Fisheries Department and the Swiss National Park launched a red deer project called *Ingio via?*. In the Engadin language *Rumantsch*, this means *where are you off to?* The aim was to investigate the spatio-temporal behaviour of the red deer using GPS locations. Of particular interest was the role of the Swiss National Park and other hunting ban areas where hunting is prohibited. As an employee with the Research and Monitoring Department of the Swiss National Park, I was put in charge of the operational management of the project. After a few years, the idea arose of analysing the data as part of a dissertation. And so, I embarked on an extremely exciting journey as a doctoral student.

In addition to the *Ingio via?* data, we were able to work with GPS locations from five other study areas with hunting ban areas. Thus, thank you to the data owners of these study areas for allowing us to use the data for this research. The analysis was conducted with the generous support of the Swiss National Park and the Canton of Grisons' Hunting and Fisheries Department. Additional financial support was provided by the NUKAHIVA Foundation.

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An instructive journey accompanied by unrivalled experiences lies behind us. And I deliberately mean *us*. This dissertation would never have been possible without the great and generous support of a large number of people who unselfishly invested their knowledge and time in this project and in my personal development. In addition, I have always been able to count on many kind-hearted people who have advised and strengthened me beyond the project itself.

First and foremost, I would like to thank my supervisor, Klaus Hackländer, for his support through his professional expertise, knowledge and experience, and especially for his role as a door opener with his solution-oriented, positive and humorous manner. I would also like to thank my advisory team, who have provided me with extensive support from the conception of this dissertation right up to the publication of papers. I would particularly like to emphasise Pia Anderwald. She has guided me in all areas of scientific work, and often worked tirelessly and energetically, checking results for plausibility, proofreading and editing texts. I would like to thank all the co-authors for their valuable contributions to the writing of the publications, including Wibke Peters, Christian Rossi, Jan Schweizer, Claudio Signer, Sven Buchmann, Flurin Filli, Hannes Jenny, Benjamin Bar-Gera, Alina L. Evans and, once again, Klaus Hackländer and Pia Anderwald. I would also like to express my gratitude to Sven Buchmann and Lars Korzelius, who helped me to graphically visualize results from. I learnt a lot from all of them.

Special thanks go to the initiators of the red deer project *Ingio via?*, Hannes Jenny and Flurin Filli, who later joined the advisory team. It was only through this extremely exciting co-operation project between the Canton of Grisons' Hunting and Fisheries Department and the Swiss National Park that the idea of a dissertation came about. I would therefore like to thank the decision-makers Sonja Wipf, Adrian Arquint and Ruedi Haller for making my dissertation possible. Simon Aeschbacher also supported me in the final phase of the dissertation. It is very important to me to thank all gamekeepers and park wardens for capturing the animals, because they spent countless hours during the night doing so.

I would also like to thank my colleagues at the Institute of Wildlife Biology and Game Management at BOKU University, including the doctoral students, for the scientific exchange, and Diana Pötschacher from the Institute's secretariat.

During my doctorate I was able to attend extremely interesting courses in which I learnt specific knowledge. I would therefore like to thank all the course instructors, especially Friedrich Leisch, Gabriele Cozzi, Patrick Laube and Jan Wunder. I would also like to thank Anita Risch for accepting me as a guest in her team at the Swiss Federal Institute for Forest, Snow and Landscape Research WSL, which made some of the courses accessible to me in the first place. Last but not least, I would like to thank the reviewers for their time and effort in assessing this dissertation.

Years ago, under the wing of Klaus Robin, I was able to take my first steps in the fields of wildlife ecology and wildlife management. We have maintained an honest dialogue to this day, for which I am extremely grateful to him, as I can always rely on his advice.

I am also particularly grateful to my family. My mother Verena, who has always let me go my own way and whose kindness and helpfulness form the foundation of our family. My father Georg certainly gave me a fundamental interest in nature and wildlife. Further, I would like to thank my three siblings Maria, Maurus and Georg for shaping each other's characters and for sticking together.

The greatest thanks go to my wife Andrea, firstly for her love, then for keeping my back free during the doctoral years, and above all for her support with her mental and emotional skills. Without her, this dissertation would not have been written. And finally, she gave me three wonderful children, Anna-Lena, Tom-Aurel and Finn-Luis. I would like to thank them for their forbearance when dad was absent in thought or a little irritable. Then, they often used their unique ability to bring me straight back to simply being Papa.

Thank you all from the bottom of my heart!

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List of publications

The main part of this cumulative dissertation is composed of three scientific articles in corresponding peer-reviewed journals. In **paper I** and **II** the author contributed with first authorship. **Paper III** was based on a Master's thesis co-supervised by the author and later published by the student (Bar-Gera, 2023). The author of this doctoral dissertation acted as co-author in **paper III**. Details of the contributions are listed below.

Paper I

Rempfler, T., Peters, W., Signer, C., Filli, F., Jenny, H., Hackländer, K., Buchmann, S. & Anderwald, P. (2025). Contrasting daytime habitat selection in wild red deer within and outside hunting ban areas emphasises importance of small-scale refuges from humans. *Ecology and Evolution*, 15(8). DOI: 10.1002/ece3.71407 (*published*)

Declaration of authorship:

Thomas Rempfler, Pia Anderwald, Flurin Filli and Hannes Jenny conceived the initial idea for the study. The study design and analytical approach was refined by Wibke Peters, Sven Buchmann and Klaus Hackländer. Thomas Rempfler, Claudio Signer, Flurin Filli and Hannes Jenny organised the fieldwork. Thomas Rempfler, Pia Anderwald, Wibke Peters and Sven Buchmann conducted the statistical analyses. Thomas Rempfler and Pia Anderwald drafted the manuscript. All authors contributed significantly by editing the final manuscript.

Paper II

Rempfler, T., Rossi, C., Schweizer, J., Peters, W., Signer, C., Filli, F., Jenny, H., Hackländer, K., Buchmann, S. & Anderwald, P. (2024). Remote sensing reveals the role of forage quality and quantity for summer habitat use in red deer. *Movement Ecology,* 12(1). DOI: 10.1186/s40462-024-00521-6 (*published*)

Declaration of authorship:

Thomas Rempfler, Christian Rossi, Pia Anderwald and Flurin Filli had the original idea for the study. Jan Schweizer and Sven Buchmann refined the study design and analytical approach. Fieldwork was organised by Thomas Rempfler, Flurin Filli and Hannes Jenny. Christian Rossi and Jan Schweizer performed the statistical analyses on the vegetation characteristics, Thomas Rempfler, Pia Anderwald and Sven Buchmann on the integrated step selection functions. Thomas Rempfler, Christian Rossi, Jan Schweizer and Pia Anderwald drafted the manuscript. All authors made important contributions by editing the final manuscript.

Paper III

Bar-Gera, B., Anderwald, P., Evans, Alina L., Rempfler, T., Signer, C. (2025). Comparing the accuracy of machine learning methods for classifying wild red deer behaviour based on accelerometer data. *Animal Biotelemetry*, 13(9). DOI: 10.1186/s40317-025-00401-9 (*published*)

Declaration of authorship:

All co-authors conceived the study. Benjamin Bar-Gera designed the study with valuable inputs from all co-authors. Benjamin Bar-Gera planned and conducted the fieldwork and collected the data with support from Thomas Rempfler and Claudio Signer. Benjamin Bar-Gera performed the analyses with support from all co-authors, primarily Pia Anderwald. Benjamin Bar-Gera wrote the manuscript and visualized the results with valuable inputs from all co-authors.

Abstract

Within the framework of mountainous landscapes with a network of small-scale hunting ban areas and short and intense hunting activities, we analysed the spatio-temporal behaviour of partially migratory red deer. Based on GPS locations of 243 collared individuals from six study areas mainly within Switzerland, we applied *integrated step selection functions*. First, we analysed habitat selection within the concept of the *landscape of fear* – mainly applied to human presence in the absence of natural predators. Second, we tested for effects regarding the trade-off between forage quality and quantity in summer. We found that red deer selected against habitats with higher probability of meeting humans during the day, but an opposite selection at night. The animals preferred hunting ban areas in summer and autumn, and selected for contrasting habitat characteristics within and outside these hunting ban areas. Thus, they showed clearer avoidance of humans when outside hunting ban areas. In the region of the Swiss National Park, we detected the lowest effects, which indicates that it fulfils its function as a S*trict Nature Reserve* where all human use is prohibited except for hiking on trails and scientific studies. In open summer habitats of that area, red deer selected forage quantity over forage quality. We further developed a method to classify the behaviour types *lying*, *feeding*, *standing*, *walking*, and *running*, based on accelerometer data also recorded by the collars. We conclude that for our system humans largely influence the spatio-temporal behaviour of red deer. As even a network of small-scale hunting ban areas is effective at reducing human effects, hunting ban areas can serve as a promising tool in red deer conservation and management.

Kurzfassung

In Berglandschaften ohne nennenswerte Ausbreitungsbarrieren für Tiere, mit einem Netzwerk kleinräumiger Jagdschutzgebiete und kurzer, intensiver Jagd, analysierten wir das Raum-Zeit-Verhalten von teilweise wandernden Rothirschen. Basierend auf GPS-Positionen von 243 besenderten Individuen aus sechs hauptsächlich in der Schweiz gelegenen Untersuchungsgebieten, wendeten wir *integrated step selection functions* an. Zunächst analysierten wir die Habitatwahl im Rahmen der *Landschaft der Angst*. In Abwesenheit natürlicher Beutegreifer konzentrierten wir uns auf Auswirkungen des Menschen. Als nächstes testeten wir, wie die Rothirsche im Sommer zwischen Futterqualität und Futterquantität wählten. Die Rothirsche mieden tagsüber Habitate, in denen sie mit höherer Wahrscheinlichkeit Menschen begegneten, während sie diese nachts präferierten. Sie bevorzugten im Sommer und Herbst Jagdschutzgebiete und selektierten Habitatmerkmale innerhalb und ausserhalb dieser Jagdschutzgebiete unterschiedlich. So mieden sie den Menschen ausserhalb von Jagdschutzgebieten deutlicher als innerhalb. Im Schweizerischen Nationalpark stellten wir am wenigsten Effekte fest, was darauf hindeutet, dass dieser seine Funktion als *Strenges Naturreservat* erfüllt, in dem jegliche menschliche Nutzung mit Ausnahme von Wanderungen auf Wegen und wissenschaftlichen Studien verboten ist. Im Offenland dieses Gebiets selektierten Rothirsche für Nahrungsquantität gegenüber Nahrungsqualität. Wir entwickelten zudem eine Methode zur Klassifizierung der Verhaltenstypen *Liegen*, *Fressen*, *Stehen*, *Gehen* und *Rennen*, basierend auf Beschleunigungsdaten, die ebenfalls von den Halsbändern aufgezeichnet wurden. Für dieses System folgern wir, dass der Mensch das Raum-Zeit-Verhalten von Rothirschen stark beeinflusst. Da ein Netzwerk selbst von kleinräumigen Jagdschutzgebieten menschliche Einflüsse reduzieren kann, können Jagdschutzgebiete ein vielversprechendes Instrument für den Schutz und das Management des Rothirschs sein.

1 Introductory overview

1.1 Introduction

In this dissertation *The impact of habitat characteristics on spatio-temporal behaviour of red deer (Cervus elaphus)* is analysed on the basis of GPS locations of tagged red deer individuals from the Central Alps. It is thus located in the research field of movement ecology and aims to increase the knowledge base on red deer behaviour, which is relevant for its conservation and management.

1.1.1 Movement ecology – a rapidly growing field of research

The movement ecology framework considers four key components of movement: the internal state of the individual, its motion and navigation capacities, and external environmental factors (Nathan et al., 2008). This framework includes the organism's motivation to move (e.g. hunger), its anatomy or physiology, its orientation or memory, as well as the landscape in which it finds itself, including obstacles or the climate. Due to the development of technical devices and their continuous improvements, a dynamic field of research has opened up that is developing rapidly. Thanks to Global Positioning System (GPS) telemetry we are able to record and analyse animal movements spatially and temporally (Cagnacci et al., 2010). Observations in the field are therefore no longer absolutely necessary. In addition, data is generated from areas or habitats that are not visible to observers and also during hours of darkness.

Characteristics of an organism's movements can be determined from the simple form of its spatio-temporal information. Knowing when and where an organism was creates relationships through sequences of recorded locations. Analyses of movement trajectories of tracked individuals aim at different results depending on the semantic level of interest (Laube, 2017): from the single fix of an animal (place and time of its whereabouts) to its displacements (e.g. distance), the manner of its displacements (e.g. speed, sinuosity), or the subdivision of the trajectory into segments with the same characteristics (e.g. static or moving). GPS data are also used to describe home ranges or resource selection using a variety of methods (Manly et al., 2002; Börger et al., 2008). This often involves defining units of time that are tangible for humans (years to hours, or even a few minutes). Movement information is also linked to an additional context, for example, the distance to a point of interest, the crossing of a line or the position in relation to an area (Gschwend, 2015). An animal’s movement data are then linked to environmental data, in particular to analyse external factors in their environment such as habitat types, human land use or weather (Dodge et al., 2013). Thus, most information describing movement is derivative and is based on results of data compilation, calculation, and interpretation (Laube, 2014).

In addition to GPS sensors, today's technical devices might also contain accelerometer sensors, which are often referred to as activity sensors. For example, by averaging accelerometer values per day, fluctuations in activity over the course of the year can be visualised (e.g. Brivio et al., 2016). However, accelerometer data is also used to classify certain behaviours of animals, especially in combination with movement data (Van Moorter et al., 2010; Shamoun-Baranes et al., 2012; Schmidt et al., 2016). Behavioural patterns derived from movement data can also be used to measure the effectiveness of conservation goals, particularly for migratory species (Ellis-Soto et al., 2025).

1.1.2 Ungulates and the concept of the «landscape of fear»

Ungulates are popular study species in movement ecology. On the one hand, they are suitable because they are common and relatively easy to catch. Furthermore, they are large enough so that the use of sensor collars is unproblematic from an animal ethics point of view. Prey species, such as ungulates, react to the presence of predators by adapting their behaviour and trying to avoid risks (Brown et al., 1999). On the

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one hand, this avoidance behaviour is innate, as for example shown by the antipredator behaviour of neonates (Atmeh et al., 2024). On the other hand, ungulates are able to take other aspects into consideration through learning and experience (Stankowich & Blumstein, 2005). These include, for example, the speed and size of the predator, the individual's physical condition based e.g. on reproductive state and size, environmental factors such as topography or the availability as well as accessibility of cover, and time of day. Due to the need to forage, they develop strategies that provide the most energy at the lowest cost (Pyke, 1984; Stephens & Krebs, 1986). For data-based analyses, it is crucial that relevant habitat characteristics are available as quantitative variables at the desired spatial and temporal resolution.

The concept of the *landscape of fear* implies that a prey animal is able to perceive different levels of predation risk in its home range and to respond with different levels of fear (Laundré et al., 2010). This means that the physical landscape together with predation risk influence prey animals' risk perception, which in turn can cause behavioural adaptations, e.g. in the distribution of prey species (Gaynor et al., 2019). In addition to applying this concept to natural predators, it is also used in relation to humans, especially because hunting affects the behaviour of prey animals. In movement ecology, effects of hunting have been identified for many ungulate species. Differences have also been found between their behaviour during the day and at night, when darkness provides some level of safety (Gaynor et al., 2018). If no GPS locations are available for predators or humans, proxies for their spatio-temporal behaviour, e.g. distances to trails, streets or settlements, their densities or the human footprint index, are included as part of the habitat characteristics in the explanatory variables to assess the corresponding effects on prey animals (Proffitt et al., 2013; Tucker et al., 2018). Variables such as hunting pressure are often categorically assigned to specific areas. This is because a study area may contain sub-areas with varying intensities of hunting pressure, representing different levels of risk for the animals (Griesberger et al., 2022). For example, both reduced movement and space use by white-tailed deer (*Odocoileus virginianus*) are interpreted as avoidance behaviour in response to risk from hunters (Little et al., 2016). Similarly, roe deer (*Capreolus capreolus*) no longer positively selected their feeding sites during the hunting season based on forage availability (Benhaiem et al., 2008). Taking into account time of day, it was described that they used more forested habitats during the day, but open fields at night (Bonnot et al., 2013). In addition, roe deer used open fields more during the day with increasing distance to roads and settlements. Other findings show that they decreased the use of high-crops during the day and used protected areas as a refuge from hunters (Grignolio et al., 2011). In the days following the hunt, white-tailed deer decreased the use of areas around hunting stands during the day, but increased usage of these sites at night (Sullivan et al., 2018). Female moose (*Alces alces*) also showed a pattern of avoiding higher-risk areas more during the day than at night during and less so after the hunting season (Ausilio et al., 2025). They further avoided settlements and preferred to be close to the forest if they had lost their young due to hunting the previous year (Graf et al., 2024).

It is further known that not only hunting, but also human recreational activities trigger behavioural reactions in a comparable way to predation (Frid & Dill, 2002; Stankowich, 2008). The consequences include increased vigilance (Beauchamp, 2015), flight (Ydenberg & Dill, 1986; Schnidrig-Petrig & Ingold, 2001), changes in habitat selection (Gander & Ingold, 1997; Filla et al., 2017), or reduced activity levels (Graf et al., 2018). A pronounced aspect is that recreational activities also affect parental investment in offspring (Gill et al., 2001), the condition of parents, and their reproductive success (Frid & Dill, 2002). Such negative effects can negatively affect population size over time (Sutherland, 1996). Disturbance effects are therefore an important component to consider in ungulate conservation and management, and movement ecology analyses can help recognise them.

In this context, another finding is significant: Mammals can also adapt their behaviour in the opposite direction, namely when the presence of humans decreases. This was shown during the COVID-19 lockdowns, when mammals increasingly used areas near roads with large human footprints (Tucker et al., 2023).

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1.1.3 Safety vs. forage needs of red deer

The safety needs of ungulates in relation to natural predators, hunters and human recreational activities are the subject of considerable research interest, and a considerable amount of work has been conducted on elk/wapiti (*Cervus canadensis*) and red deer (Mattioli et al., 2022). After grey wolves (*Canis lupus*) were reintroduced to Yellowstone National Park, elk/wapiti adapted their habitat use in favour of greater safety in response to the natural predator (Hernández & Laundré, 2005). Further, red deer responded to hunting with preferences for dense vegetation, increased flight distance, and more time spent outside their core home ranges (Meisingset et al., 2022). Interestingly, differences in fear reactions were observed both within and between sexes at the onset of hunting (Lone et al., 2015): Males that moved to habitats offering more cover survived the hunt, while those that did not were shot. In addition, males moved to habitats with lower forage quality while neither effect was detected in females. This could be because male elk/wapiti already largely used habitats with good cover before the hunt began. In Canada, older female elk/wapiti reduced their movement rates and increased the use of forest and steeper terrain with increasing age, and became almost inaccessible to hunters (Thurfjell et al., 2017). They even responded differently to hunters with bow and arrow compared to those with rifles (see also Proffitt et al., 2013).

Hunting is generally perceived as a more acute threat than human recreational activities (Jayakody et al., 2008), but human disturbance effects on elk/wapiti behaviour even exceeded the effects of habitat and natural predators (Ciuti et al., 2012). As other ungulates, red deer were more vigilant in the presence of humans, especially in habitats with little cover (Jayakody et al., 2008). Red deer in alpine habitats avoided roads and hiking trails, instead preferring areas near forest cover, and thus adapted their behaviour to possible human presence (Sigrist et al., 2022). Avoidance of hiking trails was also observed even among red deer that seemed to be habituated to humans, i.e. in habitats with regular human presence (Sibbald et al., 2011; Westekemper et al., 2018). Another study on elk/wapiti and red deer identified human activity as the strongest driver of movement, even when compared with forage availability or topography (Mumme et al., 2023). Differences between the behaviour during the day and at night have also been confirmed in red deer due to the main activity of humans during the day (Godvik et al., 2009; Allen et al., 2014). Moreover, they used protected areas to avoid risk (Proffitt et al., 2009; Mikle et al., 2019). In a study area with zones of varying restrictions on recreational activities, both factors were taken into account: adapted behaviour in protected areas and a distinction between day and night (Coppes et al., 2017).

Although much is known about red deer and their behaviour, analyses of new combinations of the animals' natural needs and the influence of human disturbance can create new knowledge, especially in alpine regions. As many previous studies have tested effects on the behaviour of red deer during certain seasons, analyses that differentiate between day and night, but also over the course of the year, and take into account the influence of an entire network of hunting ban areas (see chapter 1.1.5) based on a large sample of individuals, could close existing knowledge gaps. This promises new insights into red deer biology with a focus on conservation and management.

Ungulates face a trade-off between safety and forage needs (Mysterud & Ims, 1998; Hernández & Laundré, 2005; Godvik et al., 2009). Red deer avoid humans even at the expense of forage quality (Ciuti et al., 2012; Lone et al., 2015; Mikle et al., 2019). A second trade-off exists between forage quality and quantity (Stephens & Krebs, 1986; Fryxell, 1991). Depending on their digestive systems, ruminant species have been classified into three main feeding types of browsers, grazers and intermediate feeders, each with different requirements for the quality and quantity of food (Hofmann, 1989). Red deer belong to the intermediate feeder type (Mattioli et al., 2022), and meet their high metabolic needs by consuming large amounts of food. The availability and quality of forage is higher in summer, and the animals voluntarily consume less food in winter (Zweifel-Schielly et al., 2012; Arnold et al., 2015). Previous attempts to determine the food preferences of red deer have produced ambiguous results, with some studies identifying preferences for forage quality (Zweifel-Schielly et al., 2009) and others for quantity (Schweiger et al., 2015a; Sigrist et al., 2022). The reasons for this lie, on the one hand, in the behaviour of red deer and elk/wapiti. Within populations, there are usually migrating and resident individuals that use their ability to leave unsuitable areas in favour of better ones (Mysterud et al., 2011; Peters et al., 2019) with correspondingly different forage selection patterns. Thus, migrants have better access to high quality forage (Hebblewhite et al., 2008; Bischof et al., 2012; Sigrist et al., 2022). These authors and others showed that red deer in mountainous landscapes, combine this with a shift to higher-elevation habitats in summer (Zweifel-Schielly et al., 2009; Garroutte et al., 2016; Proffitt et al., 2016; Mysterud et al., 2017; Fellmann, 2022). On the other hand, different forage selection between the sexes is to be expected due to sexual dimorphism in ruminants, with females selecting more strongly for forage quality and males for forage quantity (Barboza & Bowyer, 2000; Ruckstuhl & Neuhaus, 2002). These patterns are not necessarily observed in red deer (Clutton-Brock et al., 1982). In contrast, a study in a Mediterranean mountainous environment found that males consumed higher quality forage than females, mainly because they fed more on arboreous species (Garcia et al., 2023). However, variables for quality and quantity are difficult to obtain because both change over the course of the season and are generally difficult to separate (Langvatn & Hanley, 1993; Wilmshurst et al., 1995; Huete et al., 2002).

Today, space- and airborne remote sensing instruments are used in movement ecology to gather crucial data. Passive remote sensing instruments work by measuring the reflected sunlight of the earth's surface at different wavelengths. However, all these systems face key constraints, including limitations in spatial resolution, revisit times, and the number of spectral bands. Data vary considerably between resolutions of 2 m and 8 km, single snapshots in time and one per day, and two to 312 spectral bands (e.g. Hebblewhite et al., 2008; Hamel et al., 2009; Schweiger et al., 2015b). To predict specific variables over larger areas, the spectral information has commonly been calibrated using field samples (Hebblewhite et al., 2008; Hamel et al., 2009; Proffitt et al., 2016; Johnson et al., 2018). Taking into account the constraints of satellite data, vegetation indices were developed, especially the Normalized Difference Vegetation Index (NDVI), to generate information on the greenness of the vegetation (Cracknell, 2001; Beck et al., 2011; Pettorelli, 2013; Neumann et al., 2015). The strength of the NDVI is that it is versatile because it is related to many vegetation characteristics (Huete et al., 2002). This is precisely why it can be used as a proxy for forage quality (e.g. Hamel et al., 2009) or quantity (e.g. Hansen et al. 2009) but is not suitable for analysing the corresponding forage selection. However, imaging spectrometers, commonly referred to as hyperspectral sensors, could be used to derive forage quality and quantity (Schweiger et al., 2015a), but lack the necessary revisit time to map developments over an entire growing season. A current option is the Sentinel-2 satellite constellation developed by the *European Space Agency*, with 10 spectral bands at spatial resolution of 10 to 20 m and a revisit time of 5 days (Drusch et al., 2012). In addition to the possibility of deriving vegetation indices from surface reflectance, the spectral bands of the Sentinel-2 sensors also allow the estimation of biophysical and biochemical plant traits (Punalekar et al., 2018; Rossi et al., 2020). Using physical laws, radiation transfer models describe how vegetation interacts with light, allowing for the modelling of surface reflectance based on canopy and leaf traits (i.e. optical traits), as well as the background soil (Houborg et al., 2015). Thus, by inverting such models it is possible to derive proxies for forage quality and quantity from the remotely sensed surface reflectance at high spatial and temporal resolution despite a reduced number of bands compared to hyperspectral sensors (Raab et al., 2020). These estimates have not yet been applied to animal species but have the potential to clarify whether red deer select for quality or quantity, as they generate more specific variables that go beyond the exclusive use of conventional vegetation indices, such as NDVI. In addition, they also enable comparisons in forage selection between the sexes in heterogeneous alpine habitats characterized by short vegetation periods, again in the context of environments influenced by human activities.

1.1.4 Classification of behaviour types

Movement analyses of animals tagged with GPS collars aim at shedding light on spatio-temporal patterns. In a sense, these patterns, such as habitat selection, provide information about the animals' behaviour and can contribute to effective conservation and management of the species (Sutherland, 1998; Ellis-Soto et al., 2025). However, they have the limitation that they do not allow direct conclusions to be drawn about different types of an animal's behaviour (Laube, 2017).

GPS collars are often additionally equipped with accelerometers, which measure the relative movement of the collar as the difference in acceleration between successive measurements (Krop-Benesch et al., 2011). In other words, they measure the intensity of the collar’s - and hence the animal's - movement. Thus, accelerometer data can be used to derive an animal’s activity levels (Stache et al., 2013; Brivio et al., 2016; Figure 1). For various species of carnivores and ungulates, classification models have been used to assign specific animal behaviours to accelerometer data (e.g. Signer et al., 2010; Wang et al., 2015). Former behavioural classification models for ungulates were trained with accelerometer data of captive (Naylor & Kie, 2004) or free-ranging animals (Kröschel et al., 2017), of low (i.e. few minutes; Gaylord, 2013) or high temporal resolution (i.e. multiple measurements per second; Kirchner et al., 2023), and as binary (Roberts et al., 2016) or multiclass models (Löttker et al., 2009). While binary models classify two modes, e.g. feeding vs. walking, or active vs. inactive, multi-class models can classify more than two behaviours.

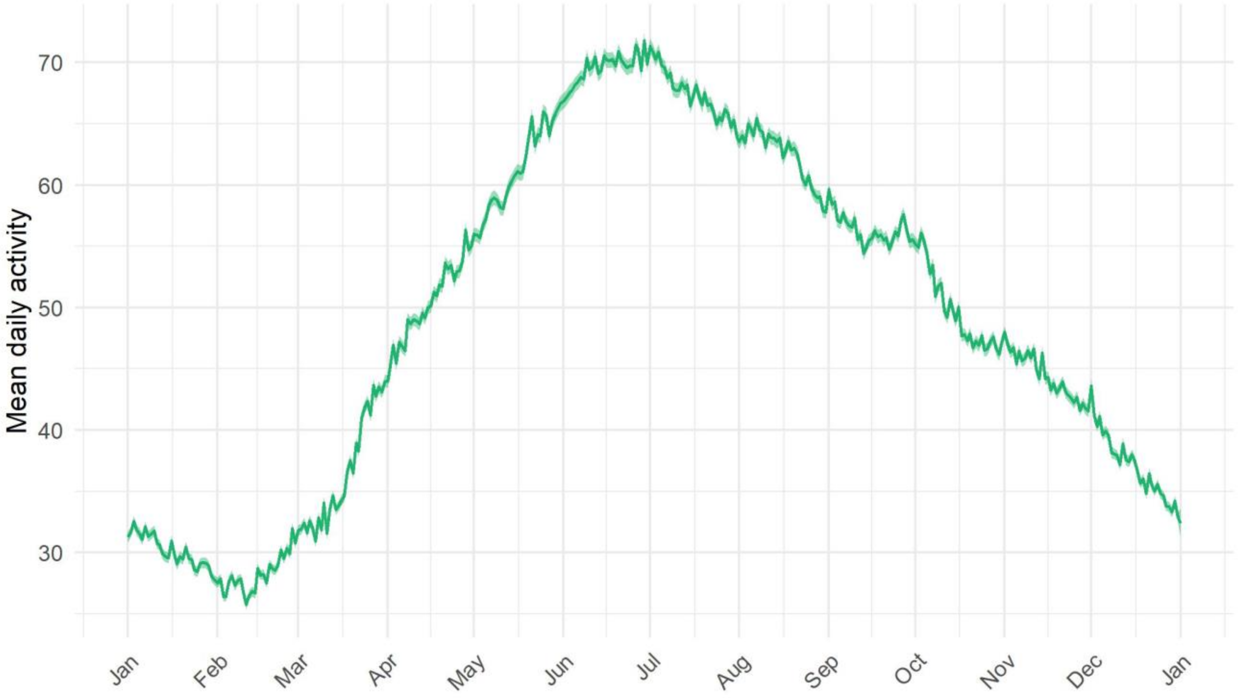

Figure 1: Mean daily activity per month of red deer from the Swiss National Park and its surroundings (years from 2010 to 2021). Mean daily activity was calculated as the daily mean root of the sum of squares of two-axis accelerometer data (forward-backward motion, left-right motion). Plot adapted from Lars Korzelius, Swiss National Park. Data by Swiss National Park, unpublished.

As with other sensors, accelerometers generate large data sets that researchers are faced with today (Tuia et al., 2022). The sheer size of such data sets makes machine learning algorithms a welcome tool for detecting patterns and thus can provide new insights into animal behavioural ecology (Norouzzadeh et al., 2018; Eikelboom et al., 2019; Schneider et al., 2019). A variety of algorithms has been developed, including discriminant function analysis (Naylor & Kie, 2004; Gaylord, 2013), recursive partitioning (i.e., classification and regression trees; Löttker et al., 2009; Heurich et al., 2012), or random forests (Kröschel et al., 2017; Kirchner et al., 2023). For griffon vultures (*Gyps fulvus*), fur seals (*Arctocephalus spp.*) and sea lions (*Neophoca cinerea*), the efficacy of different machine learning algorithms for classifying behaviour has been compared (Nathan et al., 2012; Ladds et al., 2016), but not yet for free-ranging cervids. Classification models trained on captive animals may perform well for captive animals, but they may not for free-ranging animals because their behaviour may differ (Pagano et al., 2017). So far, there is a lack of multiclass models that have been trained using low-resolution data from free-ranging cervids. In addition, the gap of comparing the accuracy of several classification models based on different machine learning algorithms was to be closed.

1.1.5 Red deer management in Switzerland – a constant challenge

In Switzerland, the management of huntable and protected species under the *Federal Hunting Law* is the responsibility of the 26 cantons (§3, Federal Hunting Law, SR 922.0). The Swiss cantons are comparable to federal states or provinces in other European countries. The law takes ecological principles into account and thus requires the preservation of biodiversity, the protection of wildlife habitats and endangered species, adequate protection from human disturbance, the designation of protected areas, and the designation of supra-regional wildlife corridors. Hunting rights are not tied to private land ownership. Cantonal hunting authorities, and in most cantons also state gamekeepers, enforce hunting legislation while each canton decides on its own hunting system. Hunting is carried out by recreational hunters. There are currently three hunting systems (Baumann et al., 2014): patent hunting, district hunting and state hunting. In 16 cantons, and thus in most parts of Switzerland, hunting is organised as a licence system (patent), whereby anyone with hunting rights can purchase a cantonal hunting permit each year and is free to choose their hunting grounds. In nine cantons, the district hunting system applies, where specific hunting grounds are leased to groups of hunters for several years. State hunting is the exception and only recognised in the canton of Geneva. There, recreational hunting was abolished by democratic decision in 1974, and state gamekeepers have since been responsible for regulating wildlife populations.

In the late 19th century, many wildlife species were extinct or greatly reduced in Switzerland. Consequently, the first hunting law was introduced in 1876 to regulate hunting. In particular, restrictions on hunting seasons, protection of mothers and young animals, and the establishment of state gamekeepers were aimed at restoring wildlife populations (Baumann et al., 2014). Protected areas in the form of hunting ban areas played a key role in this process (§1, Federal Hunting Ban Areas Ordinance, SR 922.31): Since ungulate populations were expected to recover in hunting-free areas, the cantons of the mountainous regions in particular were instructed to designate areas where hunting is banned. Until the beginning of the 20th century, 43 federal hunting ban areas were subsequently established throughout the country. In addition, many cantons had also designated cantonal hunting ban areas, among those the canton of Grisons since 1906. Europe's first hunting ban area was established in the canton of Glarus as early as 1548. The Swiss National Park was founded in 1914 as the first large-scale protected area in the Alps. According to the categories of the International Union for Conservation of Nature (IUCN), the Swiss National Park is a category Ia protected area (*Strict Nature Reserve*) where all human use is prohibited except hiking on trails (§1, National Park Law, SR 454). This area was thus removed from human use, compliance with the strict rules was ensured by park wardens, and natural processes were to be the subject of ongoing research (e.g. Haller, 2002).

From a nature conservation perspective, these measures have achieved the desired success. In the last 150 years, many populations have been able to recover and species have returned to Switzerland, including the red deer, after being largely eradicated in the 17th century (Haller, 2002). Due to the legal research mandate, park wardens in the Swiss National Park have recorded the summer populations of red deer, documenting an increase from 0 in 1914 to over 2000 individuals in the 1970s and 1980s (Figure 2). There is even reason to believe that they significantly underestimated the population from the 1950s to the 1980s (Haller, 2002). As early as 1928, the *Swiss Federal National Park Commission* called for more ecologically oriented research into ungulates (Burckhardt, 1991): "*It would be desirable if, in addition to the mere enumeration of the observed game, there is also information about the change of locations and its causes, about the ratio of sexes and of game and predatory animals, about the behaviour of the animals towards humans and, above all, about observations of all kinds regarding the effects of strict protection. This would provide the most valuable material for scientific processing and research, and probably also for the legal regulation of hunting.*"

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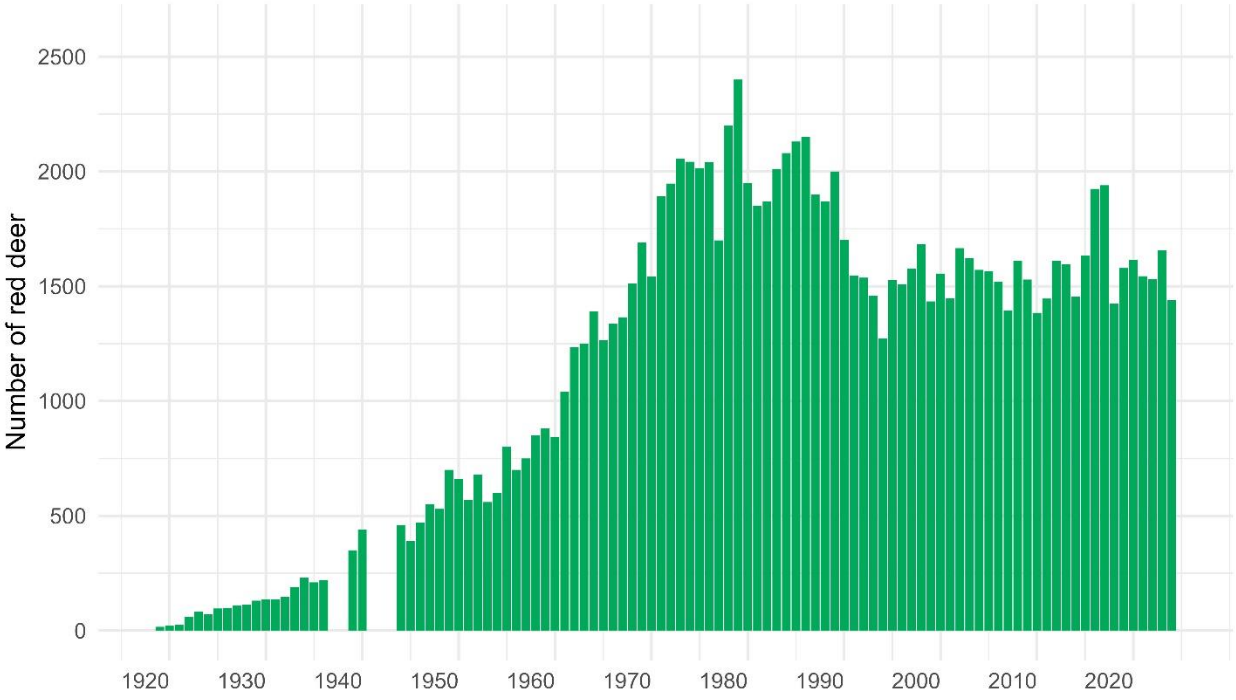

Figure 2: Red deer population development in the Swiss National Park from 1914 to 2024 after being largely eradicated in the 17th century (Haller, 2002). Data by Swiss National Park, unpublished.

The hunting legislation of the canton of Grisons, where the Swiss National Park is located, has traditionally set additional constraints as hunting red deer is limited to a maximum of 21 days in September (§11, Cantonal Hunting Law, BR 740.000). Hunting at night is prohibited. Due to the rapid population growth in the Swiss National Park and its surroundings between the 1940s and 1980s, repeated and increased winter mortality, and damage to forestry and agriculture soon occurred (Burckhardt, 1957; Haller, 2002). Efforts to regulate red deer populations clearly did not have the desired success, even though female red deer had also been hunted since the 1950s. At the time, politicians and society generally referred to the situation as the *red deer problem*, and there were no solutions. Initial tagging of red deer individuals enabled descriptions of annually recurring migrations between the same summer and winter habitats beyond the park boundaries: in summer, many red deer were inside the Swiss National Park, but outside in winter (Schloeth, 1961). At the same time, the extent of bark stripping and browsing in winter habitats outside the Swiss National Park gave cause for concern about natural regeneration in the forest (Kurth et al., 1960). In addition, malnutrition was considered to be the cause of winter deaths, affecting 60% of animals according to post-mortem examinations (Klingler, 1966). An experiment involving a hunting weekend in the surroundings of the Swiss National Park outside the traditional hunting season in late autumn 1956 was successful. However, it provoked an outcry in the media, prompting the cantonal hunting authorities to abandon this approach due to public pressure and instead focus on shooting lactating females in the surroundings of the Swiss National Park until 1966 (Haller, 2002). This in turn led to increased hunting pressure on individuals exhibiting behaviours that did not involve summer use of the hunting-free Swiss National Park, which was detrimental to long-term hunting success (Jenny & Filli, 2014). Despite a doubling of the number of hunters between 1953 and 1980 and the associated increase in hunting pressure, the hunting bag in the canton of Grisons stagnated between 1956 and 1970 at an average of 1,623 individuals (jagdstatistik.ch/gr/hunting_bag), while the red deer population continued to grow also in the Swiss National Park (Figure 2).

It stands to reason that the *red deer problem* in the surroundings of the Swiss National Park was due to the high population density relative to the resources available in their habitat (Buchli, 1979). Finally, the lifting of taboos, including culling during special hunts in November and December and culling within the Swiss National Park from 1973 to 1995, which was not provided for by law, led to the desired regulation of red deer populations (Haller, 2002): since 1995, the summer population in the Swiss National Park has averaged 1,567 individuals (Figure 2). Importantly, additional cantonal hunting ban areas of small size have been designated since the 1980s to optimize the summer distribution of red deer and to sustainably ensure high hunting success, while at the same time protecting potential rutting areas. Hunting in September nowadays ensures basic regulation across the canton considering aspects of population ecology. Thus, calves and their mothers are not huntable in order to preserve established behavioural traditions with resident individuals also ocurring outside hunting ban areas. Males at the peak of their social importance, especially during the rutting season, which takes place from mid-September to the beginning of October, are only hunted in very small numbers. Hunters use the crowns on both sides of the antlers as a proxy to identify such individuals. The ecological reason for this regulation is that, as recorded in the Swiss National Park, a shortage of older, experienced males during the rutting season resulted in only a few dominant males, which led to oversized herds and a prolonged rutting season (Klingler, 1966; Haller, 2002). During the second hunting phase in November and December, red deer populations have been culled since 1987 on a maximum of ten half-days across the canton. The number of animals is thus locally adjusted to the social and economic carrying capacity of the winter habitats, with particular attention being paid to balancing the sex ratio in the hunting quota. Over the past 25 years, an average of 5,807 hunters have practised hunting in the canton of Grisons (jagdstatistik.ch/gr/hunters). While they exert high hunting pressure on red deer during the short hunting season, there is no hunting during the rest of the year.

However, hunting authorities were aware that managing red deer did not simply mean culling animals. A more ecological approach was required, and detailed knowledge of (a) population size, (b) physical condition of individuals, (c) spatio-temporal behaviour, (d) availability and utilization of forage, and (e) extent of damage in forests and agricultural areas was henceforth considered fundamental to red deer management (Blankenhorn et al., 1979). It is crucial that standardized monitoring is established for these factors, thereby creating the basis for long-term data series. Hunting quotas were henceforth derived from standardized nocturnal censuses carried out annually in spring when the meadows in the valley bottoms turn green, in order to understand the population dynamics over the years (Buchli, 1979). In addition, wildlife officials record the sex, age, presence of calves, body weight, and the length of the hind foot and lower jaw of the hunted individuals (Baumann et al., 2014). A simple ratio of body mass divided by the length of hind foot or lower jaw is also recommended, taking into account sex and age class (Baumann et al., 2010). The theory behind this is that females living in habitats with sufficient forage and cover or protection would be expected to give birth to strong calves and be able to provide them with sufficient milk (Buchli, 1979). This would create the conditions for their calves to reach their maximum body size during their growth phase. Calves of mothers living in poorer conditions, i.e. in higher population densities and with insufficient resources, would be less well nourished, and consequently grow more slowly and do not reach their maximum body size during their growth phase. Over time, such an area would be populated mainly by small individuals. Consequently, changes in these measures over the years may indicate either an undetected increase in population, a decline in forage resources, or reduced access to these resources, e.g. due to increased human disturbance. This was incorporated into legislation, and today the cantons are required to keep statistics on the population and hunting bags of red deer (§3, Federal Hunting Law, SR 922.0).

For the management of red deer, it is further essential to understand their spatio-temporal behaviour. Based on the findings generated from tagged individuals, management units were designated in the canton of Grisons. Otherwise, there is a risk that hunting quotas are planned based on the population size in an area without considering seasonal migration (Reimoser et al., 2014; Signer et al., 2021). To gain a better understanding of this, several cantons have carried out tracking projects using GPS collars in recent years, in some cases in cooperation with the neighbouring countries Austria, France, and Liechtenstein. As part of the ongoing red deer expansion in Switzerland, these projects have additionally aimed at identifying habitat suitability or connectivity corridors (Patthey, 2003; Fischer et al., 2024), in order to comply with legal requirements. They have also described variation in red deer physiology and activity over the course of the year (Reimoser et al., 2014; Thiel et al., 2018) confirming the local minima and maxima in winter and summer metabolism (Arnold et al., 2004).

Red deer management with supplementary feeding in winter to prevent mortality and damage to forestry and agriculture failed in the canton of Grisons, although damage to the forest can be reduced through diversionary feeding (Arnold et al., 2018). Consequently, earlier attempts to optimize management based on the German and Austrian models were abandoned (Jenny & Filli, 2014). Today, supplementary feeding is even prohibited in the canton of Grisons (§29a, Cantonal Hunting Law, BR 740.000). Instead, targeted biotope management aims to improve natural food resources while providing favourable habitats with suitable cover and protection in summer and winter. In order to reduce energy losses due to anthropogenic disturbances in winter, wildlife refuges have been designated throughout the canton of Grisons and now also in most cantons of Switzerland. In these refuges access for humans is prohibited in winter or only permitted on designated paths (Baumann et al., 2010). Thus, based on the experiences gained in the Swiss National Park and its surroundings, two types of protected areas play an important role in today's Swiss red deer management: hunting ban areas in summer and autumn, and wildlife refuges in winter and spring. Knowing that low-disturbance areas can also lead to concentrations of red deer (Haller, 2002; Figure 2), offering seasonal protected areas is an option, especially in systems with seasonal migrations. With the designation of such protected areas in habitats with favourable natural conditions, it can be assumed that protection from humans makes them even more attractive to red deer (Proffitt et al., 2009; Mikle et al., 2019; Coppes et al., 2017). This strategy, coupled with a large number of smaller-scale hunting ban areas (Figure 3, taking the example of the canton of Grisons), aims to ensure that red deer are well distributed across the landscape. However, there is still a lack of scientific evidence that the summer distribution of red deer in particular can be controlled by these smaller-scale hunting ban areas, and thereby counteracting larger concentrations (Haller & Jenny, 2013).

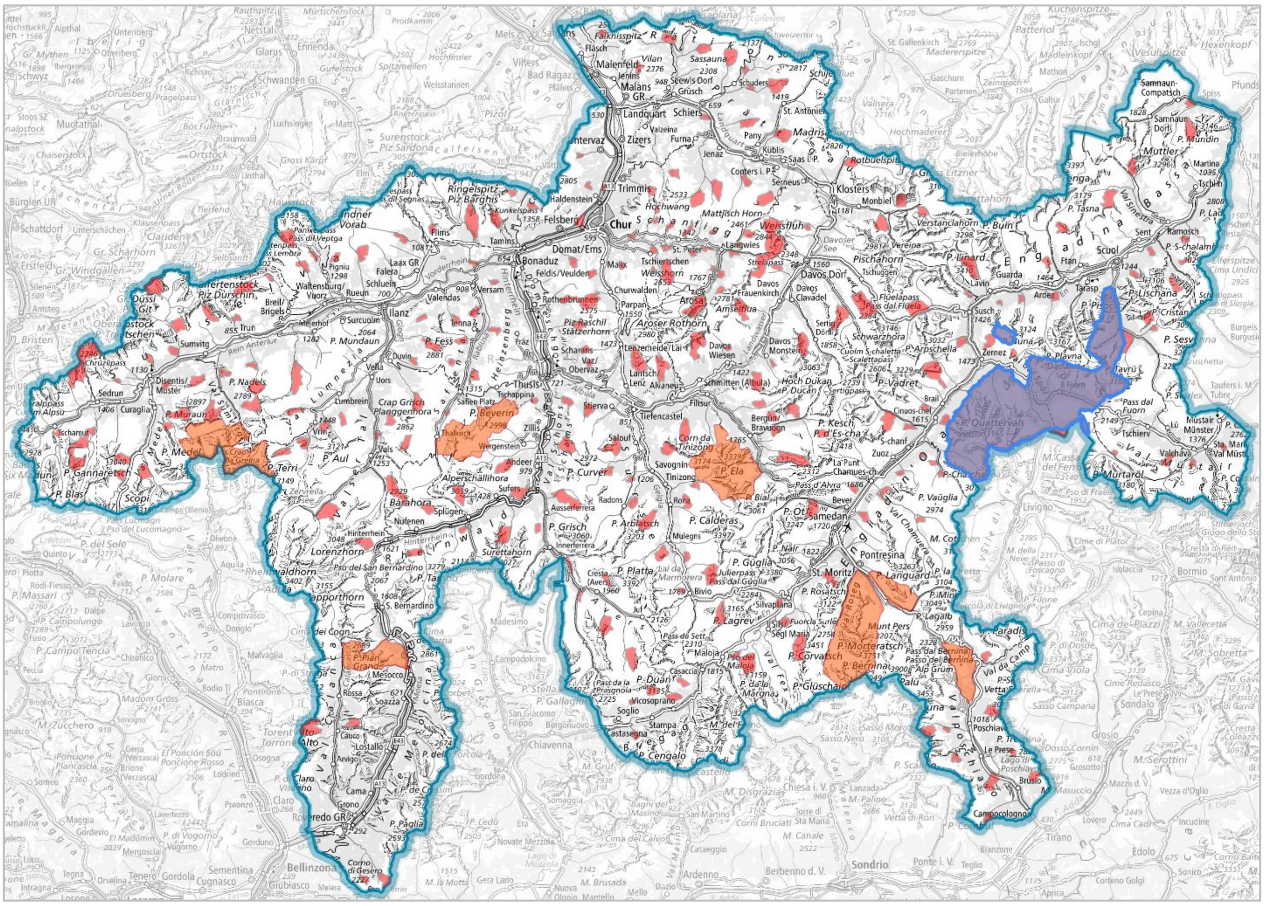

Figure 3: Hunting ban areas in the canton of Grisons including the Swiss National Park (blue), federal hunting ban areas (orange), and cantonal hunting ban areas (red). Map by Geoportal of Grisons' cantonal administration (map.geo.gr.ch/hunting_ban_areas)

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1.2 Research questions

The primary aim of this research was to refine knowledge about habitat selection of red deer with regard to two important needs: safety (**paper I**) and forage (**paper II**). Based on the broad knowledge about red deer, this research analysed their habitat selection in the Central Alps as a function of newly combined habitat characteristics, i.e. landscape variables, forage parameters, and proxies of human presence at the scale of individual movement trajectories. The second aim was to develop a method to classify behaviour types of wild red deer (**paper III**). In combination, this will provide new insights into red deer behaviour, which will serve as a basis for future conservation and management.

In **paper I**, we studied red deer habitat selection in networks of small-scale hunting ban areas in the Central Alps, which allowed us to compare their behaviour inside and outside these areas. Since large carnivores were mostly absent during the study period, humans were left as the only constant predator. We first analysed day- and nighttime habitat selection per month and study area to understand differences between day and night, as well as over the course of the year. We then focused on habitat selection specifically during the main hunting season in September, and differentiated between inside and outside hunting ban areas, and again between day and night and the different study areas. We expected red deer to select against habitat characteristics indicating human presence in all study areas during the day, but not at night. In addition, we expected red deer to select for hunting ban areas particularly during times of hunting activity. Finally, we discussed the habitat selection patterns of red deer, the differences between the study areas with a focus on human disturbances, and the impact of hunting ban areas on red deer behaviour.

While **paper I** concentrated on red deer's need for safety, in **paper II**, we integrated their need to forage with a focus on sex-specific selection of forage quality and quantity in the Swiss National Park and its surroundings. Since distinct variables for forage quality and quantity are not readily available, we first predicted dynamic parameters at high spatial and temporal resolution, and then analysed red deer habitat selection. We restricted our study to open habitats in summer (June to August), and accounted again for the effects of topography, vegetation and human disturbances. We expected red deer to select forage quantity over quality, with females showing weaker selection for quality than males. As in **paper I**, we expected both sexes to avoid humans. However, as we assumed that the Swiss National Park with its strict regulations on human use influenced red deer behaviour, the effects of habitat selection that indicate avoidance behaviour of humans could be dampened. We discussed the sex-specific habitat selection patterns of red deer, and the capability of satellite data to estimate separate variables for forage quality and quantity.

The methods in **papers I** and **II** revealed red deer habitat selection and its temporal variation. However, actual behaviour types remained hidden. We approached this task in **paper III** using accelerometer data complementary to GPS locations recorded by the collars, and collected behaviour data from red deer in the Swiss National Park by observation. We then trained classification models applying machine learning methods. In addition, we applied multiple algorithms, including different combinations and transformations of the accelerometer data, to find the most accurate classification models, and finally derived a new measure to determine which models most accurately classified red deer behaviour.

1.3 Methods

Captures of wild red deer were necessary to get the GPS locations and accelerometer data used in this research. Animals were captured by wildlife officials in accordance with national animal welfare laws and under permits issued by the cantonal and federal authorities. Unless otherwise stated, we performed calculations and analyses exclusively using R (R Core Team, 2022). For further details, please refer to the corresponding papers in chapter 2. Below we provide an insight into the methods used in the papers and explain any challenges as well as alternative methods.

1.3.1 Red deer location data and explanatory variables

GPS locations of red deer in six study areas were available at regular intervals of 1 to 4 hours over 1 to 3 years. Selecting a fix rate of 3 hours resulted in the largest sample of individuals. We had to exclude data from two other study areas, one because of irregular sampling intervals, and the other because the animals there did not have access to hunting ban areas. Thus, we used GPS locations of 243 red deer individuals (151 females, 92 males) recorded by three types of collars from VECTRONIC Aerospace GmbH, Berlin, Germany (GPS PLUS, PRO LIGHT and VERTEX PLUS). We then extracted information of landscape variables and proxies of human presence at these locations. These included *tree cover density*, *distance to trails*, *slope*, *elevation*, and *hunting ban areas* in **paper I** to analyse red deer's safety needs, and *biomass*, *relative nitrogen*, *distance to forest*, *distance to trails*, and *slope* in **paper II**. The latter analysis was carried out in order to additionally analyse the animals' need to forage in open habitats of the Swiss National Park and its surroundings, based on 66 individuals (45 females, 21 males). Except for *biomass* and *relative nitrogen*, all variables were available open source. The distance variables we calculated using the path distance tool in ArcGIS Pro (version 3.0.3, ESRI).

We chose nitrogen as a proxy for forage quality and biomass for quantity. Based on ESA's Sentinel-2 surface reflectance data (Drusch et al., 2012), we derived vegetation indices and optical traits, and modelled dynamic parameters of forage quality and quantity at a spatial resolution of 50 m and an average temporal resolution of 7.7 days (Raab et al., 2020). To achieve this, we trained two distinct random forest models to predict biomass and nitrogen using the remote sensing products as predictor variables. We used field measurements of biomass and nitrogen from 2011 to 2013 (Schweiger et al., 2015a) and 2016 to 2018 (Rossi et al., 2020, 2022) as response variables in the models. We quantified the importance of the predictor variables by grouping the variables by correlation and by variable types, i.e. surface reflectance, vegetation indices and optical traits in predicting forage quality and quantity. Next, we linked each GPS location to the temporally closest Sentinel-2 image, then used the best-performing models to predict biomass and nitrogen from the Sentinel-2 data for all GPS locations. As the absolute values (i.e. g/m^2) of nitrogen and biomass are correlated, comparing the selection of quality and quantity was difficult. We solved that using relative canopy nitrogen content (hereafter referred to as *relative nitrogen*) instead of the absolute values as a proxy for forage quality (Schweiger et al., 2015a), in the knowledge that it would cause subsequent problems: in areas where vegetation cover does not correlate with nitrogen content, e.g. in sparsely vegetated areas, the application of concentration measurements is problematic. From a radiative transfer perspective, the spectral signal of a surface is determined by the absolute amount of nitrogen rather than its concentration. To reduce these uncertainties, we used a large number of field measurements to train the random forest models and consistently excluded GPS locations with values not seen during model training from the habitat selection analysis.

1.3.2 Analyses of habitat selection

Against the background that prey species such as red deer (a) select their habitats according to their requirements for landscape features, and (b) safety needs drive them to modify their habitat selection in response to natural predators and humans (Frid & Dill, 2002; Proffitt et al., 2009; Laundré et al., 2010), we looked for methods to refine knowledge in alpine environments that contained networks of small-scale hunting ban areas. One frequently used approach for analysing GPS data are resource-selection functions (Manly et al., 2002). As the term resource-selection function is quite narrowly defined, it has been extended to habitat-selection functions, which can include environmental conditions and risks in addition to mere environmental resources (*sensu* Fieberg et al., 2021). Thus, habitat-selection functions set environmental variables, conditions or risks at locations that are used by an animal in relation to locations that are assumed to be available. In other words, habitat-selection functions model the relative probability that an available location will be used for its habitat type or value (Lele et al., 2013).

Depending on the research question, habitat-selection functions are applied at different scales (Johnson, 1980): 1st order - at the population scale (i.e. species distribution), 2nd order - at the home range scale, 3rd order - at the patch scale within home ranges, and 4th order - at the site scale. While the first three orders are often analysed using logistic regression, the 4th order is by conditional logistic regression (Boyce & McDonald, 1999; Fortin et al., 2005; Thurfjell et al., 2014). Habitat-selection functions for animal GPS data typically ignore trade-offs, e.g. between the selection of forage and cover for safety, and that these may change over the course of a day (Godvik et al., 2009; Allen et al., 2014; Coppes et al., 2017; Fattebert et al., 2019). This may lead to changes in the relative use of habitat types if availability differs among individual home ranges. So-called functional responses in habitat selection and their underlying behavioural mechanisms can be identified by estimating habitat-selection functions through mixed-effects logistic regression (Godvik et al., 2009). However, habitat-selection functions have one main disadvantage: while the used locations are given by the GPS data of tagged animals, these approaches share the challenge of defining available locations (Matthiopoulos, 2003; Lele et al., 2013).

A second popular approach for analysing GPS data are step-selection functions (Fortin et al., 2005; Thurfjell et al., 2014), and their extension to integrated step-selection functions (Avgar et al., 2016). They connect habitat-selection functions and animal movement, and offer the advantages of: (a) providing an objective method of defining habitat availability in terms of movement constraints, (b) relaxing the assumption that locations are statistically independent, and (c) including movement characteristics as predictors (Fieberg et al., 2021). The latter means that integrated step-selection functions consider the observed distributions of step lengths, i.e. the distance between consecutive locations, and of turning angles, i.e. the change of direction between consecutive locations. Thereby, each consecutive GPS location is represented as a step.

In order to analyse red deer habitat selection at the scale of individual movement trajectories, in **paper I** we fitted integrated step-selection functions (Avgar et al., 2016) in the perimeters of six study areas in the Central Alps. We first estimated ten random locations per observed GPS location based on movement-related statistics, and attributed the values of the explanatory variables to the end location of each step. We then used generalised linear mixed models (glmmTMB; Muff et al., 2020), as these have the advantage of being able to be run for all individuals simultaneously, since they account for individual-specific variation in habitat selection. Another option would have been the application of a conditional logistic regression (clogit; Avgar et al., 2016), whereby clogit is run separately per individual. To infer habitat selection of multiple individuals of a population from clogit, the results are averaged (Prokopenko et al., 2017). Thus, individuals with strong deviation from the “average behaviour” have a large effect on the estimates, while the inclusion of all individuals in the same model as a random factor increases standard errors and therefore uncertainty in the model. Because no data from males were available in the study area of the region of the Swiss National Park, we only compared females in further analyses in **paper I**. For comparing the study areas, we then pooled all those with similar trends across explanatory variables. This resulted in a comparison of the region of the Swiss National Park against all other study areas.

In **paper II**, we proceeded similar to **paper I**, but fitted integrated step-selection functions (Avgar et al., 2016) with 25 random locations per observed GPS location. We first derived proxies for forage quality and quantity based on surface reflectance values, vegetation indices, and optical traits, and then restricted to open habitats and consistently excluded GPS locations with uncertain predictions for biomass and relative nitrogen. Finally, we included steps with at least three remaining random locations (Sigrist et al., 2022), and fitted sex-specific glmmTMBs (Muff et al., 2020).

1.3.3 Classifying red deer behaviour using accelerometer data

In **papers I** and **II**, we analysed the patterns of habitat selection of red deer in relation to their need for safety and foraging, respectively, based on GPS locations. However, these analyses did not provide any information about the type of the animals’ behaviour. Powerful tools such as *State Space Models* or *Hidden Markov Models* have been developed for behavioural segmentation of animal movement trajectories, but they might fail in recognising short-lasting behaviours if the sampling interval of GPS locations is too coarse (Wang, 2019). Thus, to address these questions, in **paper III** we chose an approach using acceleration data that were also recorded by the GPS collars. Acceleration was recorded averaged over 5-minute intervals per axis and provided as a unit-free number ranging from 0 to 255, characterising the mean acceleration

(Krop-Benesch et al., 2011). A value of 0 represented no movement and 255 maximum movement. We used accelerometer data from the x-axis and y-axis which measured the forward-backward and left-right motion, respectively, of two female and two male red deer. Those four free-ranging individuals were observed in the Swiss National Park in July and August, at the time of their highest activity (Figure 1). We focused on one individual at a time, and simultaneously recorded their behaviour in the ethological app *Behayve* (behayve.com), which generated time-stamped behavioural logs for every observational session and individual. We distinguished between the behaviours *lying*, *feeding*, *standing*, *walking*, and *running*.

Since behaviours of red deer were not consistent with 5-minute intervals of the accelerometer data, we labelled the intervals as pure and mixed intervals. While during a pure interval, the animal continuously engaged in a single behaviour, during a mixed interval, the animal engaged in multiple behaviours. Mixed intervals were labelled with the longest-lasting behaviour if it lasted 2.5 minutes or longer. To link the observation data with the accelerometer data, we had to ensure that the timestamps of the two datasets matched. For the observation data, we compared the time in the app with the time in the mobile phone and a GPS watch. For the accelerometer data, we checked whether the timestamps of intervals with very low values matched those of the observed lying behaviour. We then generated a multiclass behavioural model for red deer. We divided the data into two datasets and used three quarters of the labelled intervals to train the models and one quarter to test them (James et al., 2021). In a supervised learning approach, each labelled behaviour interval served as one datapoint. While behaviour served as the output variable, the accelerometer values served as the input variables. The model then learned to predict an animal's behaviour based solely on accelerometer values when provided with a large dataset of labelled intervals.

To find the most accurate classification model, we not only used multiple machine learning algorithms, but also different combinations and transformations of the accelerometer values (Nygaard et al., 2016). For each model, the predicted behaviour of each testing interval (25%) was compared with the actual observed behaviour of that interval. Using various accuracy metrics, we were able to compare all the models' accuracies with each other.

1.4 Key findings

1.4.1 Paper I: Red deer habitat selection accounting for the need for safety

Analysing habitat selection in networks of small-scale hunting ban areas in the Central Alps, we found that red deer selected contrasting habitats during the day and at night. In terms of anti-predator behaviour towards humans we showed that during the day red deer avoided habitats where humans are likely to be encountered. In the pooled study areas (PSA), this was indicated by selection for denser tree cover, longer distances to trails, and for steeper slopes all year round. In addition, they selected for hunting ban areas in summer and autumn and therefore reduced the risk of being disturbed or even hunted. At night, they showed the opposite pattern and selected for lighter tree cover, shorter distances to trails, and flatter slopes, indicating a reduced fear of humans in the safety of darkness and a compensation for missed foraging opportunities during the day. They only selected for hunting ban areas in September. There were no effects of tree cover density and slope during winter nights, while they selected for flatter slopes during summer and autumn nights. Red deer in the study area centred on the strictly protected Swiss National Park (RSN), selected differently to red deer in PSA and generally showed fewer contrasting patterns between day and night. During the day, they selected for longer distances to trails and for steeper slopes mainly in winter. However, the selection for denser tree cover and hunting ban areas during the day, and the selection of all covariates at night, were similar to PSA. This supports the findings that red deer generally saved energy in winter, and showed no compensating behaviour at night (see also Arnold et al., 2004; Pépin et al., 2009). In addition, this indicates that the animals consumed less forage in winter and thus minimized energy expenditure on searching for forage (Arnold et al., 2015). The results for elevation in RSN during the day may be misleading because red deer selected for lower elevation in summer and higher elevation during the rest of the year, as they stayed higher up in all study areas in summer than in winter (Reimoser et al., 2014; Thiel et al., 2018; Signer et al., 2021; Figure 4). Considering that we analysed the selection on a monthly basis, it becomes clear that red deer selected for lower elevation within the generally higher range in summer.

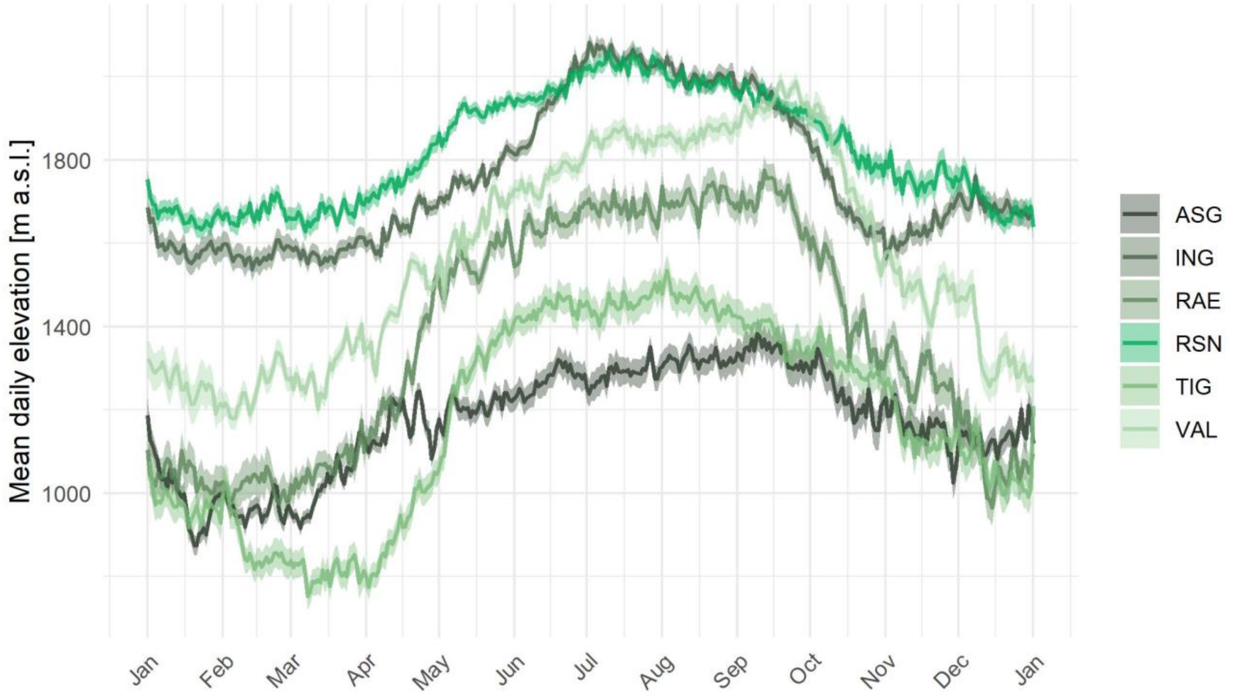

Figure 4: Mean daily elevation of red deer from six study areas between 2010 and 2021 (ASG = study area "Appenzell – St. Gallen", ING = project "Ingio via?", RAE = project "Raetikon", RSN = study area "Region of the Swiss National Park", TIG = project "TIGRA", VAL = study area "Valais"). Plot adapted from Lars Korzelius, Swiss National Park.

Second, we found differences in habitat selection between inside and outside hunting ban areas, during the day and at night, and in both PSA and RSN during the main hunting season in September. Red deer selected hunting ban areas in favour of hunted areas during the day and at night in both PSA and RSN. In PSA during the day, red deer selected for denser tree cover, longer distances to trails, and for steeper slopes, with significantly weaker selection inside compared to outside hunting ban areas. At night, red deer selected for lighter tree cover, shorter distances to trails, and for flatter slopes, thus showing a contrasting pattern of habitat selection. However, this selection was similar inside and outside hunting ban areas. In contrast, red deer in RSN during the day only selected for denser tree cover, with a weaker selection inside hunting ban areas compared to outside. Overall, this indicated a less specific habitat selection in RSN than in PSA.

Third, we ensured that effects were not caused by the seasonal behaviour of the animals, but by the influence of hunting. In PSA, red deer indeed selected for hunting ban areas due to hunting activity during the day and at night. In contrast, in RSN hunting activity had a significant positive effect only at night, but not during the day when the animals showed a selection for hunting ban areas already.

We conclude that (a) red deer generally avoided humans during the day, and this avoidance was stronger outside hunting ban areas compared to inside. We explain the less specific habitat selection in the RSN compared to PSA by the fact that red deer within the Swiss National Park do not need to (strongly) select for habitat parameters that indicate avoidance of humans. In addition, our results also show that compensation at night does not occur in this study area. Thus, we conclude that (b) the Swiss National Park, as the centre of our study area RSN, reduces the impact of human disturbance in accordance with its purpose. Finally, we conclude that (c) despite the ban on night hunting in Switzerland, hunting activities led red deer to select their habitats more cautiously, even at night. This is consistent with previous findings that red deer migrate due to the start of the hunting season (Rivrud et al., 2016) and move to protected areas (Mikle et al., 2019). However, the selection for hunting ban areas in autumn during the day and at night may also be related to undisturbed rutting sites (Frid & Dill, 2002). Due to the temporal overlap of the rut with the hunting season in Switzerland, these effects are difficult to disentangle.

1.4.2 Paper II: Red deer habitat selection accounting for the need to forage

Analysing red deer habitat selection including the trade-off between forage quality (i.e. relative nitrogen) and quantity (i.e. biomass) in open alpine summer habitats of the Swiss National Park and its surroundings, we found that both sexes selected for habitats with high biomass and high relative nitrogen, while biomass had a greater effect than relative nitrogen. Comparing between sexes, females selected more strongly for biomass than males, while males selected more strongly for relative nitrogen than females. However, due to the sex-specific model calculations, it was not possible to determine significant differences between the sexes. Our findings were consistent with those of a previous study which was conducted in the same region and used the same proxies for forage quality and quantity (Schweiger et al., 2015a), despite weekly spectral information versus one single dataset, a coarser spatial scale of 50 m versus 6 m, and a sample size of 45 females and 21 males versus two females. In addition, we confirm selection patterns found by Sigrist et al. (2022) based on a spatial resolution of 10 m, but during the green-up season and with other proxies for forage quality and quantity.

Besides analysing red deer's trade-off between forage quality and quantity, our study design allowed us to also analyse the trade-off between forage and safety needs per sex (Mysterud & Ims, 1998; Godvik et al., 2009; Mikle et al., 2019). Both sexes shared a selection for short distances to the forest, which may reflect red deer's general need for safety. However, the structure of the best-supported models indicated sexual differences in the need for safety: while for females all variables were included, for males, distance to trails and slope were excluded from the best fitting model. Keeping their distance from trails and retreating to steep terrain are part of red deer's avoidance behaviour towards humans. Since this did not seem to affect males, it is consistent with their apparent greater tolerance of human activity compared to females. On the other hand, females selected for short distances to trails and for flat slopes, which was against current theory. The explanation may lie in females' strong preference for the Swiss National Park characterized by strict regulations for humans, as their most frequently used areas were located within the Swiss National Park but in close proximity to trails. This is also evident from the mere distribution of locations: for females, 82% of locations were within the Swiss National Park, but only 46% for males. A further subdivision into day and night locations showed that for females, 89% of the locations were within the Swiss National Park during the day, but only 75% at night. This further illustrates the importance of females' need for safety. These differences were also evident in males, but at a lower level, with 59% of locations within the Swiss National Park during the day and 32% at night. Another explanation why males left the Swiss National Park at night about twice as often as females could be that they avoided high red deer densities. This could in turn be a reason why males selected lower biomass but higher relative nitrogen than females: around the Swiss National Park are alpine pastures (Rossi et al., 2020), which are grazed by cattle and sheep and therefore offer lower biomass but higher relative nitrogen. Thus, we conclude that our findings apply to higher-elevation summer habitats with little human disturbance, short growing seasons and low biomass. However, habitat selection may be different in agricultural lands with higher biomass but also higher human disturbance.

1.4.3 Paper III: Classifying red deer behaviour using accelerometer data

Developing a method to identify behaviour types of red deer based on accelerometer data, we applied multiple machine learning algorithms. In addition, we used different combinations and transformations of the accelerometer data. Although the four free-ranging red deer individuals were often in open habitats, the frequency of their observations and their behaviour was highly imbalanced as one individual was rarely observed. Similarly, we found an imbalance between observed behaviours, with lying or feeding being frequent, while standing, walking, or running were rare. In addition, the average duration of the behaviours varied. For example, lying lasted for 34.77 minutes on average, while walking lasted for only 1.16 minutes. Defining mixed intervals increased the number of intervals for these behaviours and allowed us to generate multiclass models. This would not have been possible if we had only used pure 5-minute intervals. Since the behaviours of free-ranging animals inherently include mixed intervals, relying on pure interval models can additionally lead to an inflated sense of accuracy because it is strongly biased towards the behaviours that are most commonly represented in the data (Gaylord, 2013).

As a measure to determine which models performed best in classifying red deer behaviour we introduced the *macro-balanced accuracy*. The main advantage is that high values (i.e. high accuracy) are only given if a model is able to accurately predict all behaviours, regardless of how frequently they have been observed. In contrast, the *correct classification rate*, a measure often used in previous studies to rank model performance, can still provide high values even if the model poorly predicts rarely observed behaviours (Naylor & Kie, 2004; Löttker et al., 2009; Heurich et al., 2012; Gaylord, 2013). However, the downside of using macro-balanced accuracy is that very small classes (i.e. few observations) can have an overly strong impact on the final metric. Nevertheless, we found that the macro-balanced accuracy provided the most balanced overview of the models' accuracy.

In total, we generated 144 classification models (16 algorithms * 9 model formulae). The most accurate model had a macro-balanced accuracy of 81%, and balanced accuracies of 90% (lying), 88% (feeding), 57% (standing), 71% (walking), and 100% (running) for each targeted behaviour class. This model was trained using linear discriminant analysis with the formula: $\text{behaviour} \sim x_{\text{minmax}} + y_{\text{minmax}} + \text{ratio}(x, y)_{\text{minmax}}$. With minmax-normalization, data is scaled to values from 0 to 1, while the ratio between the values remains the same as in the original accelerometer data ranging from 0 to 255. However, there was no best combination of input variables, as none consistently performed better than all other combinations. In terms of normalization methods, on average, the minmax-normalized models seemed to outperform the scale-normalized and log-transformed models. As accelerometer values of our four individuals differed significantly, we tried to improve the models for all individuals by reducing these differences using scale-normalization. However, on average, the models that retained inter-individual differences, i.e. based on minmax-normalized accelerometer values, performed better.

As with the optimal combination of input variables, there was no algorithm type that was consistently better than all the others. Although the models with the highest median macro-balanced accuracy were trained using the Gaussian process algorithm, our best-performing models were either trained with discriminant analysis or ensemble decision tree algorithms. However, discriminant analysis revealed a wide range of models with the highest and some of the lowest macro-balanced accuracies. For classification models for griffon vultures random forest algorithms which belong to the group of ensemble decision tree algorithms outperformed support vector machines which outperformed discriminant analysis (Nathan et al., 2012). For classification models in fur seals and sea lions support vector machines and random forest algorithms also performed well (Ladds et al., 2016). Although random forest algorithms also produced accurate models, discriminant analysis performed best and support vector machines performed worst. Based on the differences in that comparative studies on fur seals and sea lions and on our results, we conclude that there may not be one best algorithm for accelerometer-based behavioural classification. Instead, it is necessary to compare various algorithms, as well as combinations and transformations of input variables to obtain the most accurate classification model.

1.5 Synthesis and future perspectives

In order to assess the impact of habitat characteristics on spatio-temporal behaviour of red deer we analysed animal movement as a function of habitat parameters indicating topography, vegetation and human disturbances, with a focus on the selection of safety and forage parameters. Based on GPS locations of red deer, we have thus built on previous knowledge and refined it further. To this end, we analysed habitat selection both over the course of the year and by time of day, and took a closer look during the

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main hunting season in September. We had data available from several study areas, which had in common that they contained hunting ban areas which are nowadays used as a tool in Swiss wildlife management primarily for the purpose of controlling red deer numbers. In the end, we also wanted to quantify the impact of this measure. We further delved into the topic of foraging. Specifically, we wanted to clarify whether and how red deer select between forage quality and quantity in open alpine summer habitats, and whether there are differences between the sexes. In these analyses, in addition to the aspects of the need to forage, we also integrated and combined those relating to the need for safety. Finally, by using low resolution accelerometer data, we developed a method to identify certain behaviour types in the data that go beyond habitat selection.

In accordance with predation risk and human pressure, we found in **paper I** clear differences in the habitat selection of red deer between day and night, as they selected for habitat characteristics in opposite ways. During the day, they selected for higher tree cover density, further distances to trails, and steeper slopes. At night, however, they selected in the opposite direction, i.e. for lower tree cover density, shorter distances to trails, and flatter slopes. They preferred the hunting ban areas mainly in summer and autumn during the day. It was to be expected that red deer did not select for flat open habitats during winter nights, because they save energy and consume less forage than during the rest of the year (Arnold et al., 2015), and consequently their habitat selection is less specific in this respect. These first key findings might not be novel per se. However, they were new in the combination of analyses per month and simultaneously by day and night. Perhaps more importantly, they formed a necessary basis for further refinements. When we focused on September as the short main hunting season in our study areas, and thus the time of year with the greatest human pressure, we were able to show that red deer selected habitat characteristics less clearly during the day inside the hunting ban areas than outside. We interpret this second key finding as an effect of the hunting ban areas on the animals' need for safety, because they have less need to retreat into protective habitat structures inside hunting ban areas. On the one hand, this emphasises the function of the hunting ban areas and the fact that they are proving their worth. On the other hand, the weaker selection inside vs outside hunting ban areas and the lack of compensation at night in the region of the Swiss National Park also indicate that the restrictions on human activities (e.g. the rule to stay on trails) that apply there in addition to the hunting ban actually provide red deer with additional value. These findings are relevant for wildlife management, especially in a European context.

In **paper II**, we were able to show that in combination with empirical field measurements, remote sensing methods are suitable for the generation of fine-scale variables of forage quality and quantity in open alpine summer habitats. In addition to surface reflectance data, the inclusion of vegetation indices and previously underutilized optical traits improved the prediction accuracy of biomass and relative nitrogen in the regression models. Certain ambiguities remain in predicting relative nitrogen as a proxy for forage quality. Future hyperspectral satellite sensors potentially could take into account soil and non-photosynthetic vegetation cover, thus improving temporally and spatially high-resolution nitrogen prediction from space (Cawse-Nicholson et al., 2021; Rast et al., 2021). These could supersede the dependence on NDVI in such studies. Overall, our results suggest to use additional vegetation indices alongside NDVI, particularly given that NDVI experiences saturation issues in densely vegetated areas (Mutanga et al., 2023). If required, our models could be further refined, extended, and incorporated into global studies quantifying biomass and relative nitrogen using additional field data. We conclude that our findings are relevant for grassland ecologists, particularly in combination with wildlife ecology, in an alpine context.

Our third key finding was that although red deer in summer selected high relative nitrogen (i.e. forage quality) and high biomass (i.e. forage quantity), forage quantity was more important to them than forage quality. Although we expected that females selected more for forage quantity and males more for forage quality (Garcia et al., 2023), an inverse selection might also be possible due to sexual dimorphism (Barboza & Bowyer, 2000; Ruckstuhl & Neuhaus, 2002). Contrary to these expectations, we did not find very pronounced differences. Although these results corroborated findings from previous studies, we discussed them in a broader context: as we conducted our study in the extended region of the Swiss National Park, we integrated both forage and safety needs of red deer into the same analyses. With regard to the need for safety, we found that both sexes preferred to be close to the forest. For males, however, neither distance to trails nor slope played a role. This indicated their higher tolerance of human pressure, and was further illustrated by the fact that compared to males, females stayed far more often within the Swiss National Park with its strict restrictions on human activities. After a subdivision into day- and night locations, we learned that three quarters of the females' locations were within the Swiss National Park, even at night under the cover of darkness. By contrast, two thirds of positions of males were located outside the protected area at night. This puts the results on sex-specific forage selection into perspective in that males on alpine pastures used by livestock in the vicinity of the Swiss National Park (Rossi et al., 2020) may have selected lower biomass but higher relative nitrogen than females in their foraging patches mostly within the Swiss National Park without livestock. For another possible explanation for the selection of females for short distances to trails and for flat slopes, we combine findings from **papers I** and **II**: It is possible that these effects resulted from a predominance of selection at night, while red deer actually selected in the opposite direction during the day. We therefore highlight the fourth key finding that in studies on habitat selection, good knowledge of the study areas and their characteristics, an understanding of the animals' behaviour, and the inclusion of the relevant variables are essential for the interpretation of the results. This also requires sufficiently large samples (i.e. individuals) that allow for divisions such as day and night, and within and outside of hunting ban areas.

Following the analyses of habitat selection of red deer in the Central Alps (**paper I**) and the focus on the extended region of the Swiss National Park (**paper II**), we ultimately developed a method using accelerometer data to identify certain behaviour types in the data (**paper III**). The classification into the behaviour categories lying, feeding, standing, walking, and running corresponds to a practically relevant subdivision because it contains active and passive behaviours. As we only had low resolution accelerometer data of 5-minute intervals at our disposal, we had feared that behaviours shorter than this would be difficult to determine, including rarely observed behaviours such as standing, walking or running. The small sample of only four individuals also gave cause for concern about the success of the method development. Approximately two months of fieldwork were required to obtain 160 hours of observation data of free-ranging red deer. While collecting behavioural data from captive animals would save time, applying such a model to wild animals might be inadequate (Campbell et al., 2013; Ladds et al., 2016; Pagano et al., 2017; Kirchner et al., 2023). Wild red deer are likely to behave and move differently in their habitats than animals in captivity. Further studies could expand to other seasons besides summer. However, it must then be tested whether the summer models are also applicable to other seasons (Dickinson et al., 2020), because fur thickness and body weight are subject to seasonal changes (Mitchell et al., 1976).

In order to further refine analyses of red deer behaviour, a next step would be to investigate behavioural types and patterns derived from accelerometer data in a context of hunting ban areas and daytime. We would expect different behavioural patterns inside compared to outside hunting ban areas and during the day compared to at night. For example, the feeding and lying periods in open habitats within hunting ban areas could be more rhythmic throughout the day than outside in areas more influenced by humans. It would also be interesting to compare the patterns of behavioural types between different habitats, e.g. open habitats vs. forest. The weather could also be taken into account. And finally, it would also be possible to examine the impact of winter wildlife refuges on red deer behaviour. These have been established in Switzerland and other parts of the Alps to protect animals from human disturbance particularly in winter.

However, it would also be important to put our results into practice. The regional wildlife management in our study areas employ hunting ban areas combined with short but intensive hunting seasons. Our findings confirm impacts of habitat characteristics on spatio-temporal behaviour of red deer in several Alpine regions under the given management scenarios. They clarify that National Parks can serve as ecological baselines or controls against which the consequences of human activities and developments outside of National Parks can be evaluated (Boyce, 1998). Importantly, our findings emphasise the positive effects not only of National Parks but also smaller-scale hunting ban areas on red deer. On the one hand, we have responded to demands from almost 100 years ago, namely that we have generated information about the change of locations of the animals and its causes, as well as about the behaviour of animals towards humans, and above all about effects of strict protection (Burckhardt, 1991). On the other hand, we provide scientific evidence for the ecological principles enshrined in the *Federal Hunting Law*, which require, among other things, the protection of wildlife habitats, appropriate protection of species from human disturbance, and the designation of protected areas. Our findings thus serve as a basis for a general concept in wildlife management and could advance the use of hunting ban areas as a management tool outside of Switzerland. European countries with landscapes often dominated by humans would be particularly suitable. Based on our findings, it would not be necessary to establish large hunting ban areas, because a network of small areas already improves the situation for red deer. If wildlife managers decided to designate hunting ban areas for red deer, the grassland component should be taken into account. In other words, where possible, hunting ban areas should be designated so that they contain forest and open habitats, and thus offer opportunities to retreat from humans and to forage on pastures at the same time. The rule for visitors to stay on the trails or daytime restrictions would be suitable for this purpose. Zoning with graduated rules for humans would also be conceivable (Coppes et al., 2017).

With regard to the summer distribution of red deer, we were not able to provide direct scientific evidence that a network with a large number of smaller-scale hunting ban areas can counteract larger concentrations in a few sites. However, we can assume that red deer know the habitats in their home ranges and use them according to their safety needs (Haller, 2002; Proffitt et al., 2009; Mikle et al., 2019; Coppes et al., 2017) and that they may respond to reduced human activity in certain habitats by increasing their use (Tucker et al., 2023). From our studies we now know that red deer prefer the hunting ban areas in summer and autumn. Furthermore, we also know that in the canton of Grisons, approximately half of the hunts are carried out in the surroundings of the hunting ban areas, which corresponds to approximately 2500 individuals per year (Jenny & Filli, 2014). And finally, we have evidence from the immediate vicinity of the Swiss National Park: the number of red deer shot near smaller-scale hunting ban areas has increased over the years since their designation, while the number of red deer observed in the nearby Swiss National Park has decreased at the same time (Haller & Jenny, 2013). Thus, we reason that networks of small-scale hunting ban areas within mountainous habitats and the patent hunting system, with a short annual period of intensive hunting but mostly absent natural predators, are a means of controlling wildlife distribution and promoting sustainable regulation. Similar to a hunting for fear apporach that aims to induce behavioural adaptions in ungulates (Cromsigt et al., 2013) hunting ban areas can regulate hunting pressure and, by connecting red deer habitats, simultaneously increase hunting efficiency (Griesberger et al., 2022). In order to better understand these relationships and thus lay the foundation for further improvements in management, comparable long-term data on red deer and their ecosystems are required to ultimately estimate the social and economic carrying capacity of the system for red deer (Blankenhorn et al., 1979; Apollonio et al., 2017) and thus, the following factors should be known: (a) the spatio-temporal behaviour to designate management units; (b) the annual population size per management unit to derive hunting quotas; (c) statistics on hunting bag, carcasses and diseases, including the individual measures of physical condition, to have indicators of animal health and changes in the population or the habitats that can be indicated by changes in these values; (d) availability and utilization of forage as performance indicators of habitat productivity; (e) the extent of damage in forests and agricultural areas as measures for conflict causing red deer impact on vegetation and agricultural crops; (f) supplementary or diversionary feeding and its effects; (g) the presence of natural predators and their influence on red deer population and behaviour; (h) standardized spatio-temporal measures for human activities. No data are currently collected on the availability and utilization of forage. At least in open areas, approaches to quantifying forage using remote sensing could be useful, especially in combination with GPS locations of red deer to determine their utilization. However, forage availability and utilization within the forest should also be considered (Zweifel-Schielly et al., 2009). Regarding the extent of damage in forests and agricultural areas, at least the amounts of compensation payments are currently recorded. However, comparative data on the actual impact of wildlife on their habitats would also be important. In the forests of the canton of Grisons, this has been qualitatively estimated annually since 2021, which could one day serve as a variable in analyses (map.geo.gr.ch/ungulate_impact). Additional factors include agricultural use, especially with livestock, as this can compete with wildlife. Further, it is also important to be aware of any changes in habitat. These include, for example, areas of logging, storm damage, or bark beetle infestation in the forest, which over time provide abundant forage during certain developmental stages. Due to the rapid developments in the Alpine region, detailed information on natural predators is also needed, as is information on humans, whose diverse activities place significant demands

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on their environment. All of these factors form the basis for detailed red deer management that takes human interests in the cultural landscape into account.

Finally, I would like to emphasise the importance of knowledge about the spatio-temporal behaviour of red deer for their management and conservation on a broader scale. As a species with partial migration (Mysterud et al., 2011; Peters et al., 2019; Fellmann, 2022; Sigrist et al., 2022), it is important to know their migration routes. From a nature conservation perspective, these routes must be kept permeable for red deer or restored accordingly so that they can use routes that are currently interrupted. Communication across all political levels is therefore important, as red deer cross municipal, cantonal and national borders. Scientific consortia such as the *Global Initiative on Ungulate Migration* provide species-specific content on migration corridors based on movement data and visualise this in their *Atals on Ungluate Migration* as maps (cms.int/gium). *EuroMammals* is a less migration-focused and therefore more thematically open network from Europe that also considers mammals beyond ungulates in collaborative science for spatial animal ecology (euromammals.org). Such networks are important for understanding animal species, their behaviour, needs and habitat requirements, and thus also for management and conservation across borders. And we are glad to contribute our part.

To conclude with the words of Henry David Thoreau: "*The question is not what you look at, but what you see.*" This dissertation was very much concerned with the question of what we are looking at. For this reason, we specifically selected currently available, temporally and spatially high-resolution variables, or if not directly available, created them, in order to evaluate them using current methods of movement ecology and thus shed light on the spatio-temporal behaviour of red deer.

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2 Publications

Paper I

Rempfler, T., Peters, W., Signer, C., Filli, F., Jenny, H., Hackländer, K., Buchmann, S. & Anderwald, P. (2025). Contrasting daytime habitat selection in wild red deer within and outside hunting ban areas emphasises importance of small-scale refuges from humans. *Ecology and Evolution*, 15(8). DOI: 10.1002/ece3.71407

Paper II

Rempfler, T., Rossi, C., Schweizer, J., Peters, W., Signer, C., Filli, F., Jenny, H., Hackländer, K., Buchmann, S. & Anderwald, P. (2024). Remote sensing reveals the role of forage quality and quantity for summer habitat use in red deer. *Movement Ecology,* 12(1). DOI: 10.1186/s40462-024-00521-6

Paper III

Bar-Gera, B., Anderwald, P., Evans, Alina L., Rempfler, T., Signer, C. (2025). Comparing the accuracy of machine learning methods for classifying wild red deer behaviour based on accelerometer data. *Animal Biotelemetry*, 13(9). DOI: 10.1186/s40317-025-00401-9

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2.1 Paper I

Contrasting daytime habitat selection in wild red deer within and outside hunting ban areas emphasises importance of small-scale refuges from humans

Rempfler, T., Peters, W., Signer, C., Filli, F., Jenny, H., Hackländer, K., Buchmann, S. & Anderwald, P. (2025). Contrasting daytime habitat selection in wild red deer within and outside hunting ban areas emphasises importance of small-scale refuges from humans. *Ecology and Evolution*, 15(8). DOI: 10.1002/ece3.71407

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RESEARCH ARTICLE OPEN ACCESS

Contrasting Daytime Habitat Selection in Wild Red Deer Within and Outside Hunting Ban Areas Emphasises Importance of Small-Scale Refuges From Humans

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ABSTRACT

1. Prey species such as red deer (*Cervus elaphus*) select their habitats according to their requirements for landscape features and adapt this selection to the presence of predators and humans. We tested how networks of different types of protected areas—the Swiss National Park (SNP) without hunting but with additional regulations for humans, and smaller-scale hunting ban areas (all types together = HBAs)—influenced diurnal and nocturnal habitat selection in red deer compared with unprotected areas.
2. Using integrated step selection functions, we compared habitat selection of 243 GPS-collared individuals from six study areas across the Central Alps during day and night, during the year and specifically during the short autumnal hunting season.
3. During the day, red deer avoided habitats where encounters with humans were likely, i.e., they selected for denser tree cover, greater distances to trails, steeper slopes, and for most of the year, for higher elevation. Importantly, in summer and autumn, they selected HBAs. At night, they showed the opposite selection. This daily pattern was absent in the study area centred on the SNP, where habitat selection was less specific overall. During the main hunting season, they selected HBAs over areas without protection during both day and night, and concurrently, habitat selection was less specific inside compared with outside HBAs.
4. HBAs allow red deer to select habitat largely independently of human impact. Accordingly, compensating habitat selection at night due to human disturbance during the daytime was observed in all study areas, except for the region centered on the SNP. Our results suggest that in human-dominated landscapes, networks of small-scale HBAs can support more natural habitat selection of the animals, especially when providing additional regulations to humans.

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1 | Introduction

Prey species are sensitive to predator presence and minimise risk exposure by modifying their behaviour (Brown et al. 1999). Besides innate behaviour (e.g., neonatal antipredator tactics; Atmeh et al. 2024), individuals assess risks by combining aspects of the predator (e.g., speed, size), their own physical condition (e.g., reproductive state, size) and environmental factors (e.g., time of day, amount of cover) based on experience and learning (Stankowich and Blumstein 2005).

The landscape of fear concept represents a heterogeneous distribution of relative levels of perceived predation risk and the associated level of fear a prey animal experiences in different parts of its home range (Laundré et al. 2010). Thus, this perception of risk is related to the physical landscape and predation risk, and results in accordingly adapted behaviour, for example, distribution patterns of prey and antipredator behaviour (Gaynor et al. 2019). Animal movement is the behavioural mechanism that links the multiscale process of habitat selection in response to biotic and abiotic factors (Johnson 1980). For example, elk (*Cervus elaphus canadensis*) shifted their habitat use and fed on lower quality forage in response to wolf reintroduction in Yellowstone National Park (Hernández and Laundré 2005). This concept is not only applied to natural predators but also in relation to humans, with hunting having direct and indirect effects on wildlife: in a landscape-scale playback experiment, predators moved more cautiously when hearing human voices or became more elusive and reduced foraging activities (Suraci et al. 2019). Ungulates in turn modify their movements (Little et al. 2016) or feeding site selection to avoid hunters (Benhaiem et al. 2008). Female moose (*Alces alces*) that lost their young during the hunt stayed further away from settlements and at shorter distances from the forest the following year (Graf et al. 2024). Roe deer (*Capreolus capreolus*) modified their habitat use between day and night to avoid hunting (Bonnot et al. 2013). White-tailed deer (*Odocoileus virginianus*) are also able to recognise local risks: on days following hunting from stands, the use of areas around the stands decreased during the day and increased at night (Sullivan et al. 2018).

Human activities can affect fitness (Shively et al. 2005) and even recreational activities can cause behavioural and physiological reactions in wildlife comparable to those in response to predation (Frid and Dill 2002; Stankowich 2008). These include increased vigilance (Beauchamp 2015), flight (Ydenberg and Dill 1986; Schnidrig-Petrig and Ingold 2001), reduced activity levels (Graf et al. 2018) changes in habitat selection (Gander and Ingold 1997; Filla et al. 2017), reductions in parental investment (Gill et al. 2001) and effects on energy expenditure (Houston et al. 2012), resource acquisition, animal condition and finally reproductive success (Frid and Dill 2002). Over time and space, such individual effects can scale up to cumulative pressures at the population level (Sutherland 1996). Disturbance effects can be enhanced if humans are accompanied by dogs (Miller et al. 2001). On the other hand, during COVID-19 lockdowns with reduced human mobility, spatial behaviour of wildlife changed, for example, to increased use of areas closer to roads and high human footprint, which indicates that animals reduced their avoidance of proximity to humans (Tucker et al. 2023).

Effects of human disturbance on the *Cervus* genus are relatively well studied (Mattioli et al. 2022). For example, Ciuti et al. (2012) suggested that effects on elk behaviour caused by human disturbance exceeded those of habitat and natural predators: human presence triggered increased vigilance and decreased foraging. Among food, topography and human activity, the latter has even been identified as the strongest driver of red deer movement (Mumme et al. 2023). Animals strongly respond to disturbance from human recreational activities by increasing their level of vigilance, but their response varies with the level of cover available, and they perceive hunting as a more acute threat than human recreation (Jayakody et al. 2008). Even red deer (*Cervus elaphus*) which appear to be habituated to regular disturbance within their home ranges, may alter their behaviour and avoid hiking trails (Sibbald et al. 2011; Westekemper et al. 2018). As human activity is mainly concentrated during the daytime, one avoidance strategy used by red deer—and other mammals (Gaynor et al. 2018)—consists in altering their diurnal behaviour, i.e., avoidance of humans during the day by using refuge areas and compensation by being more active at night (Godvik et al. 2009; Coppes et al. 2017).

Habitat selection of red deer during the green-up season in a study in mountainous habitats depended, among other factors, on landscape characteristics and human presence: red deer commonly preferred shrub cover, flat terrain and lower to intermediate elevations, but avoided habitats with possible exposure to human activity, i.e., the vicinity of roads and trails, or areas far away from forest cover (Sigrist et al. 2022). The onset of the hunting season triggers fear reactions in red deer, i.e., increased flight distance, more time spent outside the core home range, and preference for dense vegetation, which may affect red deer distribution and harvesting efficiency (Meisingset et al. 2022). Reactions may differ somewhat between the sexes: for example, male red deer in Norway shifted their habitat preferences at the onset of the hunting season, while females did not, as they were already largely using cover when hunting started (Lone et al. 2015). In Canada, older female elk individually changed their behaviour as they aged and reduced movement rates to decrease the likelihood of encountering hunters (Thurfjell et al. 2017). In addition, they increased the use of secure areas (i.e., forest and steeper terrain) and adjusted their behaviour depending on the type of threat (bow and arrow vs. rifle hunters) (see also Proffitt et al. 2013). This fine-tuning of elk behaviour to avoid hunters, as opposed to just becoming more cautious during the hunting season, highlights the behavioural plasticity of this species.

In the late 19th century, the first protected areas were created to conserve iconic landscapes and provide habitat for endangered wildlife (Watson et al. 2014). At the same time, when red deer in Switzerland were just returning after their extinction in the 18th century (Haller 2002), federal and cantonal wildlife reserves were originally designated in Switzerland with the intention to increase ungulate populations by banning hunting within these reserves. As the first large-scale protected area in the Alps without any human use apart from restricted recreation, the Swiss National Park (SNP) was founded in 1914. The SNP provides the strongest degree of year-round protection, and human disturbance is greatly reduced (category Ia protected area: Strict Nature Reserve). Inside all these types of hunting ban areas (HBAs), hunting is prohibited, while the SNP and federal wildlife reserves additionally protect wildlife from human disturbance, but at different levels. Authorities and managers in the Swiss Alps have supplemented this network with small-scale HBAs, especially since the 1980s in order to manage the spatial distribution of red deer, as the species is known to use protected areas to avoid hunting activities (Haller 2002; Proffitt et al. 2010, 2013; Mikle et al. 2019). This approach is based on the expectation of the red deer's ability to reach these areas through seasonal migrations as summer habitats (Haller 2002), undertaken by parts of the populations (Fellmann 2022; Table S1).

While effects of larger protected areas on red deer are known, effects of networks of smaller-scale HBAs have not been analysed yet. These networks offer an ideal experimental study design to compare behavioural adaptations inside versus outside protected areas. In this study, we tested (a) how red deer in six study areas in the Alps select habitats during day and night, as well as over the course of the year, and (b) how habitat selection specifically during the main hunting season differs inside and outside HBAs, at day and night, and between different study areas. We expected red deer to avoid humans during the day by selecting against habitat characteristics indicating human presence in all study areas. On the other hand, we expected no such avoidance at night, especially because there is no hunting at night. We further predicted (c) a selection for HBAs particularly due to hunting activity. These compensating patterns should be less pronounced in the study area which is centred on the SNP with its strict regulations for humans.

2 | Materials and Methods

2.1 | Study Areas

We used red deer GPS data from six study areas across the Alps: from western Austria, northern Italy, Liechtenstein, as well as eastern and southern Switzerland (Figure 1 and Table S1). Settlements are typically concentrated in the valley bottoms and recreation activity is generally high in all study areas. Major highways are mostly absent, except in the study area 'TIGRA' (TIG). The main agricultural land use are pastures with cattle and/or sheep. Hunting ungulates is generally permitted outside of HBAs according to regulations. In

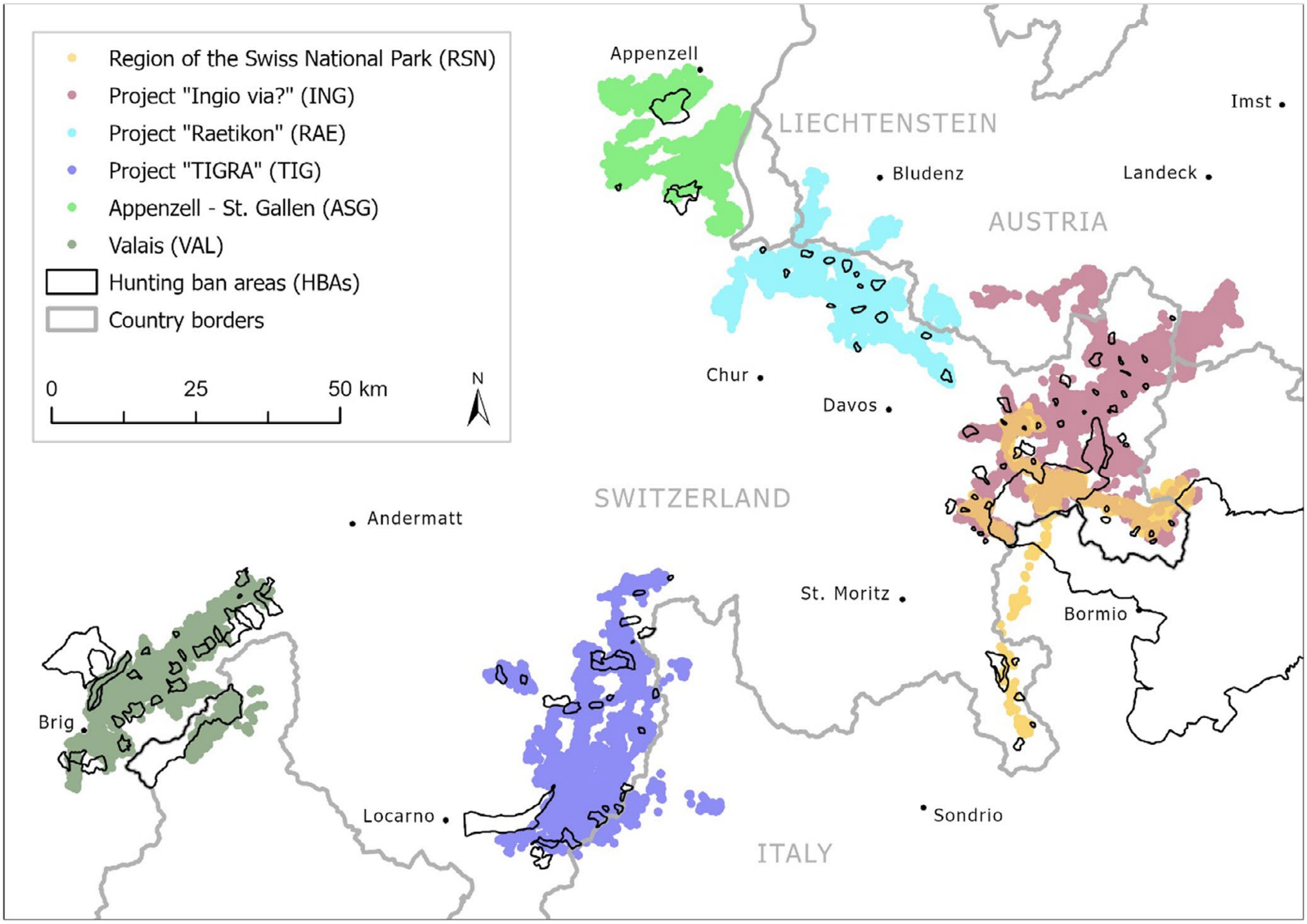

FIGURE 1 | Study areas with red deer GPS locations (coloured locations) and HBAs (black polygons). Map and data: Hunting Departments of the cantons of Appenzell Inner-Rhodes, Appenzell Outer-Rhodes, Grisons, St. Gallen, Ticino and Valais, Principality of Liechtenstein, Swiss National Park, Vorarlberg Hunting Association, swisstopo. SNP 2024/09.

most of the Swiss study areas and the respective Italian parts, a licence-based hunting system is practiced, where hunters can independently choose their place to hunt. In contrast, in the canton of St. Gallen, i.e., the main part of the study area 'Appenzell – St. Gallen' (ASG), as well as in Austria, hunting rights are linked to landownership, i.e., hunters are allowed to hunt only on specific hunting grounds (for details see Trouwborst and Hackländer 2018). Hunting in the study sites with licence hunting is mainly practiced for a period of 3 weeks in September, except for the study area 'Valais' (VAL; only 2 weeks in September, but can also include the first days of October), followed by additional hunting days in late autumn to fulfil hunting quotas. Hunting in the parts of the canton of St. Gallen in the study area ASG was practiced from mid August to mid December, in Austria and Italy from May to December. It is usually carried out from high or ground seats, without dogs, or stalking, occasionally also as drive hunts in small groups with few hunters.

In the SNP, all human activities are prohibited year-round, except for hiking on designated trails during daylight hours between ca. June and November (depending on snow conditions). Further restrictions that serve to reduce disturbance to wildlife within the park include the exclusion of livestock, visitors not being allowed to bring dogs into the park (not even on a lead), and there is a ban on overflights including paragliding or flying drones. Any violations registered by National Park Rangers are heavily fined.

2.2 | Red Deer Data

We analysed trajectories of 191 female and 118 male wild red deer that were captured and collared between 2010 and 2021. Except in Austria, there are no winter feeding stations. Individuals were immobilised with dart guns or captured in corral traps and anesthetised and equipped with GPS telemetry collars (VECTRONIC Aerospace GmbH). The collars recorded GPS locations for 1–3 years at a sampling rate of 1 or 3 h. Authorities and wildlife officials of the cantons executed the captures during winter (except for the study area of the 'Region of the Swiss National Park' (RSN), where animals were also captured in spring and early summer) in accordance with national animal welfare laws and under permits issued by the responsible bodies (GR1001411, RA 2009/2862-6743_01, SG13-12, GR2014-07F, GR2015-09, GR2017-12F, GR2020-08F, VS07-17).

We subsampled GPS locations with the package 'amt' (Signer et al. 2019) to one fix every 3 h, which was the least common denominator over all studies, with a tolerance of 3 min. In addition, we removed the data for the first 3 days and the last day in order to exclude possible effects of the capture and the removal of the collar (Morellet et al. 2009; Jung et al. 2019). We then eliminated inaccurate locations using the screening method by Bjørneraas et al. (2010). To select individuals with access to HBAs, we estimated 99% Kernel density home ranges using the R package 'adehabitatHR' (Calenge 2022) based on all GPS locations of an individual, and overlapped them with the HBAs using the R package 'sf' (Pebesma et al. 2023). In case of an overlap, we included individuals with at least 80% fix rate success per month, resulting in a sample size of 243 individuals (Table S1).

2.3 | Explanatory Variables

2.3.1 | Proxies of Human Presence

Within the study areas, there are different types of HBAs, which were available as geospatial vector data. Depending on their objectives, these designated areas restrict hunting as well as various other human activities, which may disturb wildlife or influence their behaviour (Grignolio et al. 2014). In the Swiss National Park (Strict Nature Reserve; 170 km^2) all human use is prohibited except scientific study and hiking on trails. The Stelvio National Park (Protected Landscape; 1310 km^2) is a category V protected area. Hunting is limited to a few areas, which are located outside of our analysis perimeter. The Swiss Federal Wildlife Reserves (14–26 km^2) were originally intended to increase ungulate populations by spatial hunting bans. Nowadays, they primarily aim at protecting endangered species and habitats (§ 1 federal ordinance on Wildlife Reserves), while hunting is still banned. Furthermore, several Swiss cantons have implemented Cantonal Wildlife Reserves (0.15–12 km^2) to spatially manage red deer distribution, among others the cantons of Grisons (§ 1 cantonal ordinance on Wildlife Reserves) and Valais (§ 35 cantonal hunting law). There are no HBAs within the study sites in Austria and Liechtenstein.

As the main parts of the study areas were situated in Switzerland, we used the road layer of the Swiss Topographic Landscape Model (TLM) as underlying data (Swisstopo 2015). Since we were interested in the nearest distances to trails, we only included trail categories of up to 2 m in width. For areas outside Switzerland, we used Protomaps (https://protomaps.com) to extract Open Street Map data for the project perimeter. We postedited lacking trails in ArcGIS Pro with Swisstopo's reference map 1:25′000 and combined it with the TLM. We calculated path distance from these trails, accounting for topography based on a digital elevation model with a grid size of 30 m (DEM; NASA 2020) in ArcGIS Pro (version 3.0.3, ESRI) to extract the distance values for all red deer locations in mountainous terrain, instead of planar distances.

2.3.2 | Landscape Variables

We used a DEM (NASA 2020) to derive elevation and slope (in degrees; R package 'raster' (van Etten et al. 2023)). We derived forest cover ranging from 0%–100% from the Copernicus Tree Cover Density product (Herrmann et al. 2017) by matching GPS data to the respective year of the tree cover density layer. We resampled all tree cover layers to a uniform resolution of 20 m because the respective products from 2012 and 2015 were only available at this resolution, while the product from 2018 was at a resolution of 10 m. All covariates and their expected relationships with red deer antipredator behaviour towards humans are summarised in Table 1.

TABLE 1 | Covariates and their expected links to red deer antipredator behaviour towards humans.

Covariate	Type	Expected impact	Question	References
Tree cover density	Continuous	Selection for denser tree cover reduces the risk of being detected by humans (or hunters)	(a), (b), (c)	Lone et al. 2015; Meisingset et al. 2022; Sigrist et al. 2022
Distance to trails	Continuous	Selection for larger distances to trails reduces the risk to encounter humans	(a), (b), (c)	Sibbald et al. 2011; Westekemper et al. 2018
Slope	Continuous	Selection for steeper slopes reduces the risk to encounter humans	(a), (b), (c)	Thurfjell et al. 2017
Elevation	Continuous	Selection for higher elevation reduces the risk to encounter humans	(a), (b), (c)	
Hunting ban area	Factor (inside, outside)	Selection for HBAs reduces the risk of being hunted	(a), (b) as interaction with habitat covariates, (c) as interaction with hunting activity	Coppes et al. 2017; Mikle et al. 2019
Hunting activity	Factor (yes, no)	Increased use of HBAs due to hunting activities reduces the risk of being hunted	(c) as interaction with HBAs	Proffitt et al. 2010; Mikle et al. 2019
Step length	Continuous	(Not interpreted)	(a), (b), (c)	
Turning angle	Continuous	(Not interpreted)	(a), (b), (c)	

2.3.3 | Temporal Variables

Daytime was defined as the time between sunrise and sunset, nighttime including twilight as the opposite, with the R package 'suncalc' (Thieurmel and Elmarhraoui 2022).

The hunting season differed between study areas. While it lasts until December in Italy and Austria, it is limited to a few weeks in autumn in Switzerland. For analyses on the effects of hunting activity, we limited the spatial extent to Switzerland and to the period between August 15th and October 31st which spans over the period from before hunting started until after it ended.

2.4 | Modelling Habitat Selection

In order to analyse habitat selection, we fitted integrated step selection functions (iSSFs; Avgar et al. 2016). All analyses were conducted with R version 4.2.0 (R Core Team 2022). Using the package 'amt' (Signer et al. 2019), we first calculated individual trajectories and then generated 10 random locations per observed location, based on movement-related statistics (i.e., with a gamma distribution for step lengths and a Von Mises distribution for turning angles). We then extracted explanatory variables for end locations of each step and scaled all continuous variables. To account for individual-specific variation in habitat selection, we fitted Poisson generalised linear mixed models (glmmTMB; Brooks et al. 2024; Muff et al. 2020) with random slopes per individual and year for each environmental variable, except turning angle (Webber et al. 2024). The intercept was estimated per stratum. To reduce potential bias caused by differences in movement patterns between individuals, we included the distance between two consecutive GPS locations (step length) and the cosine of the angular deviations (turning angle) in the models (Avgar et al. 2016; S2).

2.4.1 | Diurnal and Monthly Effects of Environmental Variables

For analyses of diurnal patterns, we fitted monthly step selection functions per study area separately for day and night to obtain an overview of monthly habitat selection. We next ran the same models, but separated by sex, and subsequently compared only females because no data from males was available in the study area RSN. We then pooled all study areas (pooled study areas = PSA) except for RSN, as similar trends were detected across explanatory variables in the area-specific models with the exception of RSN. In order to correct for multiple testing ($n = 264$ for all study areas separately, and $n = 48$ for PSA vs. RSN) we applied a Holm–Bonferroni correction to p values in the model outputs (Holm 1979).

2.4.2 | Effects of Hunting Ban Areas During the Main Hunting Season

To test for the effects of HBAs on red deer habitat selection specifically during the hunting season, we selected only September data, i.e., the main hunting season in all study areas. Exploratory analysis revealed similar habitat availability inside and outside HBAs. We included interaction terms between HBAs and all environmental variables in the model except for turning angles. Again, we first analysed each study area separately for day and night, and then pooled all study areas (PSA), except for RSN.

2.4.3 | Effects of Hunting Ban Areas due to Hunting Activity

Finally, we tested whether red deer selected HBAs specifically due to hunting activity or whether their selection was simply seasonal. Thus, we included an interaction term between HBA and hunting activity in the model.

3 | Results

3.1 | Diurnal and Monthly Effects of Environmental Variables

Red deer selected contrasting habitats during the day than at night, but less consistently so in RSN than in PSA (Figure 2 and Table S3). During the day, red deer in PSA selected for higher tree cover density, longer distances to trails, and for steeper slopes all year round. Except for summer, they selected for higher elevation. In summer and autumn, they selected for HBAs. At night, they showed the opposite pattern, i.e., they selected lower tree cover density, shorter distances to trails, flatter slopes and lower elevation. They only selected for HBAs in September nights. Effects were absent for tree cover density and slope during winter nights and for elevation during summer nights. During summer and autumn nights, they selected for flatter slopes.

Unlike in PSA, red deer in RSN generally showed less contrasting habitat selection between day and night. During the day, they selected longer distances to trails and for steeper slopes only in winter, and not at all for elevation (Figure 2 and Table S4). The selection at night was similar to PSA. Effects showed little difference between the sexes (Figure S5).

3.2 | Effects of Hunting Ban Areas During the Main Hunting Season

The comparison of habitat selection inside and outside HBAs is most meaningful during the main hunting season, which in all study areas is in September. With the protection from hunting, habitat selection by red deer differed inside and outside HBAs and between day and night (Figure 3 and Table S6; Figure S7). In all study areas, red deer selected HBAs to hunted areas during the day and at night. In PSA, coefficients had the same directions inside and outside HBAs. During the day, red deer selected for denser tree cover (Figure 3A.1), greater distances to trails (Figure 3C.1), and for steeper slopes (Figure 3E.1). This selection during the day was significantly weaker inside than outside HBAs. At night, red deer showed the opposite pattern of habitat selection, i.e., they selected for lower tree cover density (Figure 3A.2), shorter distances to trails (Figure 3C.2),

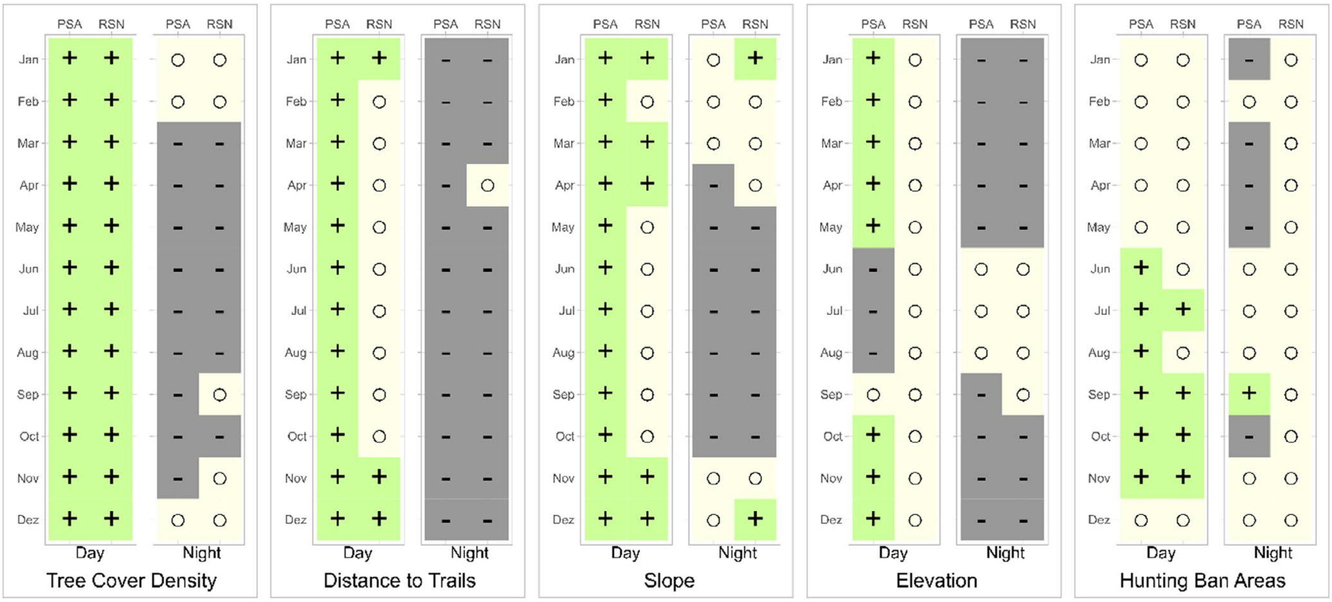

FIGURE 2 | Monthly effects of each environmental variable (tree cover density, distance to trails, slope, elevation, hunting ban areas), included in the habitat models for female red deer. Models were run separately for day and night, for the pooled study areas PSA (ING, RAE, TIG, ASG and VAL), and RSN with individual-years as random effects (green plus = significant positive, grey minus = significant negative effect, yellow circle = nonsignificant effect after Holm–Bonferroni correction).

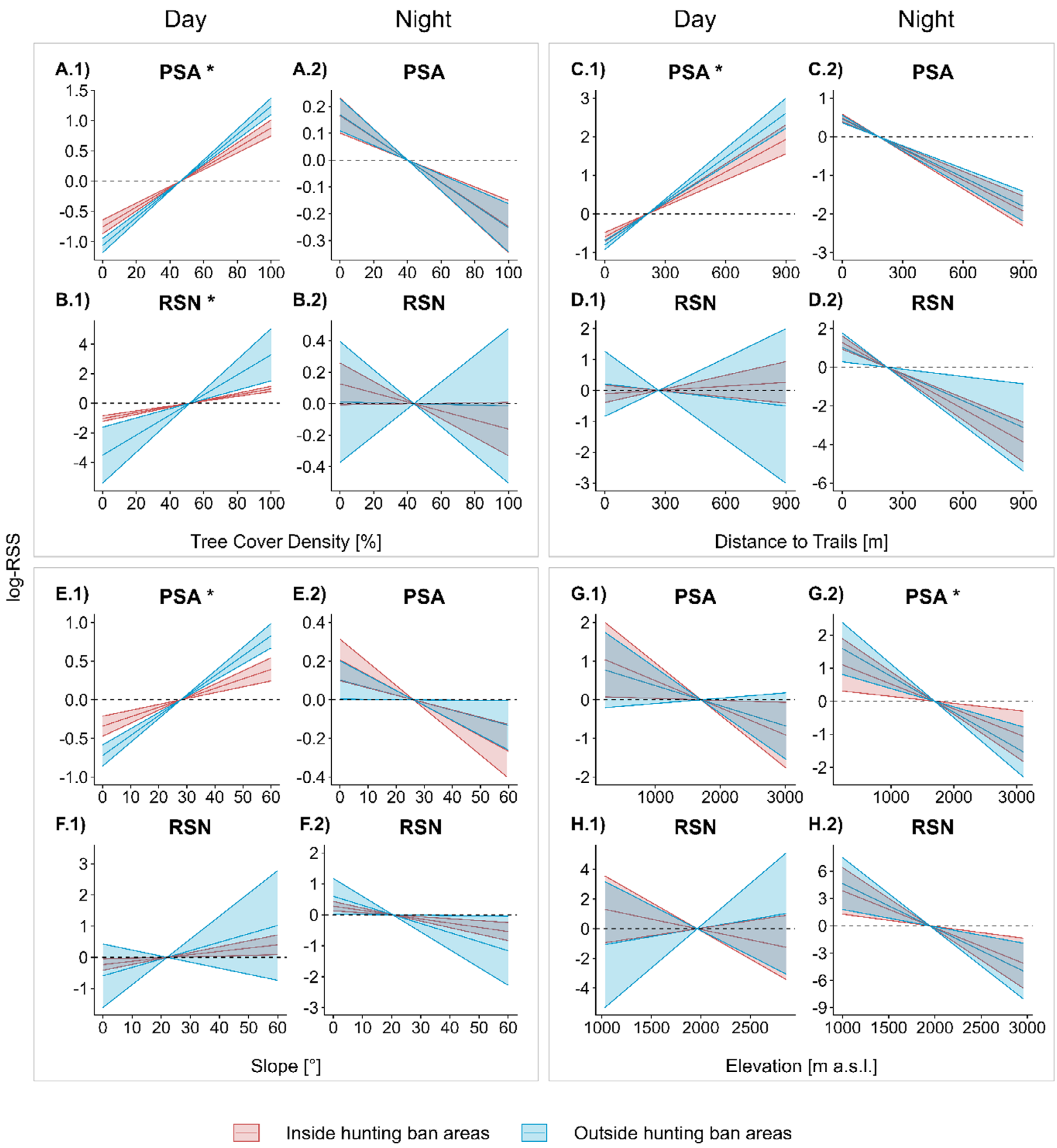

FIGURE 3 | Effects of HBAs on habitat selection concerning tree cover density (A, B), distance to trails (C, D), slope (E, F) and elevation (G, H), per study area during day and at night in September (red = inside HBA, blue = outside HBA). Log-RSS values were calculated relative to the average habitat in the study area based on a step selection analysis. * = significant difference in effect direction between inside and outside HBAs. Shaded areas encompass all pointwise 95% confidence intervals.

and for flatter slopes (Figure 3E.2). This selection at night did not differ between inside and outside HBAs.

Red deer in RSN showed less specific habitat selection than in PSA. Inside HBAs, they did not select for any covariates during the day, except for denser tree cover. This selection was stronger outside HBAs (Figure 3B.1). At night, red deer selected for shorter distances to trails inside and outside HBAs (Figure 3D.2).

3.3 | Effects of Hunting Ban Areas due to Hunting Activity

Interactions between HBAs and hunting activity in autumn for PSA showed that female red deer did indeed increase their use of HBAs due to hunting activity during the day and at night (after Holm–Bonferroni correction; Table S8). In contrast, in RSN there was a significant effect at night whereas no significant interaction was detectable during the day (Table S8) when the animals showed a selection for HBAs already (see Figure 2).

4 | Discussion

4.1 | Diurnal and Monthly Effects of Environmental Variables

Integrated step selection functions for all study areas except RSN consistently yielded monthly red deer habitat selection patterns that differed between day and night. During the day, their selection for dense forest cover and steep terrain, areas inside HBAs and further from trails indicated avoidance of areas closer to humans (Figure 2 and Figure S3–S5). These results are consistent with findings by Godvik et al. (2009), Sibbald et al. (2011) and Sigrist et al. (2022). However, they were in stark contrast to red deer habitat use at night, when the animals selected for low tree cover density, which corresponds to very low values for open areas, flat terrain and short distances to trails, but hardly chose HBAs. These contrasting patterns of habitat selection compared with those observed during the day suggest compensation in the relative safety of darkness. In agreement with Godvik et al. (2009), Coppes et al. (2017) and Gaynor et al. (2018), red deer in PSA thus avoided habitats where encounters with humans were likely during daytime but used them at night. This pattern could be encouraged by the ban on night hunting in Switzerland.

Red deer in the study area RSN, which was centered on the SNP, behaved differently from all other study areas (Figure 2 and Figure S5). Namely, they showed no significant year-round avoidance of habitat characteristics that could be attributed to human disturbance during the day, except for tree cover density. The strict protection measures from human disturbance in the SNP, and particularly the predictability of human presence on trails (i.e., guaranteed absence elsewhere), are the most likely explanation why red deer in RSN during summer and autumn neither kept large distances from hiking trails nor retreated to steep terrain and high elevations during daytime, as they did in PSA. Habituation of red deer to predictable movement of humans along designated trails versus a sensitivity to off-trail hiking has been shown in an experimental setting by Westekemper et al. (2018). Contributing factors to habituation of elk in North America have been consistent and predictable human behaviour, but also high densities, prohibited hunting, and habitats that provide winter range (Thompson and Henderson 1998). In the absence of mortality risk from hunting by humans, as in our HBAs, animals can also learn to exploit human-disturbed areas by desensitising and eventually habituating to human stimuli (Bejder et al. 2009). To some prey species, areas frequented by humans serve as refuges from predators that are less inclined to habituate to human presence (Shannon et al. 2014). This human shield effect was observed, for example, in the Yellowstone Ecosystem, where moose birth sites were located close to paved roads, which brown bears avoided (Berger 2007). On the other hand, human-habituated individuals could become bolder and thus more vulnerable to predation (Geffroy et al. 2015). In the absence of natural predators, the hunting ban in combination with the restriction of visitors to hiking trails in the SNP likely amplified the differences in habitat use compared with the other study areas. Interestingly, these differences lasted for much of the year (Figure 2), suggesting that red deer in RSN avoided humans less in spring when large parts of the population—due to seasonal migration—were in their winter habitats outside the SNP (Haller 2002). Presumably, these red deer have learned that humans do not pose a risk outside the hunting season.

Seasonal differences in habitat selection of red deer both in PSA and RSN indicated that in winter, animals saved energy during the day and did not compensate at night (see also Arnold et al. 2004; Pépin et al. 2009). They reduced forage intake in winter and thus avoided expending energy on the unproductive search for more scarcely available food (Arnold et al. 2015). During winter nights, they did not select low tree cover density (i.e., open areas in the extreme) or flat slopes. The selection for HBAs was restricted to summer and autumn, likely to generally avoid human disturbances. This is in line with a study in Germany where red deer used refuge and core zones more frequently than border zones during summer (Coppes et al. 2017). In addition, they benefited from undisturbed rutting activities in autumn (Frid and Dill 2002), and avoided hunting (Mikle et al. 2019).

4.2 | Effects of Hunting Ban Areas During the Main Hunting Season

During the main hunting season in September, red deer showed a clear selection for HBAs (Table S6). Effects of habitat selection patterns for both inside and outside HBAs had the same direction, but with contrasting directions between day- and nighttime (Figure 3). Besides the general avoidance of humans during the day, red deer avoided humans more strongly outside HBAs, as hypothesised.

The pattern of a less clear habitat selection in RSN remained after the subdivision into inside and outside HBAs (Figure 3). This can be explained by the lack of a need to select for habitat parameters associated with human avoidance within the SNP. As our results show that compensation at night is not necessary in this study area, we conclude that the SNP as the center of our study area RSN best fulfills its purpose in terms of reducing effects of human disturbance.

4.3 | Effects of Hunting Ban Areas due to Hunting Activity

Previous findings state that red deer in autumn migrate due to the onset of hunting (Rivrud et al. 2016) and seek protected areas particularly at this time of year (Mikle et al. 2019). The significant positive interaction between hunting activity and the use of HBAs for PSA during day and night, and for RSN at night (Table S8; for this analysis only inside Switzerland) indicates that more cautious habitat selection of red deer due to hunting activity extends even into the hours of darkness. We interpret this result as a direct response to hunting activities, especially because nighttime was defined as the time from dusk until dawn in our study. During the day, however, hunting activity had no additional effect on the use of HBAs in RSN, likely because the animals already showed a significant selection for HBAs during summer and autumn anyway. Another explanation for the selection of HBAs in autumn even at night may also be a selection for undisturbed rutting sites (Frid and Dill 2002). As the main hunting season in Switzerland coincides with the red deer rut, the two effects are difficult to disentangle.

In order to further refine analyses of compensating behaviour, a next step would be to compare movement behaviour, behavioural states and activity patterns during day and night, inside and outside HBAs.

5 | Management Implications

The differences in habitat selection during the day and at night, as well as inside and outside HBAs, corroborate previous findings that red deer in a human-dominated landscape are able to adapt their spatiotemporal behaviour to human activity (Ciuti et al. 2012; Mumme et al. 2023). We have shown that their selection against habitat characteristics indicating human presence depends on the time of day. We have further shown that HBAs—even at small scales—are a promising tool in red deer management. By offering spatiotemporal refuge habitats, managers in Switzerland take advantage of the capacity of red deer to recognise a landscape of fear. Increased use of lower tree cover density during the day increases red deer visibility. In a hunting for fear approach, hunting induces sufficiently strong risk effects to induce behavioural adaptations (Cromsigt et al. 2013). Consequently, we reason that especially the combination of short intense hunting periods with HBAs may lead to predictable red deer behaviour and can facilitate regulation. Thus, in human-dominated landscapes, we suggest that networks of small-scale HBAs that connect red deer habitats may aid in decreasing hunting pressure and maximising harvest efficiency (see also Griesberger et al. (2022)), especially when providing additional regulations to other forms of human use, such as restricting tourism.

Author Contributions

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data used in this manuscript are available via https://www.parcs.ch/snp/mmd_fullentry.php?docu_id=53933.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

2.2 Paper II

Remote sensing reveals the role of forage quality and quantity for summer habitat use in red deer

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Movement Ecology

RESEARCH **Open Access**

Remote sensing reveals the role of forage quality and quantity for summer habitat use in red deer

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Abstract

Background The habitat use of wild ungulates is determined by forage availability, but also the avoidance of predation and human disturbance. They should apply foraging strategies that provide the most energy at the lowest cost. However, due to data limitations at the scale of movement trajectories, it is not clear to what extent even well-studied species such as red deer (*Cervus elaphus*) trade-off between forage quality and quantity, especially in heterogeneous alpine habitats characterized by short vegetation periods.

Methods We used remote sensing data to derive spatially continuous forage quality and quantity information. To predict relative nitrogen (i.e. forage quality) and biomass (i.e. forage quantity), we related field data to predictor variables derived from Sentinel-2 satellite data. In particular, our approach employed random forest regression algorithms, integrating various remote sensing variables such as reflectance values, vegetation indices and optical traits derived from a radiative transfer model. We combined these forage characteristics with variables representing human activity, and applied integrated step selection functions to estimate sex-specific summer habitat selection of red deer in open habitats within and around the *Swiss National Park*, an alpine *Strict Nature Reserve*.

Results The combination of vegetation indices and optical traits greatly improved predictive power in both the biomass ($R^2 = 0.60$, Root mean square error (RMSE) = 88.55 g/m^2) and relative nitrogen models ($R^2 = 0.34$, RMSE = 0.28%). Both female and male red deer selected more strongly for biomass (estimate = 0.672 ± 0.059 SE for normalised values for females, and 0.507 ± 0.061 for males) than relative nitrogen (estimate = 0.124 ± 0.062 for females, and 0.161 ± 0.061 for males, respectively). Females showed higher levels of use of the Swiss National Park.

Conclusions Red deer in summer habitats select forage quantity over quality with little difference between sexes. Females respond more strongly to human activities and thus prefer the Swiss National Park. Our results demonstrate the capability of satellite data to estimate forage quality and quantity separately for movement ecology studies, going beyond the exclusive use of conventional vegetation indices.

Keywords Biomass, *Cervus elaphus*, Foraging ecology, Habitat selection, Integrated step selection functions, Nitrogen, Machine learning, PROSAIL, Sentinel-2

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Background

Animals face a trade-off between foraging and safety needs [33, 63]. The latter drive prey species to modify their habitat use in response to potential predators [51], with humans usually also perceived as a predation risk due to hunting [27, 68]. Diurnal behaviour can be altered to avoid humans during daytime [1, 20, 25, 33], and protected areas without hunting are preferred over non-protected areas [34, 58]. Foraging needs result in strategies that provide the most energy at the lowest cost, under the condition that animals can move freely and have sufficient information about their environment [71, 82]. Another trade-off exists between forage quality and quantity [28, 82]. Herbivore species specialize along a continuum ranging from the extremes of selectively feeding on energy-rich buds to mainly consuming mature, high-fiber and low-moisture leaves and wood [41, 54]. Based on comparisons of their digestive systems, ruminants have thus been classified into a continuum of three main feeding types: a) concentrate selectors (browsers), b) roughage eaters (grazers), and c) intermediate, opportunistic feeders [42]. Red deer (*Cervus elaphus*) as intermediate feeders [53] generally meet their high metabolic requirements by high daily forage intake which is matched with availability and quality in the summer diet [4, 98]. Results from studies that tested red deer preference on quality versus quantity simultaneously with separate variables have provided equivocal results in that they found either higher preferences for quantity [78, 81] or for quality [97]. In addition, within-population differences may arise from different seasonal selection patterns. Hence, analyses on tracking phenological green-up in spring considered varying selection between residents and migrants, with migrating individuals gaining better access to high-quality forage than residents [40, 81]. In closely related elk/wapiti (*Cervus canadensis*), residents selected for higher quantity, but lower quality, and migrating animals for intermediate quantity, but higher quality, respectively [40]. However, it is not clear to what extent red deer trade-off between forage quality and quantity, especially in heterogeneous alpine habitats characterized by short vegetation periods. This is due to two main reasons: because a) suitable and available variables specifically to describe quality versus quantity are difficult to approximate and can only be derived with substantial field effort, and b) studies have often focused on either quality or quantity (but not both), as they are difficult to disentangle [44, 50, 93].

A disadvantage of studies based on field sampling of biomass and nitrogen is that it can merely provide a snapshot in time and over a limited spatial scale. Various remote sensing instruments measuring the reflected sunlight at different wavelengths with varying spatial resolution, revisit times, and number of spectral bands have instead been used in movement ecology of ungulates (Additional file 1: Supplementary Table 1). The spectral information of space- or airborne data has commonly been ground-truthed with in-situ data, i.e. field samples such as the analysis of fecal samples, plant species and biomass [37, 40, 46, 69] to predict the respective variables over larger areas. Former studies predominantly relied on vegetation indices (VIs) related to green vegetation, particularly the Normalized Difference Vegetation Index (NDVI (Additional file 1: Supplementary Table 1); [8, 21, 66, 67]). The popularity of NDVI stemmed from the historical constraints of satellite data, which lacked bands in the red-edge area of the electromagnetic spectrum, such as the thematic mapper (Landsat missions), or had only the red and near-infrared bands available at higher spatial resolutions, e.g., Moderate-resolution Imaging Spectroradiometer (MODIS).

NDVI has proven a suitable proxy for green-up selection of, e.g., migrating elk/wapiti and red deer [9, 40, 64, 81], making it a suitable biomarker of the ecosystem: to approximate ground vegetation biomass [12, 38], but also primary productivity [3, 91], to correlate with fecal crude protein [37], chlorophyll concentration [17, 47] or dry matter digestibility of forage [30], and vegetation structure [44]. However, as NDVI is related to many vegetation properties [44], this method is less suitable for differentiating to which extent red deer prioritize forage quality versus quantity.

Imaging spectrometers, commonly referred to as hyperspectral sensors, measuring the reflected sunlight from a surface in hundreds of narrow spectral bands, have the potential to deliver both relative plant nitrogen content and plant biomass [79, 89]. However, they are currently limited to airborne sensors or satellite precursor missions (e.g., [15, 19]), thus lacking the necessary revisit time needed to study habitat use of wild ungulates over the entire plant growing season. Currently, an operational mission offering the necessary spatial and temporal resolution is the *European Space Agency* (ESA) Copernicus Sentinel-2 mission, providing reflectance data with 10 spectral bands at a spatial resolution of 10 to 20 m, and a revisit time of 5 days [23]. Despite the lower number of bands compared to an imaging spectrometer, Sentinel-2 sensors have proven their capabilities to derive forage quality and quantity [74]. The spectral bands of Sentinel-2 sensors allow not only to derive different VIs, but also to use physical-based radiative transfer models (RTMs) to estimate biophysical and biochemical plant traits (further referred to as optical traits) likely associated with forage quality and quantity [70, 76]. RTMs use physical laws to describe surface reflectance as a function of canopy, leaf and soil traits [43].

Determining whether to use surface reflectance, VIs, optical traits, or their combination for estimating forage quantity and quality is not trivial, as each approach has its advantages and disadvantages. For example, using reflectance values allows retaining the full spectral information and avoiding losing potentially valuable information, although raw reflectance may be less directly related to vegetation properties. VIs, while being easily derivable and robust in reducing artefacts arising from atmospheric correction processes [16], exhibit limitations like saturation at high biomass values [61] and a lack of specificity for directly estimating forage quality and quantity. The use of optical traits can enhance prediction transferability and account for viewing geometry, but their retrieval is ill-posed, meaning that there can be multiple solutions for a single spectral signature,dependent on ancillary data, and model assumptions are violated in structurally complex environments [77].

In this study, we used Sentinel-2 reflectance data, from which we derived VIs and optical traits to model dynamic parameters of forage quality and quantity at high spatial and temporal resolution. We thereby quantified the importance of surface reflectance, VIs and optical traits in predicting forage quality and quantity. Finally, we tested for the importance of forage quality and quantity on red deer habitat selection in summer using radio-collar GPS data and also accounted for the effects of topography and human disturbance. We expected red deer to select primarily for forage quantity followed by quality [78, 81] with males showing stronger preferences for quality than females [29]. We further expected both sexes to avoid humans [1, 20, 25, 33, 81]. Since the study is conducted in the region of the *Swiss National Park* (SNP), a protected area with strict restrictions on human use, we also predicted red deer to prefer the SNP over non-protected surroundings [34, 58].

Additional file 1: Supplementary Table 1 (letter landscape page as additional file: table_1_landscape_page.docx).

Methods

Study area

The study area is located in inner alpine valleys of eastern Switzerland (Fig. 1) including the SNP and its surrounding areas in the canton of Grisons (Switzerland), Tyrol (Austria), the Autonomous province of Bolzano – South Tyrol (Italy) and the province of Sondrio (Italy). Elevation ranges from 1000 to 3200 m a.s.l. and the tree line is at approximately 2200 m a.s.l. [36]. The climate is dry and cool, with an annual mean precipitation of 825 mm between the two weather stations *Buffalora* (1971 m a.s.l.) and *Scuol* (1303 m a.s.l.), and a mean summer temperature of 13.2 °C (monthly means from June to August) in the study years 2017 to 2021 [55]. Long winters are characteristic (~154 days with snow cover between October and May). Villages are located in the valley bottoms between 1000 and 1700 m a.s.l. The main agricultural land use consists of pastures with cattle and/or sheep. With 554′000 overnight stays from May to October [6] there are high levels of summer tourism [59, 94]. In the Swiss part of the study area winter feeding is prohibited. Red deer are hunted outside of hunting ban areas in September; in the neighboring countries Austria and Italy, the open season ranges from May to December. Where hunting is allowed, it is conducted during daytime only. The SNP (170 km^2) provides year-round protection to the animals. In this International Union for Conservation of Nature (IUCN) category Ia protected area, i.e. a *Strict Nature Reserve*, all human use is prohibited except for scientific studies and hiking on trails.

Red deer data

From 2017 to 2021, wildlife officials of the canton of Grisons and the SNP captured 70 adult red deer either using dart guns (n = 63) or corral traps (n = 7) in 12 spatially separated marking areas to account for potential migration in groups. All captures were conducted under permit by the federal and the cantonal governments (GR2017-12F, GR2020-08F), and in compliance with Swiss animal welfare laws. Telemetry collars (VECTRONIC Aerospace GmbH, Berlin, Germany) recorded GPS locations every 3 h over a period of 1 to 3 years. We removed inaccurate locations following Bjørneraas et al. [10] and excluded individuals with less than 80% fix rate success per month. Since we only analysed locations in open summer habitats, we filtered location data to June to August and *ESA WorldCover* raster [96] categories *grassland*, *cropland*, *bare/sparse vegetation*, and *moss/lichen* (Fig. 1). This resulted in a sample size of 45 adult females and 21 males with similar age distributions between sexes (Additional file 1: Table A1). For day and night comparisons, we defined daytime as the time between sunrise and sunset using the R package *suncalc* [85], and the opposite, including civil twilight, as nighttime.

Explanatory variables

Biomass and relative nitrogen

We estimated absolute grassland canopy foliar biomass (hereafter referred to as biomass) and relative canopy nitrogen content (hereafter referred to as relative nitrogen) for each recorded GPS location, using two separate random forest regression models in combination with variables derived from freely available satellite images.

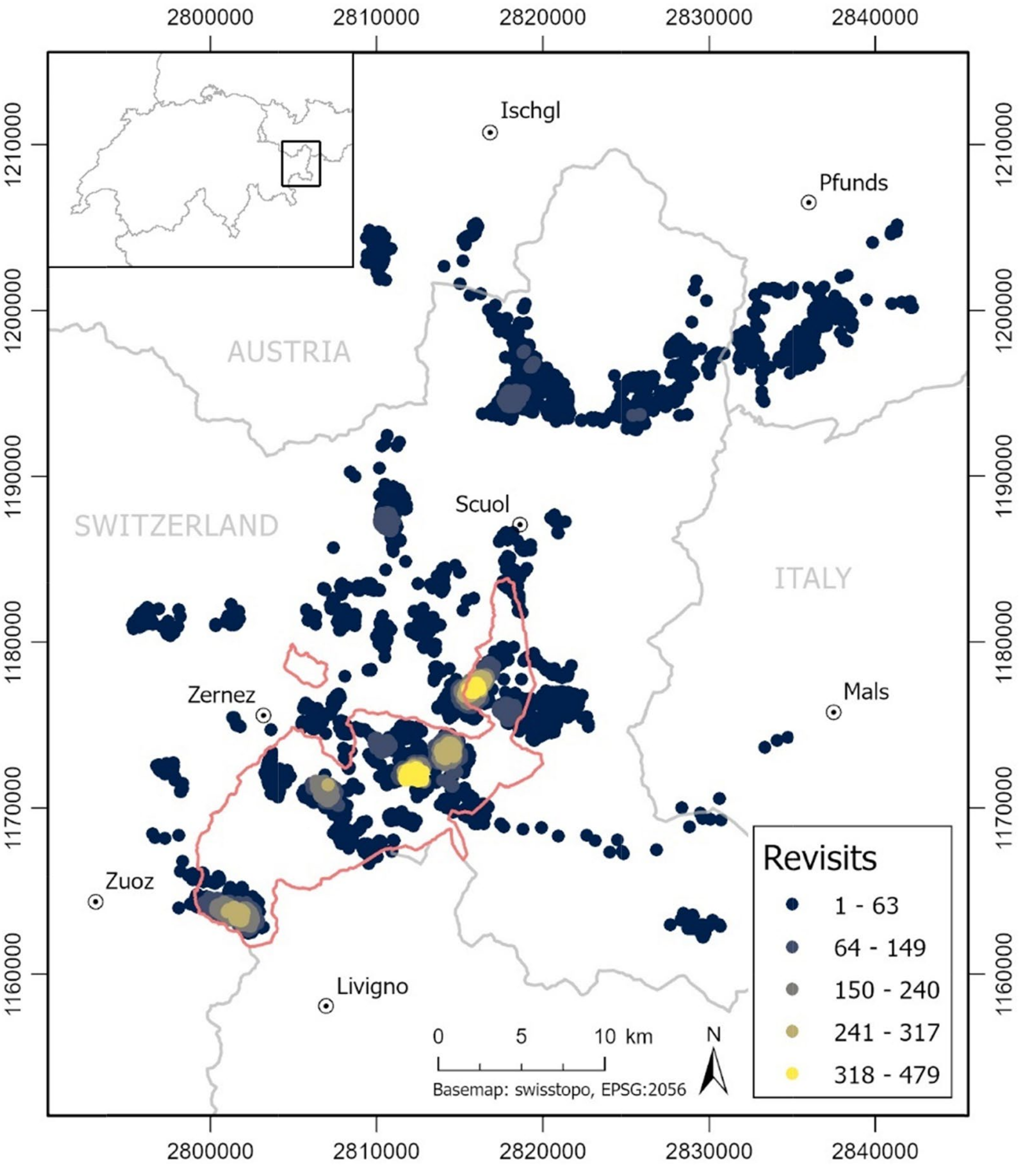

Fig. 1 Map of the study area with red deer GPS locations of 45 adult females and 21 males from June to August 2017 to 2021. To visualise the intensity of use, we calculated revisitation information within a radius of 500 m (visually determined as the optimum radius) ranging from a minimum of one revisitation (blue) to a maximum of 479 revisitations (yellow) based on the *recurse* function [13] in R. The border of the Swiss National Park is represented by red lines and country borders by grey lines

Ground reference data To train the random forest models, we used field measurements of biomass and relative nitrogen (distribution of values in Additional file 2: Figure A2) collected during the growing season in 322 plots for the SNP (2011 to 2013; [78]), as well as biomass collected in two additional studies across 52 plots in the SNP and its surroundings (2016 to 2018; [76, 77]). From 2011 to 2016, biomass in g/m^2 was clipped 1 cm above the ground on 1 m^2 per plot followed by drying at 65 °C and weighing. In 2018, dry biomass was weighed for an area of 0.2 m^2 and scaled to 1 m^2 (i.e., divided by 0.2). Chemical analysis for relative nitrogen was conducted in a previous study on one third of the samples with standard laboratory methods (TruSpec CN analyser Leco Corp., St Joseph, MI, USA; Fibre Analyser 200, Ankom Technology, NY, USA). For the remainder of the samples, a laboratory infrared reflectance spectrometer was used to predict relative nitrogen with a predictive accuracy of $R^2=0.93$ (detailed description of the method can be found in Schweiger et al. [78]). All plots were georeferenced with a high-precision

Table 1 AIC$_C$ based ranking of glmmTMBs per sex explaining model selection

	Biomass	Relative nitrogen	Distance to forest	Distance to trails	Slope	Step length	ΔAIC$_C$	AIC$_C$ weight
Females	0.67	0.12	−0.76	−0.97	−0.27	0.3	0	0.7
	0.68		−0.77	−0.97	−0.27	0.3	1.94	0.27
	0.68	0.12	−0.78		−0.27	0.3	7.14	0.02
	0.69		−0.79		−0.27	0.3	9.08	0.01
	0.67	0.13		−1	−0.27	0.29	15.28	0
Males	0.55	0.13	−0.83			0.21	0	0.32
	0.56	0.13	−0.84	0.55		0.21	0.29	0.28
	0.55	0.13	−0.83		−0.01	0.21	2	0.12
	0.56	0.13	−0.84	0.55	−0.01	0.21	2.27	0.1
	0.58		−0.84			0.21	3.51	0.06

Global Navigation Satellite System (GNSS) receiver with an expected accuracy of < 0.10 m.

Predictor variables We used three types of remotely sensed predictor variables in our random forest regression models: (1) ten Sentinel-2 spectral band reflectances [31], (2) VIs calculated from the Sentinel-2 spectral bands, namely NDVI, MERIS Terrestrial Chlorophyll Index (MTCI), Triangular Greenness Index (TGI) and Cellulose Absorption Index (CAI), and (3) optical traits (i.e. canopy structure and plant leaf traits) including leaf area index (LAI), chlorophyll content (CHL) and equivalent water thickness (EWT) obtained through the inversion of the PROSAIL RTM [45] with Sentinel-2 data. We further added dry matter (Cm) and relative nitrogen content (PROT_per), both calculated from the PROSAIL derived protein content (PROT) and non-protein carbon based constituents (CBC) to the biomass and relative nitrogen models, respectively.

Besides the commonly used NDVI, the three additional VIs were chosen since they cover different spectral regions (i.e., visible, near infrared and short-wave infrared, respectively) and provide complementary information relevant to biomass and nitrogen estimations. Specifically, MTCI is sensitive to nitrogen content in grasslands [18], TGI responds to total pigment content, which often shows a strong positive correlation with nitrogen and biomass content [86] and CAI is useful for detecting dry and non-photosynthetic vegetation contributing to the total biomass content [88].

Similarly, we chose PROSAIL optical traits related to the variables of interest: the product of Cm and LAI can serve as an estimate of biomass [72], PROT is equivalent to the nitrogen content [95], and the choice of CHL and EWT aligns with that of TGI and CAI.

To match the remote sensing data with field measurements collected previous to the launch of Sentinel-2, we resampled hyperspectral airborne surface reflectance data, acquired within days of the field data collection, to the Sentinel-2 spectral resolution. Detailed information about the derivation of all predictor variables for the GPS locations and validation data is included in Additional file 3.

Model selection We used the R package *randomForest* [52] to train separate random forest regression models for biomass and relative nitrogen. To select the most important predictor variables and identify optimal model parametrization (i.e. number of trees, minimum and maximum size of terminal nodes, and number of variables randomly sampled as candidates at each split), we used the recursive feature elimination (RFE) algorithm of the R package *caret* [49] followed by a hyperparameter optimization. Both RFE and hyperparameter optimization were performed using a fivefold cross-validation with three repeats against field-measured biomass and relative nitrogen. In doing so, we cross-validated 3456 different combinations of hyperparameters, each three times. We selected the model with the highest coefficient of determination (R^2) and also reported the root mean square error (RMSE) for the best models.

Variable importance We calculated the variable importance (i.e., increase in RMSE) of groups of predictor variables for the best random forest models using a permutation-based strategy [83]. We conducted two analyses: the first involved grouping variables with high correlation (> 0.75; Additional file 4: Figure A4), and the second involved grouping variables that belong to the same predictor type (i.e., reflectance, VIs, or optical traits). We permuted the variables from a specific predictor group for the cross-validation samples and fed them into the best random forest model to recompute the RMSE. This process was repeated 1000 times for each different group

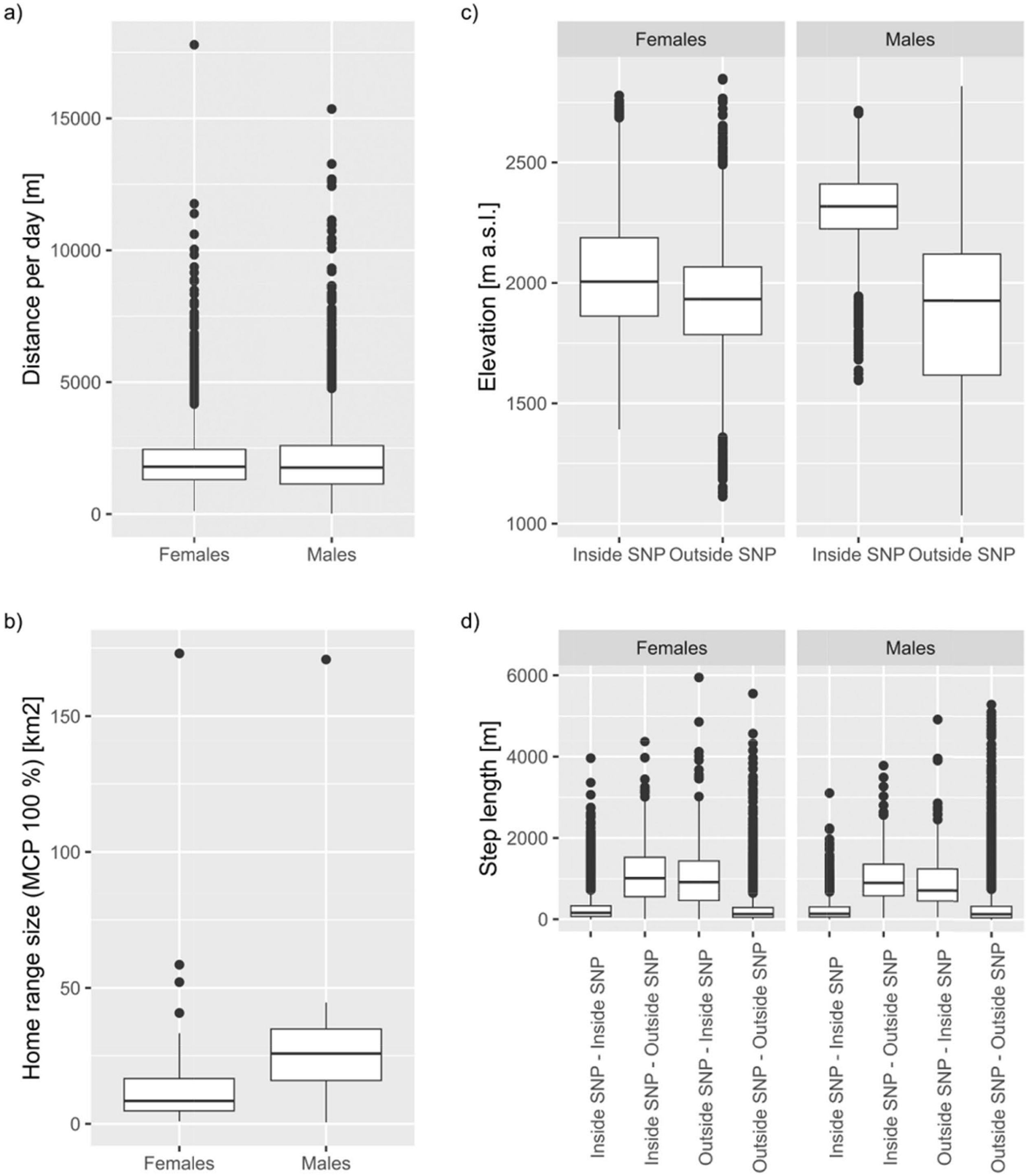

Fig. 2 Distribution of distances travelled per day (**a**) and home range sizes (**b**) by sex, and elevations covered (**c**) and step lengths (**d**) divided by sex and inside/outside the Swiss National Park (SNP)

of predictors. Subsequently, we averaged the increase in RMSE compared to the baseline RMSE values across the 1000 runs.

Prediction of GPS locations and outlier removal We assigned each GPS location to the surface reflectance data of the temporally closest Sentinel-2 image, resulting in an average discrepancy of 7.7 days between the two datasets and a standard deviation of 9.34 days. Subsequently, we used the best-performing models to predict biomass and relative nitrogen from the Sentinel-2 data for all GPS locations. Machine learning models such as random forest regression models have difficulties extrapolating predictions to data that differ from the training data. However, the dissimilarity index (DI) as proposed by Meyer & Pebesma [57] can be used to quantify the similarity between a data point to be predicted and the training data. We used the R package *CAST* [56] to calculate the DI for all GPS locations and removed DI outliers based on the interquartile range, thus only including values lower than $Q_3 + 1.5 * (Q_3 - Q_1)$, with Q1 and Q3 representing the first and the third quartile, respectively.

Further habitat variables

Close proximity to forest, as well as avoiding trails, are considered avoidance responses to humans [81]. The same applies to steep slopes, as human activity tends to be higher in flat terrain. Based on the input digital elevation model [65] we calculated slope using the *terrain* function of the R package *raster* [24]. We extracted the category *tree cover* from *ESA WorldCover* [96] in ArcGIS Pro (version 3.0.3, ESRI) and then calculated path distance to forest for all red deer locations (i.e. of all *ESA WorldCover* categories).

For the Swiss parts of the study area, we extracted trails from the streets layer of the *Swiss Topographic Landscape Model* [84] by filtering for trail categories of up to 2 m in width. For the Austrian and Italian parts of the study area, we extracted Open Street Map data using Protomaps (https://protomaps.com/downloads/osm/18343d18-d905-440e-9b45-6bcc41608e16). We post-edited lacking trails in ArcGIS Pro with Swisstopo's reference map 1:25′000. Combined with the trails in Switzerland, we also calculated path distance of red deer GPS locations to trails.

Step length

Step length, i.e. the distance between two consecutive GPS locations, serves as a measure of movement intensity. It was calculated while processing integrated step selection functions (iSSFs; see section *Modelling habitat selection*). The inclusion of step length into the model reduces potential biases due to the variability in red deer's individual movement behaviour [26].

Modelling habitat selection

iSSFs [5] were applied to estimate habitat preferences. In a first step, we used the R package *amt* [80] to generate individual trajectories. Based on the distribution of step lengths and turning angles, we estimated 25 random locations per observed location. Since we had to restrict the analyses of GPS locations to open habitats for reliable biomass and relative nitrogen values, we restricted our dataset to steps in open habitats with at least three random locations following Sigrist et al. [81]. We scaled all explanatory variables to mean zero and standard deviation 0.5 combining the female and male datasets [32], and then ran sex-specific generalized linear mixed models using Template Model Builder (glmmTMB,[60]). Individual was included as a random effect to correct for individual-specific variation in habitat selection and sample size. Model selection was applied using the R package *MuMIn* [7],Table 1). All analyses were conducted in R version 4.2.3 [73].

Results

Movements of red deer

Divided into the categories of the *ESA WorldCover* raster [96], 74% of red deer summer locations in open habitats were in grassland, 24% in moss and lichen, 2% in bare / sparse vegetation and 0.07% in cropland. Daily distances travelled, home range sizes (100% Multiple Convex Polygons) and step lengths inside and outside the SNP, respectively, were similar for both sexes (Fig. 2). Elevations covered outside the SNP were also similar, but males inside the SNP stayed at higher elevations than females. Since step lengths from movements between inside and outside the SNP accounted for only 2% they had little influence on the results for either sex.

Modelling biomass and relative nitrogen

We observed a strong performance of the best biomass model ($R^2 = 0.60$, RMSE = 88.55 g/ m^2, ntree = 1000, nodesize = 5, maxnodes = 25, mtry = 8). Tuning the hyperparameters resulted in only slight changes to the outcomes, as we found a mean R^2 of 0.578 with a standard deviation of ± 0.01 across all models. Based on the RFE analysis, we found eight variables to be sufficient in predicting biomass (Fig. 3a), with MTCI resulting as the most important variable followed by the group including NDVI, CAI and LAI. The optical trait CHL was also an important predictor.

Moderate predictive accuracies were found for relative nitrogen (best model: $R^2 = 0.34$, RMSE = 0.28%,

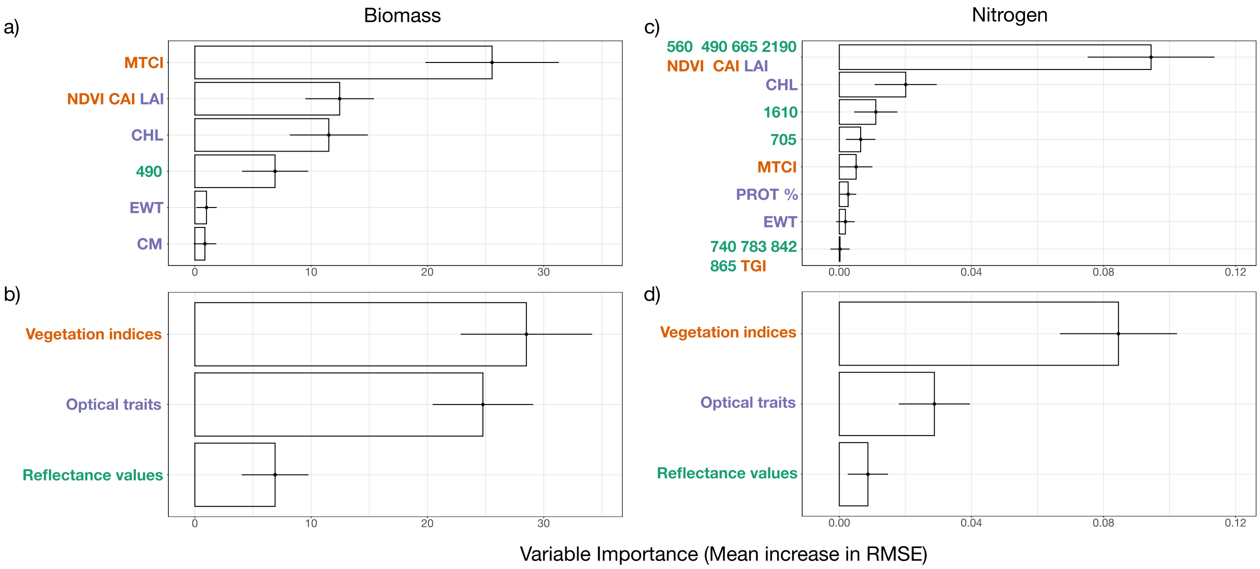

Fig. 3 Average variable importance and their standard deviation over 1000 permutations of the random forest regression models for biomass grouped by correlated variables (**a**) and by variable type (**b**), and accordingly for relative nitrogen in (**c**) and (**d**). We included three types of variables: reflectance values of Sentinel-2 bands, represented by their central wavelength in nanometers (green), and derived from them vegetation indices (orange) and optical traits derived using the radiative transfer model PROSAIL (blue)

ntree = 500, nodesize = 7, maxnodes = 23, mtry = 18) with an average R^2 of 0.31 and standard deviation of ± 0.01 across all models. All 18 variables were retained for nitrogen prediction based on the RFE analysis (Fig. 3b). We found the group including spectral bands in the visible part of the spectrum as well as NDVI, CAI and LAI, as the most important variable, followed by CHL (Fig. 3c).

VIs were the most important variables in both biomass and relative nitrogen models. However, optical traits also contributed additional value, particularly in the biomass models (Fig. 3b). While spectral bands appeared to be significant in the models for relative nitrogen, they did not provide additional value compared to VIs and optical traits, and were marginal in the biomass models (Fig. 3d).

Habitat selection of red deer

The best supported model for female red deer in open summer habitats corresponded to the full model, while the best model for males excluded distance to trails and slope (Table 1). Red deer of both sexes selected habitats with high biomass and high relative nitrogen (Fig. 4, Table 2), with biomass having a greater effect than relative nitrogen. The comparison between the sexes showed that females tended to select habitats more strongly for biomass than males, but males selected habitats somewhat more strongly for relative nitrogen than females. However, a statement on significant differences between the sexes is not possible because we calculated sex-specific models.

Regarding the variables indicating safety needs, females preferred to stay close to the forest and to trails, and in flat terrain. Males selected for short distances to forest. Both sexes showed high step lengths indicating more movement, with females moving longer distances than males.

For both sexes, GPS locations in open summer habitats were relatively evenly distributed between day and night (Additional file 5: Table A5): For females, 47% of the locations were recorded during the day and 51% for males. While 82% of the females' locations were within the SNP, this applied to only 46% of the males' locations (Fig. 5a). Of these, 89% of female locations were inside the SNP during the day and 75% at night, while for males 59% were inside the SNP during the day and 32% at night (Fig. 5b).

Discussion

Using iSSFs, we identified summer habitat preferences of free-ranging red deer in a heterogeneous open alpine landscape. We detected effects of variables indicating human disturbance and vegetation characteristics estimated based on remote sensing and field samples (Fig. 4, Table 2). The method combined simultaneous estimation of individual movement and resource selection parameters and thus enabled a likelihood-based inference of resource selection within a mechanistic movement model [5].

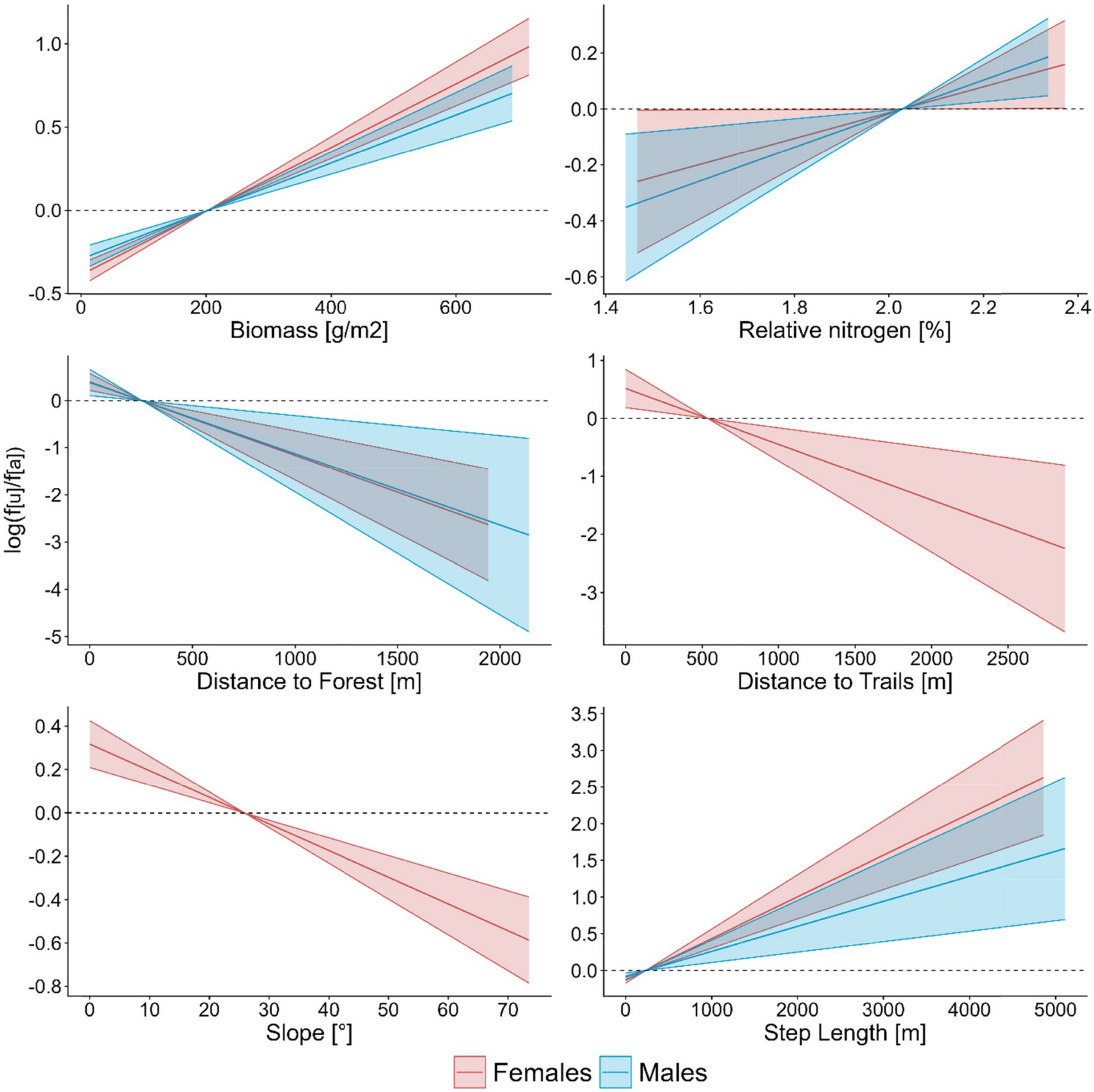

Fig. 4 Habitat selection by red deer in summer with respect to biomass, relative nitrogen, distance to forest, distance to trails and slope, as well as step length, with 95% confidence intervals. $f_{[u]}/f_{[a]}$ refers to the frequency ratio between used and available locations. Values > 0 indicate preference, values < 0 avoidance. Models were run separately per sex. Note the different scales in the plots. Only significant results are shown

Habitat selection of red deer

Red deer face a trade-off between forage quality and quantity and are under pressure to employ foraging strategies that provide the most energy for the lowest cost [28, 71, 82]. Several studies have shown that in seasonal and predictable habitats, red deer prefer higher altitudes in summer than in winter due to greater availability of high-quality forage [9, 30, 40, 64, 69, 81, 97]. We found that red deer selected more strongly for biomass than for relative nitrogen (Fig. 4, Table 2). Thus, in our study they preferred forage quantity over quality. This is largely in line with results from Hebblewhite et al. (40, 78]. The comparison with Schweiger et al. [78] who examined forage preferences earlier in the season also indicates that preferences for biomass over relative nitrogen in our study were not caused by a beginning of brown-down in August

Table 2 Results of the best supported glmmTMBs for female and male red deer in open summer habitats. SE = standard error, CI = confidence interval. Significance levels for *p* values * < 0.05, ** < 0.01, *** < 0.001

Predictor	Females		Males	
	Estimate (SE)	95% CI	Estimate (SE)	95% CI
Biomass	0.672 (0.059)***	0.555, 0.788	0.507 (0.061)***	0.388, 0.626
Relative nitrogen	0.124 (0.062)*	0.002, 0.246	0.161 (0.061)**	0.041, 0.281
Distance to forest	− 0.764 (0.175)***	− 1.107, − 0.421	− 0.741 (0.272)**	− 1.274, − 0.207
Distance to trails	− 0.97 (0.316)**	− 1.590, − 0.351		
Slope	− 0.27 (0.047)***	− 0.361, − 0.178		
Step length	0.299 (0.046)***	0.210, 0.388	0.179 (0.053)***	0.075, 0.284

or by early depletion of nutrient-rich forage. Different findings by Zweifel-Schielly et al. [97] may be explained by different elevational ranges between their and our study: Their study was conducted down to a minimum elevation of 470 m a.s.l. (versus 1000 m a.s.l. in ours), and also included nutrient-poor vegetation on the forest floor. As expected, differences in sex-specific selection of forage quality and quantity [9, 11] were weak. However, the fact that females in summer tended to select patches with higher quantity but lower quality than males was in line with patterns found for spring and autumn diets [29], which is not unusual for intermediate feeders [62].

Since our study area is characterized by strict protection regulations inside the SNP, where no human activity is permitted except for research and hiking on trails, it provides a good basis to analyse the trade-off between foraging and safety needs of red deer [33, 58, 63]. Predators were absent during the study period, except for one single resident female wolf in part of the study area in the years 2017 to 2022. Red deer preference of areas close to forest may be due to reasons of thermoregulation (e.g. [2], for chamois) or indicates their need for safety [81], which we have identified for both sexes. As previous studies showed, female red deer, especially those with offspring, choose safe habitats even at the expense of forage quality [9, 11]. We know from summer counts inside the SNP that 48% of females (two years and older) had calves over the study period (SNP, unpublished data) and assume that this rate also applies to tagged animals. The increased frequency of GPS locations of females within the SNP during the day (89%) compared to night-time (75%) indicates the overriding need for safety (Fig. 5, Additional file 5: Table A5). Males also showed this pattern, but at a lower level (59% during the day and 32% at night), which indicates clear sexual differences concerning the need for safety, and differences between day and night. Thus, males left the SNP at night about twice as often as females, which could also be interpreted as avoidance of high red deer density. As the SNP is surrounded by alpine pastures [76], which are grazed by livestock (cattle and sheep) and therefore offer lower biomass but higher relative nitrogen, this may have influenced the result of males selecting lower forage quantity but higher quality than females. Our results are applicable to relatively undisturbed summer habitats at higher elevations (>= 1000 m a.s.l.), which are characterised by short vegetation periods and overall low biomass. However, in more intensively cultivated landscapes with high biomass, e.g. agricultural lands, relative preferences may differ.

Sexual differences in habitat selection were also indicated by the different structure of the best-supported models (Table 1): for males, the variables *distance to trails* and *slope* were not included. Since avoiding trails and seeking out steep terrain are considered responses to human activity, it is fitting that these should not affect males which appear to be more tolerant to disturbance than females. The preference by females to both proximity to paths and flat terrain (i.e. areas with more

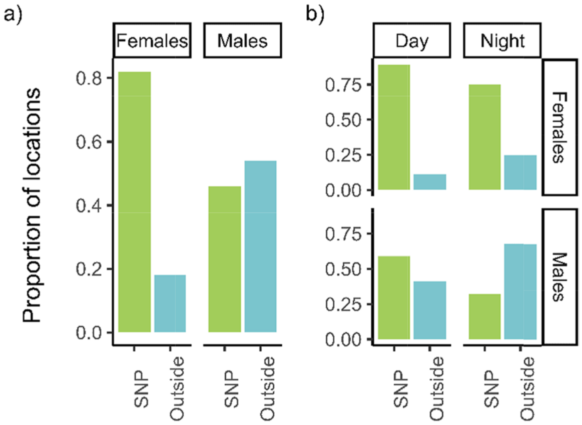

Fig. 5 Proportions of summer GPS locations per sex inside (green) and outside the Swiss National Park (SNP; blue) (**a**), and the respective proportions divided into day and night (**b**)

human activity), appears to contradict current theory. However, this might be explained by females' pronounced preference for the SNP, where human activity is strictly limited to trails and visitor flows are predictable: the most frequently used areas were inside the SNP, but in close proximity to trails (Fig. 1).

Modelling biomass and relative nitrogen

We modelled biomass and relative nitrogen at a spatial resolution of 50 m, and thus took into account the accuracy of the GPS locations (11.3 m ± 4.7 m as measured in Schweiger et al. [78]). Compared to that previous study in the same region based on a single remote sensing dataset [78], our study included weekly spectral information from June to August, and a higher sample size of red deer ($n = 66$ versus $n = 2$), but a coarser spatial scale (250 m^2 versus 36 m^2). Despite the different remote sensing approaches used, the predictive accuracies of forage quality and quantity between Sentinel-2 and hyperspectral data [78] were comparable. While our biomass model performed slightly better over multiple years ($\Delta R^2 = 0.03$), our relative nitrogen model performed slightly worse ($\Delta R^2 = -0.09$). Red deer selection patterns of biomass and relative nitrogen were consistent across both studies. This also corroborates selection patterns of forage quality and quantity in open habitats using a spatial resolution of 100 m^2 [81], although the remotely sensed instantaneous rate of green-up as a measure for forage quality and NDVI for quantity was used in their study.

A major limitation of our study and remote sensing of forage quality and quantity in general is predicting relative nitrogen, reflected in the moderate accuracy and complexity, i.e., retention of all predictor variables by our model for relative nitrogen. Similar studies relied on the use of vegetation indices as approximations of forage quality without validating them against ground reference data [9, 58, 64, 81]. Therefore, while our model explained only a third of the variance in relative nitrogen, the inclusion of ground reference data marks a significant improvement and raises questions about the reliability of certain vegetation indices as proxies for relative nitrogen content.

The reflectance of plant communities is mainly determined by the absolute content of nitrogen (g/m^2) in leaves and not its concentration relative to other leaf constituents [48]. The problematic use of concentration measurements for nitrogen is enhanced in areas where the vegetation cover is uncorrelated to the nitrogen content, a scenario possible in vegetation-poor areas. Therefore, from a remote sensing point of view, using the absolute nitrogen content should be preferred, despite its strong correlation with biomass (Additional file 6: Table A6, [93]), rendering a comparison of the selection of quality and quantity difficult. To partially mitigate the uncertainties associated with using remotely sensed relative nitrogen, we have used a substantial number of field samples to train the remote sensing models and excluded data points from the habitat selection analysis with ranges unseen during model training. Other mitigation strategies could involve the estimation of vegetation cover and non-photosynthetic vegetation from remote sensing data to actively exclude vegetation-poor areas from the analysis or improve the relative nitrogen models with such additional information. In this regard, future operational and spaceborne hyperspectral sensors [14, 75] promise more accurate predictions of forage quality.

As shown in other studies [35, 74], the inclusion of VIs in predicting forage quality and quantity improved the prediction accuracy. VIs remain the most suitable choice in forage quality and quantity estimations in grasslands due to their simplicity and strong relevance. MTCI, which uses bands from the red-edge and near-infrared region, was particularly useful. Red-edge and near-infrared regions are strongly related to chlorophyll and nitrogen content in plants [18, 22]. Overall, our results suggest to use additional VIs alongside NDVI, particularly given that NDVI experiences saturation issues in densely vegetated areas.

Similar to VIs, we found optical traits to improve the forage quality and quantity prediction. In particular, the biomass models strongly profited from the inclusion of optical traits. PROSAIL is highly sensitive to LAI, which is directly related to biomass [90]. While VIs are commonly used in predictive models, optical traits are rarely used or have shown no added value for grassland quality and quantity indicators [74]. However, Raab et al. [74] used a hybrid inversion of RTMs [92] implemented in the Sentinel Application Platform (SNAP) to derive optical traits, which differed from our look-up table (LUT) inversion. As shown by Hauser et al. [39], an optimised trait retrieval from RTMs with a LUT outperformed the SNAP application. Furthermore, hybrid approaches without further fine tuning can be ineffective in predicting optical traits in heterogeneous grassland. Overall, our results suggest that the inclusion of optical traits derived with an LUT approach increases the predictive power of forage quality and quantity models, but also highlight the challenges of relying solely on them, underpinned by the marginal importance of PROT_per in the relative nitrogen model. Nevertheless, the use of such optical traits next to VIs is motivated by the underlying physical foundation and therefore higher transferability of the models to unseen data [87]. This could especially be the case when a limited amount of field data is available to calibrate the models.

Conclusions

Red deer in open summer habitats selected forage quantity over quality. Centred on an alpine *Strict Nature Reserve*, their habitat selection was also strongly influenced by their need for safety: Females responded more strongly to human activities than males and therefore preferred the SNP.

Remote sensing data has proven to be valuable for the estimation of forage quality and quantity in open habitats over large areas and multiple years and months. In particular, the inclusion of vegetation indices and rarely used optical traits in regression models for biomass and relative nitrogen has increased prediction accuracies. While biomass can be mapped with high accuracy, certain ambiguities remain in remote sensing of relative nitrogen. Future studies could leverage on forthcoming hyperspectral satellite sensor to take into account soil and non-photosynthetic vegetation cover, potentially enhancing nitrogen prediction from space.

Abbreviations

APEX	Airborne prism experiment
AVHRR	Advanced very high resolution radiometer
CAI	Cellulose absorption index
CBC	Non-protein carbon based constituents
CHL	Chlorophyll content
Cm	Dry matter
DI	Dissimilarity index
ESA	European space agency
EWT	Equivalent water thickness
glmmTMB	Generalized linear mixed models using template model builder
GNSS	Global navigation satellite system
iSSFs	Integrated step selection functions
IUCN	International union for conservation of nature
LAI	Leaf area index
LUT	Look-up table
MODIS	Moderate-resolution imaging spectroradiometer
MTCI	MERIS terrestrial chlorophyll index
NDVI	Normalized difference vegetation index
PROT	Protein content
PROT_per	Relative nitrogen content
RFE	Recursive feature elimination
RMSE	Root mean square error
RTM	PROSAIL radiative transfer model
SNAP	Sentinel application platform
SNP	Swiss national park
TGI	Triangular greenness index
VIs	Vegetation indices

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40462-024-00521-6.

Additional file 1
Additional file 2
Additional file 3
Additional file 4
Additional file 5
Additional file 6

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Author contributions

TR, CR, PA and FF had the original idea for the study. JS and SB refined the study design and analytical approach. Fieldwork was organised by TR, FF and HJ. CR and JS performed the statistical analyses on the vegetation characteristics, TR, PA and SB on the integrated step selection functions. TR, CR, JS and PA drafted the manuscript. All authors made important contributions by editing the final manuscript.

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Availability of data and materials

The dataset supporting the conclusions of this article is available from the corresponding author on reasonable request.

Declarations

Competing interests

The authors declare no competing interests.

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Publisher's Note

2.3 Paper III

Comparing the accuracy of machine learning methods for classifying wild red deer behavior based on accelerometer data

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Animal Biotelemetry

METHODOLOGY **Open Access**

Comparing the accuracy of machine learning methods for classifying wild red deer behavior based on accelerometer data

Benjamin Bar-Gera[1*], Pia Anderwald[2], Alina L. Evans[3], Thomas Rempfler[2] and Claudio Signer[1]

Abstract

Background Effective conservation requires understanding the behavior of the targeted species. However, some species can be difficult to observe in the wild, which is why GPS collars and other telemetry devices can be used to "observe" these animals remotely. Combined with classification models, data collected by accelerometers on a collar can be used to determine an animal's behaviors. Previous ungulate behavioral classification studies have mostly trained their models using data from captive animals, which may not be representative of the behaviors displayed by wild individuals. To fill this gap, we trained classification models, using a supervised learning approach with data collected from wild red deer (*Cervus elaphus*) in the Swiss National Park. While the accelerometer data collected on multiple axes served as input variables, the simultaneously observed behavior was used as the output variable. Further, we used a variety of machine learning algorithms, as well as combinations and transformations of the accelerometer data to identify those that generated the most accurate classification models. To determine which models performed most accurately, we derived a new metric which considered the imbalance between different behaviors.

Results We found significant differences in the models' performances depending on which algorithm, transformation method and combination of input variables was used. Discriminant analysis generated the most accurate classification models when trained with minmax-normalized acceleration data collected on multiple axes, as well as their ratio. This model was able to accurately differentiate between the behaviors lying, feeding, standing, walking, and running and can be used in future studies analyzing the behavior of wild red deer living in Alpine environments.

Conclusion We demonstrate the possibility of using acceleration data collected from wild red deer to train behavioral classification models. At the same time, we propose a new type of metric to compare the accuracy of classification models trained with imbalanced datasets. We share our most accurate model in the hope that managers and researchers can use it to classify the behavior of wild red deer in Alpine environments.

Keywords Cervus elaphus, Swiss National Park, Behavioral classification, Acceleration data, Data imbalance, Overall accuracy, Balanced accuracy, Specificity, Sensitivity, Neural networks, Discriminant analysis, Random forest, Support vector machines, Decision trees

Background

In order to effectively protect and manage a species, it is important to understand its behavior [1]. Although visual observation is the most effective method to learn about an animal's behavior, observing wild animals such as red deer (*Cervus elaphus*) can be difficult as they are often elusive, may live in habitats with tree cover, are

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nocturnal, move over large distances, and can easily be disturbed by the observer [2]. To overcome these challenges, GPS collars and other telemetry methods have been used to study the spatial movements of red deer, resource selection and seasonal migrations, as well as other factors affecting their movements, such as human activity [3–5]. While these methods can provide valuable knowledge about the spatiotemporal behavior of animals, they suffer from various limitations, most notably that it can be difficult to infer which behavior the animals are engaging in [6].

Accelerometers have become a frequent component of GPS collars [6]. They measure the collar's and thus the animal's intensity of movement as the difference in velocity between two consecutive measurements. Accelerometers usually record multiple measurements per second. The data is then either saved raw (i.e., high-resolution [7, 8]) or averaged over predefined time intervals, such as 1, 5 or 10 min (i.e., low-resolution [2, 9–11]). While resolution can also pertain to the device's sampling frequency or bit-resolution, we solely use this term regarding whether the acceleration data has been averaged over predefined time intervals or left in its raw state. Averaging and reducing the amount of data can be useful when animals wear the collars over long periods and the amount of data storage is limited [12]. Additionally, working with low-resolution data requires less computing power and tends to be more accessible from a technical point of view than working with high-resolution data.

Acceleration data can be used to infer an animal's relative level of activity as a result of time, seasonality, weather, sex or age [13, 14]. Combined with a classification model the acceleration data can provide knowledge about the animal's behavior and has been used for a variety of species in the wild, including pumas (*Puma concolor*) [15], Alpine ibex (*Capra ibex*) [16], polar bears (*Ursus maritimus*) [17], or various cervids [2, 7–9, 11, 18]. Previous behavioral classification models for cervids can be categorized by whether they were trained with captive [11] or wild animals [7], whether they use low- [9] or high-resolution [8] acceleration data and whether they are binary [18] or multiclass [2] models. A binary model classifies only two different modes, such as two behaviors (e.g., feeding vs. walking) or whether the animal is active or inactive, whereas a multiclass model has the potential to classify more than two behaviors (e.g., running, feeding, or standing).

To the best of our knowledge, no multiclass models have been trained using wild cervids *and* low-resolution acceleration data. While models trained on captive animals can be very useful in certain circumstances, previous studies have illustrated that such models may perform worse than models trained with wild animals when classifying the behavior of wild animals, due to differences in behavior and/or habitat [17]. As there is always a tradeoff between the resolution of accelerometer data and memory capacity, long-term studies on wild animals frequently use collars that only save low-resolution acceleration data. For these two reasons, our first goal was to generate a multiclass behavioral model that is based both on low-resolution acceleration data and behavior of wild cervids.

With the adoption of sensors such as accelerometers, researchers are increasingly confronted with large datasets [19]. Machine learning (ML) algorithms can help find patterns in these datasets to generate new ecological insight (e.g., estimating animal populations with unmanned aerial vehicle footage [20]) or automate previously manual tasks (e.g., classifying trail camera images [21, 22]). As ML algorithms have become an increasingly popular tool in the field of ecology, they have also become easily accessible through R packages [23–31].

However, with so many different algorithms, it is difficult to know which ones to use. Previous studies have used discriminant function analysis [9, 11], recursive partitioning (i.e., classification and regression tree) [2, 10], or random forest [7, 8]. Nathan et al. [32] compared the efficacy of various ML algorithms for classifying the behavior of griffon vultures (*Gyps fulvus*) and Ladds et al. [33] did the same with fur seals (*Arctocephalus spp.*) and sea lions (*Neophoca cinerea*). However, to date no such comparison has been performed for cervids. Our second goal was therefore to fill this gap by using a variety of ML algorithms and analyzing which ones generate the most accurate classification models.

GPS collars usually include multiple accelerometers that can measure the movement on different axes (e.g., left–right, up–down, forward–backward). For our third goal, we generated models using different combinations of the axial acceleration values and their derived counterparts (sum, difference, and ratio). This allowed us to analyze not only which algorithms, but also which combination of input variables generate the most accurate models. We also applied various normalization methods to the acceleration data to identify which ones generated the most accurate models.

Methods

Study area

All field observations were conducted in and around the Swiss National Park (SNP), which covers an area of approximately 170 km^2 in eastern Switzerland [34]. The SNP is classified as an IUCN 1a conservation area (highest class of protection, wilderness area). Visitors must remain on the provided paths, plants may not be removed except for scientific reasons, meadows cannot be mowed, and all hunting is forbidden. The SNP has a diverse topography typical for the Central Alps, with elevations ranging from 1380–3173 m a.s.l. The tree line varies between 2200–2300 m a.s.l. Most of the SNP's area is subalpine and composed of around 31% forest and 17% meadow, while the rest is free of vegetation. The mean annual temperature (1991–2020) at the weather station Buffalora was 1.1 °C, the coldest month being January (− 9.1 °C) and the warmest July (11 °C) [35]. Mean annual precipitation is 936 mm, with July and August being the wettest months with 118 and 130 mm of rain, respectively. Buffalora is located just outside the SNP and at a similar altitude (1971 m a.s.l.) as the observational locations.

Study animals and telemetry collars

In the SNP and surrounding areas, wild red deer have been equipped with GPS collars since 1998 as part of various research and management efforts. Wildlife officials of the canton of Grisons and the SNP immobilized and anesthetized the animals with dart guns and 3 ml Hellabrunn mixture containing 125 mg xylazine and 100 mg ketamine per ml. Capturing and collaring was conducted according to Swiss animal welfare law (permit GR2015-09). The animals wear the collars for a maximum of 2 years, after which they are released via a remote drop-off mechanism. Every individual receives a unique combination of colored ear tags, allowing visual identification. During the fieldwork period, we observed four individuals in the wild. These included two stags (No. 779 and No. 783) and two hinds (No. 761 and No. 762). At the time, they were estimated to be 7, 9, 13 and 9 years old, respectively. Both hinds were rearing a calf and were additionally accompanied by a yearling.

The observed red deer were equipped with two different types of GPS collars from VECTRONIC Aerospace GmbH, Berlin, Germany: PRO LIGHT and VERTEX PLUS [36, 37]. Besides the location, these collars measure intensity of movement using multiple accelerometers. The antenna and electronic housing, including the accelerometer, are located on top of the collar and thus on the back of the animal's neck. The accelerometers measure acceleration continuously at 4 Hz on each axis as the difference in velocity between two consecutive measurements. Acceleration is averaged over 5-min intervals per axis and provided as a unit-free number ranging from 0–255, with 0 representing no movement and 255 maximum movement. Henceforth, these values will be referred to as acceleration values or acceleration data. The different types of collars are equipped with accelerometers on either two (x, y) or three axes (x, y, z), where the x-axis measures forward–backward motion, the y-axis sideways (i.e., left–right) motion, and the z-axis up–down movements. However, as two (762 and 779) of the four observed individuals wore collars which only measure x- and y-acceleration, we only used these two axes to generate the models. Acceleration data can be downloaded from the collars via UHF and VHF in the field or directly from the device after drop-off.

Behavioral observations

Animal observations took place during July and August 2022. As hunting is prohibited and human activity inside the SNP is restricted to hiking trails, red deer are often active and visible in open habitats during the day. We observed the animals from a distance between 250–1200 m using a spotting scope, focusing on one collared individual at a time, as long as it was visible [38]. The behavior was logged simultaneously in the ethological app "Behayve", which generated time-stamped behavioral logs for every observational session and individual [39]. While using Behayve proved to be very effective in collecting observational data, we additionally filmed most behavior through the spotting scope using a digiscoping adapter and a smartphone. The Android app "Timestamp Camera Pro" [40] was used for filming, as it displays the current time as a watermark. The filmed behavior served as a point of reference in case of any logging errors and was also used to distinguish specific behaviors more clearly.

Similar to previous studies [2, 7, 9–11], we distinguished between the behaviors lying, feeding, walking, running, standing, and fighting (Table 1). We also

Table 1 Observed behavior of wild red deer in the Swiss National Park

Behavior	Description
Lying	Lying on the ground either resting or ruminating
Feeding	Grazing with or without moving from one spot to another; we observed no instances of browsing
Standing	Standing in one spot, either vigilant and/or ruminating
Walking	Moving slowly from one spot to another without grazing at the same time
Running	Moving quickly from one place to another, either trotting or galloping
Fighting	Stags only: clashing antlers with another stag

Table 2 Formulae used to train the behavioral classification models

$behavior \sim x_{minmax} + y_{minmax}$
$behavior \sim x_{scale} + y_{scale}$
$behavior \sim x_{log} + y_{log}$
$behavior \sim x_{minmax}$
$behavior \sim y_{minmax}$
$behavior \sim sum(x,y)_{minmax}$
$behavior \sim diff(x,y)_{minmax}$
$behavior \sim ratio(x,y)_{minmax}$
$behavior \sim x_{minmax} + y_{minmax} + ratio(x,y)_{minmax}$

recorded whether the animals were ruminating or not while lying, as well as their vertical head position while walking and feeding. However, our preliminary analyses suggested that our models would not be able to distinguish between these modes, which is why we did not include them further in our study.

Data analysis

After completing the behavioral observations, the acceleration data was downloaded remotely from the GPS collars via VHF/UHF and the behavioral data was exported from the Behayve app on the smartphone. The workflow of generating the classification models consisted of preprocessing the acceleration and behavioral data, model-training, and model-testing (see Additional file 1: Fig. S1 for a schematic overview of the data analysis process).

Preprocessing involved checking the behavioral and acceleration data visually for errors, normalizing, transforming, and labeling the acceleration data with the simultaneous behaviors, and splitting the data into a training (75%) and testing (25%) subset. To train the classification models, various algorithms were employed, with the acceleration data serving as input variables and the behavior as the output variable (Table 2). Model-testing was conducted with the testing subset to assess and compare the different models and their accuracy [8, 9, 41]. Data analysis was conducted with the R programming language [42] and using RStudio [43].

Normalizing and transforming the acceleration data

As the tightness of a collar can significantly affect the acceleration data, and the individuals wore different collar types, we tested whether inter-individual differences in the acceleration data existed [44]. We hypothesized that such differences might negatively affect the models' ability to classify behaviors across all individuals [45]. Because we detected significant inter-individual differences (Kruskal–Wallis $\chi 2 = 7745.7$, $df = 3$, $p < 0.001$ for x-acceleration and $\chi 2 = 4979.8$, $df = 3$, $p < 0.001$ for y-acceleration), we separately applied scale-transformation to each individual and axis, thereby reducing these inter-individual differences [45].

Additionally, we applied minmax-normalization, which retains the original distribution of the values but projects them onto a 0–1 scale, improving the speed at which models can be trained. We also applied log-transformation to test whether this might have a positive effect on the models' accuracy (see Additional file 2: Table S1 for a detailed description of the normalization methods and Additional file 3: Fig. S2 for a visualization of their effects).

Similarly, we generated derived acceleration values, including the sum $(acc_x + acc_y)$, difference $(acc_x - acc_y)$ and ratio $(\frac{acc_x}{acc_y})$ of both axes. Having access to the variously transformed and derived acceleration values allowed us to compare their efficacy in generating accurate classification models.

Combining acceleration and behavioral data

The challenge in linking behavioral and acceleration data is that the acceleration intervals always last 5 min (12:00–12:05, 12:05–12:10, …), but behaviors of red deer are not consistent with these intervals. As a solution, two types of labeled acceleration intervals were generated: pure and mixed intervals (Fig. 1). During a pure interval, the animal engages continuously in a single behavior. During a mixed interval, the animal may engage in multiple behaviors, but, more

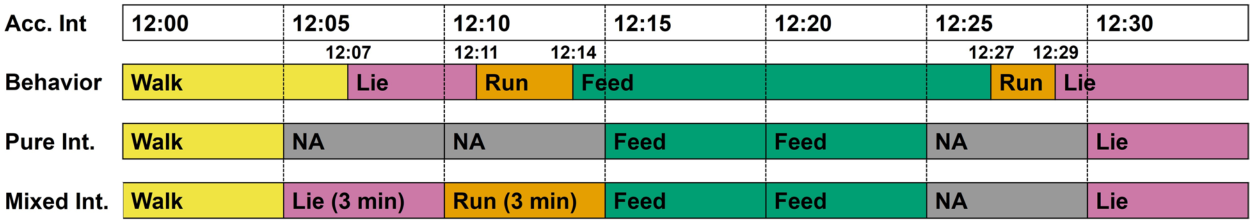

Fig. 1 Time-dependent linkage of acceleration intervals (constant time interval of 5 min) and behavioral data (variable duration). Every pure acceleration interval starts and ends within the same continuous behavior. Mixed acceleration intervals include all intervals during which a single behavior was engaged in for at least half the duration (> 2.5 min) and hence also include all pure intervals

importantly, engages in one behavior for at least have the acceleration interval (>2.5 min). As such, by this definition, mixed intervals also include pure intervals.

Acceleration data from wild animals will always include mixed intervals, especially when intervals are as long as 5 min. For the rare and short behaviors, standing and walking, the number of mixed intervals was significantly higher than the number of pure intervals (Table 4). Using mixed intervals allowed us to include these behaviors and generate multiclass models. Additionally, by training and testing models with pure intervals, for behaviors that are likely to include a high proportion of mixed intervals, we risk generating artificial and inflated estimates of the models' accuracies [9, 46]. For these reasons, we decided to use mixed intervals to train and test all our models. Due to the rarity of fighting, we were able to generate only two mixed intervals for this behavior and did not include this behavior in our subsequent analysis.

Train–test split

To train and test the classification models, we split the data into mutually exclusive datasets: 75% of the labeled intervals were used for training, and 25% for testing the models [41]. This was done separately for each behavior, ensuring that they roughly reflected the proportion of behaviors in the overall dataset.

Model-training

The models were trained using the labeled training intervals and a supervised learning approach [41]. For every interval, the model was provided with the acceleration values and the corresponding behavior. By providing the model with a large dataset of labeled intervals, it "learns" to predict which behavior an animal engaged in based purely on acceleration values. Behavior always served as the output variable, whereas the input variables consisted of different combinations of the acceleration values and their derivatives (Table 2).

In our initial analysis, we found that models trained with minmax-normalized acceleration values classified behaviors more accurately than the models trained with log- or scale-transformed data. Therefore, all subsequent models were based on minmax-normalized data (Table 2).

For each of the mentioned formulae (Table 2), we trained models with various ML algorithms. Similarly to using different combinations of input variables, the purpose of using different algorithms was to find out which ones generated the most accurate classification models. The used algorithms, relevant literature and employed R packages are described in Table 3. Some of the algorithms allow the use of class weights to mitigate the sample size imbalance between the different classes (i.e., behaviors). In our preliminary analyses, we found that using custom weights did not improve the models' accuracy, which is why we decided against employing them.

Model-testing

After training the models, their accuracy was evaluated using the testing subset (25%) [9, 41]. Each model was used to predict the behavior of the testing intervals based on the acceleration values. The predicted behavior of each interval was then compared to the actual observed behavior of that interval (Additional file 1: Fig. S1) and a confusion matrix was generated.

To efficiently compare the different models, however, it is useful to have a single descriptive value. Previous studies have frequently used the correct classification rate (CCR), also known as overall accuracy [2, 9–11, 32]:

$$\text{Correct classification rate} = \frac{\text{Number of correctly classified intervals}}{\text{Total number of intervals}}$$

Table 3 Algorithms used to train the classification models, respective literature and employed R packages

Algorithm and useful literature	Employed R packages
K-nearest neighbor (KNN) [47]	"Caret" [27]
Multinomial logistic regression [41, 48]	"nnet" [31]
Support vector machines (SVM): linear, polynomial, radial or sigmoidal [32, 41, 49]	"e1071" [29]
Discriminant analysis: linear (LDA) and flexible (FDA) [32, 41, 50]	LDA: "MASS" [31]; FDA: "mda" [25]
Artificial neural network (ANN) [32, 51]	"neuralnet" [24]
Naïve Bayes [52, 53]	"e1071" [29]
Gaussian process [54]	"kernlab" [26, 55]
Classification and regression tree (CART; simple and pruned) [41]	"tree" [30]
Ensemble decision tree models: Boosted regression trees (BRT; simple and tuned) and random forest (RF) [56]	BRT: "xgboost" [23]; RF: "randomForest" [28]

Unfortunately, CCR does not consider a dataset's imbalance. In our case, the most frequently labeled intervals were either of type lying or feeding (Table 4). A model that is capable of accurately classifying these two behaviors might therefore receive a high CCR, even though it poorly classifies rare behaviors (Fig. 5).

Recent studies [7, 8] have included precision (i.e., positive predictive value) and sensitivity (i.e., recall or true positive rate), which are calculated for each behavior separately and provide a fuller picture for imbalanced datasets [57]:

$$Precision = \frac{True\ positives}{False\ positives + True\ positives}$$

$$Sensitivity = \frac{True\ positives}{True\ positives + False\ negatives}$$

As some of our models predicted 0 intervals for some behaviors (0 false positives and 0 true positives), precision would divide by 0 and could therefore not be used. Specificity proved to be a useful alternative to precision [57]:

$$Specificity = \frac{True\ negatives}{True\ negatives + False\ positives}$$

Whereas sensitivity measures a model's ability to detect a positive case, specificity measures a model's ability to detect a negative case. For the behavior of running, sensitivity evaluates a model's ability to detect running intervals, whereas specificity would evaluate the model's ability to classify that interval as not running (i.e., any other behavior such as feeding). A model can receive a high sensitivity or a high specificity for running by either classifying all intervals as running or 0 intervals as running, respectively. Balanced accuracy counteracts this possibility by calculating the mean of sensitivity and specificity for each behavior [57, 58]:

$$Balanced\ accuracy = \frac{sensitivity + specificity}{2}$$

After evaluating balanced accuracy for each model and behavior, the unweighted mean of all these balanced accuracies per model was calculated. We termed this average the macro-balanced accuracy (MBA). Because the balanced accuracy for each behavior is weighted equally in this metric, a model can only receive a high MBA if it can predict each behavior sufficiently well, regardless of how rare or frequent it is (Fig. 5). The MBA allowed us to compare the different models with each other and draw conclusions about which combinations of input variables and ML algorithms generate the most accurate models.

Table 4 Number of observations, durations, and number of mixed/pure intervals per behaviors

Behavior	Lying	Standing	Feeding	Walking	Running
Observations (N)	142	148	312	156	18
Mean (min)	34.77	1.49	14.11	1.16	2.39
Median (min)	23.51	0.66	7.19	0.54	1.42
Minimum (min)	0.03	0.03	0.03	0.03	0.18
Maximum (min)	211.18	20.12	119.70	11.67	10.43
Pure intervals (N)	752	5	601	2	4
Mixed intervals (N)	884	25	771	26	5

The number (N) of observational instances per behavior with their mean, median, minimum, and maximum duration in minutes (min), and the respective number (N) of pure and mixed intervals. Pure intervals are defined as intervals during which the animal engaged in only one behavior. Mixed intervals are defined as intervals during which a single behavior was engaged in for at least half the duration (> 2.5 min), and hence also include pure intervals.

Results

Behavioral observations

We were able to observe the four collared red deer on 35 out of the 57 field days, resulting in a behavioral data set of 160 h. However, the frequency at which we observed individuals and behaviors was strongly imbalanced (Fig. 2). While we frequently observed the animals lying or feeding, we rarely observed them running, walking, or standing. Further, we were rarely able to observe individual 783.

Additionally, some behaviors occurred for a much shorter duration than others. While the animals lay down, on average, for 34.77 min at a time, they walked, on average, for only 1.16 min at a time (Table 4). As a result, there were little to no pure intervals for the short duration behaviors walk, stand, and run (Table 4). Including mixed intervals provided a significant increase in the number of intervals for these behaviors and allowed us to generate a multiclass model, which would have been impossible with pure intervals only.

Model performance

In total, we generated 144 classification models (16 algorithms * 9 formulae). The performance of each model is listed in Additional file 4: Table S2. The most accurate model had an MBA of 81%, and balanced accuracies of 90% (lie), 57% (stand), 88% (feed), 71% (walk), and 100% (run). The model was trained using linear discriminant analysis. The models trained with flexible discriminant analysis performed almost always equally well as the

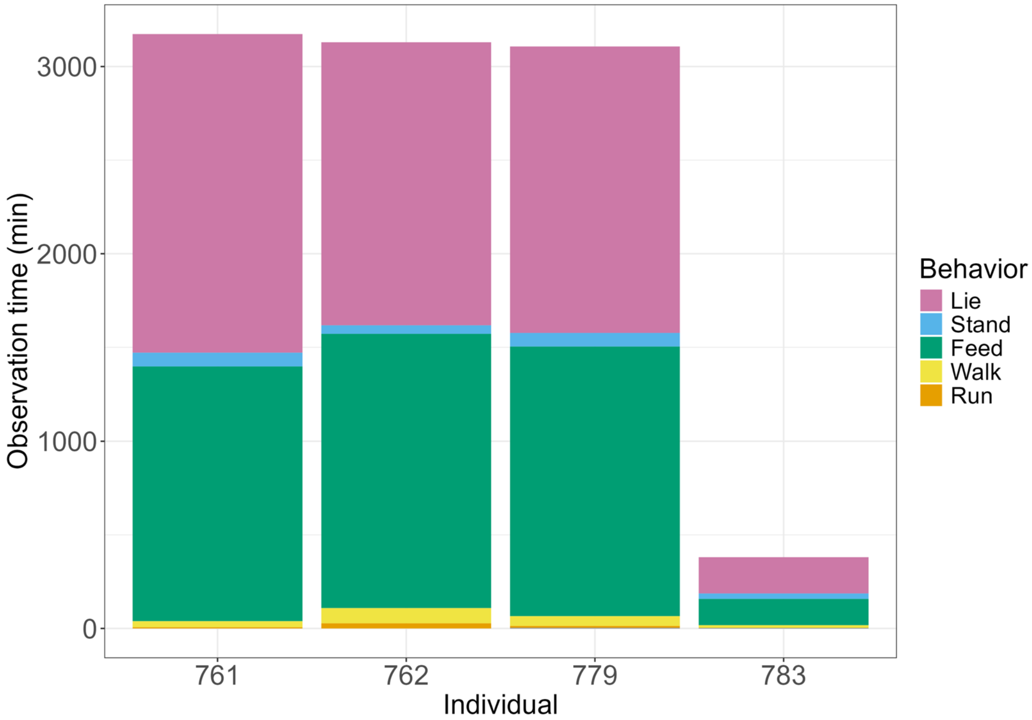

Fig. 2 Duration of observed behaviors per individual (females 761 and 762, males 779 and 783)

linear model. The model was trained using the following formula:

$$behavior \sim x_{minmax} + y_{minmax} + ratio(x, y)_{minmax}$$

The model generated the confusion matrix detailed in Table 5.

There were significant differences in the performance of the models according to the input variables used to train them (Kruskal–Wallis $\chi 2 = 79.855$, $df = 8$, $p < 0.001$; Fig. 3). The six models with the highest MBA were all trained using either the input variables $x_{minmax} + y_{minmax} + ratio(x, y)_{minmax}$ or $x_{minmax} + y_{minmax}$. These two groups of models also had a higher median MBA than all other formula groups. The models trained with the input variables $diff(x, y)_{minmax}$ and $ratio(x, y)_{minmax}$, on their own, had the lowest median accuracies. However, when combined with $x_{minmax} + y_{minmax}$, using $ratio(x, y)_{minmax}$ generally improved the MBA. The models trained only with x_{minmax}, y_{minmax}, or $sum(x, y)_{minmax}$ were intermediate with regard to their median classification accuracy. In terms of normalization methods, the minmax-normalized models seem to outperform, on average, the scale-normalized and log-transformed models.

The type of algorithm also had a significant impact on the models' MBA (Kruskal–Wallis $\chi 2 = 21.043$, $df = 8$, $p = 0.007$; Fig. 4). The models with the highest median MBA were trained using the Gaussian process

Table 5 Confusion matrix for the most accurate classification model

		Observations				
		Lying	**Standing**	**Feeding**	**Walking**	**Running**
Prediction	Lying	204	1	22	1	0
	Standing	0	1	0	0	0
	Feeding	16	4	166	2	0
	Walking	1	0	5	3	0
	Running	0	1	0	1	2

Confusion matrix of the model with the highest macro-balanced accuracy (MBA). The model was trained using discriminant analysis and the input variables $x_{minmax} + y_{minmax} + ratio(x, y)_{minmax}$

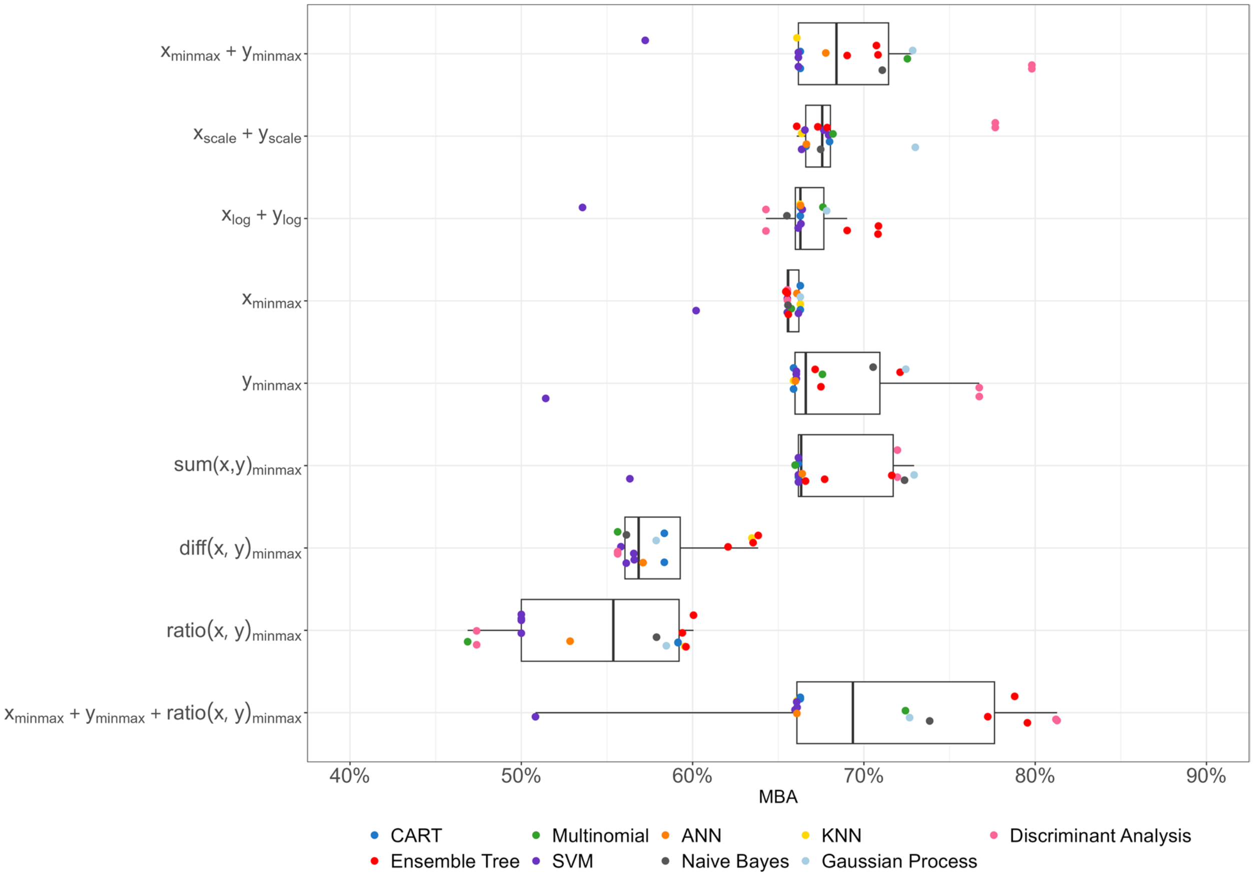

Fig. 3 Boxplot visualizing each model's macro-balanced accuracy (MBA) (Additional file 4: Table S2). Each model (point) was trained with a different combination of input variables and algorithm. In this figure, the models are vertically grouped by the combination of input variables that was used to train them

algorithm. However, the 11 models with the highest MBA were all trained using discriminant analysis or ensemble decision tree algorithms (Additional file 4: Table S2). Interestingly, discriminant analysis generated the models with the highest and some of the lowest MBA. The models with the lowest median MBA were trained using KNN, ANN, SVM, and CART. In general, there was no algorithm that always outperformed all others. However, discriminant analysis and ensemble decision tree models generated the most accurate models when combined with the right set of input variables and performed relatively similar at their upper end.

Figure 5 visualizes the benefits of using the MBA as a metric. Each point represents a model. While the vertical axis denotes that model's MBA and CCR, respectively, the horizontal axis denotes its balanced accuracy for the behavior running. Running serves as an example for any of the rare behaviors, including standing and walking. Plot **a** demonstrates that a model's ability to accurately classify running has as significant effect on its MBA ($R = 0.7$). If the model is unable to accurately predict running, it will not receive a high MBA. Plot **b** demonstrates that a model's ability to accurately classify running has little effect on the CCR ($R = 0.24$). The model can still have a high CCR even though it predicts the rare behavior poorly. The MBA therefore provides a more balanced perspective on a model's ability to classify all behaviors, regardless of how frequent or rare they are.

Discussion

Generalizability of the models

There have been a number of studies that have generated multiclass classification models for cervids in captivity [2, 8–11] or binary models for wild cervids [18, 59–63]. However, so far there have been fewer studies to have generated multiclass models for wild cervids [7] and, to our knowledge, no such studies for wild cervids living in an alpine environment or using low-resolution (5-min) acceleration values.

The most obvious reason for a lack of models trained with wild cervids is the significant increase in the effort

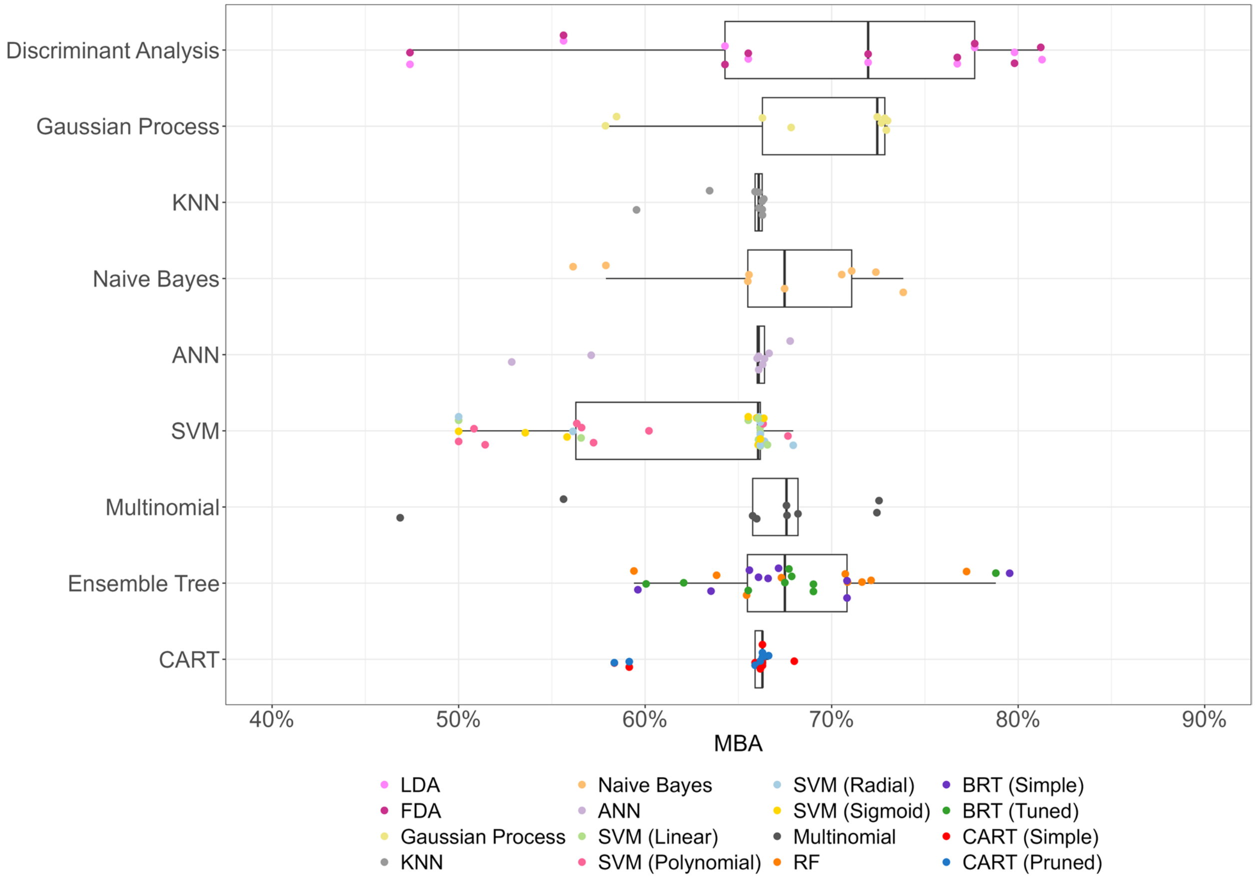

Fig. 4 Boxplot visualizing each model's macro-balanced accuracy (MBA) (Additional file 4: Table S2). Each model (point) was trained with a different combination of input variables and algorithm. In this figure, the models are vertically grouped by the category of algorithm that was used to train them

it takes to collect sufficient behavioral data. For the 160 h of behaviors we observed, we spent roughly 570 h in the field. Collecting this amount of behavioral data would, most likely, be much more time-efficient with captive animals. However, this raises the question whether a model trained on captive red deer would be generalizable to wild animals [8, 17, 33, 64]. Red deer in captivity might show different behaviors than wild red deer or move differently, depending on the landscape they live in. Although observing captive animals might be much more time-efficient than observing wild animals, we argue that it is worthwhile collecting observational data from wild animals, even if only used for testing the models.

Spreading the fieldwork phase over a longer period might allow for models that are generalizable to different seasons and might also provide observational data of additional individuals and behaviors. Most of the red deer in the SNP move from their alpine summer habitats to their winter habitats at lower elevations around October and November [4, 65]. Due to differences in their habitat and possibly in their behavior, the animals might move differently in the winter than in the summer. Additionally, as red deer undergo seasonal changes in their body weight, it would be valuable to test whether the "summer models" are still generalizable to red deer in the winter [44, 66].

Data imbalance

Similarly to previous studies, we were able to observe the behaviors lying and feeding much more frequently and over longer durations than other behaviors such as running, fighting, standing, and walking (Fig. 2; [2, 7–9, 11]). Additionally, some behaviors tend to occur for less than the duration of the 5-min acceleration intervals (Table 4). For these behaviors, we only had access to a very small number of pure intervals and would have been unable to generate a multiclass model (Table 4). While having access to shorter acceleration intervals (e.g., 1 min duration) or even the acceleration data in its raw state (i.e., high resolution) would be ideal, this is not always possible. This might be due to working with older data, or, as in our case, due to memory storage constrains and the

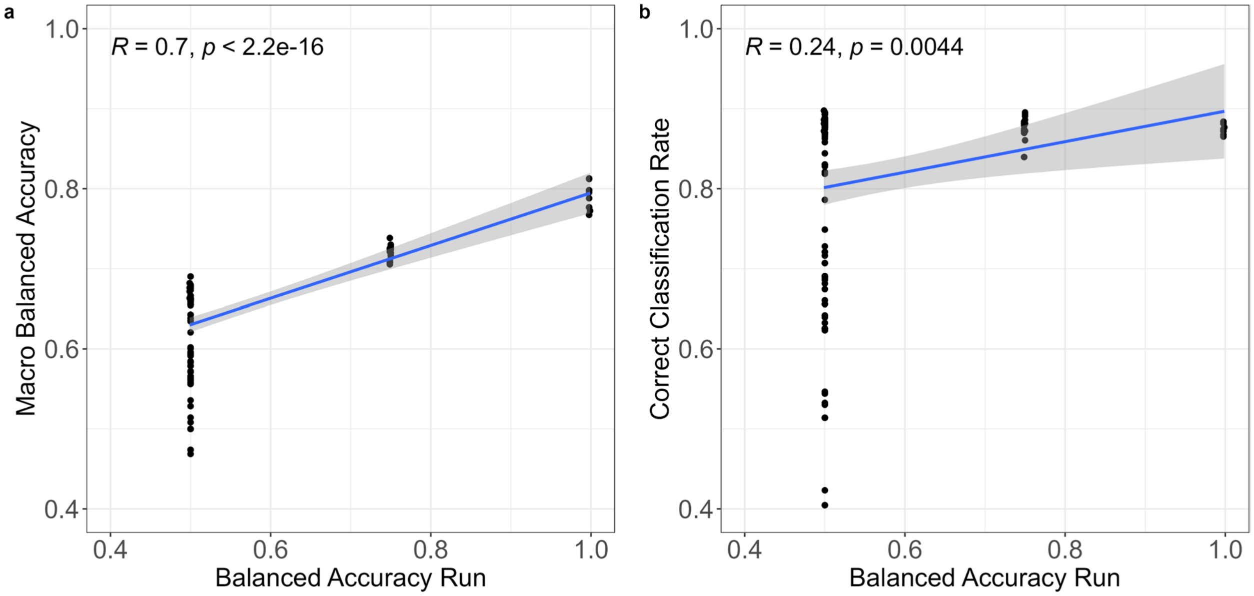

Fig. 5 Scatterplots visualizing the correlation between each models' balanced accuracy for running and its **a** macro-balanced accuracy (MBA), as well as its **b** correct classification rate (CCR). Each point denotes one model. Running correlates much stronger with MBA than it does with CCR, illustrated by the regression line (blue; 95% confidence interval), Pearson correlation coefficient (*R*) and respective *p* value

long employment period of the GPS collars (> 2 years). We were able to mitigate this issue by using mixed intervals, which allowed us to label significantly more intervals for the rare and short behaviors than if we had relied only on pure intervals. Nevertheless, we suggest that authors of future behavioral classification studies carefully consider which type of acceleration data fits their research goals, yet still complies with the technical constrains imposed by the storage capacity and employment duration of the GPS collars.

Of the studies which generated multiclass classification models for cervids with low-resolution acceleration data, only Gaylord & Sanchez [9] used mixed intervals. Loettker et al. [2], Heurich et al. [10] and Naylor & Kie [11] worked exclusively with pure intervals. The viability of using mixed intervals can be evaluated from different angles. On the one hand, every classified mixed interval is, per definition, also misclassified. To alleviate this issue, we only labeled mixed intervals where the animal engaged in one behavior for at least half of that interval's duration. On the other hand, Gaylord & Sanchez [9] argue that "datasets from free-ranging animals inherently include mixed intervals… reliance on pure-interval models to classify behaviors of free-ranging animals should be avoided" (p. 64). They argue that relying on pure intervals models can lead to an inflated sense of behavior classification accuracy.

Another issue stemming from the behavioral imbalance pertains to the evaluation of the models' accuracy. Previous studies have primarily used the CCR which evaluates a model's overall accuracy at classifying behaviors [2, 9–11]. However, when faced with a strong data imbalance, as in our case, the CCR can provide an inflated sense of a model's accuracy because it is strongly biased towards the behaviors that are most commonly represented in the dataset (Fig. 5). More recent studies have used alternatives to the CCR when evaluating the performance of behavioral classification models. Kröschel et al. [7] used CCR, sensitivity and the positive predictive value for their roe deer models. Kirchner et al. [8] used recall and precision for their moose models.

In our case, we decided to use the MBA. The MBA is the mean of each behavior's balanced accuracy and thereby weighs a model's ability to classify each behavior equally, regardless of how rarely or frequently it has been observed. As such, the MBA avoids the CCR's bias towards the more commonly represented behaviors. However, the MBA is not without its own limitations. When working with very small classes, such as running or walking, a small number of misclassifications in these behaviors can have an inflated effect on the final MBA. Whichever metric one might use, we suggest that authors of future behavioral classification models try out various metrics to test which ones fit their dataset situation and research questions [57].

Model performance

By using 16 different ML algorithms, as well as 9 different combinations of input variables, we were able to train and test 144 different models. This allowed us to draw conclusions about what generates accurate models with respect to the used input variables, normalization methods and algorithms.

While there was no combination of input variables that always outperformed all other input variable combinations, using $x_{minmax} + y_{minmax}$ or $x_{minmax} + y_{minmax} + ratio(x, y)_{minmax}$ generally generated the most accurate models (Fig. 3). Interestingly, models trained with only $ratio(x, y)_{minmax}$ as an input variable had the lowest median MBA. However, when combined with $x_{minmax} + y_{minmax}$, using $ratio(x, y)_{minmax}$ generally improved the MBA. Visually, the behaviors running and walking appear to have a higher x-to-y acceleration ratio, which might explain why using ratio as an additional input variable improves these models (Additional file 3: Fig. S2).

As there were significant differences in the acceleration values from the four individuals, we expected that decreasing these inter-individual differences might improve the models' ability to classify the behavior of all individuals. We were surprised that the models using minmax-normalized acceleration data (thereby retaining inter-individual differences) had, on average, a higher MBA than models trained with scale-normalized acceleration data (Fig. 3). Retaining inter-individual differences and the original distribution of acceleration values seems to be vital to generating accurate classification models.

Similar to the combination of input variables, there was no type of algorithm that outperformed all other algorithms for every model (Fig. 4). However, the best-performing models were all trained with discriminant analysis or ensemble decision tree algorithms. In their classification models for griffon vultures, Nathan et al. [32] found that RF outperformed SVM which outperformed discriminant analysis. While we were also able to generate accurate models with RF, we found that discriminant analysis had the highest and SVM the lowest median MBA. Similar to Nathan et al. [32], Ladds et al. [33] also found that SVM generally performed well for classifying the behaviors of fur seals and sea lions. Similar to our study, Ladds et al. [33] were also able to generate accurate models with RF and BRT. The differences in these studies' findings should underline the importance of trying out and comparing various algorithms for each new dataset and classification process.

Regarding the differences within algorithm groups, we did not find that pruning CART or tuning BRT resulted in a significant improvement in their accuracy. In fact, tuning and pruning seemed to have had a slightly negative effect on the models' MBA (Fig. 4). Similarly, whether we used flexible or linear discriminant analysis seemed to have had little to no effect on the models' MBA. However, it is possible that for other datasets, these variations improve the models' accuracy and should therefore not be dismissed [41].

The variation of the MBA was much greater within the algorithm groups (Fig. 4) than within the input variable groups (Fig. 3). This wider variation might be caused by the specific algorithms within each algorithm group performing very differently, or by the strong effect of the used input variables. Whichever the case, the different combinations of input variables should be tested just as rigorously as the algorithms, when deciding on which ones to use.

While we purposefully did not use the CCR to determine the best model, it still provides an interesting point of comparison in relation to previous similar studies. In contrast to the model with the highest MBA, the model with the highest CCR, was trained using $x_{scale} + y_{scale}$ in combination with multinomial logistic regression (Additional file 4: Table S2). The model had a low MBA of 68%, but a high CCR of 90%, comparable to the results of previous studies that used low-resolution acceleration data to generate multiclass behavioral models for cervids [2, 9–11].

Conclusion

In conclusion, this study found that while it is possible to train classification models based on the behavior of wild red deer, one is faced with a relatively small dataset, especially for rare or short-lived behaviors, such as standing, walking, running, and fighting. We suggest the use of mixed intervals to deal with this difficulty and argue that mixed intervals provide a more realistic depiction of a model's accuracy. Finally, we recommended the use of alternative metrics in addition to the CCR when evaluating the accuracy of behavioral classification models. While we decided to use MBA, there are other metrics that could be used in this scenario [57].

The behavioral classification models for wild red deer living in an alpine environment, generated as part of this study, have various potential applications. For example, such a model could be used to generate activity budgets for unobserved but collared wild red deer and analyze how human activity, seasonality, weather, or climatic changes affect their behavior. Specifically, we could evaluate how a red deer's daily activity budget changes during the hunting season or during unusually warm or cold periods. In a future project, it would be interesting to generate a web-based user interface to allow people to easily generate behavior sequences based on acceleration data, without expertise in R. For now, anyone familiar with programming in R and working with acceleration data, can use the attached R-script and model to turn their acceleration data into a timed behavioral sequence, provided the acceleration data ranges between 0–255, is averaged over 5-min intervals and includes x- and y-acceleration values (Additional file 5: Script S1). Finally, we hope that our comparative analysis of using different ML algorithms and input variables to generate classification models, our approach to labeling mixed intervals, and the suggested usage of the MBA as an alternative to the CCR can prove useful for future studies working with wild cervids and acceleration data.

Abbreviations

ML	Machine learning
SNP	Swiss National Park
IUCN	International Union for Conservation of Nature
KNN	K-nearest neighbor
SVM	Support vector machines
LDA	Linear discriminant analysis
FDA	Flexible discriminant analysis
ANN	Artificial neural network
CART	Classification and regression tree
BRT	Boosted regression trees
RF	Random forest

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-025-00401-9.

Additional file 1: Fig. S1. Simplified visualization of the data analysis process to train and test behavioral classification models based on data collected by accelerometers included in GPS collars.

Additional File 2: Table S2. Description of the normalization methods applied to the acceleration data. The methods were applied separately to each acceleration axes and individual.

Additional File 3: Fig. S2. Visualization of the effects of the various normalization methods applied to the acceleration data. Each point signifies the x- and y-acceleration value of a single 5-min acceleration interval. The plots display the untransformed (a), minmax- (b), scale- (c) and log-normalized (d) acceleration data.

Additional File 4: Table S2. The results and properties of all behavioral classification models, including the macro balanced accuracy (MBA), the correct classification rate (CCR), and the balanced accuracies (BA) for the respective behaviors.

Additional File 5: Script S1. ZIP-folder containing everything necessary to run the model with the highest macro balanced accuracy that were generated as part of this study. We included an R-script, the model file, and an example dataset (acceleration values and simultaneous behavior of a red deer individual) to run this model. The most accessible approach would be to unzip the folder and open the Behavioral_classification.Rproj file in RStudio directly.

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Author contributions

All co-authors conceived the study. BB designed the study with valuable inputs from all co-authors. BB planed and conducted the fieldwork and collected the data with support from TR and CS. BB performed the analyses with support from all co-authors, primarily PA. BB wrote the manuscript and visualized the results with valuable inputs from all co-authors.

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Availability of data and materials

The most accurate classification model trained as part of this study is provided in the additional files. Additionally, we provide an R-Script and a sample dataset to demonstrate how one can use this model with their own acceleration data. Behavioral and acceleration data, as well as additional R-Scripts, are available upon reasonable request.

Declarations

Ethics approval and consent to participate

Capturing and collaring was conducted according to Swiss animal welfare law (permit GR2015-09).

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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