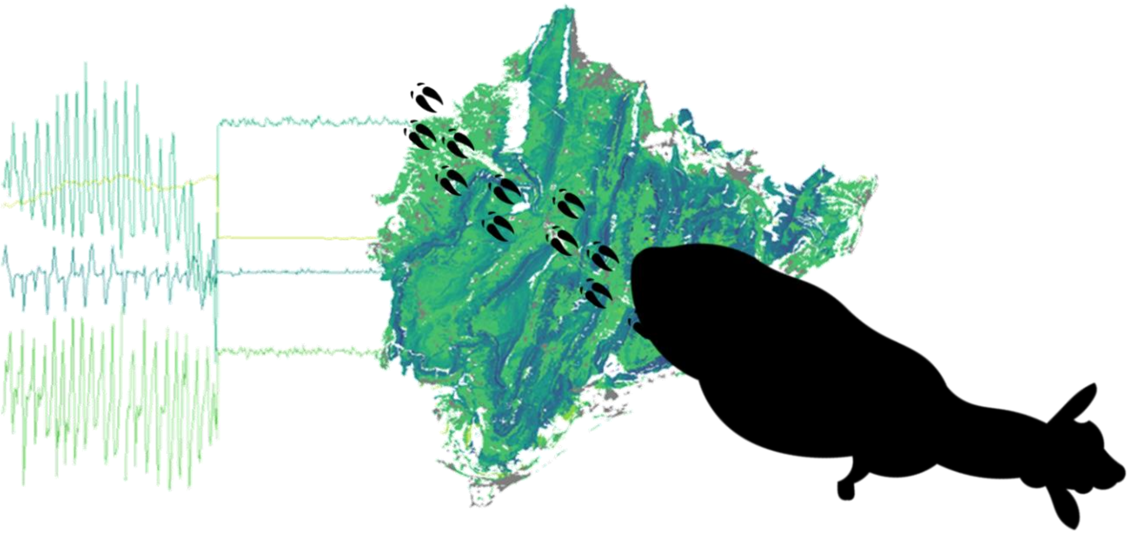
Alpine ungulate movement: Quantification of spatiotemporal environmental energetics and social interaction



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Abstract

Species movement, an animal's ability to change its location, is a fundamental property of life, and animals have diverse physical and behavioural attributes that are believed to enhance efficient travel and optimization of resources. Quantifying movement energetics and returns to examine these ideas over relevant time- and space scales is, however, problematic. In this thesis, I set out to develop and use advanced biologging tag technology to determine a second by second account of the behaviour and location of tagged animals to unveil where and when key behaviours are occurring, to answer key questions about feeding and social behaviour, allocation in space and the energetic costs associated with different movement decisions. Specifically, I used accelerometers, magnetometers, temperature and pressure sensors with GPS units in animal-attached loggers to examine key questions linking movement, energetics and feeding and aggressive behaviours in 3 wild- and 3 domestic ungulate species in mountainous landscapes in the French Alps, monitored for periods between 30 and 200 days. To obtain high-frequency data using electronic devices for long periods, I had to first design new housings to attach safely the loggers to the animals and develop methods for weather proofing the loggers. I designed, using CAD-designa and 3D printing, different housing types and used 'Guronic' resin to shockproof and waterproof circuit boards. This allowed me to obtain logging data for up to 200 days. To give a location per second but stay within ethical weight restrictions, the dead-reckoning method to reconstruct fine-scale movements between low resolution GPS fixes was adopted. To improve the accuracy of dead-reckoning estimates I improved the method using behavioural definition to identify real moves (steps, grazing, moving) and distinguish it from resting, grooming and other behaviours not leading to a displacement of the animal in space, allowing to selectively filter data to be dead-reckon. Using the data collected, I showed that central-place-based, but free-roaming, domestic goats exhibited efficient space-use by having time-dependent fanning out from their central place, which reduced local resource depletion. Models predicted that area-use increased logarithmically with herd size and duration. These finding could lead to improved livestock management in multi-functional alpine landscapes, to reduce the risk of over-grazing and manage interactions with other grazing species and clonflicts with other landuse needs. The goat grazing patterns were compared to those of wild ibex and revealed goats to be more adaptable, with the ibex being particularly vulnerable to changes in temperature, exacerbated by them preferring steep slopes with associated high metabolic costs and heat generation during ascent. These results could further inform management decisions regarding the survival of alpine ibex under projected climate change. Furthermore I developed new biologging approaches to investigate social interactions, specifically head-clashing in both species. This agonistic behaviour was associated with competition and the rut in ibex and was quantified using methods first developed for the domestic goat, where the behaviour appeared to relate primarily to competition for food. Using the goat as a surrogate species, the behaviour could be identified and mapped for the ibex, which highlighted areas and times important for head-clashing, including drastic increases during the rut. Finally, movement data and proxies for energy expenditure from three domestic species (sheep, cows and goats) and three wild species (ibex, mouflon and chamois) was utilised to produce species-specific energy landscapes across the terrains they used. This indicated that different anatomies and behaviours resulted in different, species-specific, movement costs for specific topographies and habitats. Energy use for travel across

heterogeneous space depends, therefore, on the species concerned. These findings thus highlight the importance to consider that species with different life histories and ecological needs use landscapes in contrasting ways and my results can provide a more refined evidence base for the management and conservation of these species in alpine grasslands. These biologging approaches allow now also to address further management issues such as the responses to disturbances from tourists (hiking, skiers, etc.) and even reveal how species are more susceptible to climate change.

Declarations and statements

DECLARATION

This work has not previously been accepted in substance for any degree and is not being concurrently submitted

in candidature for any degree.

Signed .[redacted]................... (candidate)

Date **31/03/2021**

STATEMENT 1

This thesis is the result of my own investigations, except where otherwise stated. Where correction services

have been used, the extent and nature of the correction is clearly marked in a footnote(s).

Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

Signed ..[redacted].............................. (candidate)

Date **31/03/2021**

STATEMENT 2

I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and

for the title and summary to be made available to outside organisations.

Signed [redacted]........... (candidate)

Date **31/03/2021**

Contents

Ethics statement and approvals

All work described in this thesis was approved by the Swansea University Ethics Committee (references beginning with 'SU'). Experiments conducted in the field, where

Concerning animals captured in collaboration with Mov-It, Grenoble university and National Hunting and Wildlife Agency (ONCFS) were approved by the Animal Welfare Ethical Review Body (references beginning 'AWERB').

The relevant approvals for each chapter are detailed in the table below

Chapter	*Relevant ethics approval number(s)*	*Notes*
2	SU-Ethics-Student-260718/762 AWERB approval: IP-1718-40	Approval for tag deployments on domestic horses (*Equus ferus caballus*) in North America (2018).
	SU-Ethics-Student-090918/981 AWERB approval: IP-1516-14	Approval for tag deployments on cows (*Bos taurus*) domestic goats (*Capra aegagrus hircus*) and domestic sheep (*Ovis aries*) in France (2017 to 2018).
	SU-Ethics-Student-090918/981 AWERB approval: IP-1516-14	Approval for tag deployments on Chamois (*Rupicapra rupicapra*), ibex (*Capra ibex*) and Mouflon (*Ovis gmelina*) in France (2017 to 2019).
3	SU-Ethics-Student-090918/981 AWERB approval: IP-1516-14-	Approval for tag deployments on domestic cows (*Bos taurus*) and domestic goats (*Capra aegagrus hircus*) in France (2017).
	SU-Ethics-Student-090918/981 AWERB approval: IP-1516-14	Approval for tag deployments on ibex (*Capra ibex*) and Mouflon (*Ovis gmelina*) in France (2017).
4	SU-Ethics-Student-090918/981	Approval for tag deployments on domestic goats (*Capra aegagrus hircus)* in France (2017).

	AWERB approval: IP-1516-14-	
5	SU-Ethics-Student-090918/981 AWERB approval: IP-1516-14-	Approval for tag deployments on domestic goats (*Capra aegagrus hircus)* in France (2017).
	SU-Ethics-Student-090918/981 AWERB approval: IP-1516-14-	Approval for tag deployments on ibex (*Capra ibex*) in France (2017).
6	SU-Ethics-Student-090918/981 AWERB approval: IP-1516-14	Approval for tag deployments on domestic goats (*Capra aegagrus hircus*) in France (2017).
	SU-Ethics-Student-090918/981 AWERB approval: IP-1516-14-	Approval for tag deployments on ibex (*Capra ibex*) in France (2017).
7	SU-Ethics-Student-090918/981 AWERB approval: IP-1516-14	Approval for tag deployments on domestic cows (*Bos taurus*), domestic goats (*Capra aegagrus hircus*) and domestic in France (2017 to 2018).
	SU-Ethics-Student-090918/981 AWERB approval: IP-1516-14	Approval for tag deployments on Chamois (Rupicapra rupicapra), ibex (Capra ibex) and Mouflon (*Ovis gmelina*) in France (2017 to 2019).

List of figures and tables

Acknowledgments

I was just going to play it cool and list names within my acknowledgements but the more I thought about the support I received the more I realised writing a bit about each person who made the work possible is the least I can do.

Massive thanks to my first supervisor Prof. Luca Borger for not only giving me the opportunity and supervision from the very beginning of my biologging journey with tortoise during my MRes, but also carrying his supervision through to a 4 year PhD. Without the unique field work and data collection arrange by him I would not be the scientist and person I am today. All the additional analytical guidance has helped me to write this thesis and without him I cannot imagine what I would be doing career wise. Thank you for taking a chance on me 5 years ago when I came to your office to enquire about Tamarin biologger backpacks, you are genuinely one of the kindest people I have met and hope to work together in the future for a long time.

I find it difficult to write about Prof. Rory Wilson without it sounding like a cliché. I therefore apologise in advance but in all honesty his enthusiasm and outstanding academic reputation while being a charismatic, down to earth person makes him an inspiration for me as a person and my work (**cue blush). His contributions to my work have been invaluable and he managed to take my simplistic ideas and bring them to life with clear guidance and supervision.

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GIW

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In addition to the candidate submitting this thesis, the following authors (with their institution; below) assisted in the research and data gathering presented in this thesis.

Name	*Institution/Organisation*	*Chapter(s) contributed to*
Luca Borger	Swansea University	1 to 8
Rory Wilson	Swansea University	1 to 8
Mark Holton	Swansea University	2 to 7
Phil Hopkins	Swansea University	2 to 7
Rowan Brown	Swansea University	3 to 7
Richard Gunner	Swansea University	3
Ewan Mortlock	Swansea University	4 and 6
Anne Loison	Université Savoie Mont Blanc	2 to 7
Mathieu Garel	Office Français de la Biodiversité	2 to 7

List of abbreviations

Abbreviation term	*Full term*
2D	Two-dimensional
3D	Three-dimensional
ABS	Acrylonitrile Butadiene Styrene
COT	Cost Of Transport
COT_{sVeDBA}	Cost Of Transport in relation to sVeDBA
CV	coefficient of variation; equation: standard deviation(x)/mean(x)
DA	Dynamic Acceleration
DD	Daily Diary
DDMT	Daily Diary Movement Trace
DR	Dead-Reckon
GLM	Generalised Linear Model
GPS	Global Positioning System
H or ΔH	height
Hz	Hertz; number of cycles per second
LoCoD	Lowest Common Denominator
Lon	Longitude
Lat	Latitude
mAh	Milliampere
Θ	Slope angle
P	Pressure
PE	Potential energy
P_0	Pressure at sea level
SD	Secure Digital
T	Temperature
sVeDBA	Smoothed Vectoral Dynamic Body Acceleration
TDC	Travelling Detection Criteria
VeDBA	Vectoral Dynamic Body Acceleration

V	Volts
VO_2	Volume of oxygen

Chapter 1

Introduction

Animal movement, or more properly 'animal travel' (because movement does not necessarily involve displacement), is a fundamental property of a species' biology, with profound implications for survival (Nathan et al. 2008). It ranges from a single step to a lifetime track (Chapinal et al. 2009, Hansson et al. 2014, Bastille-Rousseau et al. 2017, Parton et al. 2017, Mckinnon and Love 2018) and its convolutions, repetitions and reasons for taking the forms that it does have been the subject of considerable investigation (Armsworth and Roughgarden 2005, Bartumeus et al. 2005, Weimerskirch et al. 2007, Barthelemy et al. 2008, Nouvellet et al. 2009, Hills et al. 2013). Judicious movement is critical for most animals (and a very few plants) and is pivotal for enhancing lifetime reproductive success as animals react appropriately to external factors such as the likelihood of predation (Beyer et al. 2016, Pike et al. 2018), foraging opportunities (Kacelnik and Houston 1984, Bergman et al. 2001) or increased chances of finding a mate (White et al. 2011, Chirichella et al. 2014). But movement comes with a cost, both in terms of time and in the energetics associated with overcoming physical forces such as gravity, drag, and friction (Armstrong et al. 1983, Wall et al. 2006, Vandenabeele et al. 2015, Kay et al. 2019). And the rate at which this cost is implemented defines the power requirements of the animal concerned, in other words how quickly the energies used in movement are dissipated (McNab 1973, Voloshina et al. 2013, Halsey and White 2017, Wilson, Rose, et al. 2020). These are determined by metrics often used to define the particularities of movement such as the speed of travel (Pyke 1981, Chapinal et al. 2009), the rate of change of altitude (Taylor et al. 1970, Taylor et al. 1972) or depth (Fowler et al. 2006, Shiomi et al. 2008) and the precise form of the 'energy landscape' through which the species is moving or cost of transport (COT) (Shepard et al. 2013). COT is the quantification of the energetic cost for one animal to move from one location to another allowing comparison across species and even different factors at play, for example slope, substrate, or superstrate (Halsey and White, 2017; Garland, 1983). COT is calculated per unit distance travelled with basal metabolic rate taken into consideration (Schmidt-Nielsen and Knut, 1984). Therefore movement is a balance of costs and benefits (e.g. food resources acquired). Biologists assume that patterns we see in animal movement are the result of selection pressures which drive species to move judiciously, for example, maximizing net energy gain during foraging

(Ydenberg et al. 1994, Bergman et al. 2001, Wilson et al. 2012), and that the overall movement strategies exhibited by species are multifaceted, changing with the environmental conditions (Murray and Boutin 1991, Aublet et al. 2009, Elliott et al. 2014), and these strategies define how animals can best exploit their environment given their physical and physiological traits (Hildebrand and Hurley 1985, Fancy and White 1987, Crête and Larivière 2003, White et al. 2011)) – often called 'movement capacity' and 'navigational capacity' (Nathan et al., 2008).

Recognition that the drivers of movement are many, and the solutions sought by animals to deal with the multitude of both external and internal drivers of movement (Nathan et al. 2008) are necessarily going to be complex in space and time (White et al. 2011, Elliott et al. 2014). This makes any study that seeks to understand the movement of wild animals seem daunting, perhaps even foolish. And this problem is magnified by anyone who attempts to consider multi-species movements and interactions within one habitat, as this thesis attempts to do. But before despairing of all hope to define movement drivers and consequences, it is relevant to consider that there will be major elicitors of movement so that, at a basic level, we might expect the general rules behind animal movement to be primarily modulated by these few factors. In fact, the optimal foraging literature (Pyke 1981, Kacelnik and Houston 1984, Ydenberg et al. 1994, Bergman et al. 2001) effectively subscribes to this view, proposing that animal behaviour, including movement, should be largely driven by food distribution and abundance (Orians and Pearson 1979, Bergman et al. 2001, Aharon et al. 2007, Iussig et al. 2015). Specifically, foraging theory considers behaviours related to food acquisition – where to search and when to feed and when to stop, and which types of food to consume – and a common prediction is that animals should maximise energetic benefits from food, minimizing the costs involved (Pyke 2010). These principles, originally developed for fine scale decisions (food patch and diet selection), apply also to movement behaviours over larger spatio-temporal scales. This thesis therefore adopts this somewhat simplistic view, purporting that movement by animals is driven primarily by food, although social interactions and mating opportunities need some consideration, and physiological limitations will also help define what movement is judicious, or even possible.

This thesis considers the space use, resource acquisition and (metrics that act as a proxy for) energy expenditure across a suite of sympatric ungulate species in the French Alps. This area offers numerous habitats with many benefits for ungulates, including vegetation rich in biodiversity (Beniston 2006, Fischer et al. 2008, Kurtogullari et al. 2020), steep slopes to avoid predators (Forsyth 2000, Grignolio et al. 2003, Aublet et al. 2009) and a mountain range with little human disturbance (Fischer et al. 2008, Pęksa and Ciach 2018) - but see Marchand et al. (2014). But importantly within a movement ecology framework (Nathan et al. 2008), the Alps also have very variable topography, ranging from flat areas to steep slopes and cliffs, and everything in between (Beniston 2006, Marini et al. 2009, Sturaro et al. 2013), resulting in great variation in the costs for ungulates to negotiate: Movement up, and down, steep slopes requires greater energy investment to overcome gravity (Rees 2004, Wall et al. 2006, Halsey and White 2017, Dunford et al. 2020), and varying habitats, including loose scree and thick vegetation, add to movement costs in this highly heterogeneous 'energy landscape' (*sensu* Shepard *et al*. 2013). Previous studies have shown how body mass can then change and compound these relationships for example how the gradient of the trend associated with slope inclines against COT increases with the body mass of the animal (Halsey et al., 2008; Taylor et al., 1970). What drives differences in the energy costs of terrestrial locomotion however varies considerably between species and current laboratory data on net cost of transport across different species does not allow to obtain a proper understanding of the costs and constraints of terrestrial animal movement and obtaining more data from the wild will be crucial to solve these issues (Halsey & White 2019). Within this energetics framework though, this area also has highly variable climatic conditions, which impact metabolic rates (McNab 1973, Heinrich 1977, Halsey et al. 2015). The weather ranges from high winds (Beniston 2006, Giovannini et al. 2017), sub-zero temperatures (Beniston 2006, Sturaro et al. 2013) and thick snow in winter (Beniston 2006) to temperatures in summer that may exceed 30°C accompanied by high insolation (Beniston 2006, Aublet et al. 2009, van Beest et al. 2012) - for example strongly affecting ibex movements (Aublet et al. 2009). On top of this the climate is changing with global warming increasing global surface temperatures which in turn could change the snowscape (Barnes 2013, Tippett 2018). Previous work has shown ibex vulnerability to temperature may leave the species prone to climate change with higher global temperatures restricting the species movement regards to altitude and therefore time spent grazing or obtaining resources (Aublet et al., 2009; Brambilla et al., 2020; van Beest et al., 2012). This premise is associated with the 'Thermoneutral zone', a range of temperatures wherein an endothermic species does not have to expend energy to achieve homeostasis, or in other words the temperature that gives the animal its lowest basal metabolic cost (St Juliana and Mitchell, 2016). Critically, the topography of the area means that synoptic environmental conditions vary greatly with altitude, as well as with the details of the site (e.g. north- vs. south-facing slopes) and time of day or night, so that the ungulates can move to areas with favourable micro-climatic conditions, although this will entail movement costs. Other factors including predator and accident avoidance can be quantified and considered to understand the decision animals make in relation to movement resulting in landscape of fear or accidents (Gallagher et al., 2017; Wheatley et al., 2021).

Here, my aim is to use biologging technology to investigate the drivers of alpine ungulate movements, quantifying the role of spatiotemporal variation in environmental energetics, environmental conditions and habitat across multiple wild and domestic species. Specifically, this thesis considers three domestic animals, cows (*Bos taurus)*, sheep (*Ovis aries)* and goats (*Capra aegagrus hircus),* and three wild species; chamois (*Rupicapra rupicapra)*, alpine ibex (*Capra ibex*) and mouflon (*Ovis gmelini musimon × Ovis sp.*). All species are mammals from the order *Artiodactyla* (even-toed ungulates) and the family *Bovidae* and the sub-family *Caprinae*, except for the cows, which are from the sub- family *Bovinae*. All six species are ruminant herbivores and range in body size from around 600 kg for the domestic cows in this study, to 70-120 kg for the ibex, 25-60 kg for chamois, 25-55 kg for mouflon, 35-60 kg for the domestic sheep and 20-50 kg for the domestic goats. All species are considered of 'least concern' for the IUCN, except for mouflon which are considered as endangered, but are iconic species of high ecological and cultural importance in the Alps and are closely managed by the ONCFS in France.

The total population size in alpine ibex is estimated at 30,000 after recovering from near extinction (Brambilla et al., 2020), however the species originating from a small population since the early 1900s makes the low genetic pool of the alpine population vulnerable to inbreeding potentially impacting their ability to adapt to and survive changes in environmental conditions (Toïgo et al., 2007; Brambilla et al., 2020; Stüwe and Nievergelt, 1991). The species segregate sexually and spatially depending on the season with the sex groups mixing during the breeding season or rut, this lasts from December to January (Tettamanti and Viblanc, 2014; Villaret and Bon, 2010; Grignolio et al., 2010). Male ibexes species compete via head impacts all year round, assessing individuals throughout the year rather than just during the harsh winter and rut alone (Willisch and Neuhaus, 2010; Toïgo et al., 2007).

European Mouflon and chamois were selected as the other wild ungulate species due to their presence within higher altitudes and steep slopes (Pęksa and Ciach, 2018; Marchand et al., 2015). The three wild species have comparative moving strategies to negate the energetic costs of steep slopes, with chamois have sporadic movements, ibex moving conservative and mouflon somewhere in between (Biancardi and Minetti, 2017; Pęksa and Ciach, 2018). Chamois and mouflon are segregated sexually and spatially, similar to ibex (Ryser-Degiorgis et al., 2002; Marchand et al., 2015). Chamois are the least threatened of the three species, listed as 'least concern' by IUCN (Corlatti et al., 2011; Fankhauser, 2004). Mouflon population is descending due to human disturbance through habitat destruction from farming, this had lead to mouflon being listed as 'vulnerable' on the IUCN (Barbanera et al., 2012).

Cows, goats and sheep are used as livestock across the globe for meat, dairy and wool, including the French alps (Sturaro et al., 2013; di Virgilio et al., 2018; Marini et al., 2009). The alps offer a unique study site with highly varying and extreme slopes and high altitudes (Lees et al., 2013; Dickinson et al., 2021; Halsey and White, 2017). Livestock spend the warmer months in the higher altitudes, being herded up from the lower farmlands. Some livestock populations are allowed to free roam with supervision from farmers or restricted to large fenced off sections (approx. 2 km^2) (Sturaro et al., 2013; di Virgilio et al., 2018).

Goats and sheep are physically similar to the ibex and mouflon respectively making them of high interest with the species likely to obtain similar niches (Ryser-Degiorgis et al., 2002;

Fankhauser, 2004). Sharing similar roles and resources within an ecosystem could lead to robust, introduced livestock outcompeting wild ungulate species (Fankhauser, 2004; Chirichella et al., 2014). Goats and sheep are well adapted to mountainous habitats with high locomotion capacity (Dickinson et al., 2021; Dailey and Hobbs, 1989). In contrast, cows with a larger body mass are expected to struggle to move efficiently across the extreme topography making comparison of the species movement strategies of interest (Garland, 1983; Halsey et al., 2008).

The use of domestic species has obvious advantages. They are accessible, manageable, and excellent for developing and testing new biologging technology (e.g. collars) and data analysis methods on individuals that I could observe at all times. Their study is also topical because there is presumed competition between domestic and wild ungulates (Ryser-Degiorgis et al. 2002, Acevedo et al. 2007, Bro-Jørgensen 2011). Almost one third of the Alps is protected under governing bodies due to the unique natural beauty and biodiversity of the region (Fischer et al. 2008, Baur and Binder 2013) and wild ungulates are key ecological engineers to the ecosystems of the Alps through their grazing (Fischer and Wipf 2002, Probo et al. 2014, Nota et al. 2020). Aside from concerns about competition with domestic livestock, many of the wild species are also under threat due to the Alps undergoing urbanisation and the growing tourist industry, leading to species conflict with humans undertaking activities such as pastoralism, forestry and hunting.

Studies have looked into resource acquisitions for the wild ungulates within the Alps to better understand species preferable habitat types to better protect and manage the region (Macandza et al., 2012; Manly et al., 2002). Ibex were found to prefer bare rock dominated habitats (Grignolio et al., 2003) whereas chamois and mouflon selected grassland (Fankhauser, 2004; Forsyth, 2000; Marchand et al., 2013, 2015). The wild ungulate species change their space use depending on the season and rut (Willisch and Neuhaus, 2010; Marchand et al., 2015; Toïgo et al., 2007). The ungulate species generally cover more distance during summer to graze as there is higher cover of vegetation during the warmer months (Brivio et al., 2010). During the colder months and the rut, the distances moved by the wild ungulate species drop off as less time is spent on foraging and more energy is spent mating and behaviours associated (Brivio et al., 2010). Many studies have relied on data from observations or global position system (GPS) (Rutter et al., 1997; Helen et al., 2006; Alados et al., 2000; Ryser-Degiorgis et al., 2002) but little literature have utilised high resolution data (>1Hz) or monitored the species for continuous periods across seasons (Moreau et al., 2009).

The work conducted within this thesis hopefully provides further information to support previous findings while providing fine-scale insights into ungulate behaviour and ecology that might aid in management decisions and ultimately play a role in conservation. But the title of the thesis; ***Alpine ungulate movement: Quantification of spatiotemporal environmental energetics and social interaction***, underpins the overarching question of this work; ***What does the movement ecology of alpine ungulates tell us about their exploitation of their environment?*** Done properly, this would be a monumental task, but I hope, within this thesis, to have made appreciable progress at least.

To understand where, when, and why animals move, I based much of my data acquisition for this by using animal-attached sensing and recording tags, also known as 'biologgers' (Kooyman 1965, Kooyman and L. 2004, Naito 2004). Since their inception in the 1960s (Kooyman and L. 2004) these systems have become extraordinarily small, diverse, powerful and multi-sensing (Holton et al. in press). They can record data from 10 sensors or more at high frequencies (> 10 Hz) for many months in storage memories that are essentially insatiable (Holton et al. in press), giving information on things like temperature, light, pressure, acceleration and magnetic field intensity (Wilson et al. 2008). This sort of information can be inspected to reveal behaviours (Shepard et al. 2008, Williams et al. 2015, Fehlmann et al. 2017), energy expenditures (Qasem et al. 2012, Wilson, Börger, et al. 2020, Dickinson et al. subm.) and movements across 3D landscapes (Shiomi et al. 2008, Bidder et al. 2015, Wensveen et al. 2015), all in relation to select environmental variables. In particular, acceleration loggers can provide unprecedented opportunities to estimate the metabolic cost of activities of wild animals, via- so-called dynamic body acceleration (DBA) metrics (reviewed in Wilson et al. 2020). The opportunities for acceleration data to act as proxies for energy expenditure were highlighted for studies in humans since decades, and for animals since the pioneering work in great cormorants (*Phalacrocorax carbo*) by Wilson et al. (2006), and since then the theoretical and practical framework and methods have been refined (e.g. Quasem et al. 2012; Bidder et al. 2012) and the approach can now provide robust estimates for animals for which movement-related costs constitute a major part of the energy budget and if precise requirements for tag attachment and calibration are observed (reviewedin Wilson et al. 2020).

Combination of such data with ‘conventional information’, such as the distribution of vegetation types (Tronchot 2008, Moreau et al. 2009, Marchand et al. 2015), provides a potent backdrop with which to study important questions about the movement ecology of alpine ungulates (see also di Virgilio et al. 2018). For example how do habitat type and slope interact to modulate cost of transport across elevations for terrestrial animals?. Understanding these relationships should reveal how species mitigate the costs that the environment has while comparing the species ability (Garland, 1983; Halsey and White, 2017). By quantifying or mapping the COT, movement corridors are exposed, and these areas could be prioritised for management and conservation (Wheatley et al., 2021; Shepard et al., 2013).

However, to take full advantage of the potential of biologging technology, I had to solve a series of technological and methodological challenges, starting from the goal of developing collars and loggers robust enough to record for up to one year, thereby extending the duration of high-frequency multi-sensor biologging collars by orders of magnitude. Furthermore, as powerful as biologging seems, it is not without its problems, and these are particularly manifest when they are deployed on large animals that regularly engage in high impact head clashes in the variable (and sometimes very harsh) environment of the Alps. In short, tags can fail because they are not robust enough to withstand the pressures of deployments on free-living animals. Many studies using biologgers resort to the use of commercial collars, together with their tag attachment mechanisms (Rutter et al. 1997, Putfarken et al. 2008, Moreau et al. 2009, Marchand et al. 2015,), but these options are not fully reliable and can be restrictive regarding data resolution, deployment durations, and device weight. Attaching remote devices onto species come with ethical restrictions as weight and size of the logging unit being shown to have detrimental effects to the fitness of the animal (Cooke et al., 2013; Chivers et al., 2016; Vandenabeele et al., 2015). By building tags in-situ of the laboratory, the mass of each element (including battery, housing, logging circuit board, attachment method) can be controlled (Bidder et al., 2015; Walker et al., 2015). Trade-offs can be made to give the user full control of the data collection for example time window and battery capacity, therefore battery weight. Unreliable systems have animal welfare implications, because the study subjects have been caught and collared unnecessarily, inciting considerable stress (Vandenabeele et al. 2015, Chivers et al. 2016). Thus, in ***Chapter 2 (Building customised, flexible multi-sensor biologging units for short- and long-term tagging of alpine ungulates)***, I develop two types of novel collars and housings for collecting high-frequency multi-sensor biologging data on alpine ungulates. First, I develop custom-designed housings to allow flexible and targeted data collection on the domestic ungulates (cows, goats and sheep). Second, I develop a custom-designed set of housings to record data for up to one year, thus orders of magnitude longer time scales than existing technologies at the time, using the Daily Diary multi-sensor tags, attached to commercial GPS collars already deployed on the wild ungulates. I document the steps that I took to design and construct tag housings that maximized my tag deployment success and at the same time detail the main issues that lead to tag failure and loss of data. Chapter 2 specifically attempts to expand biologging solutions for the scientific community by introducing lab-built biologgers, demonstrating how the devices are designed, produced and deployed, not only to save on costs, but also to give the user control and understanding of the logger setup. In addition to this, techniques to mitigate the effects of weathering and high impacts on electronics are investigated with evidence showing how these methods improve the reliability of the customisable and affordable electronic tags.

Having successfully collected large amounts of data on domestic and wild alpine ungulates, using the collars and loggers developed in chapter 2, in ***Chapter 3 (Step in the right direction for dead-reckoning terrestrial animals)*** examines the extent to which a relatively novel technique in terrestrial animal ecology, ‘dead-reckoning’ (Bidder et al. 2015), can enhance our knowledge of space-use and movement paths by wild animals. Researchers commonly use GPS units to determine animal movement (Rutter et al. 1997, Putfarken et al. 2008, de Weerd et al. 2015). Unfortunately, communicating with a satellite to calculate position consumes a high amount of battery energy, making frequent locations (≥ 1 fix per minute) for long continuous periods impossible if ethically defensible weight restrictions loggers are to be maintained (Portugal & White 2018). In order to ensure high resolution location data (e.g. every second), dead-reckoning uses a combination of accelerometer, magnetometer and low-resolution GPS data, interpolating between GPS fixes using movement vectors (speed and heading) defined by the sensors (Bidder et al. 2015, Dewhirst et al. 2016). Much literature has explored this technique for tracking humans (Jiménez et al. 2009, Tian et al. 2014) and some work has used it on wild animals, most notably in the marine environment (Wilson et al. 1991, Shiomi et al. 2008, Wensveen et al. 2015). The method however has scope for substantial improvement in terrestrial environments (Bidder et al. 2015) but had never been attempted across time scales in excess of one week. Chapter 3 aims to not only dead-reckon the movements of four wild ungulates over long time-scales, but also to find possible solutions to minimise errors such as location drift associated with dead-reckoning. The work in this chapter was a direct attempt to reduce error in dead-reckoning paths, using information from the sensors to distinguish body movements associated with a displacement of the body over space, and movements of the body whilst the animal remained in the same geographic position. The aim was to develop a procedure and data analysis pipeline, so that, following successful deployment of tags on animals over months, it would be possible to reconstruct high resolution paths of animal movements over seasonal time scales. This then forms the basis for work presented in subsequent chapters (see below). Part of the work in chapter 3 has also led to an additional publication which I co-authored, on a new R package for dead-reckoning (Gunner et al. 2021).

Having reconstructed fine-scale (1-second resolution) movements of ungulates over scales of weeks to months, I moved from the question of 'where' the animals moved, to the question of what they did at each point in space. Thus, in ***Chapter 4 (Move. Eat. Rest. Repeat)*** looks at ungulate food consumption and attempts to link it to locality. The GPS-enabled dead-reckoning protocol of chapter 3 detailed how animal movement paths could be constructed, but this chapter goes beyond simple description of area-use by attempting to link space-use to travel and food-finding. Specifically, the high frequency acceleration data collected by the animal attached tags are interrogated to define when domestic goats ‘rest’, ‘travel’ and ‘graze’, the suppositions being ground-truthed by watching the animals undertake these activities and then comparing them to their corresponding acceleration metrics. Chapter 4 goes on to consider how 10 individuals within a herd of 40 domestic goats manage their time and available space between grazing, travelling and resting over a month during which they roamed over large pastures (~2 km^2). Since these animals were kept in a pen overnight, they moved away from this central place to forage during the day, moving back in the evening. The work was able to define grazing pressure with locality and showed how the animals used a fanning out technique over time, which reduced their impact on the areas available to them. Such fine-scale information allows to reconsider ideas about movements and optimal foraging theory (Williams et al. 2020; Owen-Smith et al. 2010), as it allows to better connect habitat selection with movement costs. Information of this type could increase general understanding of grazing impacts on specific habitats and help understand the potential for conflict between domesticated and wild species.

Chapter 5 (Grazing on alpine slopes) adopts a similar methodology to that adopted in chapter 4, but uses the approach to study the alpine ibex, benefitting from the acceleration signals linked to behaviours in the domestic goats to identify resting, grazing and travelling in the ibex. The results from the behavioural analysis are used to identify potential overlap between the two species in habitat and slope-use when grazing. This section of the thesis also builds on previous research within the literature looking at how ibex space-use may be limited by heat, with this species being particularly susceptible to overheating. Specifically, the work looks at the energy expended by the animals to move in the way they do and dovetails it with data on altitude-linked air temperature to theorize that ascent and descent of slopes increases metabolic heat production, which needs to be built into assessments of ibex susceptibility to climate change.

Whilst resting, travelling and grazing (feeding) comprise the majority of the time budget of animals, especially ungulates, there are also other important behaviours expressed by animals, such as social behaviours. An important type of social interactions are agonistic interactions, such as head-clashing in ungulates. Thus, in ***Chapter 6 (Landscape of rage)*** I used verified behavioural observations of head-clashing interactions of the tagged animals to develop efficient head-clashing behaviour identification rules from the accelerometer data and then extended the approach to data from the wild counterpart, the alpine ibex. Subsequently, by synchronizing the precise times of head-clashing with location of the animals, determined by GPS-enabled dead-reckoning, sites and times when particularly high rates of these agonistic interactions could be identified. The work showed that most domestic goat interactions of this type appeared to occur in relation to food and were most prevalent during the day. The ibex engaged in head-clashes throughout the year but displayed a substantial increase in incidence during the rut and also favoured particular sites. The implications of this are discussed.

Finally, in ***Chapter 7 (Ungulates as cartographers),*** I brought together all methods developed and obtained fine-scale movement and space-use of the six species of ungulates in the Alps, detailing, as far as possible, where, and how, the different species expend most energy to move within the heterogeneous energy landscape defined by the topography. The different species mitigated the effects of steep slopes by going up and down them at oblique angles, with marked inter-specific differences in strategy. This, and proxies for power use, provided evidence that the different slopes did not represent a common 'energy landscape' (*sensu* Shepard *et al*. 2013) for the species but rather that animal mass and differing behavioural strategies resulted in the different species having different 'energy landscapes' for common slope angles.

Chapter 8 (The synopsis) briefly reviews the advances and setbacks that occurred during the thesis work, pointing to interesting aspects that could not be followed up due to lack of time. This chapter finally speculates on where the research area might develop in a future where animal-attached technology is set to make an ever-greater mark on our understanding of animal movement ecology.

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Chapter 2

Building customised, flexible multi-sensor biologging units for short- and long-term tagging of alpine ungulates

Abstract

Animal-attached multi-sensor tags (‘Biologgers’) have enormous potential to markedly advance our understanding of the causes and consequences of animal movements, such as for alpine ungulates. Customised, flexible units allowing both short-term, focussed studies, as well as units for long-term (seasonal to annual scales) high-frequency monitoring of terrestrial ungulates, are however critically missing. In particular, the likelihood of tag failure, and associated animal welfare implications (including weight of the tag and methods of tag attachment), varies between different species and habitats and increases with deployment duration. The specific requirements will also change markedly depending on the aims and questions of the study. Hence, not only are commercially available devices generally very expensive, they often may not be well suited for the desired data collection. This work presents lab-based techniques to build customizable GPS-enabled Daily Diary (DD) multi-sensor tags (tri-axial accelerometers and magnetometer and environmental sensors) for Alpine ungulates (the methods and approaches can easily be extended also to other taxa), flexibly combining DD tags with commercial GPS tags and collars. I focus particularly on indications and procedures to maximize the probability that tags will function over time, including housing design, battery recommendations and weather-proofing the circuit boards. Appropriate designs, measures and costs depend primarily on the projected logging period so tag construction is presented for three periods; short-term (days; weight range 20-45 g), medium-term (several months; weight range 140-440 g) and long-term (>6 months; weight range 200-350 g). I trialled the custom-built medium- and long-term tags on over 100 domestic ungulates in the French Alps (goats, sheep, cows) over periods of weeks to > 1 month, and on 58 wild alpine ungulates (ibex, chamois, mouflon), logging accelerometer data at 20 Hz, magnetometer data at 8 Hz and temperature and pressure at 1 Hz, and GPS fix schedules ranging from 15-minutes to one location every 2 hours. Post-deployment analysis shows that appropriately treated DDs can run until either the memory card is full or the battery fully used, with an average tagging success rate of 81% (range: 5 to 27 days) for the medium term deployments and 36% (range: 7 to 220 days) for the long term deployments. The majority of failures occurred in ambitious long-term targets and consideration of possible causes has led to recommendations for future deployment which have already improved tag deployment success across three different deployment events. The work should allow researchers to minimize malfunction risk with cost-effective tag protection appropriate for the deployment conditions. Overall, the study demonstrates how custom-built biologging tags and collars, rather than "off the shelf" commercial animal tagging solutions, can have optimized weight, attachment method and design to match project aims and suit both the field conditions and the study of animal's welfare.

Introduction

Biologging, the deployment of sensor-based logging systems on free-living animals (Naito 2004), is increasingly popular for the study of wild (and equally for domestic and farmed) animal behavioural ecology as individuals can be studied seamlessly over time irrespective of environmental conditions, locality, and time of day (Rutz and Hays 2009). This can also mitigate costly and potentially biased direct observations (Altmann 1974, Cagnacci et al. 2010) which may cause disturbance in normal patterns of behaviour shown by the study animals (Canine 1990, Crofoot et al. 2010). A particular value of such tagging systems is that they can also, theoretically, log data for periods extending for months (Preston et al. 2010, Mckinnon and Love 2018) or even years (Horning and Hill 2005, Mckinnon and Love 2018). Such ambitions come at a price however, as the probability that something will go wrong increases over time because combining sensitive electronics with harsh field conditions can lead to device malfunction, losing some, or all, of the data gathered (Bidder et al. 2015), with up to 50% of deployed collars failing to record as programmed across studies in multiple taxa (Johnson et al. 2002 Allison et al. 2013, Hofman et al. 2019), with the success depending also on the specific settings of the biologgers (e.g. McGregor et al. 2016) and a documented urgent need of further improvements of biologging technology for deployment on wild animals (Dore et al. 2020). For example, tags that fail due to inability to resist the effects of weathering typically have battery problems, where ingress of water leads to corrosion across the terminals and cessation of data storage. Worse, it may sometimes even render the stored data inaccessible.

Aside from the cost implications of such tag malfunction, loss of data has ethical consequences associated with animal capture and restraint (Portugal & White 2018, Wilson et al. 2019, Baatsler et al. 2020, Soulsbury et al. 2020, Stabach et al. 2020) and highlights how every effort should be made to have tags that are as reliable as possible.

Importantly, the last few years of biologging studies have seen an appreciable shift away from workers buying company-produced tags, to construction of their own systems (Gleiss et al. 2010, Harrison et al. 2011, Fehlmann et al. 2017, Foley & Sillero-Zubiri 2020) and with this, the necessity of customising tag size and shape as well as working with attachment methods, result in devices causing as little detriment as possible (Kay et al. 2019). Tag optimisation is multi-faceted though. For example, specially selecting minimal, but appropriate, sample rates improves GPS fix success rate (McGregor et al. 2016) and may reduce battery consumption so that smaller batteries can be used and tags can be lighter (Holton, in press), with consequences on the quality of data gathered (Brown et al. 2013). Indeed, even slight changes in weight and size can have a disproportional detrimental outcome on the fitness of the species being tagged (Vandenabeele et al. 2015, Portugal and White 2018).

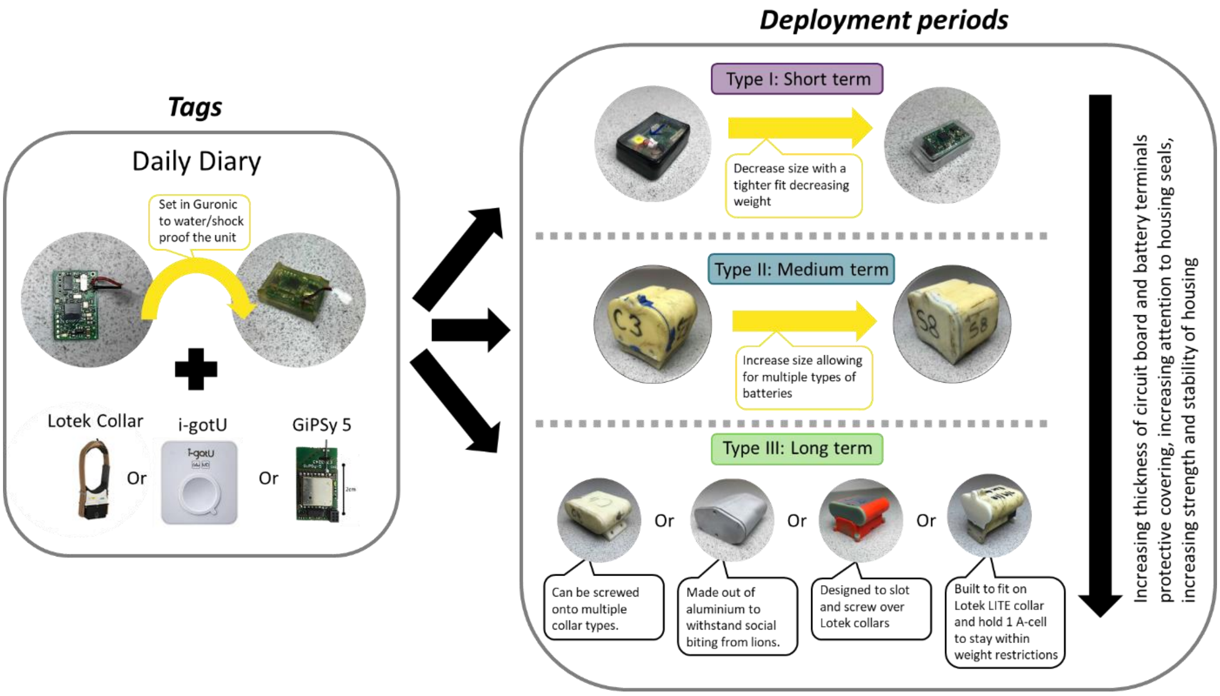
Ease of deployment and the understanding of the technology is an underestimated aspect of biologging when data are collected in the wild. Building a tag with easy custom options to access the logging units and batteries reduces tag setup time when deploying, increasing the ability of researchers to track more individuals and/or collect repeated data on the same individuals. In addition, building bespoke tags and their housings in the laboratory increases knowledge about how the technology operates. This ultimately leads to units being deployed more easily in the field and reduces the chance that there will be any reduction in sample size while maximising both the duration of logging and the length of time that the device is attached to the animal.

Here, I describe techniques used to design housings and logger systems closely tailored to the research questions and to minimize the failure of tags, and particularly expand on the benefits of using *in-situ*, custom-designed tags based on the lifestyle and habitat of the study subjects used in this thesis; alpine ungulates. I also note that lessons learnt from this research have led to our presented technology being used to customize tags on other terrestrial species including African lions (*Panthera leo),* and African hunting dogs (*Lycaon pictus*).

Methodology

Building tags for three deployment lengths

My approach assumes that tags log data continuously (Yoda et al. 1999, Martiskainen et al. 2009, Moreau et al. 2009, Fehlmann et al. 2017) rather than in bursts, as some systems do (Nishiumi et al. 2018, Rast et al. 2020), and I arbitrarily split the projected logging life into three groups (Fig. 1) based on the questions being asked in the study. The deployment lengths are; short-term (several days), where, typically, fine details of animal behaviour are examined (Shepard et al. 2008, Campbell et al. 2013, Dickinson et al. subm.), medium-term (weeks to several months), where intra-seasonal patterns of space-use and/or behaviour are of interest (Martiskainen et al. 2009, Moreau et al. 2009, Alvarenga et al. 2016, Fehlmann et al. 2017) and long-term (several months - years), where inter- and intra-annual patterns are examined (Horning and Hill 2005).



Set in Guronic to water/shock proof the unit

Decrease size with a tighter fit decreasing weight

Increase size allowing for multiple types of batteries

Can be screwed onto multiple collar types.

Made out of aluminium to withstand social biting from lions.

Designed to slot and screw over Lotek collars

Built to fit on Lotek LITE collar and hold 1 A-cell to stay within weight restrictions

Increasing thickness of circuit board and battery terminals protective covering, increasing attention to housing seals, increasing strength and stability of housing

Figure 1 – Examples of devices used within animal tags by the research group (multiple channel loggers and/or GPS loggers and transmitters) and how the housing has been developed according to the projected length of deployment periods.

The electronic hardware

Within my system, I primarily used "Daily Diaries" (DD) (Wilson et al. 2008), which record acceleration (1 g = 9.81 m.s^{-2}) in three orthogonal axes. The tags were placed on the study subjects so that these acceleration axes recorded the anterior–posterior (surge), dorso-ventral (heave) and lateral (sway) axes. The DDs also recorded magnetic field intensity *via* an orthogonal tri-axial magnetometer, temperature and pressure with the timing of recordings regulated by a quartz real-time clock. Circuit boards ranged in size from 25 x 25 x 3 mm to 20 x 17 x 3 mm, depending on the model (Wildbyte Technologies 2020). These units used a removable micro SD card on which the data were stored and typically weigh 2-3g.

The batteries used to power the DDs differed depending on the desired logging duration and recording frequency of the unit. Most medium-term deployments used rechargeable flat rectangular 3.6 V Lithium polymer cells ranging from 350 to 1000 mAh (RS Components Ltd., Corby, Northants, NN17 9RS, UK), which powered a DD for one week to one month, respectively, weighing up to 40g. To collect data for longer periods, up to two 3.6 V Lithium-Thionyl Chloride A-cells were used (3.6 Ah, LS 17500, SAFT, Speciality Battery Group, Bagnolet, France), with each A-cell powering a DD for approximately 100+ days and weighing 22g each (at 20 Hz accelerometer sampling rate).

Final line of defence; protection of electronics from water and humidity

Circuit boards were inserted into a plastic ice cube tray so that they could be encased in GURONIC casting resin for electronic boards, a rubber like material specifically conceived to block the ingression of moisture on electrical circuits and thereby prevent any corrosion from water ingression should the seals on the external housing fail or the housing crack.

First line of defence; housings for study systems

All housings were first designed using Computer-aided design (CAD) technology, in order to find the most efficient dimensions, conditional on battery size, number and types of loggers employed, and attachment method to the animals (e.g. with or without custom openings to attach to the collar belt). The tags varied in their external housings (Fig. 1), which changed according to expected environmental pressures (shocks from hitting against other animals or rocks; rain and snow; temperatures, etc.) and the projected deployment periods. Two classes of materials were used - vacuum-formed from polyethene for short term deployments, and 3D-printed shock-proof ABS resin for medium and long-term deployments.

Short-term; tests for < 1 day on domestic horses (Equus ferus caballus)

In the present thesis, short-term housings were used to test the loggers, with all data collection focussed on medium and long-term deployments, hence I refer to examples where I built these housings on side-projects on other taxa. A very efficient and cheap ‘short-term’ housings (Type I) can be designed and built using vacuum-formed from polyethene (≈2 mm thick). These housings could be splash-proofed by being wrapped in electrical tape or waterproofed (to *ca.* <0.5 m depth) by sealing with polyethylene glue. I used two housing sizes (Fig. 1), the smaller version (20 x 35 x 22 mm, ~20g) potentially allowing smaller species to be tagged but leaving no room for units other than a single DD (i.e. no GPS). This housing was tested only in domestic and captive species due to its inability to resist high forces and pressures and short-term waterproofing. In addition to horses (see case study below), I also used these housings for short (*ca.* 3h), continuously monitored periods on domestic dogs (*Canis lupus familiaris*), and Aldabra tortoises (*Aldabrachelys gigantea*).

I prepared a similar housing for a study on horse movements and energy expenditure, where on a ranch in Buffalo, Wyoming, North America, sixteen adult American Quarter horses were tagged using the type I housing described (Milne 2019). The housing held a square “Daily Diary” circuit board and a 1000 mAh rechargeable battery. The tag had a total weight of 45 g with maximum dimensions of 65 x 35 x 22 mm (Fig. 2). The housing was backed with foam and wrapped with electrical tape onto the saddle (Fig. 2) to ensure that the acceleration axes mirrored the principal axes of the horse (see above) to obtain an accurate representation of the animal’s movement (Fig. 2). The same logger was repeatedly deployed on the different individuals for periods between 30 and 150 minutes and the device was constantly observed by the rider. During the deployment period, the animals were subject to temperatures between 10°C and 23°C with little or no rainfall (NOAA 2017).

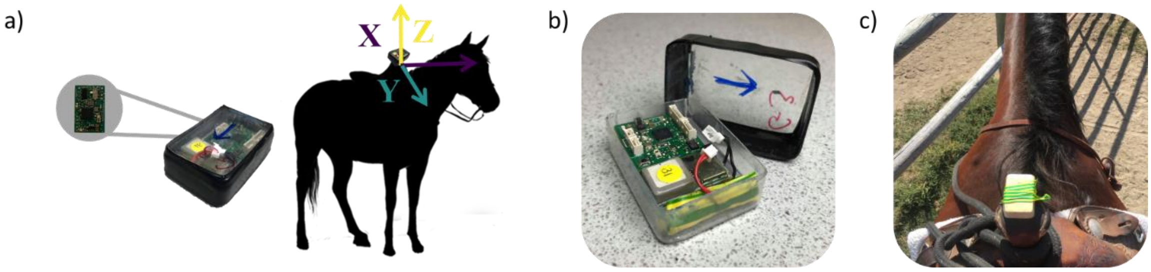


Figure 2 – (a) Diagram showing position of the DD with respect to the housing and where positioned relative to the species (b) Daily Diary and 1000 mAh battery inside a polyethylene housing for short-term data collection and (c) in place taped to the saddle of a horse.

Field performance – Study area and species

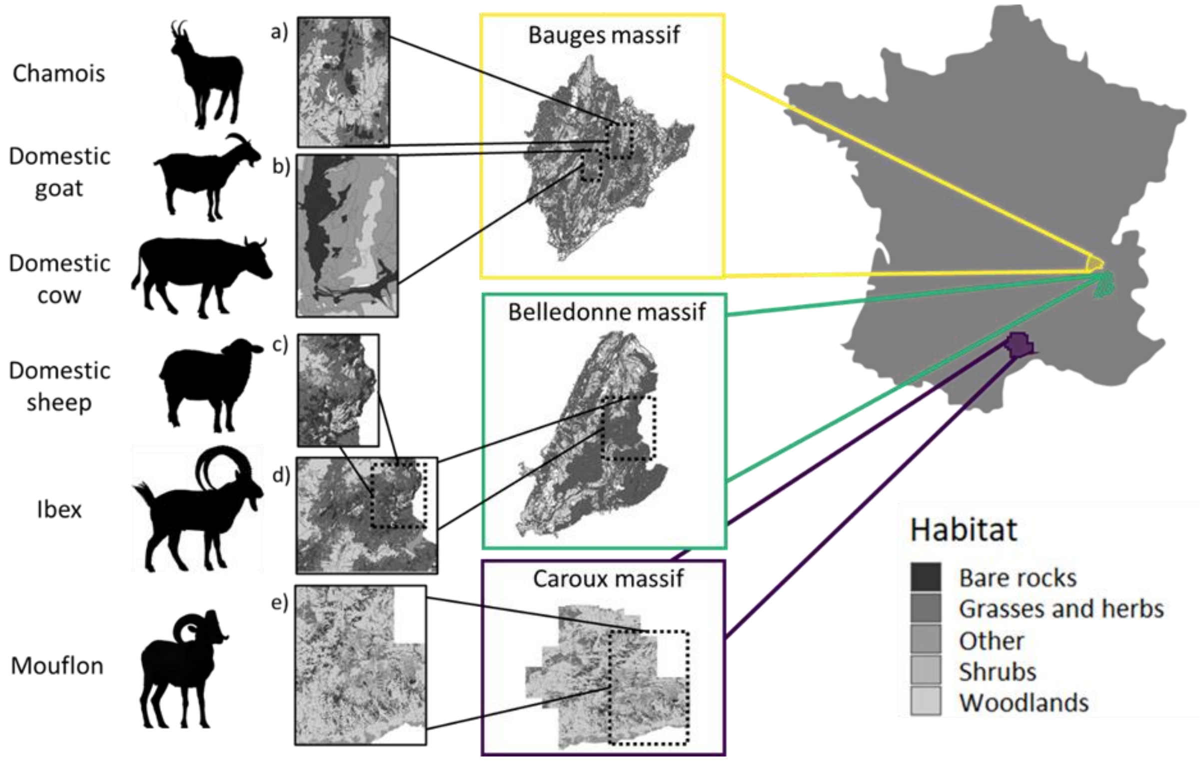


Figure 3 – Illustration of the overall study area and the position of specific relevant sites within France. (a) The Bauges massif was used for studying the chamois, (b) the domestic goat and (c) the domestic cow. The Belledonne massif was used for (c) the domestic sheep and (d) alpine ibex study while (e) the mouflon was studied within the Caroux massif. Each map has polygons outlined and is coloured based on habitat.

Medium-term; tests for < 2 months on domestic cows (Bos taurus)

The medium-term housings (Type II) were designed to be used on the domestic species (cows, goats, sheep) during the time of summer (July-August) on the French Alps – on the Bauges Mountain (Massif des Bauges, 45.61°N, 6.19°E) (Fig. 3a) for the goats and cows, and on the Combe Madame on the Belledonne Massif (La Ferrière, Isère; 45.26479°N, 6.11419°E) (Fig. 3c) for the sheep. All housings contained Daily Diary tags (Wilson et al., 2008), combined with Gipsy5 GPS tags (TechnoSmArtTracking Systems http://www.technosmart.eu), both electronic units powered by 1000 mAh rechargeable battery for each tag. All housings were attached to the animals using standard commercial nylon collars for livestock – for sheep and goats I used Kvikk Durable Plastic Collars (Collar Length 59.5 cm, Collar Width 2.5 cm, Circumference 41 -52cm, weight 52g; Shearwell Data Ltd, Minehead, Somerset, UK; www.shearwell.co.uk), and for the cows I used nylon neck collars with single roller buckle (width 40mm, length 135cm, weight 180g; Fearing Lifestyle, Durham, UK; www.fearing.co.uk). The housing was made of Acrylonitrile Butadiene Styrene (ABS) plastic (≈10 mm thick) (Olivera et al. 2016) printed in 3D, following the CAD design, to have a cavity which could hold of the required batteries and logging units. The housing was constructed so that it could be threaded onto different sized belts/collars, but mainly targeted at the cow or sheep/goat collars, respectively. The housing was made watertight for long periods by coating the plastic in acetone (which sealed the plastic filaments together) and by adding an O-ring on the lid, fastened into place using aluminium screws with an optional hole to allow outside pressure to be registered by the pressure sensor (Fig. 4).

For the remainder of this chapter for simplicity I focus on the cow collars only – the sheep and goats ones were very similar, with a lower vertical extension to accommodate the smaller body size. The housing was counterbalanced on the nylon belt with a 500 g lead diving weight, to hold the logger up dorsally on the collar (Fig. 4). The collar had a total weight ~690 g, with housing dimensions of 60 x 70 x 54 mm. The cows were collared during milking (which occurred on-site twice daily in a mobile milking station) and systems remained on the animal for between 6 to 30 days. During the deployment period, the animals were subject to temperatures between 9°C and 22°C with average monthly rainfall 56mm (NOAA 2017).

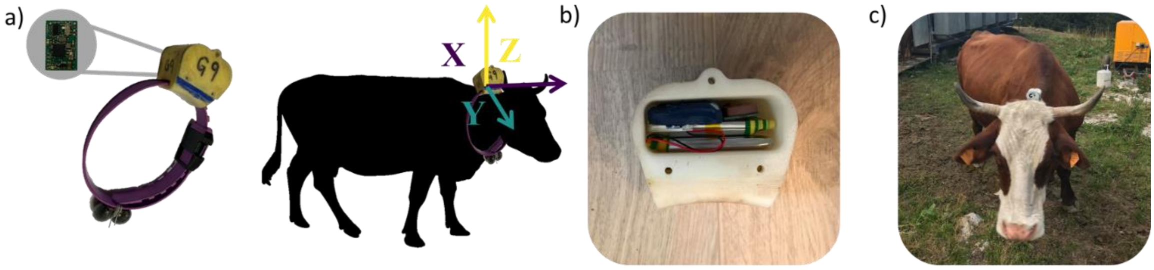


Figure 4 – (a) Diagram showing position of the DD with respect to the housing and once positioned onto the individual cows (b) the Daily Diary, GiPSy 5 and 1000 mAh battery inside the housing for the medium-term data collection, (c) Lab-built collar attached to a cow.

Long-term; tests for > 6 months on ibex (Capra ibex)

For long-term monitoring (i.e. up to 1 year of logging), I prepared 3D-printed housings made from ABS plastic (Type III), particular considerations included the ability of the system to withstands large impacts (> 2 *g*), prevent large amounts of water entering and then flooding the housing and the capacity to cope with water condensation within the housing from the changing temperatures. A key novelty of the housings was that, thanks to the 3D design, I could design housings which could be seamlessly bolted onto and encase existing housings of commercial GPS collars, used for many years on the study species, as part of long-term projects. This housing hence became an add-on to an existing, proven biologging collar, which is an advantage both from an animal ethics point of view as well as from an efficiency standpoint – the standard, long-term data collection can continue as usual and if the additional system works, novel data are collected in addition to the full set of the established ones. Specifically, I developed such housings for ibex (*Capra ibex*), mouflon (*Ovis gmelini musimon × Ovis sp.*), and chamois (*Rupicapra rupicapra*) (plus red deer (*Cervus elaphus*), as part of a different project to the current thesis). All three species are routinely monitored and tagged every year with GPS radiocollars by the Office National de la Chasse et de la Faune Sauvage, according to the ethical permits by the Préfecture de Paris, in agreement with the French environmental code.

A sample of individuals of each species is captured every year, using either drop down nets or netted pen traps with salt blocks for bait. Once captured, the ungulates were handled, masked, released from the net and had their legs restrained to immobilise the animal. Data were then collected including blood and hair samples, weight, sex and measurements of horns, hoofs and legs. Before the ungulate was released the individual was collared with the Lotek GPS with attachment time recorded. Specifically, all animals were tagged with a Lotek wireless GPS 3300S collars with radio-controlled remote release mechanism (revision 2; Lotek Engineering Inc., Carp, ON, Canada). The Lotek collars recorded a GPS position every hour and contained a VHF transmitter at the top of the collar with mortality sensor, as well as the 3D-printed housing specifically designed to be screwed onto the GPS unit. The collar with the

DD attached weigh in at 438g staying under the 3% guideline for all species. The collars are recovered after a year through a remotely triggered drop-off mechanism. Thus, using a custom-built add-on allowed me to seamlessly add an entire new level of data collection, with new sensors, to an existing set of long-term projects, without disrupting the ongoing monitoring efforts. The chamois were captured in the Massive de Bauges area (Fig 3a), the ibex in the Belledonne massif (Fig 3d), and the mouflon in the Caroux-Espinouse mountains (43.60854°N, 2.98639°E) (Fig 3e).

In detail, the 'Daily Diary' housing contained an elongated DD circuit board and two 3.6 V A-cells combined with a diode (Fig. 5; see also above), powering the single DD unit. The complete housing had a weight of 62 g and had housing dimensions of 48 x 75 x 78 mm. To allow the 2 A cells to last for (theoretically) one year, I selected a sampling schedule of 20 Hz for the accelerometers, 8 Hz for the magnetometer, and 2 Hz for the temperature and pressure sensors.

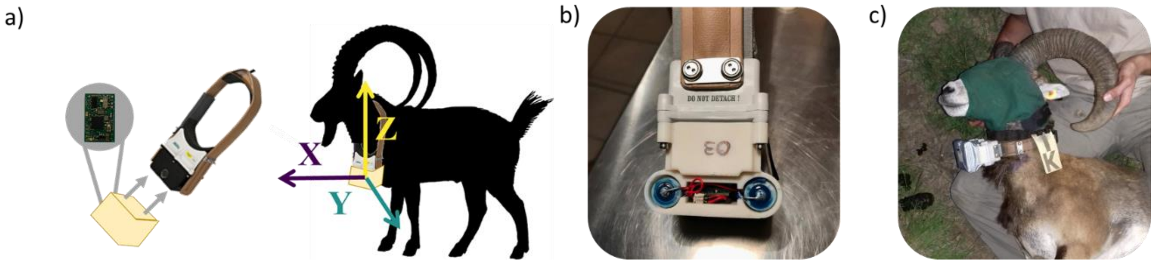


Figure 5 – (a) Diagram showing position of the DD with respect to the housing and where positioned relative to the species (b) Daily Diary and A-cells within the housing showing how the unit fits over the top of the commercial collar, (c) similar collar setup attached to a mouflon.

During the deployment period, the tags were subject to temperatures between -11°C and +36°C (average 10.8°C), as recorded by the internal temperature sensor, with precipitation (rain- or snowfall) varying between monthly means of 70 and 172 mm (NOAA 2017).

Results

The three housing types all successfully collected data for the minimum desired amount of time across the required channels (Table 1) with high resolution. However, some failures were noted following this.

Table 1 - Comparison of the different housing types, the average amount of data collected and the logging success of the tags.

	Time scale		
	Short-term (Type I housing)	*Medium-term (Type II housing)*	*Long-term (Type III housing)*
Average logging time in days (at 20 Hz using chosen battery sizes)	<1	12	200
Amount of deployments (number of individuals (n))	26 (n=16)	134 (n=85)	58 (n=58)
Average data points including all channels (at 20 Hz using chosen battery sizes)	1.27E+06	9.12E+07	1.52E+09
Percentage of devices treated with Guronic	0%	87%	94%
Percentage of data successfully collected compared to maximum potential data collected with respect to battery capacity	100%	81%	36%
Breakdown of logger failures with possible causes (if no data is recoverable)			
Device incurring electronic failures due to water ingression (device logged for part of the time)	0 (0%)	20 (80%)	3 (8%)

Devices that completely failed to record at all (likely due to human error in programming and set up)	0 (0%)	5 (20%)	7(19%)
Corroded and corrupt SD cards losing all data	0 (0%)	0 (0%)	9 (26%)
Housing found damaged or missing	0 (0%)	0 (0%)	17 (47%)

In the short-term study using the type I housing, out of 26 deployments, no units failed, providing 100% of the expected data.

The type II housings were deployed 68 times on three domestic ungulate species across the months of July and August in 2017 and 2018 and provided 81% of the expected data. 20 failures occurred in the devices that did not have their circuit boards covered in Guronic. In these units, the circuit boards were visibly corroded. Three of the recovered housings (2%) had cracks resulting from robust inter-individual interactions, or the action of hitting the collars against rocks or the metal bars during the daily milking operations, none of which (0%) had resulted in damage to the DDs.

The type III housings recorded alongside a Lotek GPS collar on 14 wild ibex. Three tags failed to log data due to corruption on the SD card although the reason was not clear, three tags logged for <60 days in circuit boards that were not covered in Guronic (see above), and three units logged for >200 days. A total of 27 tags were deployed on mouflon in 2017, 2018 and 2019; 17 tags were deployed on chamois in 2017, 2018 and 2019. Just under half the units (47%) were not successfully recovered accounting for most of the data lost. The SD cards failed for 13 and 2 of the tags for mouflon and chamois, 3 for the ibex. Thus, 6 (69%), 11 (41%) and 6 (35%) of the collars successfully recorded useable Daily Diary biologging data, respectively for ibex, mouflon and chamois – a non-significant difference (Pearson's Chi-squared test, X squared = 4.2498, df = 2, *p-value* = 0.1194). These loggers provided 20 Hz accelerometer, 8 Hz magnetometer, and 4 Hz environmental data (temperature and barometric pressure) for over three months on average (range 5 – 220 days; Table 2).

Table 2 – How biologger collars performed using type III housing, across three wild ungulate species.

Species	*Deployed*	*Successfully recovered*	*Units with recovarable with data*	*SD card failures*	*Days of data (median)*	*Days of data (range)*
Ibex	14	9	6	3	218	52-220
Mouflon	27	24	11	13	80	5-220
Chamois	17	8	6	2	150	97-173

Using the temperature sensor data allows to explore if tag failure was associated with below-zero temperatures (leading to battery failure). Using the ibex data, whilst there was a clear relationship between battery voltage and temperature (Fig. 6), the end of data recording did not coincide with the expected end of data recording.

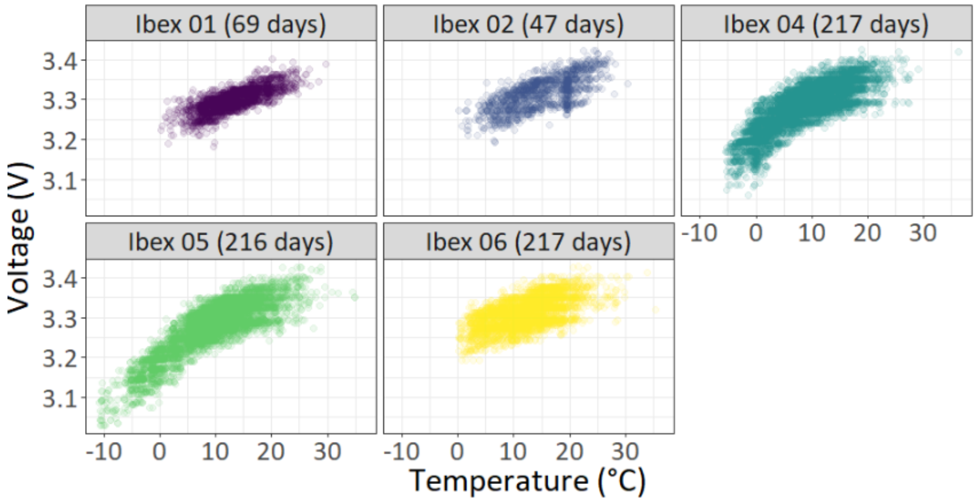


Figure 6 – Scatter plot showing how voltage of electronic DD logger changes how temperature register by DD logger, across five individual ibex.

Discussion

This study highlights how housings for logging systems on wildlife must address a series of issues which vary considerably according to the study species and the projected deployment period. The tagging success rate was very high for the short term and medium-term deployments and whilst the rate was considerably lower for the long-term deployments on wild animals, it was still within the average rate for wildlife biologging studies, even using expensive commercial devices (Johnson et al. 2002, Allison et al. 2013, Hofman et al. 2019). On the other hand, specific commercial devices have shown considerably higher success rates and there are strong challenges and risks in developing custom-built devices ((see Foley & Sillero-Zubiri 2020) and references therein), counterbalanced however by the lower costs and the ability to collect data better suited to the project aims and with closer consideration of specific animal welfare requirements. I discuss here in detail procedures to be used to further improve tag success rate.

Aside from the housing having to be robust enough to withstand the forces to which the animals subject them, including interspecific interactions (e.g. Jung & Kuba 2015), perhaps the single most important element is the value of covering the circuit board with Guronic, a product fabricated specifically to protect electronics from moisture and reduce the impact of mechanical shock. Although the Guronic layer added little to short-term deployments (although the test conditions did not cover extremes of weather), temperature changes within the air spaces of housings due extreme temperature cycles, even over just a few days, can lead to repeated cycles of condensation where water forms droplets on the circuit board, before being re-vaporised. An unprotected circuit quickly becomes corroded under such circumstances, often due to short-circuiting between the power lines on the board and will generally stop logging even resulting sometimes in loss of data. I would therefore recommend, where the weight of the tag is not critical, that all circuit boards be covered in Guronic (or similar types of coatings for electronic circuit boards), even for short-term deployments. Where weight becomes a strict issue (Vandenabeele et al. 2012) , I suggest using “plasti dip”, an aerosol designed to protect circuit boards from moisture that can be applied in thin layers. Although I did not explicitly use this product within my trials, this would add an extra layer of protection and, whilst this layer will not protect against vibration of shocks in the same way as the rubberized Guronic, it would seem markedly better than nothing.

Vacuum-formed polyethylene housings are cheap and rapid to produce (typically taking 1 person approximately 2 days to prepare 10 tags, which includes building batteries and unit testing). However, such housings are only appropriate for short-term deployments and should be checked regularly (every three days at least) for signs of weakness. The probability that such housings will fail to protect the logger depends on the species concerned, its environment, the specific site of logger attachment and the projected logging duration. Workers need to determine the likely forces to which the housings may be subjected (such as the effect of head-butting in ungulates) and test the housings with these forces (which can be simulated with weights) to check that they withstand the process. Deployments within humid environments or environments subject to highly variable temperatures makes any breach of the housing (including simple cracks) critical since water can enter the system and/or condense within the housing. Indeed, such cracks generally lead to water accumulating within the housing as water condenses, or moves inside *via* capillary action, and is joined by more water as repeated condensation- or precipitation events occur. Finally, the specific site of attachment determines, to some extent, the likelihood of the housing eliciting problems. To exemplify, I use data from a previous work (Redcliffe 2017), where a transparent housing mounted dorsally on a collar can have internal temperatures that exceed 45°C when subject to intense insolation due to a ‘greenhouse effect’ (He et al. 2018) (Fig. 7).

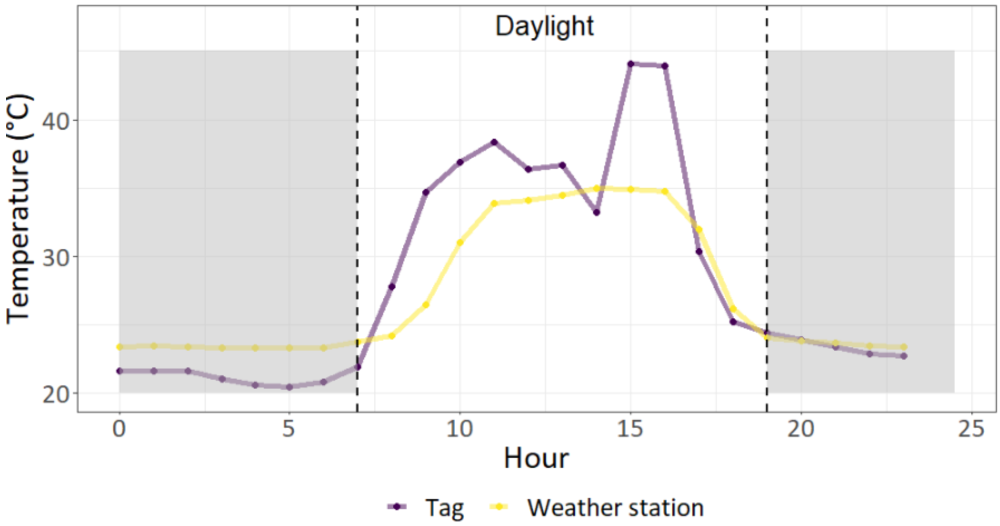


Figure 7- Hourly mean temperature recorded by a DD tag encased in vacuum-sealed housing and attached to an Aldabra tortoise (Aldabrachelys gigantea)) and compared to the weather station data as a function of hour of day. The data that were collected over approximately two days during the dry season May to June 2016, in Mauritius, with the dashed line representing approximate sunrise and sunset. Note: species behaviour and movement will dictate some temperature readings e.g. seeking shade midday.

Not only does this serve to vaporise water within the housing, only to condense later when the temperature cools, but it may also lead to pressure build-up within the housing which may lead to cracks in the glue and subsequent water ingression. I would recommend that such housings be only used for deployments not exceeding a few days in any event but that the deployment period be decided depending on the harshness of the operating environment, including animal forces and the weather. Vacuum-formed housing are, however, ideal for studies on captive animals, such as the horse study described here, since they can be easily deployed and removed.

3-D printing using ABS plastic can mitigate many of the problems of vacuum-formed housings and are therefore more suitable for medium-term projects (see also Foley & Sillero-Zubiri 2020). This is, however, more costly and time-consuming (each housing may take several hours to print, and must subsequently be water-proofed, so that it takes about 1 week to fully prepare 10 tags). The specific advantage of the 3-D printing process is that housing wall thickness can be varied easily so that expected forces can be taken into account. It is important, however, to seal the units properly with acetone since the printing process layers filaments together, leaving spaces between them so that they are not, otherwise, waterproof. There is little information on the stability of ABS plastic over time under conditions experienced by wild animals (Boldizar and Möller 2003, Olivera et al. 2016) but some degradation of capacity is expected so I would recommend such housings for no longer than about 6-12 months. Further long-term tests will be important to clarify this.

Deployment periods that exceed 6 months require a much greater investment of time and resources. Specifically, an engineer’s time is required to consult, design and build housings, making this the costliest option. Such housings can, however, be made to be fully durable (if made in aluminium for example – if the body weight of the study species allows this; this was not an option for the wild ungulate species in my thesis), reducing the chance of the unit becoming damaged when on the animal, even over extended periods. Reasons for tag failure stemming from such housings tend to centre around inadequate provision of batteries or using poor quality memory cards (see e.g. Table 2). Both of these problems can be easily dealt with.

Choosing the right housing for the study

To aid users undertaking a project using biologgers, I present a flow diagram (Fig. 8) to help understand the requirements of the study and identify the most appropriate housing.

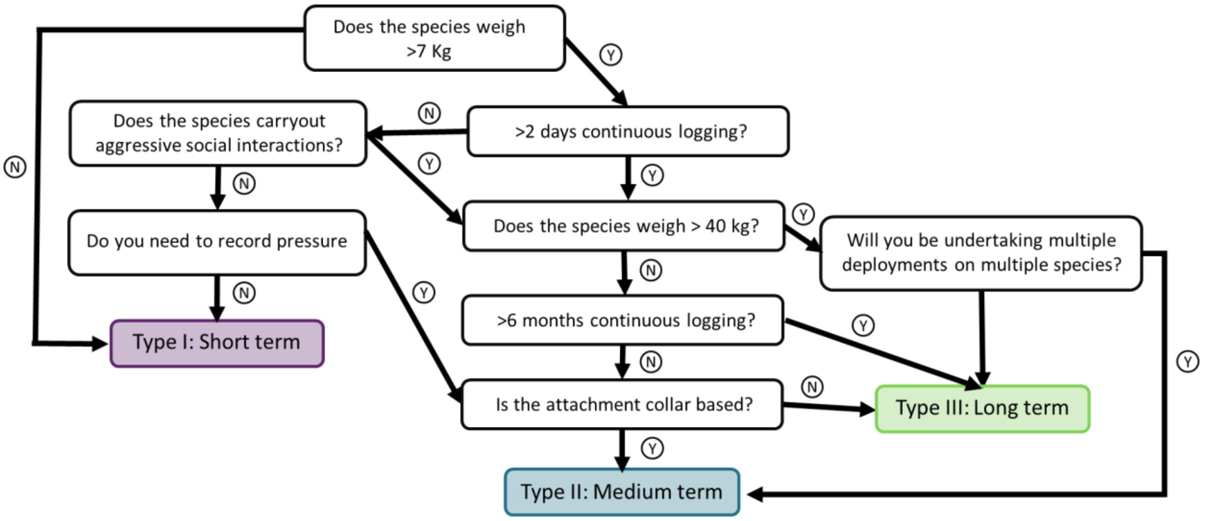


Figure 8 - Flow chart relating the study species and the desired logging period, to help identify the optimal housing for data collection in ungulates.

Future improvements

The proportion of device failures in my study from both short-term and medium-term tags implies that housing recommendations for these deployments are good. I note however, that collar mounting, especially loose collars, creates noise within the acceleration and magnetometer data (Wilson et al. 2019) lowering data quality, and making behaviour signals less consistent. I would suggest that researchers working with such sensors minimize this by considering a more flexible, tighter fit, perhaps using more elastic material for the collar, and adding padding, if possible, considering animal welfare.

I noted the several tag failures due to corrupt SD cards, tag corrosion and housings being smashed during the long-term study. To prevent the housing cracking on further deployments, I recommend fortifying the structure by changing the internal structure filament print of the housing and rounding off the edges of the ABS plastic. To reduce electronic failures, water and shock-proof Guronic should be used on all deployments and high quality durable micro SD cards used for memory. As yet, I have done no systematic test of the ability of different SD cards brands to provide a robust memory but this is urgently needed because I had memory card failure in housings that were fully intact when recovered.

The implication is that temperature changes may have been responsible for data corruption but this is conjecture.

Conclusion

The in-laboratory-designed biologging collars are not only cheaper but offer more data at a higher resolution than most company-built animal collars. The techniques used to shockproof and waterproof the terrestrial electronic devices have been improved over the past three years and this has increased the success of data collection. This study highlights the importance of design and attachment methods to acquire the best quality acceleration and magnetometer data. The short-term housing and attachment method produced clear consistent signals, however the medium-term collars acceleration data were lower quality due to the noise in the signals caused by the loose fitting of the collar. It would be beneficial to the community if other researchers building tag housings, including those working in the marine environment, were able to disseminate their successes and failure, perhaps *via* a forum in the biologging society.

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Chapter 3

Step in the right direction for dead-reckoning terrestrial animals: Using behavioural definition analysis to improve the accuracy of dead-reckoned locations

Abstract

Dead-reckoning is a method which uses vectors of heading and speed to allow calculation of vehicle movement paths. It has also been shown to be a powerful tool for deriving high resolution (>1 Hz) travel paths of terrestrial animals for a fraction of the battery consumption and, under some circumstances, less error in location than global positioning system (GPS) loggers, with a higher resolution of turns and also in locations without GPS signal reception (dense canopy, under cliffs, etc). Despite this, the approach is underused and when it is, few specifics are provided, making it hard for researchers to replicate the treatment, and often with insufficient consideration of the error sources. This work uses 20 Hz data from GPS-enabled Daily Diary tags (GPS frequency ranging from 15 minutes to 2 hours) on 27 free-living, mountain ungulates – 8 domestic cows (*Bos taurus*), 10 domestic goats (*Capra aegagrus hircus*), 6 wild alpine ibex (*Capra ibex*) and 3 Mediterranean mouflon (*Ovis gmelini musimon × Ovis sp.*) to assess the errors of GPS-enabled dead-reckoning in reconstructing movement tracks, according to different rules derived from the accelerometers to indicate travelling – an approach missing from all current standard methods. By using example data, over time scales of 14-20 hours, from the study species, four different 'travelling detection criteria' (TDC) were tested, all of which demonstrated the extent to which simple filtering can improve estimates of animal location, speed and distance travelled with error accumulation ranging between 9 and 117 m/h according to species and TDC. This study therefore highlights the value of dead-reckoning to interpolate between GPS fixes in collar-tagged free-roaming ungulates. In particular, careful consideration of how to determine when tagged animals are travelling leads to surprisingly accurate information about animal movement pathways, even when GPS fixes are only taken at hourly intervals.

Introduction

Two or three dimensional animal paths can reveal key aspects of species energetics (Parker et al. 1984, Lempidakis et al. 2018, Wilson et al. 2020), decision-making (Helen et al. 2006, Grignolio et al. 2007, King and Cowlishaw 2009), home ranges (Christiansen et al. 2017, Cohen et al. 2018) and behaviour (Carbone et al. 2007, Hein et al. 2012) and can lead to a better understanding of a suite of important phenomena including the spread of disease (Patz et al. 2008), habitat utilisation (Aarts et al. 2008, Roper et al. 2001) and social interactions (Bandeira de Melo et al. 2007, Handcock et al. 2009, Calabrese et al. 2018, Barkley et al. 2020).

Typically, animal paths are obtained from locations sampled at regular times from the continuous trajectory of an animal, using animal-attached biologging sensors or transmitters, and are reconstructed by joining the sampled locations with straight line sections (Calenge et al. 2009). With high resolution paths in particular, behaviours can be identified from the characteristics of the path (Edelhoff et al. 2016), for example track tortuosity (Benhamou 2004) and step lengths (Ungar et al. 2005, Bandeira de Melo et al. 2007, de Weerd et al. 2015). To obtain these locations, satellite-based systems such as Global Positioning Systems (GPS) are commonly used, derived from tags attached to the study animals. Since this system uses the position of orbiting satellites, communicating *via* radio transmission, GPS-acquired positional quality is affected by any environment that inhibits the passage of radio-waves e.g. through salt water or when an animal is under cover (e.g. tree cover) (Gamo et al. 2000, Quaglietta et al. 2012, Camp et al. 2016), leading to biased if not entirely missing locations in certain habitats. Thus, although GPS-acquired position is regarded as a 'gold standard', it is not reliable under some circumstances and may not be viable under others (Gamo et al. 2000, de Weerd et al. 2015). Radio transmission also requires a relatively high amount of power and GPS uses particularly high power to calculate position (Dewhirst et al. 2016). For example, typically, to collect GPS fixes for a high-resolution path (at e.g. 1 Hz) for one day requires~500 mAh of power or ~3.5 g in A-cell battery weight (see appendix, Table 1). Thus, to collect high frequency long-term GPS data requires a bulky, heavy and financially costly battery that must be carried by the species being tracked. The extra mass and bulk affect the cost of movement (Vandenabeele et al. 2012) and therefore likely the fitness of the animal (Wilson et al. 2004, Rasilius et al. 2014, Bodey et al. 2017). Therefore, researchers seeking to minimize such effects by keeping batteries small have to choose between short-term high temporal resolution tracks or longer-term, low temporal resolution tracks (Frair et al. 2005, Oksanen et al. 2015). Low resolution GPS paths however result in the loss of key details of the path's tortuosity, which has consequences for my understanding of animal movement, e.g. by leading to poor estimates in distance travelled or time spent in particular habitats (Rowcliffe et al. 2012).

Dead-reckoning (Kao 1991), which uses information on animal heading, speed and change in height/depth in vectorial calculations (Shiomi et al. 2008), offers a solution to this. Specifically, in terrestrial animals, it produces high resolution paths with fewer GPS fixes by filling in the gaps between the infrequent 'true' locations by using tri-axial acceleration metrics as a proxy for speed and tri-axial magnetometer to derive heading (Bidder et al. 2015). The data necessary for dead-reckoning can be collected using electronic devices combining accelerometers and magnetometers, e.g., "Daily Diaries - DDs" (Wilson et al. 2008) in tandem with the GPS loggers (important for error correction, see below). DDs consume markedly less power than GPSs because there is no signal transmission and no complex calculation on the tag. The dead-reckoning procedure does not, however, render the GPS obsolete because ground-truthed locations are required periodically to prevent any drift caused by cumulative errors as a result of slightly offset orientation of the tag relative to the animal (Bidder et al. 2015, Dewhirst et al. 2016), noise in the acceleration data and inaccuracies in the speed *versus* acceleration metrics (Bidder et al. 2012). In short, GPS-derived positions allow the dead-reckoned data to be converted into locations that can be mapped, making a combination of GPS and dead-reckoning a powerful method for deriving high resolution animal movement paths.

GPS-corrected dead-reckoning has been used to project paths in studies for aquatic species (Wilson et al. 1991, Mitani et al. 2003, Shiomi et al. 2008, Wensveen et al. 2015), for pedestrian navigation (Jiménez et al. 2009, Tian et al. 2014) and terrestrial animal studies have tested the methodology on domestic species, including domestic dogs (*Canis lupus* *familiaris*), cows (*Bos Taurus*) and horses (*Equus ferus caballus*) (Bidder et al. 2015, Dewhirst et al. 2016). However, few studies have used this approach on wild species for periods longer than a day, and no studies have used the technique on freely-moving wild species over long time scales.

The use of dead-reckoning for terrestrial animals was first described by Bidder et al (2015) with its benefits highlighted. Bidder *et al*. (2015) mention, however, how using Vectoral Dynamic Body Acceleration, a derivative from tri-axial acceleration data (Wilson et al. 2019), as a proxy for speed, has its limitations due to the relationship between true speed and VeDBA changing with substrate, incline and the change in step gait from walking to running. In the most simplistic approach though, the suggestion is that VeDBA extent appropriately codes for travel speed even though animals may have high VeDBA values when not moving (e.g. when shaking themselves or grooming). This is obviously problematic and makes a strong case for identifying translocational movement before applying any speed conversion to the VeDBA data. However, there are multiple approaches for identifying behaviour from acceleration and magnetometer data (Fehlmann et al. 2017, Williams et al. 2017) with corresponding potential to enhance dead-reckoning-derived tracks.

In this work, I examine the extent to which behaviour identification enhances dead-reckoning path definition in moving animals using data from free-living, domestic cows (*Bos Taurus*), domestic goats (*Capra aegagrus hircus*), wild alpine ibex (*Capra ibex*) and wild mouflon (*Ovis gmelini musimon × Ovis sp.*). The specific aims of this study are; (i) to examine various acceleration-based metrics to indicate when animals are travelling and stationary, (ii) to consider how these metrics tie in with VeDBA/speed relationships, (iii) to assess how both of these affect the viability of GPS-enabled dead-reckoned tracks before (iv) making recommendations as to how researchers can best use acceleration and magnetometry data to produce the paths in GPS-enabled dead-reckoned data that most likely correspond to the real paths taken by study animals. This forms an important element that informs the methods used in subsequent chapters in this thesis.

Methodology

Acceleration and magnetometer data were collected using Daily Diary (DD) multi-sensor biologgers (Wildbyte Technologies 2020) and GPS systems – Gipsy 5 (Technosmart) or Lotek 3300S (Lotek.com) – see chapter 2 for more detail. I here summarise the main information – on 4 wild and domestic ungulate species living in alpine mountain areas in France (Table 1; see chapter 2 for further detail). The DDs recorded multiple data points per second on 8 channels including, tri-axial accelerometers (at 20 Hz), tri-axial magnetometry (at 8 Hz), temperature (at 2 Hz) and barometric pressure (at 2 Hz). The GPS units recorded fixes at different rates, dependent on the species, location and projected logging period (Table 1).

Table 1- A list of data used within this study detailing the individuals used, GPS sampling frequency and tagging duration.

Species	*Number of individuals*	*Time window of sample data*	*Sample data duration*	*GPS fix rate*	*Location*
Domestic goat	10	August 2017	14 hours	1 fix every 15 minutes	Bauges massif, France
Domestic cow	8	August 2017	14 hours	1 fix every 15 minutes	Bauges massif, France
Ibex	6	May to June 2017	24 hours	1 fix every 2 hours	Belledonne massif, France
Mouflon	3	June to July 2017	16 hours	1 fix every 30 minutes	Caroux parc, France

Two data sets were taken from deployments using tags on domestic animals; cows and goats in the Bauges massif (45.60485°N, 6.18295°E). For these two species, the laboratory-built collars were made from nylon belts equipped with 500 g lead weight and flexi-plastic with a 100g lead weight, respectively. Both species' collars had the same tag housings (weight; ~50 g, dimensions; 60 x 70 x 54 mm) constructed of ABS plastic (see chapter 2) containing a DD and GPS Gipsy 5 unit (TechnoSMart 2020) that took one GPS location every 15 minutes (Table 1).

Two data sets were derived from wild species, one from alpine ibex tagged in the Belledonne massif (45.2241°N, 6.0305°E) and the other from mouflon residing in the Caroux mountains (43.6059°N, 2.9868°E). The DD housing for both species (weight: 150 g, dimensions: 48 x 75 x 78 mm) was also constructed of ABS plastic and was fitted over, and screwed onto, a collar-mounted GPS Lotek 330s collar (Lotek 2020), programmed to take a fix once every two hours for the ibex and once every 30 minutes for the mouflon (see chapter 2).

In the procedure detailed below, a single 24 h period, picked at random from each individual from each species was selected for analysis.

Nominal dead-reckoning procedure for terrestrial animals

The simple, nautical dead-reckoning technique (Cotter 1978) begins by taking a known start point (in my case, where the animal was at the start of the selected 24h period). If the heading of the vessel (or animal) is known as well as its speed, the trajectory of that vessel can be plotted over time using vectorial calculations. In essence, the moving body continues in a straight line with a movement rate determined by its speed until either speed or heading changes (Cotter 1978, Kao 1991, Bidder et al. 2015). In the times of old sailing vessels, headings and speeds were maintained for long periods, making the calculation relatively simple (notwithstanding issues with drift due to currents). Application of this technique to animal movement necessarily involves frequent (sometimes > 1 Hz) assessment of both heading and speed since animals may change both at any time. This is achievable with modern logging systems (Kao 1991, Jiménez et al. 2009, Bidder et al. 2015), which can compute heading and speed for fractions of seconds (Bidder et al. 2015, Dewhirst et al. 2016). Today, animal dead-reckoners are generally based on using inertial measurement units (IMUs) (Johnson and Tyack 2003) such as found in the DDs. However, this is complex and requires several transformations to convert the magnetometer and acceleration data into distance and heading and then to convert these into GPS decimal coordinates. These are briefly described below although more details can be found in Bidder *et al*. (Bidder et al. 2015, Gunner et al. 2021, Walker et al. 2015). To undertake the dead-reckoning process and all the calculations associated with it, I used bespoke software; Daily Diary Movement Trace (DDMT) (Wildbyte Technologies 2020).

Magnetometer data correction

The magnetometer data are subject to a number of errors including sensor bias (which is due, in part to ferrous material in the tag or adjacent tags such as the GPS), scale factors (because the earth's magnetic field is not constant across its surface), sensitivity errors and iron deposits in rock types in the surrounding areas of where the animals move (Caruso 2000, Guo et al. 2008, Vasconcelos et al. 2011). To correct for these issues, the tri-axial magnetometers tag must be calibrated. This involves subjecting them to a series of extensive, defined rotations so that a tri-axial plot of the magnetic field intensity logged by the sensors (also called the M-sphere (Williams et al. 2017)) can be formed (Fig. 1). This is supposed to be a perfect sphere but is typically distorted in a number of ways due, for example, to the presence of ferrous material in or near the tag, and so must be corrected (Fig. 1) (for details see Bidder *et al*. 2015).

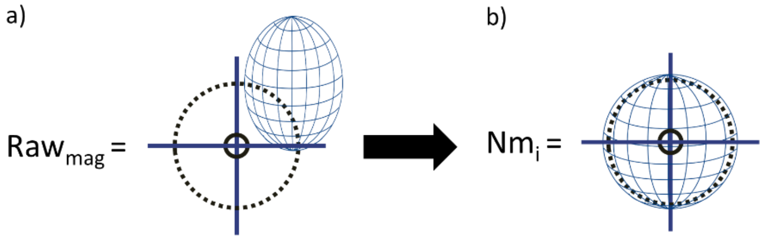
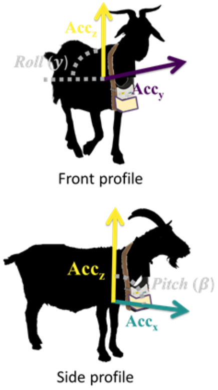


Figure 1 – Calibration of the magnetometers by rotating them extensively produces data that, when plotted as a tri-axial graph, produces a sphere (the M-sphere – see Williams et al. (2017). To be useful in dead-reckoning, this sphere, which is typically distorted (a), has to be normalised (b) so that it becomes perfectly spherical and so that the vectorial sum of the magnetic field vectors are constant at all points on the sphere, which centres the sphere about a defined origin.

Derivation of tag orientation to prepare for animal heading calculations

The procedure for deriving animal heading requires, first, that the tag orientation be defined. This is done by deriving the 'static' acceleration (that component due to the earth's gravity acting on the body of the animal, also when the animal is immobile) by smoothing the raw acceleration, typically over a window of 2 seconds (Shepard et al. 2008), and then using these values to define tag pitch and roll (Fig. 2).



$$\text{Static acc. } (S_i) = \frac{1}{n} \sum_{i=0}^{n=1} Acc_i - i$$

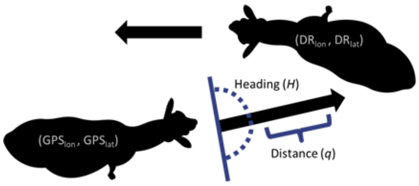
$$Pitch(\beta) = \left(\alpha \tan 2\big(S_{y.} \sqrt{S_x \cdot S_x + S_z \cdot S_z}\big) \cdot \frac{180}{\pi} \right)$$

$$Roll(\gamma) = \left(\alpha \tan 2 \left(S_{x.} \sqrt{S_y \cdot S_y + S_z \cdot S_z} \right) \cdot \frac{180}{\pi} \right)$$

Figure 2- Alignment of the tri-axial sensors with respect to the animal carrying the tag and summarized description of how tag pitch and roll is calculated from the 'static' acceleration (the acceleration component due to gravity). Note that the x and y refer to the acceleration axes shown in the stylized animal drawings.

Derivation of animal heading

The details of the derivation of the animal heading are given by Bidder *et al.* (2015) and Walker et al. (2015). In short, the animal pitch and roll angles are used to interpret the normalized (Fig. 1) magnetometry data. Specifically, the heading angle is determined by using the *atan2* function in the relevant two axes of the normalised magnetometer data and this is then converted to radians (Fig. 3).



Heading (H)

$$atan2(y,x) = 2arctan\frac{y}{\sqrt{x^2 + y^2 + x}}$$

$$RNm_i = Nm_i \cdot R_x(\gamma) \cdot R_y(\beta)$$

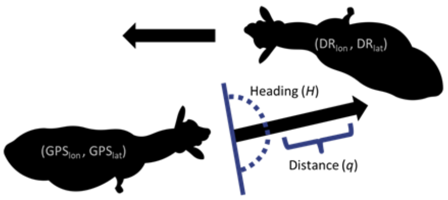
$$R_i(\gamma) = modified\ pitch\ and\ roll\ angle\ using\ matrices$$

$$H = \big(atan2(RNm_{y.} - RNm_x)\big) \cdot \frac{180}{\pi}$$

Figure 3 – Calculation of animal heading involves the integration of the pitch and roll data (x and y) with corresponding axes in the normalized magnetometer readings (N and m terms).

Distance travelled

Bidder et al. (2012) provides evidence that the Vectorial sum of the Dynamic Acceleration (VeDBA) (see Qasem et al. 2012) scales linearly with travel speed in terrestrial animals. VeDBA is calculated by deriving the dynamic acceleration for each axis by taking the static (smoothed) acceleration away from the raw acceleration before the 3 axes are added vectorially (Wilson et al. 2019) (Fig. 4).



Distance (q)

$$Dynamic\ acc.(DA_i) = Acc_i - S_i$$

$$VeDBA = \sqrt{(DA_x^2 + DA_y^2 + DA_z^2)}$$

$$Speed\ (s) = (VeDBA \cdot m) + c$$

m=coefficient to express how VeDBA interacts with true speed

$$Distance(d) = t \cdot s$$

t= time recorded by internal clock of logger

$$Distance\ with\ curvature\ of\ earth(q) = \frac{d}{R}$$

R=Radius of earth (6.371 x 10 ^{6}m)

Figure 4 – The distance travelled by an animal has been found to be accessible by using VeDBA as a proxy for speed (Bidder et al. 2015). To calculate VeDBA, the dynamic acceleration from each acceleration channel (which is the raw acceleration minus the smoothed – see Fig. 2) is added, vectorially, to the dynamic acceleration values from the other two channels. The speed versus VeDBA relationship is linear, with a non-zero VeDBA threshold intercept at a speed of 0. The distance travelled is simply the calculated speed multiplied by the time spent travelling at that speed.

The linear relationship between true speed and VeDBA is described by a gradient and intercept, which vary according to species and, to some extent, terrain (Bidder et al. 2012, Qasem et al. 2012). The values of these parameters can be found for some species in the literature or calculated using the GPS points: Here, time-defined GPS points are superimposed on the equivalent (again time-defined) dead-reckoned points and the gradient and intercept values in the VeDBA *versus* speeds relationship changed iteratively until the distance (and angle – because the tag might not be placed perfectly aligned with the longitudinal axis of the animal's body) between the two points is minimised. Corrected dead-reckoned points can then be converted to GPS-type co-ordinates (Fig. 5).

Converting to GPS coordinates

$$DR_{lat} = a\sin(\sin GPS_{lat} \cdot \cos q + \cos GPS_{lat} \cdot \sin q \cdot \cos H)$$

$$DR_{lon} = GPS_{lon} + atan2\big((\sin H \cdot \sin q \cdot \cos GPS_{lon}), (\cos q - \sin GPS_{lat} \cdot \sin DR_{lat})\big)$$

Figure 5 – The dead-reckoned data, which in the initial steps consists of distances in metres and heading in degrees, are positioned so that they best accord to infrequent GPS-fixes, which follow a standard co-ordinate system. The approach then has to convert all data to a standard geographic co-ordinate format.

After GPS correction has taken place any speed estimates derived from the path, will have a strong relationship with VeDBA with key alterations made by extending or limiting the path length based on GPS locations (Bidder et al., 2015). This helps to account for distribution within the linear relationship between VeDBA and true speed caused by differences in walking gait, across individuals, on substrate and superstrate (Bidder et al., 2012). This correction makes VeDBA and true speed estimates independent of one another.

Four approaches to defining travelling behaviour for dead-reckoning

The precise way in which speed is derived is critical for the viability and accuracy of the dead-reckoning approach (Bidder et al. 2015). The two central issues in this regard, are to decide precisely <u>when</u> an animal is travelling and <u>how fast</u> it is travelling. I used four different rules to deal with these issues and examined their potential for error by dead-reckoning the movements of four ungulate species (Table 1). For this, I extracted randomly selected data from each individual of the four species and dead-reckoned paths for; a single 14h stretch for each individual of both the domestic cows and goats, for the mouflon over 16 h and over 24 h for each individual ibex (periods chosen to reflect different GPS fix frequencies (Table 1). I illustrate the approach I took by highlighting data from a goat from a start point (GPS-determined) to a point 14 h later (also determined by GPS). With this animal, as with all the animals within this chapter (Table 1), the iterative correction described above, which would usually be used to correct the VeDBA/speed relationship between all GPS points, was only applied to every other GPS point gathered between the start and end points of the periods used for analysis (Table 1). As a result, the positions calculated by the dead-reckoning procedure coincided exactly with the GPS positions for half the GPS fixes, deviating in the other GPS points by an extent that was dependent on the validity of the rules used to define travelling behaviour (see below) and the extent to which the parameters defining the relationship between VeDBA and speed (Fig. 4) held true.

The four different rules used to define true travelling (travelling detection criteria – TDC) were; (i) no VeDBA threshold (ii) VeDBA threshold (iii) definition of steps and (iv) implementation of movement modes.

(i*) No VeDBA threshold*

Although VeDBA has been found to be a good proxy for speed, (Bidder et al. 2012, 2015) VeDBA signals are also produced when animals move their bodies without travelling, such as when they shake themselves (Shepard et al. 2008). Clearly, conversion of the VeDBA values during such periods into speed and therefore travel is wrong and leads to erroneous movement patterns. Despite this, many dead-reckoning studies do not state that the speed of the study animal (e.g. by using a VeDBA/speed relationship) has been filtered for any acceleration data that might indicate that the animal is not actually travelling (Mitani et al. 2003, Shiomi et al. 2008, Jiménez et al. 2009, Wensveen et al. 2015). In order to address the effect of not filtering non-travel-produced VeDBA, my start position was to dead-reckon between GPS points assuming a linear relationship between VeDBA and speed (cf. Fig. 4) with an intercept that goes through zero for both parameters (Fig. 6a).

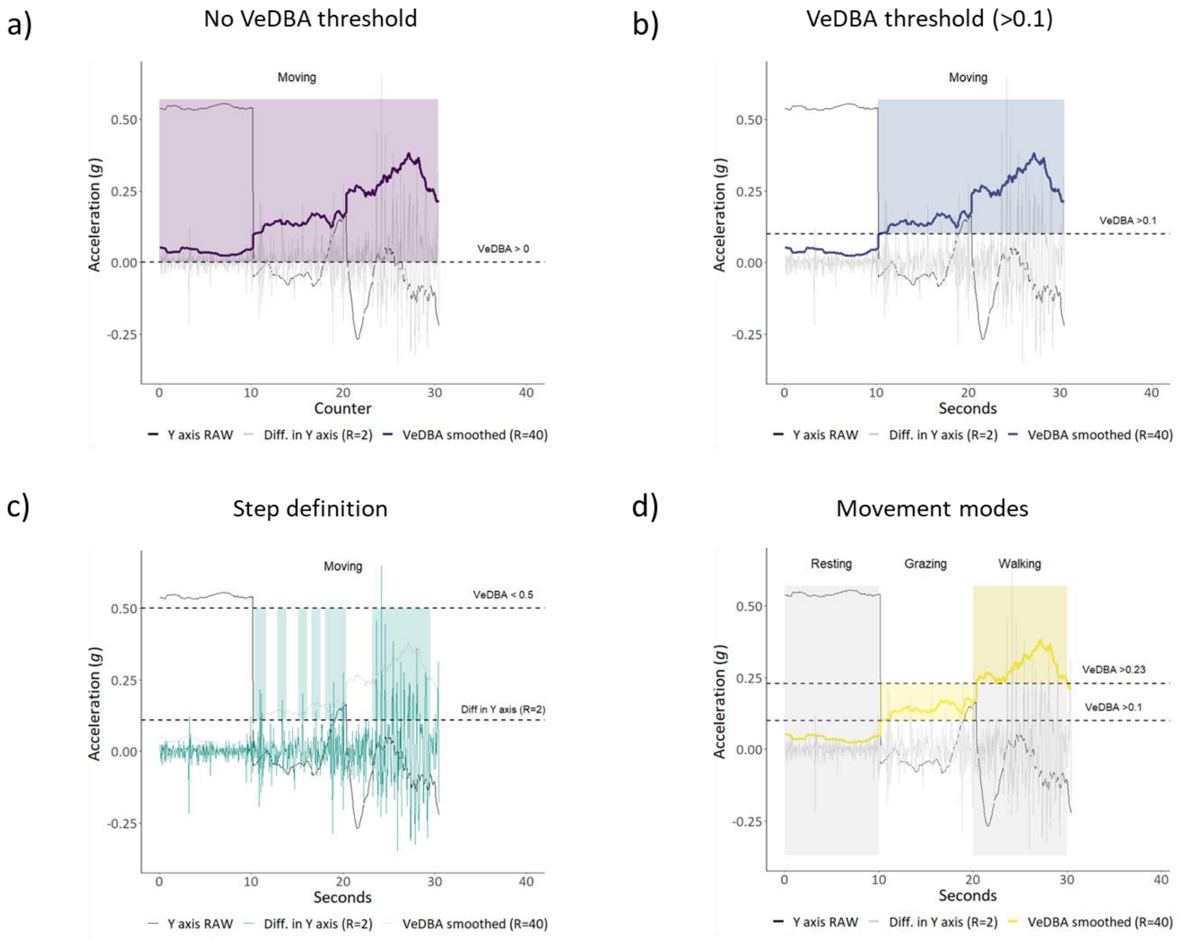


Figure 6 – Derivation of movement versus non-movement rules for ungulates equipped with collar-mounted DD tags. Graphs are of select acceleration channels (recorded at 20 Hz) over time for one dataset from a domestic goat tagged in August 2017 within the Bauges, France, illustrating the different approaches used to filter the data before being used in the dead-reckoning procedure. In all cases, the raw y-axis data is shown as well as the same data smoothed (over 0.1 s), the differential of the y axis across 0.1 seconds and the VeDBA, smoothed over 2 s. (a) shows when travelling was inferred (purple box) based on any value of VeDBA > 0.0, (b) shows when travelling was inferred (blue box) for any time that the VeDBA exceeded a threshold of 0.1 g. (c) shows travelling (green bars) based on a Boolean algorithm that interrogated acceleration data to determine when steps had taken place and (d) shows inferred travelling based on VeDBA thresholds to define behavioural states (resting, grazing and walking).

(ii) VeDBA threshold

The VeDBA threshold method (Walker et al. 2015) assumes that low-value VeDBA estimates occur when animals are not travelling. Thus, to identify travelling, I implemented a rule that ensured that no dead-reckoning was undertaken unless until the VeDBA values exceeded a defined amount (>0.1 *g* in the example in Fig. 6b). This threshold value is presumed to vary between species and biologger setup so travelling behaviour should be ground-truthed with observations when possible. In the case of my animals, I defined this threshold by observation of the domestic animals and comparing travelling behaviour with VeDBA. For the wild animals, I compared their raw acceleration data to those of the domestic animals and set the threshold to occur at a VeDBA value that was marginally lower than the lowest VeDBA associated with acceleration signals that indicated footfalls (see below).

(iii) Definition of steps

One of the most obvious delineators of travelling behaviour should be the identification of steps (or strides), assuming they can be defined within the tag data. I used a particular form of analysis based on a Boolean approach as suggested by Wilson et al. (Wilson et al. 2018), the Lowest Common Denominator (LoCoD) approach, which can be used to define individual steps within an animal’s movement. This approach looks for specific changes and defined patterns in e.g. acceleration signals, that occur during movement, that are predictable with each step, and which only occur during travelling behaviour. In my use of the LoCoD approach, I attempted to quantify the presence of steps (Fig. 6c) so that the VeDBA/speed relationship could be applied to dead-reckon at any time when steps were identified. To implement this, I synchronised video observations/recordings of tagged goat and cow movement with their respective DD data to define the sensor-dependent features of steps. Following this, I produced an algorithm within the DDMT software (Wildbyte Technologies 2020) which implements the LoCoD method, that searched for steps within any prescribed ungulate data (see Wilson *et al*. 2018 for more detail). For the specific example of the goat, I calculated a difference in the accelerometer y-axis readings (the rate of change of acceleration or jerk) across 2 data points (0.1 seconds, as acceleration was recorded at 20 Hz). The step was marked as such when the jerk was > 0.11 *g* and VeDBA smoothed (across 40 events/2 seconds) was less than 0.5 *g*. Each marked step was then extended by half a second either side assuming each step would take at least a half second to carry out, which also allows the algorithm to link steps within continuous travelling behaviour. The equations used for the other species, which were grounded in observations for the cows but using the similar distinctive patterns in steps in the wild species, can be found in the appendix (see appendix, Table 2).

(iv) Movement modes

The LoCoD method (Wilson et al. 2018) was also used to identify three general behaviours, two of which typify ungulate movement (the third being resting) (Fig. 6d): VeDBA smoothed (across 40 events/2 seconds) windows were used to define the behaviours when animals were ‘resting’ (where VeDBA smoothed for goats was < 0.1 *g*), ‘grazing’ (VeDBA smoothed > 0.1 *g*) and ‘walking’ (VeDBA smoothed <0.23 *g*) (cf. chapter 4). Cross-checks with observations (see appendix, table 7) showed that this basic approach successfully identified the behaviour on a second by second basis and matched the observed behaviours >80% of the time (see chapter 4 for the goat example) (see appendix , Table 2 for behaviour definition rules). Each behaviour or movement mode was then allocated with a different speed coefficient (the gradient of the relationship between VeDBA and speed (Fig. 4) - see below for details) to calculate the distance travelled (Fig. 4). These speed coefficients were initially determined by finding data that corresponded to animal travel (both grazing or walking) that had occurred continuously between two adjacent GPS-defined points so that the correct gradients could be determined *via* iteration (see above). This same approach was used in the domestic cows and attempted in the two wild ungulate species by examination of the acceleration data and comparing them to the domestic species. During the iterative procedure when the dead-reckoned path was being fitted to the GPS points, the (different) gradient coefficients for grazing and walking, respectively, were changed in tandem, but maintaining the same ratio to each other.

GPS cleaning

GPS locations can be notoriously inaccurate under certain conditions (Cagnacci et al. 2010), one of which is mountainous terrain because the topography shields access to satellites (Rutter et al. 1997, Gamo et al. 2000, Ungar et al. 2005). To correct for such problems, GPS screening was used to clean the raw GPS data (Bjørneraas et al. 2010). Here, outliers from median speed and acute angles in movement, manifest as departures from an otherwise regular trajectory and taking the form of spikes (cf. Gunner *et al.*, in 2021), were filtered from the GPS locations. R-studio was used to carry out the GPS cleaning (RStudio Team 2020).

Errors in dead-reckoned vs GPS positions and animal travel speed

The distance between the locations of the dead-reckoned paths (for each of the 4 rules used to identify travelling for the 4 ungulates) and their time-synchronized GPS positions was calculated using the following equation:

$$Distance = a\cos(\sin Lat_{DR} \cdot \sin Lat_{GPS} + \cos Lat_{DR} \cdot \cos Lat_{GPS} \cdot \cos(Lon_{GPS} - Lon_{DR})) \cdot 6371$$

This calculation was carried out using the package 'fossil' within R-studio. The same package was used to calculate animal travel speed.

Statistically comparing travelling detection criteria

I used linear mixed models, fitted using the lme4 package in R (R Core Team, 2019), to test for differences between TDC methods in average error. I accounted also for differences between species and compared models with and without an interaction between species and TDC method. To obtain the *p*-values I used the lmerTest package, which applies a Satterthwaite's degrees of freedom method.

Results

The dead-reckoned tracks using the four different travelling detection criteria (TDC) overall showed broadly similar patterns in movements over the 14 h, as the path was brought back to the GPS positions each time, but within this broad pattern there were clear distinct differences in the reconstructed fine-scale path (Fig. 7). The most obvious differences were between the ‘no-threshold VeDBA’ travelling criterion and the other three travelling criteria. For example, in my illustration of the process with a single goat (Fig. 7), the no VeDBA threshold method showed no extensive southwest deviation in the path taken towards the beginning of the track, whereas the final part of the path was rather similar in all cases.

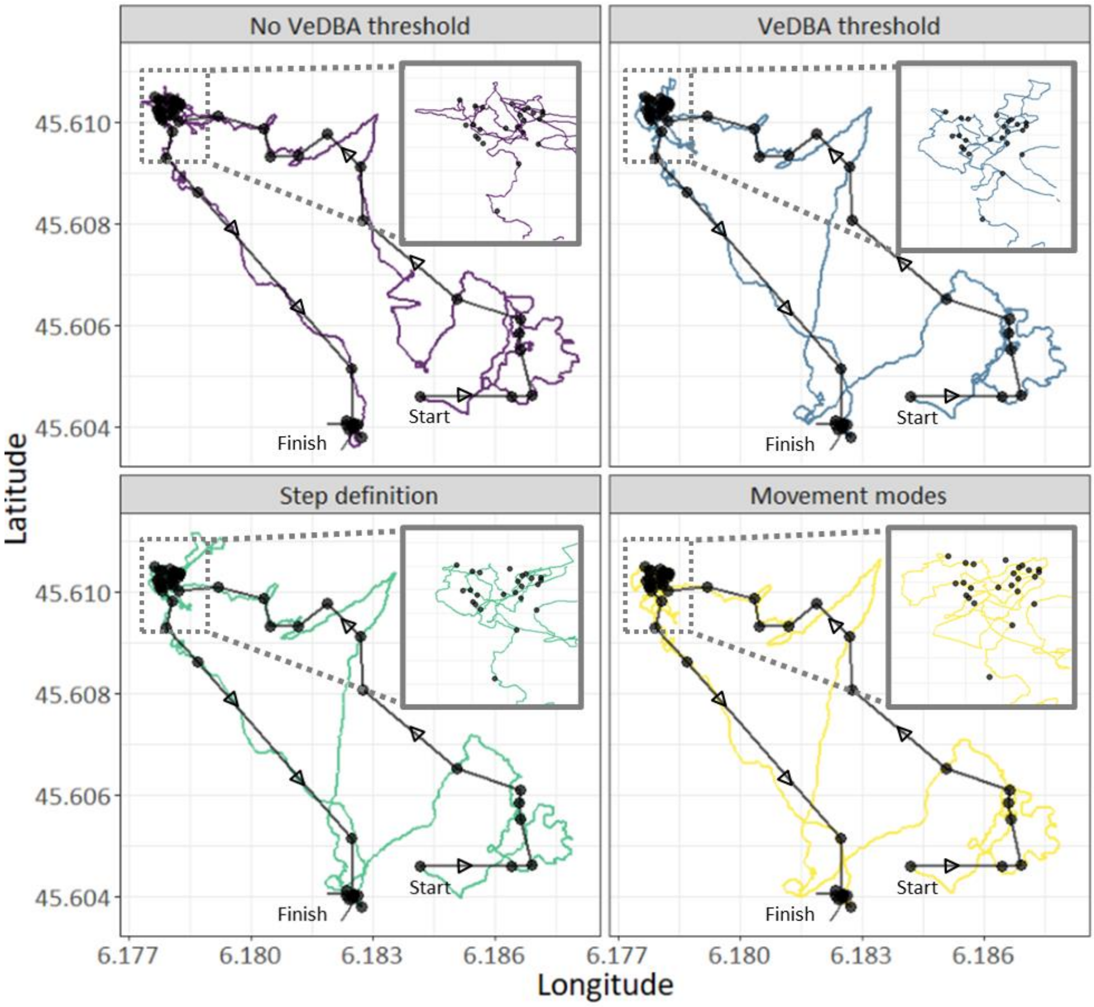


Figure 7 – An example of how the movements of terrestrial animals can be elucidated using GPS-corrected dead-reckoning. The figure shows the movements of a domestic goat tagged in August 2017 within les Bauges, France, over 14 h as determined using GPS fixes at 15 min intervals (black dots joined by black lines and arrowed to show direction). The dead-reckoned path was interpolated between every other one of these points (i.e. for GPS fixes separated by 15 mins) according to one of four travelling-discerning criteria (see methods). The grey dashed boxes in the top left-hand corner show areas which have been magnified to highlight differences in finely resolved tracks.

The coherence between any of the four different TDC methods was less obvious when very fine-scale movements were considered (see insets in Fig. 7) although, again, the similarities were most apparent between the 'VeDBA threshold', the 'step definition' and the 'movement mode' approaches.

By allowing the dead-reckoning process to superimpose dead-reckoned tracks with GPS fixes for every other GPS fix, I was able to examine the extent to which the dead-reckoning process drifted away from the 'true' position over even short time scales (assumed here to be the GPS fixes – but see discussion) for the positions where the dead-reckoned track and the GPS fixes were not aligned. This can be illustrated by a cumulative error plot where the cumulative error in dead-reckoning compared to GPS fixes is plotted over time (Fig. 8). This plot shows pairs of points where the error does not accumulate, corresponding to where the GPS fixes and dead-reckoned points are aligned *via* the iterative error-correction process outlined in the methods, alternating with pairs of points where the GPS and dead-reckoning process are not aligned, and the two paths can diverge.

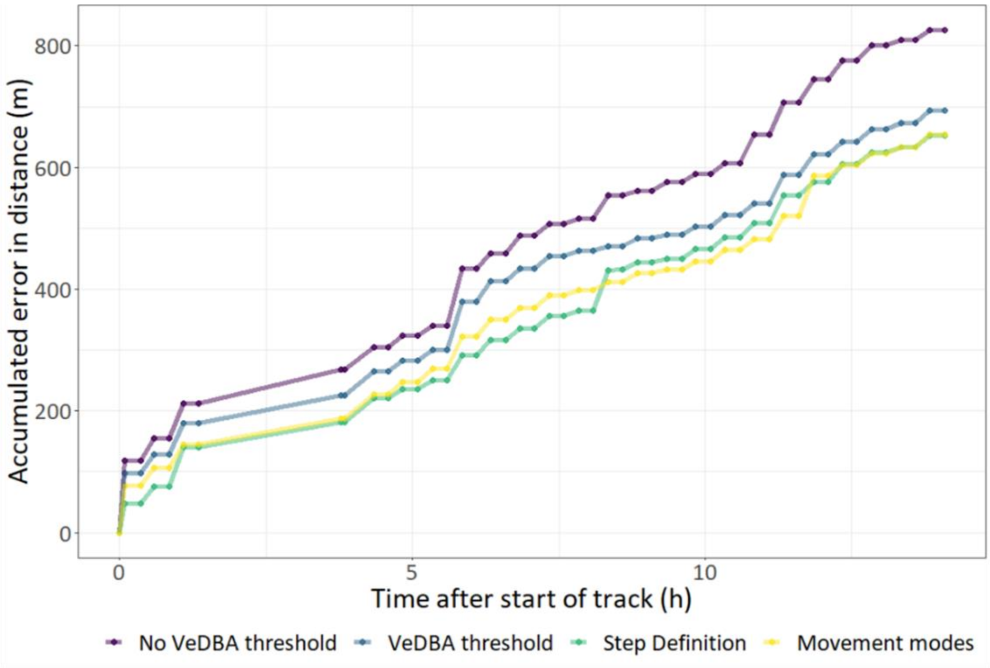


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Figure 8 – Graph showing the extent of deviation between GPS- and dead-reckoned fixes across time in GPS-corrected dead-reckoning procedures (using 14 hours from a domestic goat tagged in August 2017 in the Bauges,

France) with travelling specified according to one of four criteria (see text). Here, the GPS and dead-reckoned paths were superimposed at every other GPS fix so that the accumulating error jumps in the y-axis at every other point (see text).

The 'No VeDBA threshold' method has the highest location error rate across all study species (by between 14 and 41%) than those of the other TDCs, a lower movement speed by between 12% to 29%), and longer total paths, by 5% to 26% (Table 2). Using 'No VeDBA threshold' lead to significantly larger errors (*t*-value = 2.168, *p*-value = 0.030), whereas the estimated average error was essentially the same for the other methods. There was also no significant difference between species in the effect of TDC methods on average error (i.e. no support for an interaction). Conversely, average error was larger for ibex (*t*-value = 3.369, *p*-value = 0.0028). There was also no significant difference between species in the effect of TDC methods on average error. Conversely, the characteristics of the movement path are very similar among the three dead-reckoned tracks with a travelling detection criterion, total path length was significantly larger for 'No VeDBA threshold' (*t-value* = 4.449, *p-value* <0.001), with no difference among the other 3 TDC paths. Speed output, was found to be markedly and significantly quicker for 'Step definition', whereas significantly slower than the others for 'No VeDBA threshold' (when compared to 'Movement modes', No VeDBA threshold: *t-value* = -9.044, *p*-value <0.001, Step definition: *t-value* = 11.392, *p*-value <0.001, VeDBA threshold: *t-value* = -3.687, *p*-value <0.001).

Table 2 - Mean error in concurrence between GPS fixes and dead-reckoned fixes for alternate non-aligned fixes (see text) for each of the travelling detection criteria used across all species. The distance between each non-aligned GPS and dead-reckoned step was also used to give speed and path distance.

Species	*Travelling detection criterion*	*Mean error for alternate GPS correction (m)*	*Total path length (m)*	*Average speed (when moving)* ms^{-1}
Domestic goat	No VeDBA threshold	35.02	7871.46	0.15
	VeDBA threshold	25.11	6610.78	0.25

	Step definition	24.79	6324.45	0.41
	Movement modes	25.21	6496.72	0.28
Domestic cow	No VeDBA threshold	17.19	4763.68	0.09
	VeDBA threshold	15.13	4603.69	0.13
	Step definition	15.23	4512.52	0.26
	Movement modes	14.84	4609.09	0.18
Ibex	No VeDBA threshold	117.68	11541.79	0.13
	VeDBA threshold	90.11	9799.96	0.15
	Step definition	83.75	9487.26	0.34
	Movement modes	83.28	9128.69	0.20
Mouflon	No VeDBA threshold	31.30	5330.68	0.08
	VeDBA threshold	21.05	4684.95	0.10
	Step definition	23.21	5231.31	0.26
	Movement modes	21.90	4610.04	0.14

Discussion

Integration of dead-reckoning with GPS

This work clearly shows the value of dead-reckoning as a method for providing information about the movement paths of animals between GPS fixes, elucidating remarkable detail in the minute by minute movements of the animals, even when GPS fixes were only available every two hours. The frequency of verified locations, which need not take just the form of GPS fixes (Gunner et al. 2021), is clearly important for maintaining a good approximation of how the animals relate to environmental space (as e.g. determined by vegetation surveys (Fischer and Wipf 2002, Mancilla-Leytón et al. 2013, Oksanen et al. 2015), topography etc. (Dailey and Hobbs 1989, Wall et al. 2006, Dunford et al. 2020)). However, I also note that the forms of the paths taken by animals themselves (tortuosity (Nams 2014, Ihwagi et al. 2019), speed (Pyke 1981, Wilson et al. 2015), step lengths (Hildebrand and Hurley 1985), turn angles (Wilson, Griffiths, et al. 2013, Wilson, Mills, et al. 2013) etc.) are important for understanding a suite of animal movement issues, such as species diffusion (Hein et al. 2012), food location strategies (Kacelnik and Houston 1984, Wilson et al. 2012) and vigilance (Vasquez 2002, Lashley et al. 2014), thus, accurately reconstructing the movement path is of paramount importance.

An important point about the utility of GPS-enabled dead-reckoning, is that it allows animal movement to be studied in fine detail and over much longer periods than by conventional GPS alone because system power requirements are considerably lower (Holton et al. in press). Specifically, calculation of GPS fixes typically draws a current of 30-50 mA over several seconds (Bidder et al. 2015, Dewhirst et al. 2016) whereas DDs, such as used in this study, use *ca*. 1.3 mA. The consequence of this is that GPS systems alone require batteries that have a capacity that is around 30 times higher than dead-reckoning systems if they are to be used virtually continuously in a comparable manner. Since battery capacity is directly related to battery volume and mass (Kay et al. 2019, Williams et al. 2020), this translates to study animals having to carry disproportionately large tags, with all the ethics consequences that these engender (Vandenabeele et al. 2015, Williams et al. 2020). For my studies on alpine ungulates, which were conceived to cover many months of tracking, this equates to prohibitively large packages if the space use were to be determined using GPS alone.

Within the context of this thesis, absolute resolution of animal position in space is important though, thus it is relevant that the errors in dead-reckoning be considered. My process does assume, however, that the GPS locations were perfectly correct, and the fact that I had to remove erroneous points because the speed or the position were impossible, makes this obviously untrue. So, although I assume that all system errors were due to the dead-reckoning processes, GPS inaccuracy should be borne in mind. In fact, dead-reckoned tracks and GPS fixes taken with low temporal resolution are complimentary because they both allow determination of position but suffer from quite different errors (see de Weerd et al. 2015 and Gamo et al. 2000 for discussion). More in-depth work could consider the extent to which GPS and dead-reckoning should be given different weightings according to conditions (including the frequency of GPS fixes); for example, di Virgilio et al. (2018) use a Bayesian approach to include also GPS error into account in dead-reckoning. In a pragmatic and general sense for the moment though, I note that for GPS-enabled dead-reckoning, authors recommend one GPS fix every two hours or less, depending on the activity of the species tagged and quality of data (Bidder et al. 2015, Dewhirst et al. 2016) and I have worked within these limits.

Travel detection criteria

A key aim was to evaluate more biologically realistic specific criteria that could be used to determine when animals were travelling (rather than just moving their bodies without travelling), in order to improve the application of dead-reckoning – in particular avoiding that the algorithm makes the trajectory move when in reality the animal was moving some part of the body but was not moving the body across space. The results clearly indicate that even over very short overall times scales (< 24h) and also very short specific time scales (2-4 hours), a non-negligible and detectable error accumulated (Table 2), and that any type of TDC should be employed, as opposed to use dead-reckoning without a form of TDC, in order also to avoid obtaining movement paths with misleading characteristics (total distance moved, speed, etc. – Table 2). Furthermore, whilst the difference is smaller, the biologically more realistic TDCs, based on step or movement mode identification, consistently outperformed fixed VeDBA - threshold rules. Interestingly, movement paths reconstructed using the step-based TDC, i.e. where the path is dead-reckoned only when a clear step was identified in the accelerometer signal, lead to movement paths with the faster average movement speed between locations (Table 2). This suggests that this criterion may be the most biologically realistic, being better able to identify the instances when the animal was truly moving. This is intuitive since there are clearly occasions when animals produce a VeDBA signal but are not moving. Examples would be shaking or inter-animal interactions without travel (Gregorini et al. 2006, Pipia et al. 2008, Aublet et al. 2009). The ‘no VeDBA threshold’ would incorporate these into the travel, which is obviously erroneous, not least because it would tend to underestimate travelling speed (Gregorini et al. 2006, Manning et al. 2014, Biancardi and Minetti 2017, Moseby et al. 2020) as well as produce parts of the pathway that never existed.

Thus, in an attempt to define a single approach that could be used within this thesis as standard, I chose the ‘movement modes’ approach which, across species, had either the lowest rate of error or close to it. This gave error rates of between about 16 and 44 m/h (see appendix, Figure 1, Table 3 for further details). This option is advantageous in that it does not have the complexities of defining single steps (which may be particularly challenging for species that cannot be observed) and is not as simplistic as having just a VeDBA threshold, which may be expected to vary more in different habitats than the movement modes approach. Separating behaviours into essentially three phases (stationary, grazing and travelling), where the two travelling modes may have different gradient coefficients, may also account to some extent for gait changes that may occur between grazing and travelling. This may be appropriate because it has already been noted that the relationship between VeDBA and speed changes with gait (Chapinal et al. 2009, Bidder et al. 2012, Dickinson et al. subm.). Ultimately though, any of the three TDCs that incorporated a more sophisticated travel would seem to produce excellent path resolution (Tables 2 & 3) with errors of less than 0.5 m/min.

The general value of the TDCs within the GPS-enabled dead-reckoning approach is exemplified in Fig. 7, which shows a large deviation from the GPS-defined track just after the start of the monitored period (Fig. 7), where the animal moved some distance in a south-westerly direction before reversing its direction of travel (evident in all TDC except the ‘No VeDBA threshold’) to almost join its previous position. Activity based on GPS position alone would have concluded, at this time, that the animal moved very little whereas it was, in fact, particularly active. The dead-reckoning approach therefore obviously provides a great deal of information beyond just position, mostly particularly speed (Table 2), something that is hard to define except in a rather vague sense, for GPS positions spaced in time.

Although this study focussed only on short time scales, it highlights the value of terrestrial dead-reckoning for elucidating the movement paths of ungulates, even in a topographically variable environment. Not only is GPS-corrected VeDBA a useful metric for defining travel speed, and thereby relating to distance travelled, but the linear relationship between speed and VeDBA seems extraordinarily robust given the instability of collar-mounted tags. Consideration of rules that define when, precisely, animals are travelling is important though, and I recommend that researchers give this proper consideration in future attempts to verified position-corrected dead-reckoning in terrestrial animals.

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Chapter 4

Move. Eat. Rest. Repeat: *Habitat preferences and space-use of a herd of domestic goats (Capra aegagrus hircus) in the French Alps*

Abstract

Elucidation of the space-use and habitats selected for grazing by free-roaming domestic ungulates can help farmers manage the ecological impact of their livestock and enhance animal welfare. This study utilised high frequency, continuously logging accelerometers and magnetometers combined with infrequent GPS location data collected on free-roaming domestic goats (*Capra aegagrus hircus*) within a region of the French Alps with summer alpine pastures. First, tagged goats were observed during grazing, travelling and resting and, by pairing observations with accelerometer signals, algorithms based on a Boolean approach were produced to define the behaviours. This method resulted in an efficient behavioural definition with an ≥ 85% accuracy rate (85% grazing; 87% moving; 100% resting), providing information on behaviour for every second of data. A range of data collected (5 to 25 days) across ten individuals was then used to define when and where the goats were grazing. Dead-reckoning was used to reconstruct high-resolution 1Hz movement maps, which combined with the behaviour identification procedures allowed to map movements and behaviour across the study area and for all available habitats. Goats adopted a central place foraging strategy because they were trained to come back to the farm pen periodically, where cover and salt licks were provided and goats were milked. Outside the pen, which they could leave freely, movements were not restricted within their foraging range. Goats tended to graze on the most abundant habitats but avoided forested areas and showed a preference for rocky habitats (e.g. scree), grasses (e.g. alpine lawns, semi-arid lawns) and grazing herb formations. The area covered during grazing increased approximately logarithmically with both time and the number of individuals, giving a crude estimate of 1.1 km^2 space used over 25 days for a herd of 10 individuals. The work and results show how loggers can be used to identify and record very fine behaviour and movement data, used to examine the impact of livestock

during free-roaming grazing while defining the space and habitats needed for domestic species. The behavioural identification rules are based on explicit algorithms which can easily be applied to other studies, including wild species.

Introduction

Grazing impacts by domestic livestock are now topical (Dong et al. 2020, Nota et al. 2020), not least because of the detriment to the environment, such as reducing biodiversity (Fischer et al. 2008, Ravetto Enri et al. 2017). Specifically, over-grazing changes the recruitment of vegetation by driving out species vulnerable to grazing impacts while allowing species adapted to this pressure to flourish (Mayer and Erschbamer 2011). Grazing also leads to soil becoming compacted, decreasing the soil quality and discouraging vegetation growth in excessively grazed areas (Vidal et al. 2020). Cessation of livestock grazing does not always seem to be the solution for this though, with studies in the Alps showing how the absence of grazing amongst the highlands allows for the invasion of less desirable shrubs and subsequent reforestation (Sturaro et al. 2013, Probo et al. 2014). This, in turn, causes habitat loss for valuable semi-natural vegetation communities (Marini et al. 2009). Thus, grazing by livestock can be an effective approach for managing and conserving grasslands and the associated wildlife (Watkinson & Ormerod 2001, Kotsonas et al. 2021)

Although pastures within the higher altitudes of the Alps have been formed over thousands of years of livestock grazing, the last 50 years has seen grazing meadows abandoned as the practice becomes economically marginal (Fleury and Gibon 2000, García-Martínez and Bernués 2009, Bernués et al. 2011). This shift in grazing impact has resulted in lower species richness, triggering initiatives seeking to protect the pastures, with *Nardus*-based pastures being recognised as being of particular conservation interest (Kurtogullari et al. 2020) due to the high productivity and connectivity of this habitat (Parolo et al. 2011). In addition, the reduction of summer grazing high up the mountain slopes puts more grazing pressure on the lowlands all year round, resulting in altitudinal over-grazing (Sturaro et al. 2013).

It has been suggested that strategies to protect the valuable alpine environment should balance grazing pressure with space over time. However, this approach requires detailed information on precisely how livestock exploit the landscape in time and space (Bernués et al. 2011, Sturaro et al. 2013, Probo et al. 2014), a non-trivial undertaking, especially with the more mobile livestock. To this end, quantifying in fine detail variation in space use and habitat selection is of paramount importance. In fact, a number of studies have looked at the spatio-temporal variation in grazing of cows (Probo et al. 2014, Pittarello et al. 2016) and sheep (Pittarello et al. 2017, Ravetto Enri et al. 2019) within the Alps. Against this, although previous work in the Alps has sought to identify vegetation selection and daily movement patterns of goats using simple location data (Iussig et al. 2015), the scales over which this, and other, studies can provide information depends on the frequency of location fixes – and if these locations are frequently taken (> 1 fix per minute) the logging period is typically short (Moreau et al. 2009, Pittarello et al. 2017). Thus, combining location data with accelerometer-based behaviour identification provides exciting potential for conservation grazing and precise livestock farming (Moreau et al. 2009, di Virgilio et al. 2018).

There is however, potential for this to change as biologgers, animal-attached recording tags, become smaller, more powerful and more accessible (Holton *et al*. in press), providing exciting new possibilities for research and management (Williams et al. 2020). Indeed, tri-axial accelerometers recording at tens of Hz are now regularly used to quantify behaviours in both wild animals (Wilson et al. 2008, Brownscombe et al. 2014, Fehlmann et al. 2017) and domestic livestock (Martiskainen et al. 2009, Moreau et al. 2009, Lush et al. 2018) and acceleration metrics in tandem with magnetometer data are also now being used to dead-reckon the paths of wild (Bidder et al. 2015, Dewhirst et al. 2016) and farmed animals (di Virgilio et al. 2018) to give detailed movements of species where GPS data are sparse (Wilson et al. 1991, Shiomi et al. 2008, Wensveen et al. 2015). A prime value in such biologger data is that it is cost-effective and allows unbiased data to be collected (Canine 1990, Rutz and Hays 2009) for long continuous periods (months) (Preston et al. 2010, Mckinnon and Love 2018), including at times when the study subject cannot be seen (Brown et al. 2013) for example during night or within mountainous or heavily vegetated environments (Gamo et al. 2000, Camp et al. 2016).

In this study, I used biologgers on domestic goats *(Capra aegagrus hircus)* to examine their movement and grazing patterns in an extensive alpine pasture in France. I aimed to determine goat habitat- and vegetation preferences by; (i) determining their movements with unprecedented 1 second resolution by using GPS-enabled dead-reckoning, (ii) quantifying the three major behaviours found in ungulates (resting, grazing and moving (Festa-Bianchet et al. 2008, Martiskainen et al. 2009, Moreau et al. 2009)) using a Boolean approach based on the Lowest Common Denominator method (Wilson et al. 2018) before (iii) marrying the marked behaviours to the locations calculated in to map out grazing and understand space use associated with the behaviour, and finally (iv) conduct a resource selection analysis to unveil habitats that are avoided or selected by the goats to suggest vegetation that is selected when grazing and map and quantify the area grazed over time by herds of goats.

This approach is an important step to understanding habitat and space use by goats in the Alps that should contribute to informing management plans seeking to optimize both habitat conservation and economic benefits.

Methods

Study Site

The study was conducted in 2017. The site chosen was a pasture valley within the Bauges Massif, a game and wildlife national reserve situated in the French pre-Alps (Fig. 1). The valley is made up of mostly limestone rock types, which dictate the vegetation, resulting in mostly calcareous alpine grassland and coniferous forests (Mathieu et al. 2009, UNESCO 2015). Bare rock and scree become more prevalent higher up the side of the valley as the topography becomes steeper.

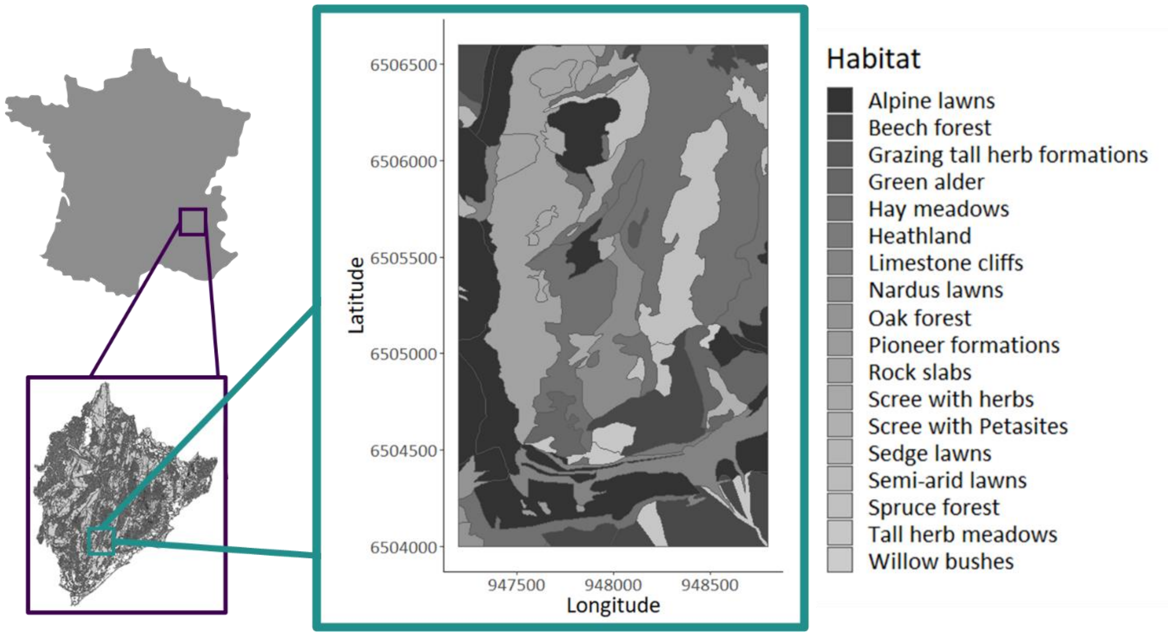

Figure 1 – Map of the massif in relation to France and the study site in relation to the massif with each habitat outlined and coloured by habitat.

All year round, the study site supports two wild ungulate species, chamois (*Rupicapra rupicapra*) and Mouflon (*Ovis gmelini musimon × Ovis sp.*). Between June and October, the valley is shared with grazing livestock; domestic dairy cows (*Bos taurus*) and domestic dairy goats (*Capra aegagrus hircus*). The goats used in this study came from a goat farm where the livestock were free to browse an area of 2 km^2 hectares within the valley (but importantly their movements were not restricted by fences and the goat farmer reported that a few individuals remained in the area after summer and survived the winter, in the years before my study).

The goat herd comprised 40 females and 1 male. Of these, I selected twenty females for data collection with an average weight of approximately 30 kg. The animals were milked most mornings and were kept in a pen overnight but were free to roam and leave the pen during the day and during nights.

Biologgers

The domestic goats were collared with lab-built collars (see chapter 2), using commercial soft nylon livestock collars, lead weights and the logging units (Daily Diary and GPS). A 100 g of lead was attached to the bottom of the collar to act as a counterweight to keep the biologger dorsally positioned to provide consistent acceleration signals and increase the chances of the highest quality GPS fixes.

The biologger featured a waterproof 3D-printed ABS plastic housing containing a GiPsy 5 GPS (TechnoSMart 2020), set to record a location every 15 minutes, and a "Daily Diary" (DD) multi-sensor biologging unit (Wilson et al. 2008, Wildbyte Technologies 2020), comprising tri-axial accelerometers and magnetometers and environmental sensors, each powered by a separate 1000 mAh lithium battery (see chapter 2). The Daily Diary unit was programmed to collect both acceleration and magnetic field intensity in three orthogonal axes, temperature, light and pressure at a range of sampling rates (Table 1). The DDs were covered in Guronic (te Connectivity 2020) to keep the devices waterproof, shock-proof and insulated. The device recorded the data onto a removable 2GB micro-SD card, sufficient to record data up to one month at 40 Hz. The total weight of the collar and tags was 240 g, staying within the ethical guidelines of 3% of the animals' body weight.

Table 1- A list of variables the Daily Diary (DD) collected with corresponding recording frequency, units of measurement and range.

Channel	*Recording frequency (Hz)*	*Measurement*
Accelerometer X axis Surge (Forward – Backward)	20	0 to 6 *g*
Accelerometer Y axis Sway (Side – Side)	20	0 to 6 *g*
Accelerometer Z axis Heave (Vertical)	20	0 to 6 *g*
Magnetometer axis 1	8	Max. of earth's magnetic field
Magnetometer axis 2	8	Max. of earth's magnetic field
Magnetometer axis 3	8	Max. of earth's magnetic field
Barometric pressure	2	100 to 2000 mbar

External Temperature	2	-20 to 60°C
Light	2	0 to 100 000 lux

Deployment

Before attaching the collars to the animals, the DDs were calibrated by engaging them in a defined set of movements, conceived to provide proper 3-dimensional coverage for the G- and M-spheres (Williams et al. 2017) – see also chapter 2. Collars were then attached in the morning when the goats were still within their pen. All individuals selected were docile and required little to no restraint. The ear tag number was taken from each individual and used as a corresponding study number. The attachment and tag recovery times were noted, with tag recovery also taking place in the morning after defined wearing periods. There were three deployments using a range of randomly selected individuals; two one-week deployments, where behavioural observations were undertaken, and a one month continuous deployment.

Behavioural observations

Behavioural observations were recorded using the *ab-libitum* focal sampling method (Altmann 1974) noting time carefully so that behaviours could be synchronised with acceleration data to ground-truth all behaviours.

Quantifying behaviours

The DD data was visualised using bespoke software Daily Diary Movement Trace (DDMT) (Wildbyte Technologies 2020). The software produces interpolated time-based plots to show how acceleration and other channels change over time at high resolution (in my case, 20 Hz). Time-stamped behavioural observations were imported into DDMT to visualise how behaviours appear in the accelerometery data. Based on this, Boolean-based rules using acceleration metrics were used as algorithms (Wilson et al. 2018) to search for and highlight behaviours within all data sets including times the individuals were unobserved. This Lowest Common Denominator (LoCoD) approach (Wilson et al. 2018) was chosen because this method was found to be particularly time-efficient, allowing many different rules for different behaviours to be tested across large data sets, and can be directly employed and used by other studies (e.g. as opposed to machine-learning based approaches). The single most appropriate metric to define grazing was vectoral dynamic body acceleration (VeDBA), calculated using;

$$VeDBA = \sqrt{(DBAX)^2 + (DBAY)^2 + (DBAZ)^2}$$

Where DBA is the dynamic acceleration in the three axes (X, Y and Z). The dynamic acceleration was calculated by subtracting static acceleration (the raw acceleration smoothed with a running mean over 2 seconds (Shepard et al. 2008) from the raw acceleration. A further running mean across 40 data points (or two seconds) was used to smooth VeDBA to reduce noise (Wilson et al. 2020) while producing more consistent waves (hereafter called sVeDBA).

Resting, grazing and moving behaviours were defined using simple sVeDBA thresholds and limits (Fig. 2). The classification rules identified the peak of sVeDBA wave during active behaviours (grazing, walking, other). Where behaviours apparently changed from one to another and back within a second, it was marked as the predominant behaviour either side of the change.

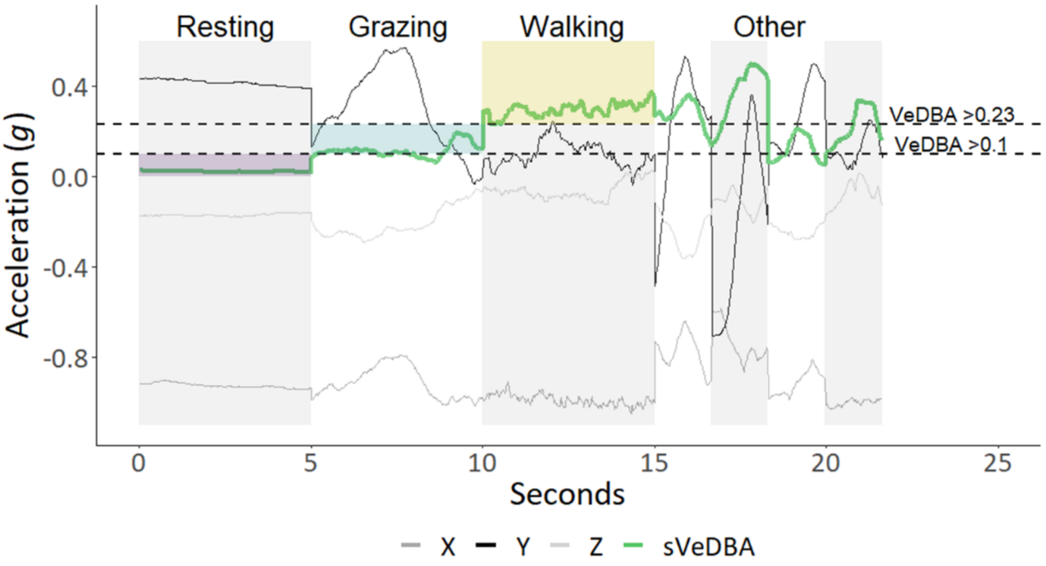

Figure 2- A plot of acceleration smoothed in all 3 axes and smoothed VeDBA *(sVeDBA) over 2 s showing how it changes over time as the goat changes behaviour. The thresholds used to define the three behaviours are shown using the dashed lines with the specifics of the conditions indicated. Other behaviours are flinching, head-clash, drinking and using salt lick in this order.*

GPS-corrected dead-reckoning

I dead-reckoned the movement paths of the goats using the magnetometry data in tandem with the accelerometers to derive heading (Bidder et al. 2015) and VeDBA as a proxy for speed (Bidder et al. 2012) to reconstruct fine-scale movements between GPS location fixes (see chapter 3). This produced a 1 Hz GPS corrected dead-reckoned path using DDMT (see also chapter 3). The GPS data used was cleaned using the GPS screening method of Bojorneaas et al. (Bjørneraas et al. 2010).

Mapping behaviours

The quantified behaviour was allocated a location from the 1 Hz dead-reckoned path by synchronising behaviour and location times. R (R Core Team, 2019) and R Studio (RStudio Team 2020) were used to map these behaviours with a combination of packages including ggmap, and ggplot2. Mapping data from Google Maps (Google 2020) and shape files were used to gain detailed information about space use and habitat type used by the goats. The shape files have areas of habitat represented by polygons that have an associated National Inventory of Natural Heritage (INPN) (Callou et al. 2011) habitat code with detailed description of that habitat and dominant vegetation (Table 2). This mapping data was supplied by Grenoble University and the National Hunting and Wildlife Agency (ONCFS) management team (Tronchot 2008).

Table 2 – A list of habitats found within the study site with dominant vegetation; habitat INPN code which links to the habitat description (link: https://inpn.mnhn.fr/); and study code used to abbreviate habitat for figures.

Habitat	*Dominant vegetation*	*Study code*	*INPN habitat code*
Alpine lawns	*Sesleria sp, Laserpitium siler and Carex sempervirens*	*AL*	*36.4311/ 36.4312*
Beech forest	*Fagus sp./Acer pseudoplatanus*	BF	41.133/ 41.15
Grazing tall herb formations	*Rumex alpinus, Senecio alpinus, Cirsium spinosissimum* and *Peucedanum ostruthium*	GTH	37.88
Green alder	*Alnetum viridis*	GA	31.611
Hay meadows	*Trisetum flavescens*	HM	38.3
Heathland	*Rhododendron ferrugineum*	H	31.42
Limestone cliffs	*Potentilla sp.*	LC	62.151
Nardus lawns	*Nardus stricta*	NL	36.311
Oak forest	*Quercus sp.*	OF	41.571
Pioneer formations	*Fraxinus excelsior*	PF	41.39
Rock slabs	None	RS	62.3
Scree with herbs	*Thlaspion rotundifolii*	SwH	61.22
Scree with petasites	*Petasites sp.*	SwP	61.231
Sedge lawns	*Carex ferruginea*	SL	36.412
Semi-arid lawns	*Brachypodium pinnatum*	SAL	34.323

Spruce forest	*Picea abies*	SF	42.215/42.2121
Tall herb meadows	*Adenostyles alliariae*	THM	37.81
Willow bushes	*Salix pentandra* and *S. appendiculata.*	WB	31.6213

To visualise the high resolution location data and to quantify the time spent per location, the "recurse" package was used to calculate and define 'revisits' by animals if locations on one day were within 10 metres of a site used on another day. This metric was used to colour points on the map to produce a 'heat map' effect.

Calculating distances moved

To calculate the distance between adjacent locations, step length was calculated using the following equation from the "fossil" package in R;

$$Err = a\cos(\sin Lat_{DR1} \cdot \sin Lat_{DR2} + \cos Lat_{DR1} \cdot \cos Lat_{DR2} \cdot \cos(Lon_{DR2} - Lon_{DR1})) \cdot 6371$$

where; Lat_{DR1}= Latitude of dead-reckoned step 1, Lat_{DR2}= Latitude of dead-reckoned step 2,Lon_{DR1}= Longitude of dead-reckoned step 1, Lon_{DR2}= Longitude of dead-reckoned step 2.

Estimate for space use

To quantify the space used by each goat and the whole herd, all location data was subset to provide 1 location every minute. The location limits were then used to produce a polygon by interpolating the most outer locations. The "sf" package in R was used to calculate the area of the polygon shape drawn in relation to the polygon projection.

Selection coefficients

To quantify habitat use and preference of the goats, I used standard Resource Selection Analysis (RSA) procedures, to compare used against available resources ('habitat'), based on the central assumption that the distribution of animals is proportional to the quality of the resources (Manly 2002). I defined all habitat types within the outline of all locations visited by the herd of goats as 'available' (i.e. corresponding to a within-home range level). The 1 Hz dead-reckoned movement path data were defined as 'used' locations. More specifically, and a point of novelty of this chapter, is that thanks to the behaviour identification from the accelerometer data, I was able to identify and select the grazing locations only, without using all locations, as done in standard resource selection analysis based on GPS data. To generate the 'available' locations I distributed randomly points across the availability polygon (with a specified minimum point differences >5 m). Given the very high volume of 'used' data, using the same amount of available 'random' locations allowed to quantify well the availability space. I then used standard logistic regression, implemented using Generalised Linear Mixed Models to account for individual variation (individual ID fitted as random intercept), to relate the vector of used and available locations (coded as 0/1) to the habitat covariates (i.e. the type of habitat at each location) and to estimate the regression coefficients, which directly provide the selection coefficients (negative values indicate avoidance, positive values indicate selection for, or preference, for a habitat type). All analyses were done in R using the "lme4" package. The abundant, but regularly grazed, rock slab habitat was coded as the reference habitat type and only habitats that were grazed on a reasonable proportion (> 1% of locations) were included, (see appendix, Fig. 2, Table 4 for all habitats).

Results

Behaviour identification

124 focal observations over ~6 hours were made across six individuals during the first week of data collection and were used to validate the definitions of behaviour using the Boolean-based rules (see appendix, Table2). As the equations defined behaviours to the second, the equations were tested on a second by second basis. All behaviours had a high reliability

(≥85%), with the most frequent error being that some moving was defined as grazing (Table 3).

Table 3 – List of defined behaviours with corresponding seconds that match the observed behaviours which was then used to calculate the reliability of the behavioural rule used (see text). Data used for this were from varied logging periods (5 to 7 days) from six domestic goats tagged July 2017 within les Bauges, France.

		Seconds of Observed behaviour				
		Moving	Grazing	Resting	Other	*Accuracy*
Seconds of defined Behaviour	Resting	0	0	345	0	100%
	Grazing	120	971	8	50	85%
	Moving	825	73	0	48	87%

Behaviour and space use

The mean number of hours spent on each behaviour showed little variation between individuals (Levene's test for variance: *F*-value =0.013, *p*-value=1), (Fig. 3) with resting accounting for most time (69%), grazing second (24%) and moving the least time (7%).

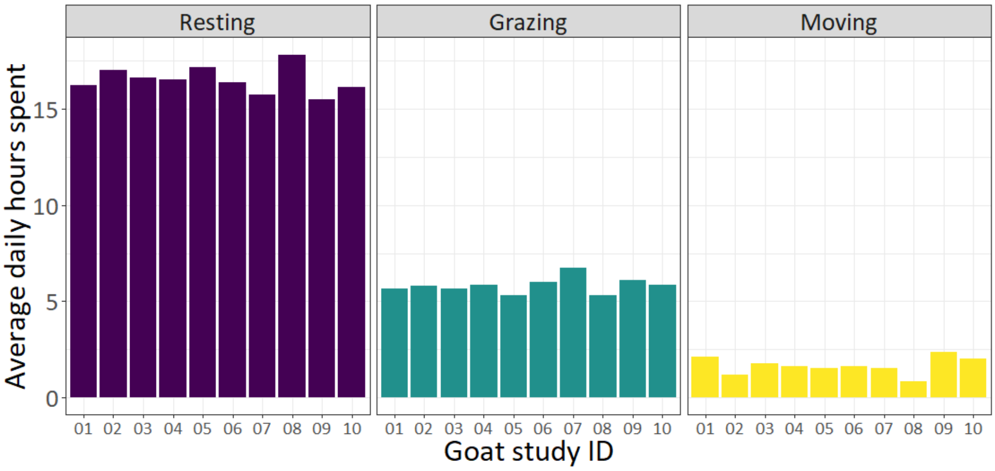

Figure 3 - Average daily time spent engaged in defined goat behaviours showing the variation between individuals. Data taken from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within les Bauges, France.

The GPS-enabled dead-reckoning, combined with the behaviour identification algorithms, produced unprecedented detail of the behaviours and movements of all tagged goats. This showed that goats typically adopted central place movement (Orians & Pearson 1979), radiating from their central place (their pen) in the morning and returning either at night or for a brief period during the day before moving out again (Fig 4).

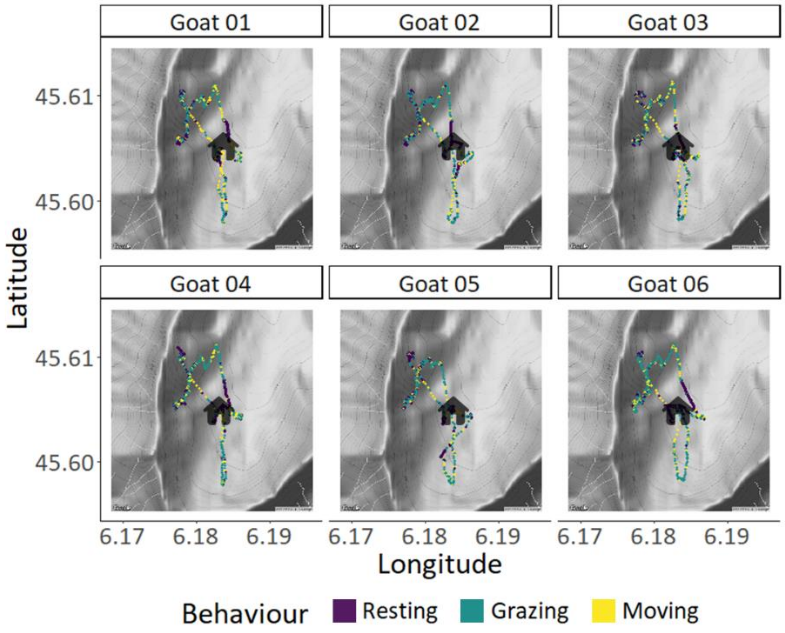

Figure 4 – Example movements of 6 individual goats, each over the same single day, showing their outward movement from the pen (black house logo) and illustrating the extent of group cohesion. On this day, the herd executed two forays from the central place. Note the tendency for increased grazing to occur at greater distances from the pen.

Over time, these movements showed a tendency for the animals to fan out, covering an ovoid shape, rather than repeatedly returning to the same place (Fig. 5).

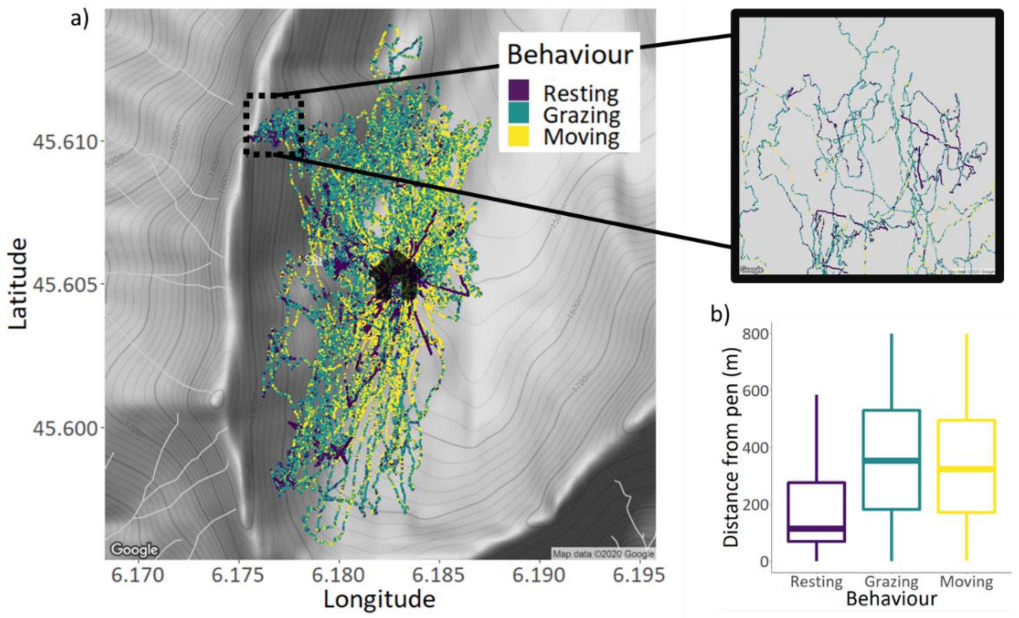

Figure 5 - Mapped goat behaviour across space (by linking acceleration-defined activity with GPS-enabled dead-reckoned paths). The data are from a 25-day logging period from a single domestic goat tagged August 2017. Although this movement roughly also represents that of the herd (cf. Fig. 7b). 5b - Boxplot (horizontal lines show median, box limits show upper and lower quartile and whiskers show range excluding outliers) showing how behaviour changes with distance from the pen. Data from varied logging periods (5 to 25 days) from one domestic goats tagged August 2017 within the Bauges massif, France.

Within this general fanning out pattern, goats grazed more at locations more distant from the pen, rested closer to the pen and moved (with reduced or no grazing) between the pen and grazing spots (Fig. 5a, b). The fanning out behaviour over time meant that the area grazed by individuals, and therefore the herd, increased significantly over time during the 25 day continuous data collection (Fig. 6a), both for individual animals and for all ten goats classified as herd (Simple linear regression on all individuals for log scales for time (t) and area used for grazing (A) (Fig. 6b) this gave $A = 0.88t - 2.14$ (*p* <0.001, R^2=0.90) for all individuals and $A = 0.44t - 1.11$ (*p* <0.001, R^2=0.94) for the whole herd of 10).

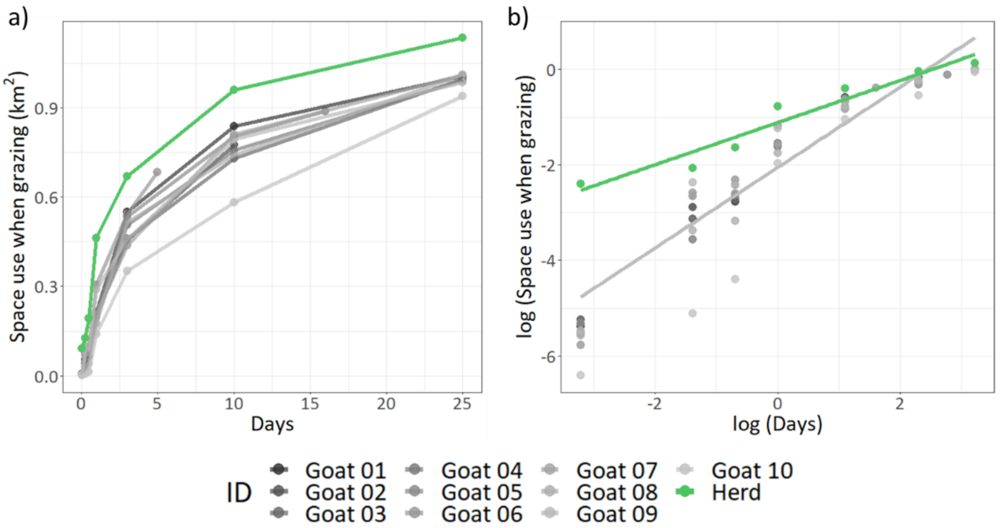

Figure 6 – (a) Relationship between overall area used for grazing and time for individual goats and for all 10 considered together (herd). (b) The same variables with both space use and time on a log scale to show logarithmic relationship with linear regression lines for both individuals and the herd. Data from varied logging periods (5 to 25 days) from ten domestic goats tagged August 2017 within les Bauges, France.

Resource selection analysis

The resource selection analysis showed clear selection for/against specific habitats (Fig. 7a). In particular, there was evidence that Forests and *Nardus* lawns were selected against for grazing, while tall herb formations, semi-arid lawns, scree with herbs and tall grazing formations all were used more likely for grazing than based on their availability in the within the 'herd home range' (Fig. 7).

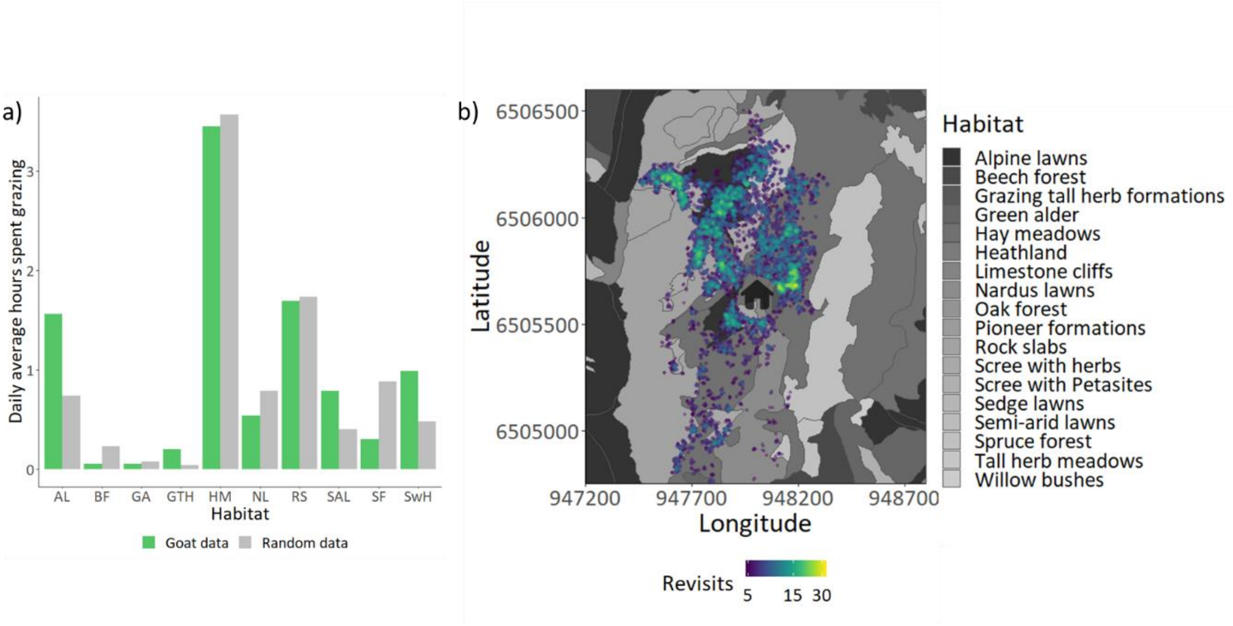

Figure 7 – (a) The daily hours grazed for random modelled data and average real goat data for each habitat (where the daily hours grazed >0.05). (b) – Grazing mapped on a habitat map to reveal areas revisited with location data thinned to be one fix per minute. Grazing locations are coloured by revisits, with revisits being defined as two or more time-spaced locations sharing the same 10 m^2 grid. Black house logo represents pen/farm location. Data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within les Bauges, France.

Examination of grazing patterns over time showed that the time spent in different habitat types changed over the summer month (the 25 days tagging period), also compared to a random selection (Fig. 8) (see appendix, Fig. 2 and Table 4 for all habitats) linked, in part, to changing area use with varying habitat type availability (Fig. 8, 9).

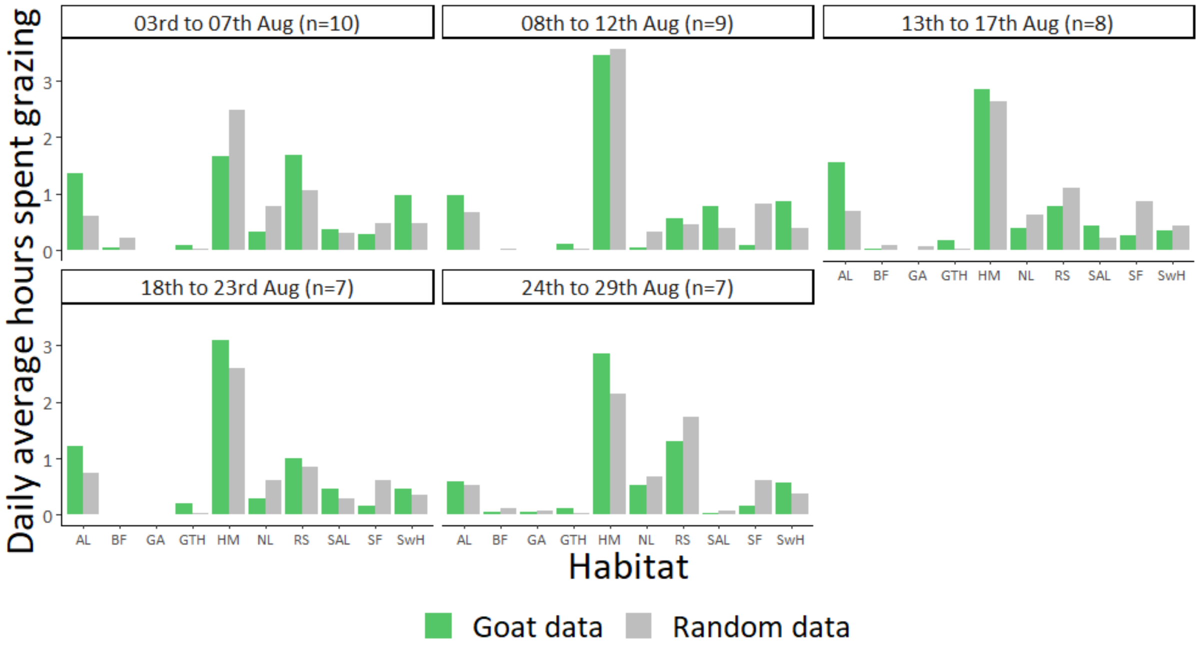

Figure 8 – The daily hours grazed for random modelled data and average real goat data for each habitat (where the daily hours grazed >0.05) across different time periods. Data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within les Bauges, France.

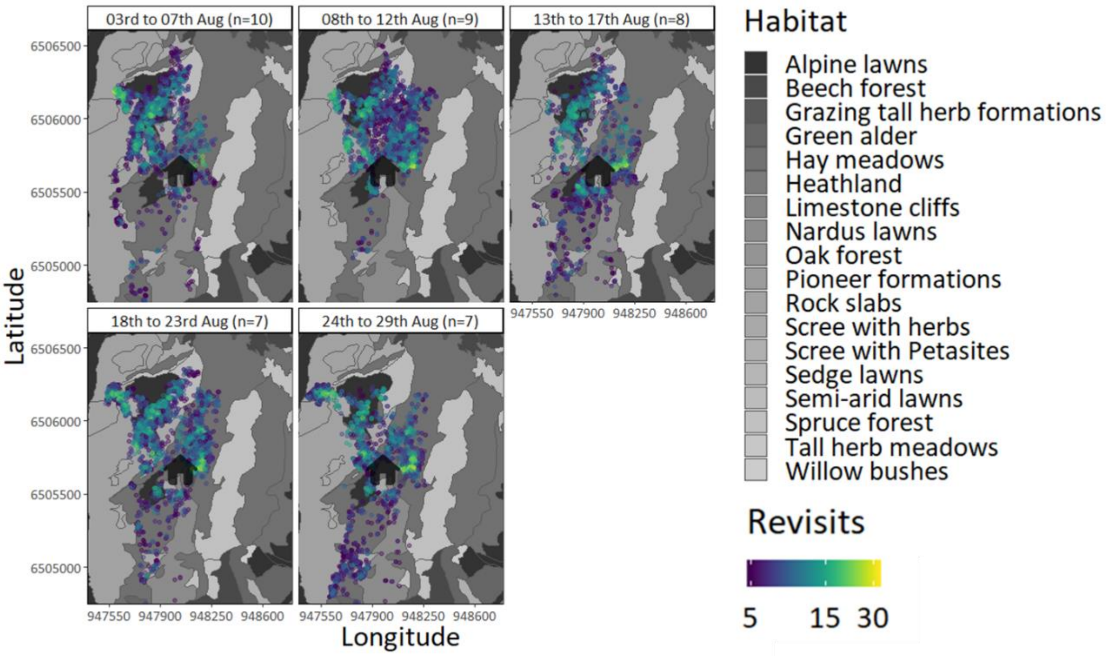

Figure 9- Grazing mapped on habitat to reveal revisited areas (location thinned to one fix per minute). Grazing locations are coloured with a heat map depicting revisits (see Fig. 7 for definition) and are repeated for the specified time period. Black house logo represents pen/farm location. Data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within les Bauges, France.

This was reflected in the observed changes in the selection coefficients (Table 4), as out of 12 habitat types, only 'Tall herbs' were always selected for, and only 'Nardus lawns' were always selected against. The forested areas, 'Spruce forest, 'Green Alder' and 'Beech forest', were also always selected against except for one time period. Selection coefficients for the remaining habitat types repeatedly switched between positive and negative values (Table 4). This coincided also with changes in the areas used by the herd over the 25-day time period, Fig. 9, Table 4), using more areas further south in the latter part of the tag deployment period.

*Table 4- List of selection coefficients for each habitat compared to the rock slab habitat, giving data for each data collection period as well as an overall coefficient (*** = p< 0.001, ** = p<0.01). Data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within les Bauges, France.*

Habitat	*03rd to 07th August*	*08th to 12th August*	*13th to 17th August*	*18th to 23rd August*	*23rd to 29th August*	*Overall*
Alpine lawns	1.033***	-0.070***	0.589***	0.402***	-0.306***	0.550***
Beech forest	-2.566***	Not grazed	10.516	-4.137***	-1.175***	-2.725***
Grazing tall herb	0.600***	0.756***	1.185***	1.233***	1.025***	1.300***
Green alder	0.121***	Not grazed	-0.065***	-1.850***	-0.841***	-1.495***
Nardus lawns	-0.418***	-3.810***	-0.396***	-0.942***	-0.333***	-0.701***
Rock slabs	0.644***	-0.656***	-0.528***	0.030***	0.248***	-0.282***
Scree with herbs	0.796***	0.072***	-0.373***	-0.176***	0.097***	0.217***
Scree with Petasites	0.520***	-0.244***	0.205***	-0.598***	-3.658***	0.104***
Sedge lawns	0.587***	-0.297***	1.621***	-11.649	-1.015***	-0.192***
Semi-arid lawns	0.418***	0.215***	0.466***	-0.084***	-1.206***	0.156***
Spruce forest	0.095***	-1.045***	-0.696***	-2.548***	Not grazed	-1.342***

Discussion

Applicability of approach in defining feeding areas and preferences

Our GPS-enabled dead-reckoning approach provided extraordinary resolution of goat movement, both in terms of defining individual movement, and that of an appreciable proportion of the herd, even though the GPS position was only sampled approximately once per 15 minutes. This, together with good resolution of habitat type, and the identification of the behaviour at each location (grazing, moving, resting) provided an excellent and rather unprecedented picture of overall habitat use. The quality of the allocation of specific areas of the habitat to behaviours depends, however, on our ability to resolve behaviours. Various authors have used accelerometry (and other) techniques in attempts to define ungulate behaviours, notably grazing (Festa-Bianchet et al. 2008, Martiskainen et al. 2009, Moreau et al. 2009), with various levels of success. For example, Moreau et al. (2009) used a combination of loggers and acceleration data and similar approach to that adopted in this study by using acceleration thresholds to successfully define grazing in goats for >73% of the time, while Putfarken et al (2007) looked at GPS data alone to define grazing in both cows and sheep, with rates of success of 94% and 89%, respectively. Our method used a simple sVeDBA threshold to provide data on resting, moving and grazing with over 85% accuracy (Table 3). Within this, resting was identified with certainty (100%), as expected due to low values of acceleration in all three orthogonal acceleration axes. Similarly, substantive movement was well defined by high VeDBA values because walking and trotting in tetrapods provides high heave and surge acceleration values (Martiskainen et al. 2009, Moreau et al. 2009) and sometimes sway (Fehlmann et al. 2017), which all feed into the calculation of VeDBA (Qasem et al. 2012). Grazing was least accurate for two reasons. Firstly, transition between moving and grazing and *vice versa* involves a gradual change in VeDBA which depends on the length of time over which the transition occurs. Under these conditions, the precise point at which one activity begins and the other ceases does not seem to be reflected by a precise value of VeDBA (and it may be different depending on whether the goat goes from walking to grazing or *vice versa*). Secondly, linked to this, and perhaps more importantly, goats engage in walking and grazing where the two behaviours are effectively mixed. Indeed, multi-tasking is a common feature of mammalian herbivores, with multiple overlapping behaviours during foraging (Fortin et al. 2004). Under such conditions, the weighting to one or the other activity depends greatly on the time allocated to each element, the length of the transition period and the 'vigour' of each of the two elements. I suspect that resolution of such phenomena would be challenging for any method used to define behaviours from accelerometry data (Fehlmann et al. 2017, Chakravarty et al. 2019), with grazing and moving being located more on a continuum as opposed to binary, exclusive categories. I also note that our approach did not allow us to differentiate between grazing and drinking or salt-licking. However, the prevalence of these two behaviours compared to grazing is trivial. Similarly, other infrequent but dynamic behaviours (e.g. headbutting, flinching and shaking) likely were categorized as 'moving', but given their very low occurrence this would have affected the time allocation to our three principal activities only minimally.

In light of the widespread ungulate multi-tasking, achieving a ≥ 85% classification success is actually very encouraging, even more so considering that certainty for animals operating in very variable terrain, in terms of vegetative cover and slope, both of which affect patterns of movement (Wall et al. 2006, Shepard et al. 2013, Dunford et al. 2020) and VeDBA (Bidder et al. 2012) making identification more problematic. Certainly, our simple approach makes recognition of potential errors easier and more apparent, at least, than is the case with many machine-learning approaches (Fehlmann et al. 2017, Chakravarty et al. 2019). We note, however, that machine-learning approaches may be particularly valuable for more refined definitions of transient behaviours (Valletta et al. 2017), although this was not the subject of this study.

Grazing and movement patterns

In a general sense, the calculated times spent grazing, moving and resting (Fig. 3) by the goats matched activity budgets for a suite of other goat species for similar data logged over intense grazing periods (table 5) (Aharon et al. 2007, Vas and Andersen 2015). However, the activity budgets over the daytime period showed that this population rested more frequently and generally moved more frequently than in these other studies (Shi et al. 2003, Moreau et al. 2009, Pokorná et al. 2013). Overall, it is clear that many factors will influence patterns, including breed, landscape (indoor or outdoor), climate or even vegetation quality and this may explain differences. In contrast, my results could highlight observation bias toward grazing if the focus of the study surrounds the grazing behaviour. Another cause for the high resting levels found within my study could be the strict classification for grazing to reduce false positives. This would underestimate overall grazing frequency although I do not expect it to change comparisons between times spent grazing within different habitats. Lastly, my definition only indicates grazing during the active part of the behaviour, on a second by second basis, which leads to chewing between bites and momentarily pauses for vigilance being marked as resting when lower resolution methods would define this as grazing. Including more time-based decision rules in the classification algorithms could be a potential solution.

Table 5 – List of studies with corresponding details to compare the result of time budgets as proportion time spent

Species	*Author*	*Data collection*	*Resolution*	*Date(s)*	*Purpose of study*	*Proportion of time spent*			
						Resting	*Grazing*	*Moving*	*Other*
Feral goats	Shi et al (2003)	Observations	NA	Daytime 06h to 20h (Jan and Dec 1981; May and Nov 2000)	Activity budgets	0.32	0.55	0.07	0.06
Domestic goats (Thüringer Waldziege × Toggenburg crossbred)	Moreau et al (2009)	Accelerometer and observations	>1Hz	Daytime for 4h periods (June to August 2007)	Grazing	0.32	0.65	0.03	NA
Domestic goats (Mamber breed)	Aharon at al (2007)	Observations	NA	Daytime (total: 164 hours)	Grazing	0.33	0.32	0.35	NA
Domestic goats (Norwegian)	Bruun (2015)	Video recordings	NA	1.5 hour intervals during feeding	Activity budgets	0.43	0.44	0.05	0.08
Domestic goats (Norwegian)	Vas and Andersen (2015)	Observations	NA	1.5 hour intervals during feeding	Activity budgets	0.25	0.5	NA	0.25
Domestic goats	Pokorna et al (2013)	Observations	5min intervals	Daytime 06h to 20h (Aug to Sept 2008)	Activity budgets	0.35	0.61	0.04	NA
Domestic goats	This study	Accelerometer	1Hz	Intense grazing periods for 26 days (Aug 2017)	Grazing	0.4	0.47	0.13	NA
Domestic goats	This study	Accelerometer	1Hz	Daytime 06h to 20h periods for 26 days (Aug 2017)	Grazing	0.58	0.32	0.1	NA

It gives confidence in my methods that this data ties in so well with the diurnal pattern of other species (see chapter 5, Fig. 4), but also shows that the goats behaved in a manner considered typical for ungulates in their habitat (Shi et al. 2003, Festa-Bianchet et al. 2008). The lack of variation between individuals in the time spent engaged in each behaviour is fully expected for such a socially dependent species that moves collectively as a herd (O'Bryan et al. 2019). Indeed, asynchrony between individuals within the herd is presumably what leads to the extent of spreading out of the herd over the day (Couzin and Krause 2003, O'Bryan et al. 2019), with the situation being reversed when they return to the pen at night.

The dual phenomena of the goats being herd animals and in this context being a species that forages in a central place manner (Orians and Pearson 1979) is what likely accounts for the change in space use over time observed in my study goats (Fig. 9): All central place animals tend to deplete food resources closest to their central place, a phenomenon that has been called Ashmole's halo in marine systems (Birt et al. 1987, Elliott et al. 2009), thus it benefits individuals to radiate out beyond this halo to forage. More generally this is a case where accessibility becomes restricted, in this case due to the central place foraging behaviour, affecting space use of animals (Matthiopolous 2003). Where animals forage in groups on static resources, such as plants, the exploitation in the space used by the group can be extreme, particularly when inter-individual spacing is small (Elliott et al. 2009). Thus, optimization of movement patterns of herd animals such as goats, has to balance the distance (and associated cost) that the animals travel away from their central place with the energetic benefits of unexploited (or little exploited) areas with increasing distance (Pyke 1984, Houston and McNamara 1985). In addition, movement direction has to be factored in, because by adopting a fanning out pattern over time, animals can exploit closer areas to their central place than they could if they always maintained a single heading when setting out to forage. Indeed, time-based exploitation of different areas based on radiating from the central place gives time for the vegetation to regrow and should, other things being equal, result in a logarithmic increase in space use with time, as observed in my goats (Fig. 6). The effect of distance and direction on exposed area can be made apparent by using the simple example of a circle representing the limits of daily movement of a central place foraging animal such as these goats. Because the total available area increases according to Area = πr^2, where r is the radius of the circle, small increases in radius produce a disproportionate increase in available area. In this case, this would effectively rapidly limit the necessary transit distance between pen and feeding site. In fact, in my study, the area topography apparently somewhat limited fully radial movement, with a steep incline being present to the West of the pen, which tended to flatten the potential radiation circle into an ovoid. Nonetheless, the observed space-use by our animals over time (Fig. 6a) gives a good estimation of how much area a herd of 10 goats will exploit at that time of year – levelling off at about 1.1 km^2. I note, however, that most of this space is also presumably used for the rest of the herd of 40 animals so that extrapolation of space-use and herd size needs attention, unless the entire herd is monitored. A plot of the area grazed against number of animals for defined periods of time shows increasing area with increasing numbers in the herd as well as increasing areas over time (cf. Fig. 10). Extrapolation of these lines to different numbers of animals in the herd should help give an idea of how herd size relates to area exploited. However, strictly speaking, this will not be truly representative of area use if the herd were solely made up of the indicated number of animals since the data were derived from a herd of 40 animals which, itself, will affect the results. Nonetheless, the approach at least gives an approximate idea.

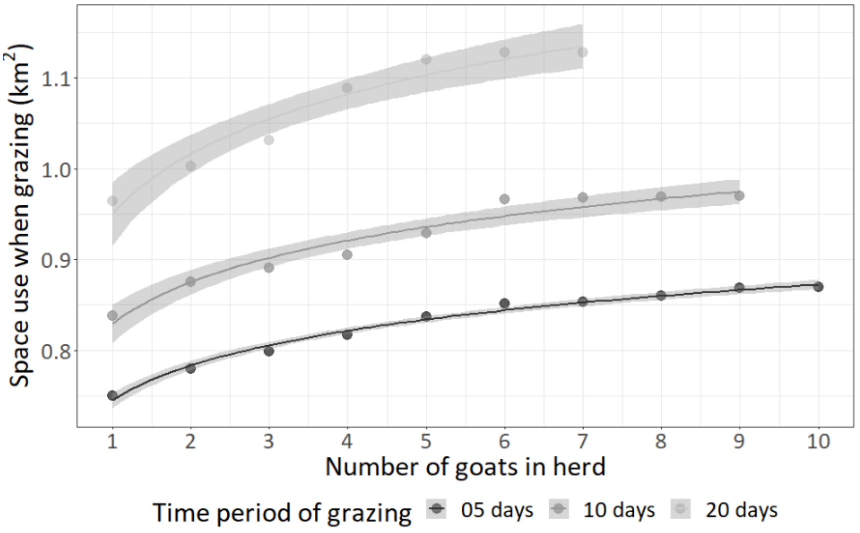

Figure 10- Area grazed by goats in an Alpine setting as a function of the number of goats in the herd. Note that this data was derived from individuals with a 40-animal hard and so does not represent the situation that would occur were the goat herd were to be strictly limited to the number suggested. Nonetheless, the graph shows important trends.

Beyond this, if food is indeed a determinant of space-use, central place foraging theory would predict greater space use in less productive times of the year and this is also expected to change according to habitat composition.

Habitat exploitation

The data clearly shows habitat preferences (Fig. 7, table 4), which therefore affects the details of space-use. For example, I note that there was an usually high number of revisits to a spot in the centre East of the overall grazed area (Figs 7b & 9), a space that was predominantly grazing tall herb formations surrounded by hay meadow vegetation. Although I cannot know precisely what plant species the goats were targeting within this, and other habitats (Sanon et al. 2007, Mancilla-Leytón et al. 2013), preference for grazing in certain habitats should allow somewhat modified predictions as to the overall space that goats may require in different areas of the Alps according to herd size and the habitat composition. For example, knowing that the animals tend to avoid forest habitats and sedge lawns would indicate that areas of the Alps with high proportions of these habitat types are likely to suffer increased consumption on the other, relatively less abundant, habitat types, such as Alpine lawns, Scree with herbs and semi-arid lawns. Ideally, studies should attempt to determine what, exactly, goats favour within the different habitat types so as to build up a more comprehensive picture of goat impact over time and space. Such as reconstruction of the foodscape of an area for a specific species has recently been achieved in the same study area for a wild species, the chamois (Duparc et al. 2020). By combining data on animal movements with unprecedent detailed data on the quantity and quality of edible resources in the landscape (via vegetation sampling, remote sensing, and diet DNA barcoding), the authors were able to show that in reality the foodscape of the chamois contained only a low proportion of available biomass (<18%) and a low spatial covariation between plant phenology and biomass. This led to the chamois constantly selecting for plants in the flowering stage, avoiding areas with low edible biomass, leading to shifts in the home range selection ratios for/against more advanced plants over the summer period. Thus, to understand habitat selection and foraging patterns, it is crucial to consider the actual foodscape for a species, especially when the traits of edible plants differ from those of all available plants.

The high amount of grazing on rock slaps was unexpected as, despite the presence of vegetation, the habitat is described as mostly bare rock (Devillers et al. 1991) which implies that there would be more effort required to seek out the vegetation. A similar argument can be made for the preference for scree with herbs. Based on this, I assume that the vegetation on rock slabs (spp.) and within herb screes (spp.) must be particularly beneficial, such as having a high energy density. More detailed studies, including using the collar-mountain videos used by Newmaster et al. (2013), could examine this in more detail.

Goats avoided forested areas, which included spruce, green alder (*Alnus alnobetula*) and beech habitat when grazing. This was expected as there are few herbs and grasses due to the shading effect of the tree canopy (Mancilla-Leytón et al. 2013). However, wild alpine ungulates may use the forested areas to avoid the heat (Marchand et al. 2015), which seems to be less of a problem in the domestic species. Interestingly, the only period when there was a significant preference for wooded habitat was during the first 5 days of tagging, when green alder had a high selection coefficient.

Overall, hay meadows were preferred over rock slabs but this did not stay consistent over the logging period. I expected to see a preference, with high grazing rates at these sites as this habitat is specifically planted by farmers for livestock to graze (Devillers et al. 1991). This expected result further supports this methodology and analysis to define and locate grazing. Alpine lawns were preferred, as expected, due to diverse grass species being present, which make up the preferred diet of most goat species (Sanon et al. 2007, Iussig et al. 2015), but this picture will become further clear by including diet selection data to understand the species-specific foodscape (Duparc et al 2020).

Grazing herb formations were the most preferred habitat for grazing. This habitat is usually associated with cattle (Devillers et al. 1991) that were also present within the valley. This result might show the benefit of having multiple species grazing within one pasture valley if the goats prefer vegetation that forms uniquely in the presence of domestic cows.

Semi-arid lawns were not preferred for all logging periods but overall did have a positive selection coefficient. This habitat is a result of over-grazing or nutrification (Devillers et al. 1991, Mayer et al. 2009) but this data shows that the habitat still offers grazing opportunities for livestock. As part of this, depending on the resilience of the vegetation, this habitat could be restricted from goat grazing to allow the habitat to recover and increase in biodiversity, especially since these results show that goats seek out and graze on the habitat. Nardus lawns are similar, in being associated with over-grazing, with resulting in reduced biodiversity. Although goats did graze in this habitat, there was no specific preference for it.

Despite the methodological limitations (see above), the results do show what habitats are preferred by domestic goats for grazing and this information should be useful for farmers, allowing them to better manage the land, and protect habitats from being over-grazed. Indeed, this type of study could be run for longer periods, with more detailed analysis of the foodscape, to define trends over seasons so as to understand what could be done to manage grazing impacts. As part of this, more detailed analysis could specifically determine vegetation-, rather than just habitat preferences (Duparc et al. 2020).

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Chapter 5

Grazing on alpine slopes: Effects of habitat, slopes and temperature on grazing behaviour and behaviour budget in domestic goats (Capra aegagrus hircus) and Alpine ibex (Capra ibex).

Abstract

Domestic ungulates have been introduced into every continent across the globe and can compete with native ungulate species for resources. This can be especially critical in mountain grasslands, where steep slopes and rocky areas restrict available habitats, with environmental change, such as rising temperatures, further exacerbating the impact of domestic livestock on wild ungulates. Understanding resources selection, conditional on topography and environmental conditions, of both wild and domestic mountain ungulates can hence markedly inform management as well as further our understanding of their movement ecology. Here, I used multi-sensor biologging technology and novel methods to study two closely related species, the domestic goat (*Capra aegagrus hircus*) and the alpine ibex *(Capra ibex),* living in two nearby study sites in the French Alps. Movement data from both species were collected using collar-attached accelerometers, magnetometer and global position system (GPS) devices, fine-scale (1Hz) movement paths were obtained over summer months (July-August) by dead-reckoning and the behaviour at each point in space and time was reconstructed using the 'Lowest Common Demnominator (LoCoD)' Boolean behaviour identification method, and grazing locations, and time spent grazing, were analysed in a resource selection framework, in relation also to topography (slopes) and environmental temperature. The ibex and goats shared four habitat types, with both species selecting herb habitat and avoiding conifer forests when grazing. The time spent grazing as a function of the slope of the topography depended on incline in goats, with a slight preference for steeper inclines when grazing. The ibex also selected steeper slopes for grazing, preferring even steeper inclines than the goats (but related also to availability of inclines). Importantly, ibex showed a markedly stronger response to temperature than domestic goats, in line with the

documented heat stress sensibility of the former. The results show that global warming may prove critical for the management of alpine grasslands and that domestic species may negatively impact wild species, due to their shared habit preferences and being less critically affected by environmental change, likely due to the support received by the farmers and shepherds.

Introduction

For conservationists, how invasive- and deliberately introduced species interact with their adopted habitat and the native species is key to understanding how to preserve ecosystems (United Nations 1993). Invasive species can, for example, alter an ecosystem by *inter alia* posing a threat to native species *via* predation (Caut et al. 2008, Cheng et al. 2016), competition (Côté 2005, Dugger et al. 2011), habitat alteration (Wardle et al. 2001) or habitat destruction (Fordham et al. 2007). A common example of potentially detrimental introductions is in the form of ungulate livestock competing with their wild counterparts: Livestock grazing accounts for over one quarter of the world’s land use (Steinfeld et al. 2006) and, in many instances, these livestock have to share resources with wild herbivores. The competition and negative impacts of domestic species on wild animals is the subject of much debate (Chaikina and Ruckstuhl 2006, Allred et al. 2013), with domestic ungulates often providing social and economic benefits but negatively affecting biodiversity (Spear et al. 2009) and the key need to understand the contrasting impacts of native and introduced/domestic grazers for the conservation of grasslands (Allred et al. 2013).

Livestock management within the French Alps is a particular case, with free-range grazing livestock present at the higher altitudes during the summer months (Tasser and Tappeiner 2002). Studies show that there are some benefits of this grazing to the vegetation biodiversity and connectivity (Fischer and Wipf 2002, Mayer et al. 2009). It improves the alpine ecosystem generally and can even promote relevant habitat availability for the wild ungulates (Zweifel-Schielly et al. 2009, Espunyes et al. 2019).Governing bodies actively encourage farmers to adopt site-specific seasonal grazing (Baur and Binder 2013) which leads, in some areas, to livestock and wild species appearing to share the same spaces in the summer months (Ryser-Degiorgis et al. 2002, Fankhauser et al. 2007, Chirichella et al. 2014). The extent to which this leads to space- and time overlap for grazing by wild and domestic ungulates is unclear.

The locations, extents and times spent grazing by ungulates are critical to their fitness (Bergman et al. 2001) because all species need to spend a substantial part of their life feeding (Arnold 1985). Indeed, anything that diminishes this time can have a significant impact on fitness (Bergman et al. 2001, Janis 2008). It is little surprising, therefore, that studies have shown that ungulates choose judiciously where and when to forage in relation to predators (Gazzola et al. 2005, Gude et al. 2006), habitat type (Pearson et al. 1995, Forsyth 2000) and temperature (Aublet et al. 2009, Pęksa and Ciach 2018, Herfindal et al. 2019). Critically though, few studies have considered how wild species compare with potentially co-occurring domestic livestock in these regards, and how this might affect competition (Ryser-Degiorgis et al. 2002). An exception to this was Martinez (2002), who investigated ibex (*Capra pyrenaica*) and sheep (*Ovis aries*) conflicts in sympatry but found that sheep adopt such different feeding behaviours to ibex species that competition seemed unlikely. Comparisons between congeners are expected to be more telling though, because similar species are more likely to favour similar conditions which can result in niche displacement for the weaker species (Pépin and N'Da 1991, Fankhauser 2004, Ferretti and Mori 2020). This may explain why domestic goats (*Capra aegagrus hircus*) have been shown to displace the iberian ibex (*Capra pyrenaica*) to suboptimal (woodland) habitats, with both species being reported to prefer grasses and herbs in areas of allopatry (Acevedo et al. 2007). In fact, for this reason, goats may be problematic to wild congeneric species, with a particular case for concern being the Alpine ibex (*Capra ibex*). This species faced near extinction at the beginning of the twentieth century due to excessive hunting although careful re-introduction has now allowed numerous populations to establish across the Alps (Stüwe and Nievergelt 1991). While the current estimated population totals some over 50,000 individuals (Stüwe and Nievergelt 1991), the low genetic diversity of this species puts it at risk of inbreeding and makes it vulnerable to environmental pressures (Grossen et al. 2020),. The Alpine ibex habitat preferences for grazing have been previously described in a number of their alpine populations (Grignolio et al. 2007, Herfindal et al. 2019, Brambilla et al. 2020) particularly those in France (Villaret and Bon 1995). The results showed that the species spent long periods on bare rocks and scree but considering abundance favours grass habitats (Grignolio et al. 2003), higher altitudes (Grignolio et al. 2003, 2007, Aublet et al. 2009, Herfindal et al. 2019) and avoids midday high temperatures (Aublet et al. 2009, Herfindal et al. 2019). However, both the behavioural analyses and space-use were based on the use of low-resolution GPS, radio-tracking or simple observations and therefore could not definitively allocate space-use and temperature to grazing. Thus, here my aim was to provide an analysis of very fine-scale movements, behavioural budgets, and space use, including response to slope and temperature, of alpine ibex and domestic goats. Especially the combination of behaviour identification and movement data allows for a considerably more refined analysis of foraging behaviour and to this end combining a wild species and a closely related domestic one, tagged in two different areas, provides the opportunity to apply this approach to data showing a large range of behavioural and environmental differences.

This study used continuous, high resolution (≥1 Hz) animal-attached loggers to determine the second-by-second location and behaviours of domestic goats and Alpine ibex foraging in two different areas within the French Alps. The aims of the work were; (i) to verify tag sensor-defined behaviours (resting, grazing and moving) by observation of logger-equipped domestic goats and applying these values, with modification, as necessary, to wild ibex, (ii) to determine the extent to which temperature affects the grazing of both species, (iii) to identify grazing preferences with regards to habitat and slope and thereby (iv) allude to the extent to which the two species might compete for resources or space if farming practice leads to sympatry.

Methods

Study sites

The domestic goats were collared in a pasture valley (45.60485°N, 6.18295°E) within the Bauges Massif, a National Game and Wildlife Reserve in the northern French Alps (Fig. 1a).

The vegetation in the Bauges is dominated by beech *Fagus sylvatica* and fir *Abies alba* forests (with a preponderance of conifer forests in the specific study area here), Alpine pastures and rocky areas (Duparc et al. 2020). In the summer months, daylight averages 15 hours, temperature ranges from 12°C to 27°C and there is regular rainfall (NOAA 2017).

The ibex were collared near Allemond (45.13610°N, 6.04020°E) in the Belledonne-7 Laux Reserve (Isere, France) on the Belledonne mountain range (Fig. 1b). The Belledonne massif attitude range is greater than that of the Bauges, with several peaks higher than 2700 m above sea level, and deep valleys. The topography determines the vegetation, and there are larger areas of bare rock and scree compared to the Bauges. There are however, several shared habitat/vegetation types shared, including extensive grasslands and fragmented forest, including conifer, deciduous, mixed, and open woodland (Michallet et al. 1988). The summer has temperature highs of 25°C and lows of 10°C with regular rainfall and an average of 15 hours of daylight (NOAA 2017).

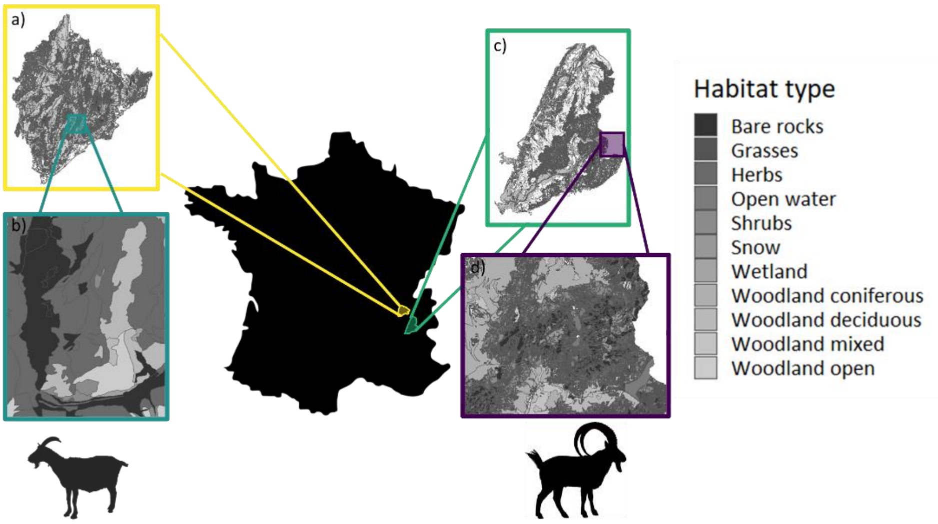

Figure 1 – (a) A shape file of the Bauges massif and its position within France, (b) – the site used for the domestic goat study and its location within the massif and (c) - a shape file of the Belledonne massif and its position in relation to France. (d) shows the site used for the alpine ibex study and location within the massif. Each shape file had polygons outlined and coloured based on habitat.

Study species

Domestic goat: The free roaming herd of goats studied was composed of 1 male and 40 females, of which ten were selected for data collection. The average weight of the selected goats was approximately 30 kg. The animals were milked every morning and were kept in a pen for most nights, which predetermined their movement habits appreciably. The goats used in this study came from a goat farm that was easily accessible where the livestock were free to browse a segregated area of 2 km^2 within the valley (Fig. 1b). The goat herd shared space with domestic dairy cows (*Bos bos taurus*), wild chamois (*Rupicapra rupicapra*) and wild mouflon (*Ovis gmelini musimon × Ovis sp.*).

Wild Ibex: The ibex population within the Belledonne massif were reintroduced in 1983 with 20 Alpine ibex from Mont-Pleureur (Switzerland), with the population continuously monitored since then through capture–mark–recapture methods (including GPS collars) by the Office National de la Chasse et de la Faune Sauvage (Toigo et al. 2013). Specifically, Ibex are captured and ear-tagged each spring, using tele-anaesthesia, cage traps, leg-holdsnares, or drop nets, using methods approved by the French Environment Ministry. Six ibex individuals were captured and collared for this study in the eastern part of the mountain range (Fig. 1d). The ibex population shared the massif with other ungulates including wild chamois (*Rupicapra rupicapra*) and domestic sheep (*Ovis aries*).The average weight of the selected individuals was 80 kg, all Ibex were males with an estimate age ranging from 7 to 12 years (determined from counts of horn growth rings at capture).

Biologgers

Domestic goats: The goats were collared with lab-built collars containing accelerometer and magnetometer units ("Daily Diaries" - DD) (Wilson et al. 2008) (Fig. 2a) and Global Position Systems (GPS) (GiPsy5, TechnoSMart). The GPS was programmed to record position once every fifteen minutes, while the DD recorded tri-axial acceleration at 20 Hz, tri-axial magnetic field intensity at 8Hz and temperature and pressure at 2 Hz (for further details of the collar setup and DDs see chapter 4 methods) (Fig. 2b). The highest collar weight was 150 g, staying well within the 3% ethical guidelines (0.5%).

Wild Ibex: The ibex were collared with Lotek 3300S GPS collars (Lotek 2020) with a lab -built housing fitted and fastened to the commercial battery housing at the base of the collar (Fig. 2c). The ABS plastic housing contained two A-cell 3.7 volt batteries and a DD that recorded acceleration (Fig. 2d) and magnetic field intensity in three orthogonal axes as well as temperature and pressure using the same regime as for the goats. The Lotek GPS collar had an injection mould plastic housing at the base containing batteries to power VHF and GPS units within the collar. The collars themselves were constructed of re-enforced artificial leather and had a remote triggered release. The combined weight of the logging collar with all components was, on average, <500 g, weighing in as 0.7% of the average ibex weight capture, staying far below the recommended 3% maximum tag weight (Casper 2009).

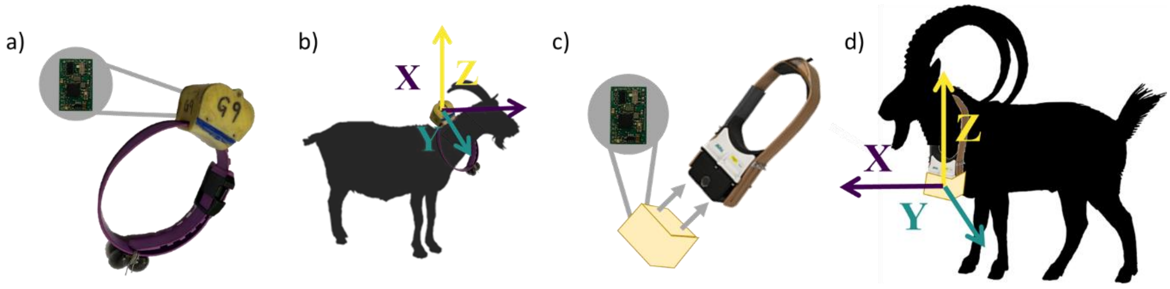

Figure 2- (a) Placement of the Daily Diary (DD) housing and the way it fits in relation to the lab-built collar, (b) - the orientation of the three acceleration axes in relation to the collar and goat, (c) - placement of the Daily Diary (DD) housing with respect to its fitting onto the exterior of commercial Lotek collar and (d) - the orientation of the three acceleration axes in relation to the collar and the ibex.

Deployment and collection

Before collars were attached to the animals, each GPS and DD device was turned on and the DD was then calibrated. Calibration of the DD involved carrying out a defined series of movements to; (i) provide a key within the data for synchronised time and (ii) to allow the 3 magnetometers to sample the magnetic field intensity in all orientations to calibrate the overall magnetic field intensity (Williams et al. 2017) and to enable hard- and soft-iron corrections to be implemented (Guo et al. 2008, Vasconcelos et al. 2011).

Domestic goats: The collars were attached to the goats in the morning when the herd was enclosed in an indoor pen. The individuals were selected randomly and required minimal handling. Attachment time and ear tag number was recorded for each collared individual.

Wild Ibex: The captures for the wild species used a drop net trap, triggered remotely, and baited with salt licks to lure the ibex (Toigo et al. 1999, Jullien et al. 2001). All methods were approved by the French Environment Ministry. Individuals of suitable weight and size were selected to be collared, with horn length and weight noted at capture.

Data analysis

All biologging data were handled and analysed for behaviour identification and dead-reckoning using the DDMT software (Wildbyte Technologies 2020). All other analyses, including mapping and statistical analyses, were conducted in R (R Core Team, 2019) and R Studio (RStudio Team 2020). In particular, statistical analysis involved the use of linear models and generalised linear mixed models.

Dead-reckoning

To give an estimate location every second, dead-reckoning (Bidder et al. 2015) between GPS fixes was used. In essence, this involves using accelerometers and magnetometer to derive animal heading with respect to magnetic North (subsequently corrected to true North) and Vectorial Dynamic Body Acceleration (VeDBA) (Bidder et al. 2012, Qasem et al. 2012) as a proxy for speed (see chapter 3 methods for further details). To clean the GPS data, the Bjørneraas GPS screening (Bjørneraas et al. 2010) method was used within a package through R-studio (RStudio Team 2020).

Pressure to altitude

To convert the pressure and temperature channels from the DD to altitude the following formula was used:

$$h = \frac{\left(\left(\frac{P_0}{P}\right)^{\frac{1}{5.257}} - 1\right) \times (T + 273.15)}{0.0065}$$

Where h is altitude or height in metres, P_0 is pressure at sea level, P is the pressure reading from the logger and T is temperature.

Behaviour definition

Definition of the behaviours of wild Ibex, where tagged animals effectively cannot be observed, is not trivial. The normal protocol is to observe a tagged animal and correlate the details of acceleration signals to behaviour so that machine-learning or other protocols can be used to find specific data within extended datasets from unobserved animals (Shepard et al. 2008, Brown et al. 2013, Fehlmann et al. 2017). This option is not available for wild cryptic species and one suggested solution is to use a similar animal captive counterpart (e.g. a congener) to provide the necessary calibration (Campbell et al. 2013, Rast et al. 2020). This is naïve if the expectation is that a machine-learning algorithm for a particular behaviour in a captive animal is to be transposed to a wild counterpart because even small morphological differences between the wild animal and its observable counterpart can make a large difference in acceleration metrics (Wilson et al. 2020, Dickinson et al. subm.). However, there are generalities in the accelerometer patterns produced by moving animals, especially useful if animals share the same Bauplan and mode of locomotion, as for example ungulates. With ungulates, the variability in the raw heave, surge and sway acceleration data as well as in the smoothed VeDBA signal, clearly indicate grazing, resting or travelling (chapter 4). This is possible, not least because the data from any acceleration sensor in a tri-axial (orthogonal) group of three, is a defined and predictable response to the movement of the tag. Specifically, the sensor returns an acceleration value along its measurement axis that incorporates; (i) the static acceleration from the earth's gravitational field (which depends on the angle of the sensor axis with respect to the earth's surface) with (ii) any linear acceleration produced by the animal and (iii) any centripetal acceleration invoked by the animal. Given this, and the fact that the sampling frequency of the three axes determines the extent to which observable waveforms within the data are due to, for example, an animal's stride, it is not difficult to see how particular animal movements produce recognisable acceleration patterns. This can be formalised within an efficient and repeatable framework, the Boolean time-based decision-tree template (Wilson et al. 2018).

With this in mind, I visually examined Ibex acceleration data after spending extensive time examining goat behaviour manifest in the acceleration data (Chapter 4). I had developed a protocol for differentiating this goat behaviour into its three main elements, resting, travelling and grazing, based on thresholds in smoothed VeDBA (over 40 data points) (Chapter 4) (Fig. 3a): I used this as a basis to transpose Ibex acceleration data and identify the three behaviours within the wild Ibex dataset, verified by simple 'expert inspection' (Fig. 3a,b). Specifically, an offset was needed to correct for the difference in noise in the acceleration signature of the Lotek collar compared to the lab-built collar: The Lotek collar was heavier than the lab-built collar, and was padded, which led to a more stable (less variable) signature during periods of animal immobility (resting). Comparison of the resting sVeDBA for the two species showed that the goats produced an average sVeDBA that was 0.05 *g* higher than the Ibex. Thus, the sVeDBA thresholds for all behaviours previously defined for the goats (Chapter 4) were offset by 0.05 *g* to act as thresholds for the 3 major behaviours within the ibex data (Fig. 3b). Inspection of the acceleration signals corresponding to resting, travelling, and grazing in the Ibex data using this offset identified, as far as the 'expert user' could tell, the behaviours perfectly. Once quantified, the behaviour (from both species) could be linked to other variables (temperature, pressure and location [see above]) recorded by the DD *via* time (see appendix, Table 2 for rule definition table).

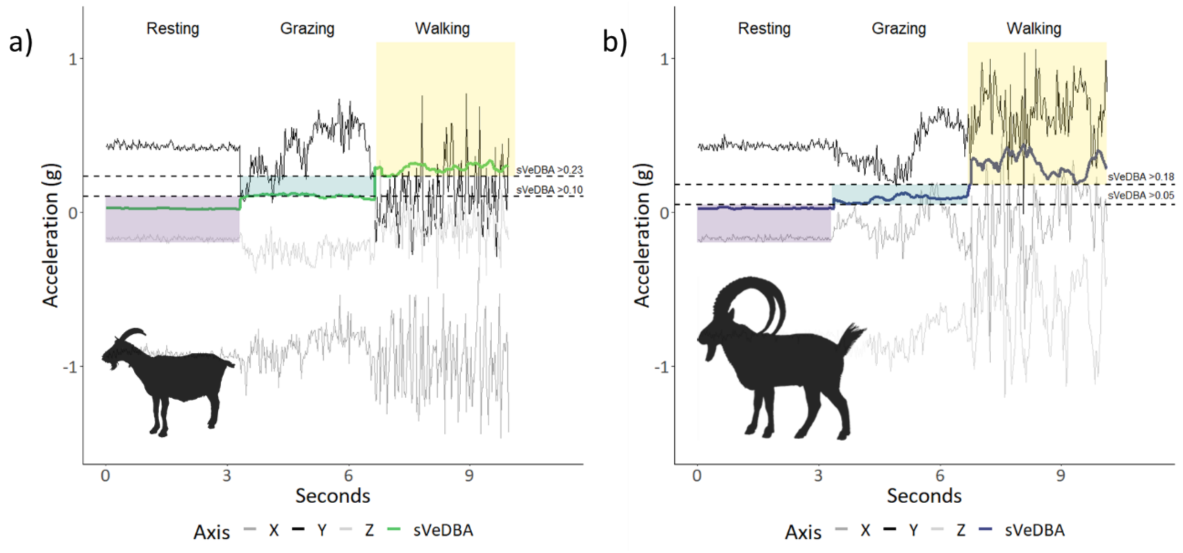

Figure 3- (a) A plot of acceleration smoothed (over 40 events (2 s)) over all 3 orthogonal axes (grey lines) and sVeDBA (green line) to show changes over time with changing goat behaviour. The thresholds used to define the three behaviours are shown using the dashed lines with the thresholds specified. (b) - shows an equivalent plot for an Ibex (sVeDBA - blue line) using a 0.05 g sVeDBA offset applied to all thresholds used to define the three behaviours.

Mapping

"ggmap" and "raster" packages within R (R Core Team, 2019) and R studio (RStudio Team 2020) were used to map the 1 Hz dead-reckoned paths onto shape and raster files. Details including slope and habitat could then be extracted from the maps to link grazing to the environment: habitat type was extracted from shape files and slope incline (as %) (using a map with 25 m^2 resolution) from the raster plot. Mapping data was supplied by Grenoble University and the National Hunting and Wildlife Agency (ONCFS) management team (Tronchot 2008). The shape files describing the habitat for Belledonne and the Bauges used different habitat definitions, so the French maps were translated and unified for standardization (Table 1). To quantify overall space-use for each species and identify space-use according to grazing, the locations of grazing for each individual were used to outline a polygon, executed using the "sf" package in R studio, which then allowed the area used to be calculated.

Table 1- List and break-down of how the habitat information supplied was combined to define shared habitats with new habitat descriptions.

Study habitat ID	*Description*	*Belledonne habitats*	*Bauges habitats*
Bare rock	Predominately exposed rock in the form of rock face or loose scree. Vegetation can be present including pioneer species, grasses and herb species.	Rock shadow, exposed rock	Scree
Grasses	Grass species making up lawns that have a variety of biodiversity- and productivity types including Nard, Laiche and Seslerie species	Diverse lawns	Nard, Laiche, Seslerie, Dry grass, Forage (mowing meadows)
Herbs	Herbs species with a variety of biodiversity and productivity including Megaphorbiaie	Herbs	Megaphorbiaie
Open water	Open bodies of water in the form of lakes and rivers	Water	Not present
Shrubs	Mixture of open, fruit-bearing, closed, low and tall shrub species	Closed shrubs, open shrubs, low shrubs, shrubs with fruits	Shrubs
Snow	Snow present, note: not known if this habitat is date dependent as snow is present at some altitudes all year round	Snow	Not present
Wetland	Habitat where the water table is high, resulting in seasonal or permanent flooding	Low swamp	Not present
Woodland coniferous	Forest made up of conifer species including spruce and larch	Spruce, Conifers in islets, larch	Spruce

Woodland deciduous	Forest, made up of deciduous species including beech, birch, alder and a mix of deciduous species	Beech, Birch, mix of hardwoods	Beech, Alder
Woodland mixed	Forest made up of a mix of deciduous and conifer species	Mix of conifers and deciduous trees	Not present
Woodland open	Sparse forest including a variety of species	Loose forest	Not present

To condense the high numbers of data points (hundreds of millions), the “recurse” package within R studio was selected, where, if two or more grazing locations were withing 10 m^2 of one another, it was counted as a revisit. This revisit metric was then used to indicate areas that were used most frequently.

Selection coefficients

In a manner similar to chapter 4, a logistic regression within generalised linear mixed models (using the “lme4” package in R) was used to analyse use-available data within standard resource selection analysis (Manly et al. 2002). Used locations were the locations with identified grazing behaviour. Available locations were distributed within the polygon enclosing all locations of the herd or tagged individuals. The results produced a selection coefficient for each habitat compared to bare rock (reference standard). The same process was also used to highlight preferences for grazing on different slope inclines with slope as a percentage.

Results

Overview of captures

The six Ibex captured were all male and weighed between 77 and 85 kg, with estimated ages ranging between 7 and 12 years (Table 2).

Table 2- List of the individual Ibex (all male) tagged with the data noted at the time of capture and the corresponding values associated with their behaviour for the following 30 days after release. Each of the six animals was tagged in June 2017 within Belledonne, France.

Study ID	*Total grazing hours*	*Total distance travelled (km)*	*Space use (km^2)*	*Space use when grazing (km^2)*	*Weight (kg)*	*Estimated age (years)*
Ibex 1	286.48	210.78	4.85	4.81	77.7	7
Ibex 2	288.43	213.03	5.87	5.81	85	12
Ibex 3	273.24	201.24	5.24	5.31	78.3	9
Ibex 4	259.85	188.5	5.28	5.17	81.2	12
Ibex 5	279.63	152.43	1.52	1.51	79.4	7
Ibex 6	303.6	63.11	3.47	3.46	79.8	9
Mean	281.87 ±14.84	171.52 ±57.54	4.37 ±1.61	4.34 ±1.60	80.2 ±2.6	9 ±2

Behaviour

The second by second data stemming from a total of 30 ibex days from 6 individual Ibex showed that the animals spent a mean of 53% of their time resting (standing or sitting), 8% moving (without grazing) and 39% grazing. This was similar to the goats, that spent a mean of 69% of their time resting (standing or sitting), 7% moving (without grazing) and 24% grazing (Chapter 4). As with the goats (Chapter 4), there was little variation in overall activity across individual Ibex (Levene's test for variance: *F*-value = 0.018, *p*-value = 0.99), with a maximum of 17% difference in time spent grazing between the most active and least active grazers (Table 3). Activity in both species depended on time of day though. Both species predominantly rested at night and around mid-day and had peaks in grazing activity in the morning and afternoon/evening, with periods of heighted travel preceding and during grazing (Fig. 4).

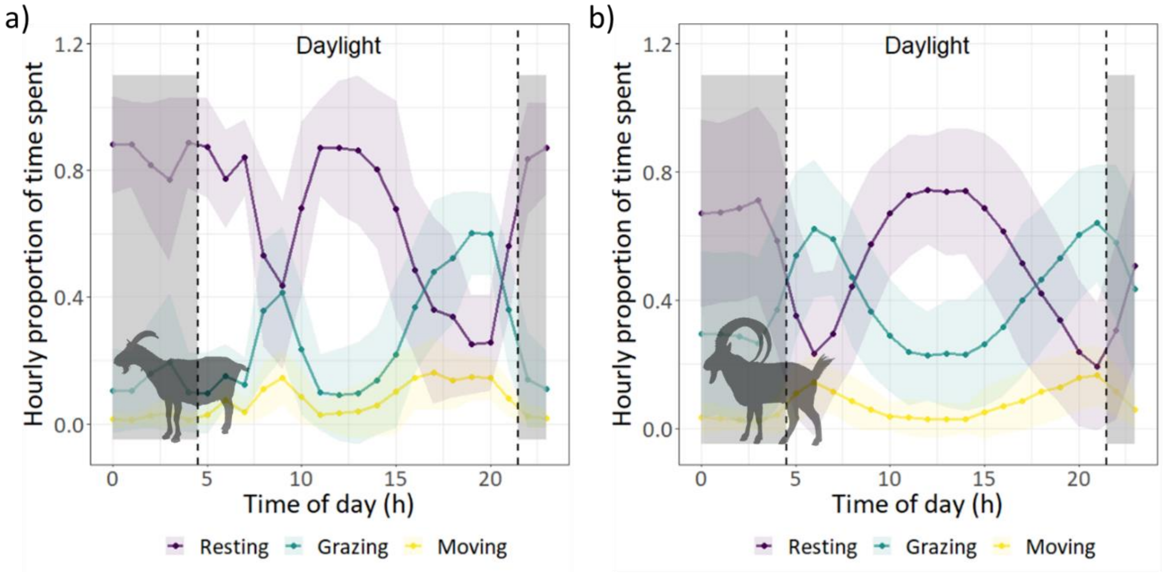

Figure 4 – Mean proportion of time spent per hour engaged in grazing, resting and travelling by (a) tagged goats and (b) tagged ibex during the study period. Error shading shows SD across individuals for each behaviour. Ibex data from 30 days from six wild ibex tagged in June 2017 within Belledonne, France. Goat data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within the Bauges, France.

The sVeDBA associated with the three major activities was highest in walking animals, being approximately 10 times that of the lowest sVeDBA activity, which occurred in resting animals in both species (Table 3). Grazing was intermediate in both species and was approximately five times higher than resting (Table 3).

Table 3 – Mean values of DBA for both domestic goat and ibex in relation to behavioural state

	Goat		*Ibex*	
Activity	*Mean sVeDBA (g)*	*SD*	*Mean sVeDBA (g)*	*SD*
Resting	0.03	0.04	0.03	0.01
Grazing	0.15	0.04	0.10	0.03
Walking	0.31	0.16	0.24	0.14

As a reflection of the activity-specific VeDBAs (Table 3) and the varying proportion of behaviours allocated to different hours of the day (Fig. 5), there were clear trends in mean VeDBA-values per hour, with highest VeDBAs associated with movement (travelling and grazing) between 6h and 10h and 15h and 20h for the goats and between 5h and 9h and 17h and 22h for the Ibex (Fig. 5).

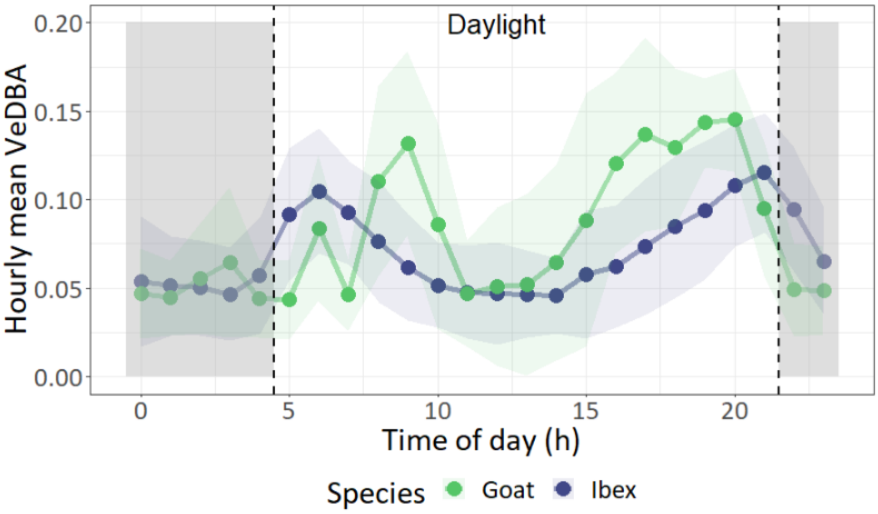

Figure 5 – Variation in VeDBA over the course of the 24 h cycle in 10 tagged domestic goats (green line) and 6 tagged wild Ibex (blue line). Error shading shows SD across individuals for each species. Ibex data from 30 days from six wild ibex tagged in June 2017 within Belledonne, France. Goat data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within the Bauges, France.

Area-use

Information on the goat area-use is covered extensively in chapter 4 (see Figures 6 and 9 in this chapter). In essence though, these animals displayed a central place foraging pattern because they returned to their pen on most nights. In addition, because the goats travelled as a herd, individual differences were minimized, which was not the case for the Ibex (see below). Overall, for the monitored period, the goats radiated out from their central place spending most time in their central place with diminishing time with increasing distance from that central place (Fig. 5, Chapter 4). An exception to this was an enhanced revisit frequency in a single northwest axis extending out from their pen (Fig. 7b, Chapter 4).

Individual Ibex varied appreciably in their use of space (Fig. 6) and in the distances that they travelled (Chapter 6, Table 4). For example, Ibex 5 remained for the whole of the monitored period within small areas (<3.5 km^2), with a higher incidence of revisits to grazing patches (Fig 5). The other individuals exploited larger areas during the data collection, ranging from 4.28 km^2 to 6.70 km^2, with lower mean revisits to the defined grazing patches and greater distances travelled (Fig. 5). One individual (Ibex 2) exploited two substantially different areas during the tagging period, spending approximately half the time in one area before moving to the other (Fig. 5).

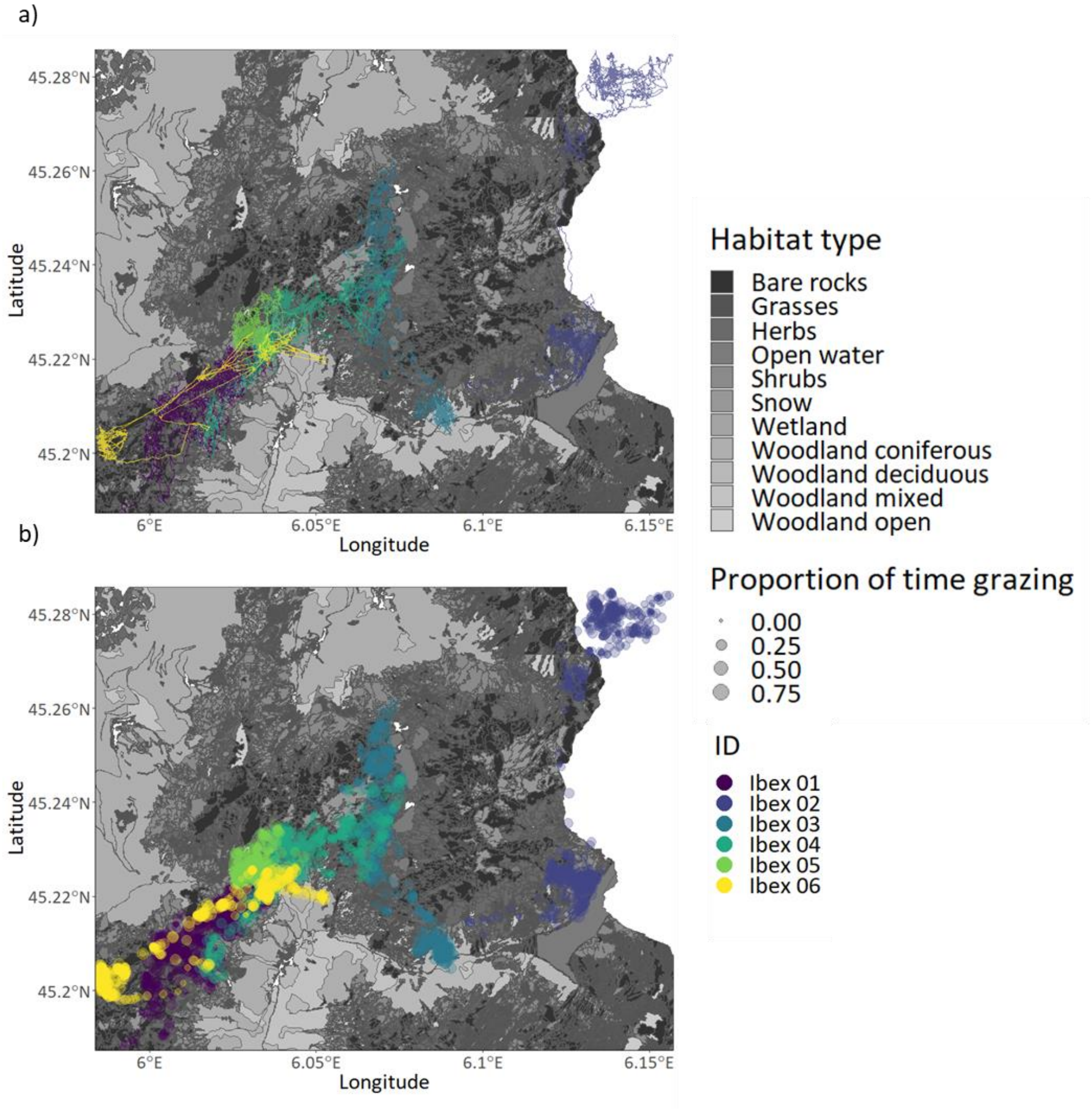

Figure 6 – (a) Dead-reckoned paths coloured by individual, sub sampled to 1 location per minute to show area and movement range used by each individual. (b) Mean locations for hourly periods coloured by individual with size of each point to show proportion of that hour spent grazing. Map coloured by study habitat type. Data from 30 days from six wild ibex tagged in June 2017 within Belledonne, France.

Temperatures

The hourly variation in temperature to which the goats and Ibex were exposed was very clear from the DD data, with maxima around 14h and minima around 6h in both species (Fig. 7a) although the goats were exposed to temperatures that were almost 8°C higher than the Ibex. A histogram of the proportion of time spent grazing by the two species revealed that the ibex grazed throughout the 24 h cycle but for appreciably longer periods in the hours around dawn and dusk. By contrast, although the goats grazed appreciably in the mid-morning, they grazed most substantially in the mid- to late afternoon (Fig. 7a). Consideration of the mean proportion of time grazing per hour of day against hourly mean temperatures showed a significant negative relationship between grazing (y) and temperature (x) for the Ibex (y=-0.06x+1.23, R^2= 0.83, p<0.001) but not for the goats (y=-0.02x+0.73, R^2=0.06, p>0.1) (Fig. 7b).

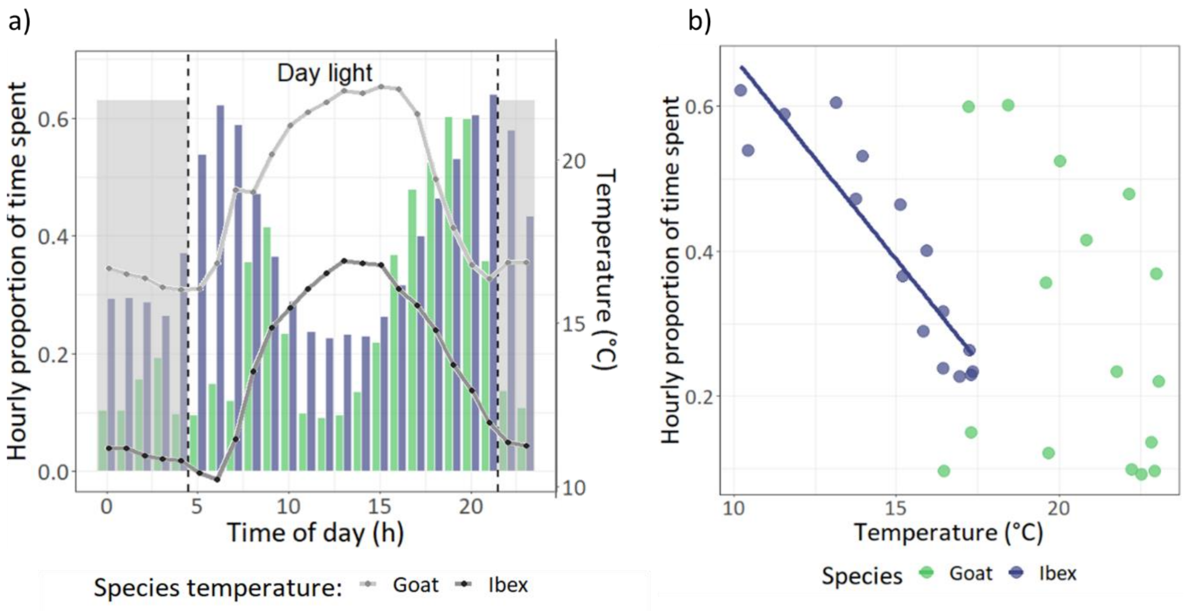

Figure 7- (a) The mean temperature (derived from the DD data) to which goats (grey line) and Ibex (black line) were exposed during the tagged periods overlaid on the mean proportion of time that the two species spent grazing per hour (goats shown by green bars and ibex by blue bars). (b) Scatter plot of the mean proportion of time per hour spent grazing as a function of mean temperature per hour during daylight hours for both ibex (blue symbols) and goats (green symbols. Each data point represents mean hourly temperature for all individuals of that species and the mean hourly proportion time spent grazing compared to other two defined behaviours (rest and moving) for just daylight hours (6h to 21h). Ibex data from 30 days from six wild ibex tagged in June 2017

within Belledonne, France. Goat data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within the Bauges, France.

Altitudes

The two species exploited two markedly different altitudes during their tagged periods, with the Ibex and the goats grazing at mean altitudes of 2166 m and 1538 m (Fig. 8b,c), respectively. Beyond this, the ibex moved over a greater altitude range (225 m) that was approximately twice that of the goats (112 m) (Fig. 8a). The hourly proportion of time spent grazing by goats (y) increased with increasing relative altitude (x) in the ranges they selected according to $y=0.003x+0.178$ ($p < 0.05$, $R^2=0.33$) whereas the Ibex grazed less with increasing relative altitude within the ranges they selected ($y=-0.002x+0.719$ $p<0.0001$, $R^2=0.80$) (Fig. 7a).

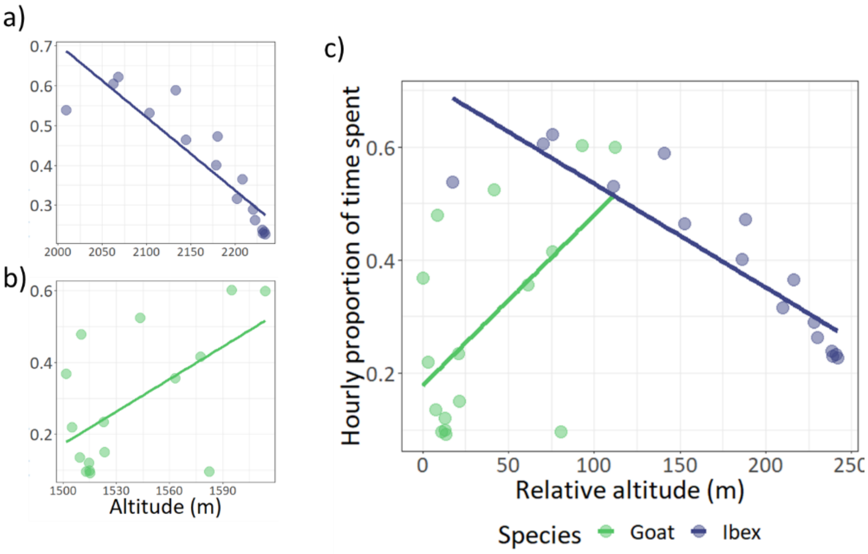

Figure 8- Scatter plot showing how the mean proportion of time spent grazing changed with altitude for (a) ibex and (b) goats. (c) shows the mean proportion of time spent grazing as a function of relative altitude where 0 is the lowest altitude encountered at any time per individual over the tagged period. Each data point represents mean hourly temperature for all individuals of that species and the mean hourly proportion time spent grazing compared to other two defined behaviours (rest and moving) for just daylight hours (6h to 21h). Ibex data from 30 days from each of six wild ibex tagged in June 2017 within Belledonne, France. Goat data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within the Bauges, France.

The altitudes exploited were, however, dependent on time of day. The goats spent the night at a relative altitude of just under 100 m, generally descending to graze during the day (Fig. 9). By contrast, the Ibex spent the night at their lowest relative altitudes, climbing some 250 m during the day, peaking around mid-day, before descending again for the night (Fig. 9).

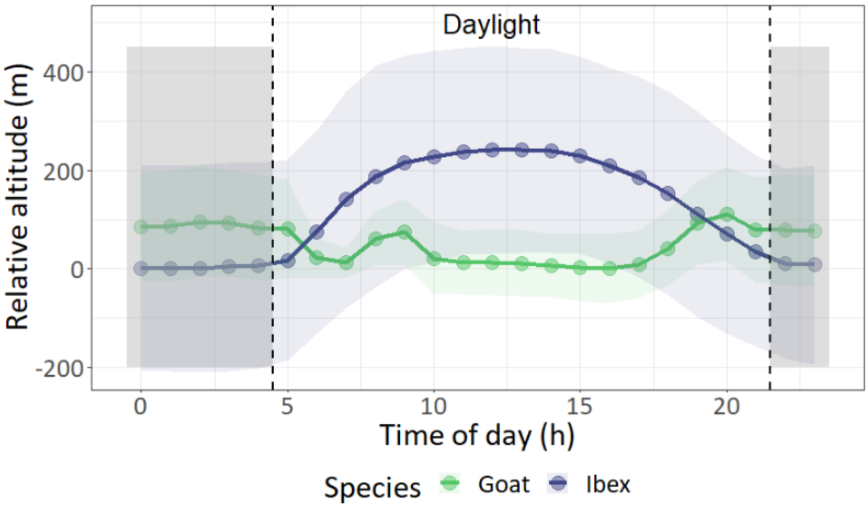

Figure 9 – Mean relative altitude of goats (green symbols) and Ibex (blue symbols) as a function of time of day (cf. Fig. 8a) across the full period the animals were tagged. Error shading shows SD across individuals for each species. Ibex data from 30 days from six wild ibex tagged in June 2017 within Belledonne, France. Goat data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within the Bauges, France.

Grazing habitat

Ibex grazed more in herb- and shrub habitat type than available, with slight avoidance of grassland habitat (Fig. 10). Ibex also avoided coniferous woodland but preferred deciduous woodland. By contrast, goats grazed more than expected from available on bare rocks and grasses while avoiding all types of wooded areas (Fig. 10). The two species only shared four habitat types between them, within which the goats spent most time grazing grasses (5.36 hours) whereas Ibex grazed mostly on herbs (2.76 hours) and shrubs (2.54 hours). The Ibex also grazed within other habitat types present in their movement range, including snow and shrubs.

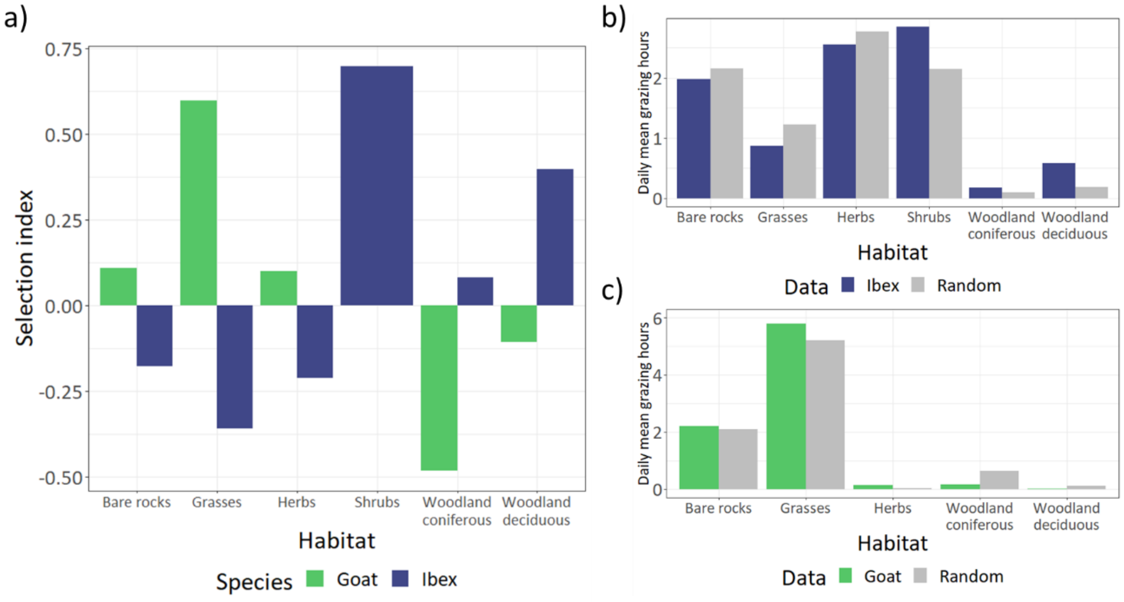

Figure 10 – (a) Bar plot highlighting the selection index for each habitat shared by the goats and ibex. The histogram shows the mean time spent grazing in each habitat type for the study animals (coloured bars) compared to available; (b) Ibex and (c) domestic goats. - Ibex data from 30 days from each of six wild ibex tagged in June 2017 within Belledonne, France. Goat data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within les Bauges, France.

Slope

The proportion of time spent grazing as a function of slope compared to available in the area revealed that Ibex appeared to graze most on steeper slopes, with the highest proportion of time spent on slopes with gradients of between about 35 and 60 degrees (Fig. 11a). This meant that a simple linear regression analysis showed a significant positive trend of time spent grazing (y) against slope (x) for these animals (y=6.00e^{-5}x+6.35e^{-3}, p <0. 05, R^2=0.07). By contrast, the goats appeared to graze less with increasing slope, spending most time grazing on slopes between 0 and 40 degrees (Fig. 11b). This pattern meant that there was a significant negative trend in time spent grazing (y) against slope (x) according to y= -1.95e^{-4}x+1.64e^{-2} (p <0, R^2=0.46). Worth noting there was a high amount of flat (0% slope) available to the ibex, producing predicted 0.07 proportion (total 2179 hours for the 29 days) time spent, this is not displayed on the plot below.

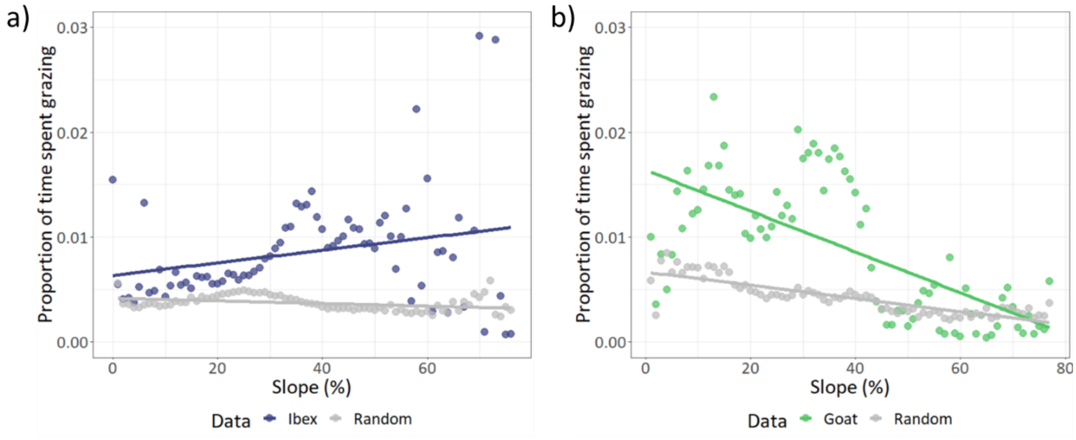

Figure 11 - Scatter plot showing how the proportion of time spent grazing changed with slope (%) for (a) ibex and (b) goats. Proportion time spent grazing was calculated by comparing to other two defined behaviours (rest and moving) with a mean for each rounded slope value. To do this for random data, random data was sampled at the same quantity for each individual within a circle encompassing the range of observed movements, so comparisons could be drawn comparing availability of the slope to the goats. Ibex data from 30 days for each of six wild ibex tagged in June 2017 within Belledonne, France. Goat data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within the Bauges, France.

The resource selection analysis at individual level showed appreciable variation between individual ibex with habitat type but less so with slope; five of the ibex selected steeper slopes to graze on compared to slopes available (Table 4). Most ibex had a preference for shrub habitat for grazing (compared to the bare rock) but all other habitats had appreciable variation between individuals with no obvious species preference even though the selection index implied that woodlands would be preferred (see above). The goats showed much less variation between individuals, as expected given they were from the same herd, than the ibex. Most had a strong preference for grasses and herbs over bare rocks but appeared to prefer exposed rocks over woodland areas (See appendix, Table 5 for all habitat types occupied by Ibex when grazing).

*Table 4- List of selection coefficients for each habitat compared to the bare rock habitat and slope (%) giving data for each data collection period as well as an overall coefficient (*** p< 0.001). Ibex data from 30 days for each of six wild ibex tagged in June 2017 within Belledonne, France. Goat data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within the Bauges, France.*

	Grasses		*Herbs*		*Woodland coniferous*		*Woodland Deciduous*		*Shrubs*		*Slope*	
Study ID	*Goat*	*Ibex*	*Goat*	*Ibex*	*Goat*	*Ibex*	*Goat*	*Ibex*	*Goat*	*Ibex*	*Goat*	*Ibex*
1	0.17***	0.21***	1.50***	0.31***	-1.25***	-5.48	-2.27***			0.11***	0.013***	0.006***
2	-0.17***	0.83***	0.86***	0.98***	-1.07***		-11.74	0.74***		1.51***	0.004***	-0.001***
3	0.07***	-0.36***	1.27***	0.16***	-1.29***		0.89***	1.55***		0.39***	0.009***	0.019***
4	0.29***	0.24***	1.55***	0.23***	-1.16***	-1.31***	-2.34***	-1.51***		0.35***	0.007***	0.017***
5	0.36***	-1.26***	1.61***	-0.68***	-0.52***		-4.12***	-12.87		-0.64***	0.015***	0.036***
6	-0.49***	-0.12***	0.19***	-0.20***	-0.61***	0.51***	-11.64	-0.40***		1.10***	0.019***	0.046***
7	0.13***		1.52***		-1.41***		-14.57				0.009***	
8	0.20***		1.23***		-1.48***		-2.13***				-0.002***	
9	0.06***		1.49***		-1.49***		-2.88***				0.009***	
10	0.08***		1.53***		-1.60***		-2.28***				0.003***	
Mean	0.07	-0.08	1.28	0.13	-1.19	-0.40	-2.16	0.09		0.47	0.009	0.021

Discussion

Viability of adopting goat-derived signals for behaviour for wild Ibex

A critical step within this study is the use of sVeDBA, with specific thresholds for particular behaviours and visually verified for goats, for ibex (du Toit and Yetman 2005, Sanon et al. 2007, Pokorná et al. 2013). To make this approach applicable, however, the sVeDBA thresholds had to be modified by subtracting a noisier baseline apparent in the 'resting' goat data but absent in the ibex. This was then used to derive ibex activity, based on effectively minimally modified thresholds and confirmed by visual inspection. I believe that this approach, which called on 'expert knowledge' to recognise particular patterns in the acceleration data linked to specific behaviours, was justified for a number of reasons. Firstly, and perhaps most importantly, it is effectively impossible to record the behaviour of tagged wild ibex. This situation is not unique to ibex though, since there are many species that cannot be observed to 'validate' acceleration data. The idea that no attempt to determine the activities of these animals should be made simply because it is impossible to validate is patently absurd because, as mentioned earlier, accelerometers give precise outputs to defined movements of the tags and many patterns of behaviour are similar among related species, as shown by classical ethograms obtained from visual observations. Secondly, there were broad and easily recognisable patterns in the form of the acceleration data for just three very different behaviours; resting, travelling and grazing goats, and these patterns were similarly clear for the ibex (Fig. 3). Thirdly, the offset of 0.05 *g* in the sVeDBA represents a relatively small change given the range of sVeDBA in the data. Finally, given that ungulates typically spend >95% of their total time engaged in resting, travelling or grazing (Shi et al. 2003, Pelletier et al. 2009, Pęksa and Ciach 2018), the only real imperative of this study was to be able to distinguish between these three, all other behaviours (such as head clashing – see chapter 6) being so transient as to be insignificant with regard to feeding sites. Thus, although the data on sites and environmental conditions used for grazing in this study are dependent on broadly correct identification of grazing, I am confident that this was the case.

In fact, the activity time budgets and daily patterns for the ibex in this study matched the literature using behavioural focal observations for caprinids (Hamel and Côté 2008, Aublet et al. 2009, Ma et al. 2012) in ibex species (Aublet et al. 2009, Grignolio et al. 2010, Büntgen et al. 2014), with the species spending most of its overall time resting (both standing and sitting down) while most of its active time was spent grazing. This also lends confidence to the methods used to distinguish between the behaviours of the ibex (see above).

The physiological consequences of altitude and activity

Ibex body- and environmental temperature as a function of altitude.

The tag-derived observations of the behaviour of the ibex can be used to summarize their activities and examine how these relate to the environment and the synoptic conditions. This is important because not only are ibex particularly susceptible to higher temperatures (Aublet et al. 2009, Mason et al. 2017) but the very act of climbing to allow animals to move up the mountainside to higher, cooler altitudes (Parker et al. 1984, Halsey and White 2017, Dunford et al. 2020) is energetically onerous (Büntgen et al. 2014, Mason et al. 2017) and results in large amounts of heat production, which could exacerbate temperature problems. In brief summary, this data show that the ibex fed little at night (Fig. 4b), primarily resting on the lower slopes (Fig. 8a, 9) where they were exposed to moderate temperatures (ca. 11°C) (Fig. 7). However, around dawn, they moved up the slopes (Fig. 8), feeding as they went, with high levels of grazing within the first 100 m relative increase in altitude (Fig. 9). As they did this, the temperature they experienced rose due to the normal changes in temperature that occur during the 24 h cycle. This temperature continued to rise as the animals also continued to climb while decreasing their incidence of grazing. Their average relative altitude reached a maximum at around 250 m by 12h (Fig. 8), by which time they were exposed to mean temperatures of 17°C (Fig. 7a) and were only grazing for 20% of their time (Fig. 7). As the day progressed, and the temperatures at altitude began to fall, so the Ibex increased their incidence of grazing (Fig. 7a) and moved down the slopes (Fig. 9). Their grazing diminished abruptly at around 20h (Fig. 7a), after which they descended further, attaining their night-time status and altitude at around 21h (Figs 7 and 9).

All this points to specific benefits of both maximum and minimum relative altitudes. The reduced incidence of grazing at night, replaced by resting, indicates that the lower slopes are used for sleep and likely rumination while these ibex are exposed to temperatures that are within their (likely) thermoneutral zone. This will minimize the energetic costs of metabolic rate at night and possibly also help reduce the incidence of predation (by, for example, wolves *(Canis lupus lupus)* – in another study using these tags in the area, a mouflon was actually depredated by a wolf during the study). The extent to which the lower slopes provide appropriate, or preferred food, however, is not clear. This is because animals move rapidly up the slopes around dawn, and continue to do so, increasing relative altitude by about 200 m, until about 10h (Fig. 9). During this period, initially directed movement gives way to a greater incidence of grazing until there is a grazing peak around 6h (Fig. 4, 6a). Given that ibex have been shown to be highly sensitive to high temperatures (Aublet et al. 2009), this altitudinal migration, which has been described by Aublet et al. might be ascribed to either their movement to preferred feeding areas or attempts to minimize high temperature stress because the temperature decreases by 0.2°C for every 30m change in altitude. In fact, this altitudinal migration is likely to be a combination of both feeding in an appropriate area and temperature regulation.

The extent to which movement and temperature regulation due to altitudinal migration interact, can be examined in a general manner by using a simple energetic model built on using calibrated data from another goat species acting as a proxy for ibex. Dickinson et al (subm.) present data on the metabolic rate of pigmy goats (*Capra aegagrus hircus)* as a function of DBA metrics during resting and walking at different speeds and inclines on a treadmill. They specifically present results for DBA as Overall Dynamic Body Acceleration (ODBA) (Qasem et al. 2012) rather than VeDBA (Wilson et al. 2020) as used here, but these are essentially interconvertible by dividing ODBA by 1.44 to calculate VeDBA. This conversion is used throughout to convert data presented in Dickinson et al (subm.) to standardize units.

Derivation of an indicative relationship between VeDBA and oxygen consumption

Firstly, I note that the VeDBA values reported by Dickinson et al. (subm.) for Pygmy goats both resting and moving (at specific speeds) (being 0.028 *g* and [interpolated to 1 m/s – the regression only goes to 0.83 m/s] 0.29 *g*, respectively) are strikingly similar to the values reported here for both goats and ibex (cf. Table 3). This gives general confidence in a comparative approach because the accelerometers on the Dickinson et al. (collars (which were identical to those used in this study) are seemingly reacting in much the same way with regard to DBA as those in the current study even though they are deployed on different species.

Dickinson et al (subm.) report that their pygmy goats walking on the level had a mean oxygen consumption of 82.2 mL/min at VeDBA-values of 0.097 *g*, increasing by 4.33 mL/min for every 0.00694 *g* VeDBA-value increase after that. This translates to;

$$VO_2 = 1860VeDBA + 2.171 \qquad (1)$$

with units being mL O_2 per minute per animal or a mass-specific (mean mass of the goats was 25.9 kg) relationship of;

$$VO_2 = 17.342VeDBA + 1.488 \tag{2}$$

in units of mL/min/kg. In turn, using Schmidt-Nielsen's (Llobera and Sluckin 2007) conversion of oxygen into energy of 20.1 J being released for every mL of oxygen used, this converts to;

$$Power_{(at\ 0°)} = 150.47VeDBA + 12.91 \tag{3}$$

in units of W/kg. By contrast, pygmy goats walking up a 15° slope, had a mean oxygen consumption reported to be 183 mL/min at VeDBA-values of 0.096 *g*, increasing by 17.93 mL/min for every 0.00694 *g* VeDBA-value increase after that. Using the same approach as above, This converts to;

$$Power_{(at\ 15°)} = 623.09VeDBA + 0.73 \tag{4}$$

again, in units of W/kg. Note that the intercepts in both eqns (3) and (4) cases do not correspond to oxygen consumption at RMR because animals have a positive VeDBA signal even when resting (e.g. Table 3).

Derivation of mass-specific energy expenditure as a function of slope

The relationships above, derived from Dickinson et al (subm.), only allow for calculation of power on level ground and ascending slopes of 15°, and it is clear from these that the VeDBA vs Power relationship depends critically on slope. In order to approximate the effect of a variable slope (within the 0-15° range) in terms of power and VeDBA, I suggest that I can linearly interpolate between the slopes of eqns (3) and (4) because the rate of change of potential energy for an animal moving up a slope at a constant speed is linearly dependent on that slope. As such, the difference between the slope gradients from the two equations and their intercepts can simply be divided by 15 to give the increment in energy expended per degree slope increment. If these values are multiplied by the slope angle and added to the values for the 0° relationship, it should approximate a relevant relationship between

VeDBA and power for a given slope within that range. Applying this process results in the following relationship gives;

$$\text{Power}_{(0\text{-}15°)} = ((150.47+[31.508 \text{ X } \theta]) \text{ X VeDBA}) + (12.9-[0.911 \text{ X } \theta]) \tag{5}$$

where θ = slope angle and the power has units of J/s/kg or W/kg.

Power ties in closely with cost of transport (COT), a quantification of the energy relative to metabolic rate required for an animal to change location (Halsey and White, 2017; Shepard et al., 2013). The more power required to overcome potential energy posed by slope angle, the higher COT to move across this slope (Halsey, 2016; Halsey and White, 2017; Dickinson et al., 2021).

Approximation of the angle of the slope during the ascent

Eqn (5) gives an approximation for the power required to walk up a slope of a given angle for a given value of VeDBA. However, in order to put this into context, the slope angle taken by the ibex during the morning altitudinal migration needs to be calculated. This cannot simply be the slope of the area over which the animals are moving (see e.g. slope index earlier) because ungulate tracks in mountains rarely move directly up the slope, with the animals, instead, walking tangentially (Dailey and Hobbs 1989). I allude to the slope angle by another process. During the morning ascent, the ibex gained altitude at a rate defined by the difference in altitude between hourly mean values (ΔH) while walking at a speed of v (m/s) with the mean walking VeDBA defined in Table 3 for the fraction of the time within that hour when the animals were walking (F_{walk}) (I assume that no specific directional movement occurred during grazing). Assuming this to approximate the situation, the slope angle is given by;

$$\Theta = \text{asin}(\Delta H/v \text{ X } 3600 \text{ X } F_{walk}) \tag{6}$$

where v is 1.0 m/s (see earlier), ΔH is in metres and the 3600 ensures that the speed, given in m/s, is multiplied to change it into the distance travelled within that hour.

Adopting this process calculates the effective slope for each of the hourly blocks during which the ibex moved up the mountain and indicates that angles when animals moved uphill varied between 0.3 and 9° (Fig. 12).

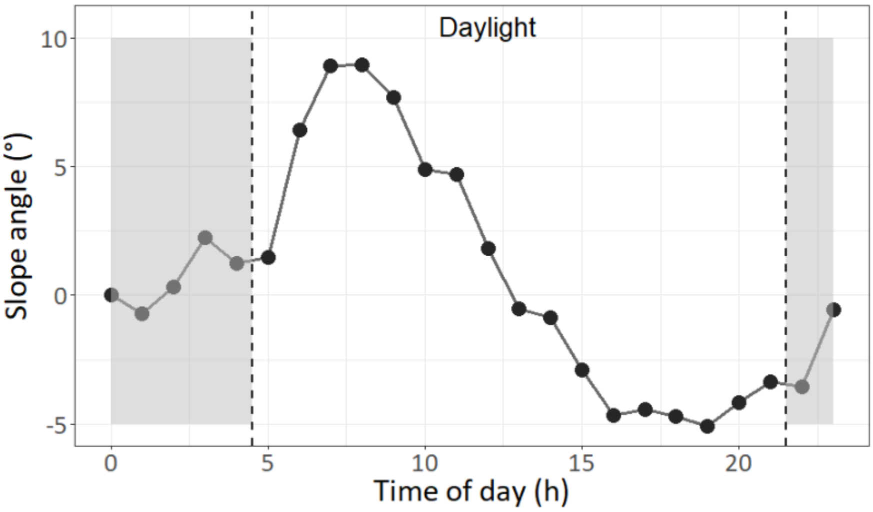

Figure 12 – Estimated slope angle traversed for ibex engaging in daily altitudinal migration based on relative altitude change per hour, assuming walking speed estimate is a consistent (see text). Positive angles indicate animals moving uphill, negative, downhill.

Indicative energetic costs of climbing

Assuming that the pygmy goat data can be used as a proxy to indicate trends in ibex energetics for animals climbing up variable slopes defined by our process (see above), I can use eqns (5) and (6) together with the known mean VeDBA of walking of 0.24 *g* (Table 3) to calculate the Mass-specific energy used in climbing as a function of time of day. This can be multiplied by the mean body mass of our animals (of 80.2 kg – Table 3) to produce a whole animal estimate of the power used for the animals to walk up the slopes. The total amount of energy specifically used during walking the ascent phase per hour is then given by multiplying the power by the number of seconds in that hour spent walking (multiplying the fraction of the time spent walking by 3600 [the number of seconds in any hour]) (Fig. 13)

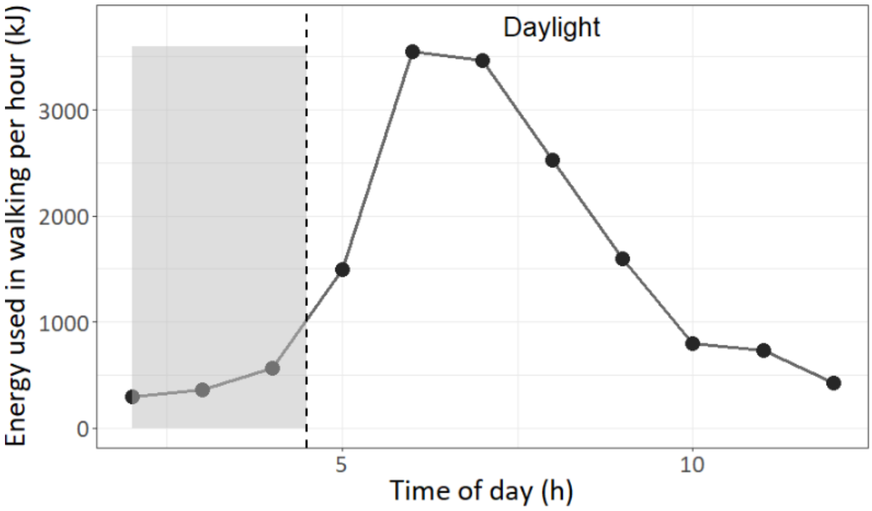

Figure. 13 – Theoretical amount of energy used by ibex by walking during the ascent phase of their daily altitudinal migration based on relationships between energy expenditure and slope determined for a congener, the pygmy goat.

I note that these costs are extremely high but accord with data gathered on bighorn sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*) by Daily and Thompson (Aublet et al. 2009, Mason et al. 2017) who noted that the energy expended by the sheep and goats for raising 1 kg of body weight by one metre vertically (on a 21.5 slope) exceeded the highest cost documented for quadrupeds.

Thermal consequences of climbing

Given that the ibex is reported to be particularly susceptible to higher temperatures (Heinrich 1977), it is useful to consider how the theoretically high energy costs of walking up slopes during the altitudinal migration might lead to thermal load, which can be expressed in terms of projected body temperature increment (although the animals presumably adopt heat-loss mechanisms to counteract it). For this, the total energy used per hour to climb (Fig. 13) should be multiplied by 0.80, since about 80% of energy expenditure is due to heat generation (Hodgson et al. 1993, Sandro Campos Maia et al. 2014), and then divided by the specific heat capacity of Ibex tissue multiplied by the Ibex mass. This can be expressed as;

$$\text{Temperature increment} = (\text{Energy used to climb per hour} \times 0.8)/(\text{SHC}_{(\text{Ibex})} \times \text{Mass}_{(\text{Ibex})}) \qquad (7)$$

where the mass is in grams, the SHC is the specific heat capacity (in J/g/°C) and the temperature increment is in °C. If I assume that ibex body temperature is normally maintained by metabolic processes other than walking (resting, grazing etc.), I can allocate the heat generated by walking to a temperature increment over the whole body. For this, I assume that the specific heat capacity of ibex tissue is roughly the same as that of muscle at 3.42 J/g/°C (https://itis.swiss/virtual-population/tissue-properties/database/heat-capacity/). The calculations indicate that, in the absence of cooling mechanisms (e.g. increased radiation, evaporation etc. (McNab 1973)) ibex body temperatures during the altitude gain phases of their altitudinal migration would rise by up to about 1C per hour (Fig. 14), which serves to illustrate the rough magnitude of the expected thermal load.

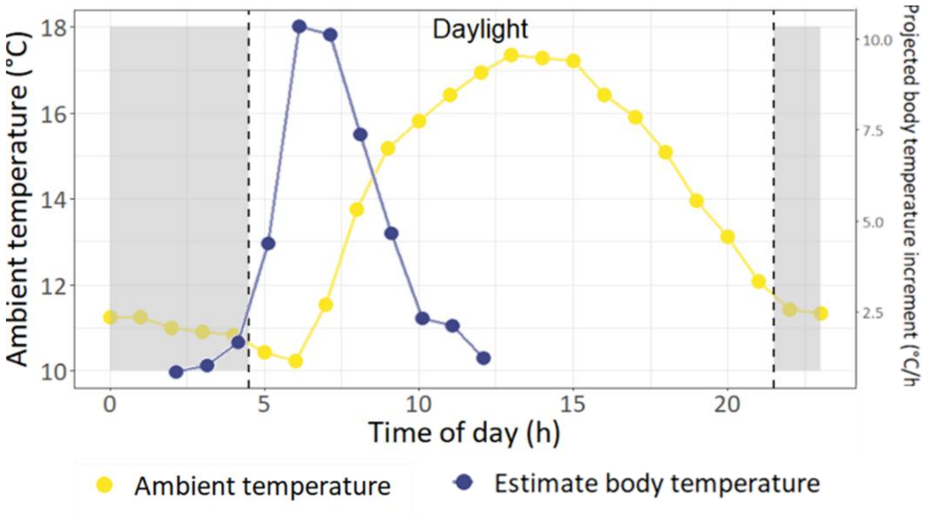

Figure 14– Blue-line; theoretical heat production expressed by body temperature increase that could be sustained by Alpine ibex (in the absence of cooling mechanisms) due to uphill slope walking during the daily altitudinal migration based on the energetics of walking using data from pygmy goats. The yellow line shows the mean ambient temperature as measured by temperature sensors associated with the ibex tags (cf. Fig. 7a). Note how the highest predicted temperature increments occur at the lowest ambient temperatures, with these rapidly dropping off as the ambient temperatures increase.

Although the exercise of predicting the heat increment of climbing in ibex is subject to many assumptions (not least of which is that the overall mass-specific metabolic rate of pygmy goats is comparable to that of ibex when the elephant-shrew curve would have it higher

(Aublet et al. 2009, Mason et al. 2017)), it does serve as a useful pointer to the rough extent of heat production and how it is predicted to vary during the climb.

Consequences of the model for understanding Ibex altitudinal migration

Two things are striking about the output of the model, one being that the heat produced during walking is very significant. The other is that the ibex climb the most, and therefore produce most heat, at the coolest part of the day (at *ca.* 6h) (Fig. 14), rapidly diminishing their climbing activity as the ambient temperatures rise. Certainly, this accords with observations that ibex are easily heat-stressed (Fuller et al. 2016). This suggests that these animals have to balance activity, and specifically high metabolic cost (heat-producing) behaviours, with ambient temperature carefully (Maloney et al. 2005, Aublet et al. 2009, Sheila et al. 2010). Such higher metabolic costs presumably also include grazing, where the mean VeDBA estimates are some 4-5 times higher than resting (Table 3). I suggest, therefore, that the early morning and early evening grazing activities at lower ambient temperatures (Fig. 7a,b) could allow the animals to feed and minimize heat stress (Haase and Underwood 2013). In addition, the altitudinal migration would seem to be a balance of the ibex moving up to higher altitudes where temperatures are lower, which should allow them to remain as close to their thermoneutral zone as possible, with the thermal consequences of having to climb (Pyke 1981) Judicious management of the climbing process (travel speeds (Halsey and White 2017) slopes selected (Halsey 2016) percentage time spent walking etc. (Villaret and Bon 1995, Bon and Joachim 2001) would seem critical in this. But all this also hinges on them finding appropriate food in the spaces they can access using their movement strategies.

Consequences of environmental temperatures for goats

By comparison with the ibex, the goats undertake a trivial, and less definitive, daily altitudinal migration, tending to descend during the day but by less than 100 m (Fig. 9). This means that, as a result, they do not have to deal with prolonged heat-producing activities compared to the ibex and will encounter only marginally increased altitude-related temperatures onto which the daily ambient temperature cycle is superimposed (Fig. 7a). This moderated pattern is, in part, almost certainly due to the goats having to forage as central place animals, having to return to their pen at night, which severely limits the extent of their behavioural patterns (see Chapter 4). Worth noting that this finding is comparing male ibex and female goats, but studies have shown male ibex to be more heat sensitive than female ibex and could account for the differences found in this study (Aublet et al., 2009; Grignolio et al., 2010). More generally, sex differences in movements and habitat use can occur in ungulates due to sex differences in weather sensitivity (e.g. in deer; Conradt et al. 2000), nutritional needs (e.g. deer; Conradt et al. 1999), predation avoidance (e.g. kudu; Du Toit 1995), thus the differences observed here between female goats and male ibex are likely driven also by sex differences.

Space-use by Ibex and goats

The smaller numbers of ibex used in the study compared to the goats, and their greater variability in habitat selection, both in terms of slope index (Fig. 11) and vegetation type (Fig. 10), belies an important distinction between the two species and sampling protocols. This is that the goats all essentially acted as one herd, making collective decisions about (Sumpter 2006, Delgado et al. 2018) where to move and forage (Laundré et al. 2010) with concomitant reduced inter-individual variability (Chapter 4). By contrast, the studied ibex were from different groups, moving in different areas.

Inter-specific differences in movement patterns and grazed habitat

The ranging patterns of the goats were typified by that of central place and have been discussed at length in chapter 4. Briefly though, over time, the herd took trajectories that resulted in a fanned-out pattern from the central place (the pen). This resulted in them exploiting a wide variety of vegetation and, importantly, ostensibly not over-visiting any particular area so that resources were presumably not over-grazed (Parker et al. 1984, Halsey and White 2017).

The ibex were clearly not bound by a central place, either as a group or as individuals. Indeed, one individual (Ibex 2) exploited two areas that were separated by a distance of ~5.8km over two distinct time periods (Fig. 6). However, there was over a fourfold variation between individuals in the total distance they covered (range 63-213 km) although this was reduced to less variation if the areas in which they actually grazed are compared (Table 3, Fig. 6). This indicates that this species will travel extensively, either to feed or perhaps for other reasons, such as to find areas with minimum disturbance, but is able to find sufficient food in relatively small areas which appear as distinct patches within the overall area within which they might forage (Fig. 6).

Within their frequented areas, both goats and ibex showed clear preferences for habitat types (Fig. 10). Again, the goat data are discussed at length in chapter 4, with animals selecting grasses and vegetation on bare rocks preferentially while the ibex preferred shrubs, deciduous woodlands and herbs. This accords with Lussig et al. (Iussig et al. 2015) who noted that domestic goats prefer grass or herbs species, and Villaret and Bon (Villaret and Bon 2010), who found that ibex in the Alps predominantly feed on rock, more precisely scree habitat (plants associated with rocky areas) over grass habitats during the summer. It is notable, however, that not all habitat types were common to both species so that is how goats might respond to snow habitats and ibex to areas for farming is not known. Superficially therefore, it would seem that there is some overlap in diet between the two species but also appreciable divergence. The reality is likely to be more complex though because studies such as these, in assessing habitat-, and therefore feeding, preferences, assume that all other things are equal. This is not the case, not just for thermal reasons (see above), but also, notably, with respect to elevation and topography and hence energy landscapes (Llobera and Sluckin 2007, Lempidakis et al. 2018)

Energy landscapes

The energy landscape concept (Dunford et al. 2020, Shepard et al. 2013) assumes, all other things being equal, that animals will use the path of least energy cost to move between two points. This can include substantial deviations from a straight-line course to a resource to be exploited (Stüwe and Nievergelt 1991). Since moving up and down inclines, particularly steep ones, are some of the most energetically taxing behaviours that animals can engage in (Pereira et al. 2009), I expect both goats and ibex in our study areas to be adopting paths that follow shallow gradients, even if they are on steep slopes (van Beest et al. 2012, Marchand et al. 2015). This is not only responsible for the zig-zag tracks of ungulates moving up steep slopes (Marchand et al. 2015) but will also act as a deterrent for animals to exploit steep slopes in general. This may be particularly the case when these animals engage in altitudinal migration, as was the case with the tagged ibex. Superimposed on this, it has been pointed out that moving up inclines is proportionately more onerous for larger animals (because the metabolic cost is a larger fraction of the mass-specific metabolic rate (Wall et al. 2006)). As a consequence, I would expect the ibex, with a mean mass of 80.1 kg (Table 3), to be more steep slope-shy than the goats (mean mass <25Kg– chapter 4) and therefore, perhaps, tend to favour vegetation that grows on shallower slopes.

However, the goats preferred gentler slopes than the ibex to forage (Fig. 11) and it is not immediately obvious why. The answer might, in part, be due to selection pressures for life on steep slopes. Aside from being energetically onerous (Laundré et al. 2010, Gallagher et al. 2017), steep slopes are considered to constitute an 'accident landscape' with a high probability of slips and trips in tandem with a high likelihood of detriment (Wheatley et al. 2021). Whilst all goats are well adapted to steep slopes, the selection for this movement ability likely has been less stringent for domestic goats which have been domesticated in a variety of habitats, including flatlands, and selected for different aims (Laundré et al. 2001). Thus, I suggest that the preference for shallower slopes in the goats, as to ibex, a highly specialised mountain species, might be related to this difference, too.

I also propose that the steeper slopes used by the ibex could potentially reduce thermal problems (see above) if these slopes were more northerly facing by being more likely to be in shadow, especially at diminished sun zenith angles. I did not determine the extent to which slope choice showed directional bias and did not analyse effects and selection for aspect (e.g.

north vs. south facing) but, given that many ungulates show shade-seeking behaviour (Ciuti et al. 2012), e.g. by resting under trees (García-Martínez and Bernués 2009, Sturaro et al. 2013), this would be an interesting aspect to examine.

Landscapes of fear

Inter-specific area-use differences, in both grazing habitat as well as slope incline preferences generally (Fig. 10) may also be partially explained within the concept of the landscape of fear (Beniston 2006). This notion recognises that animals may prefer not to frequent particular areas due to potential for predation associated with those areas (Aublet et al. 2009, Mason et al. 2017). Certainly, prime foraging areas are avoided by some ungulates if they are more likely to be depredated in these habitats (Aublet et al. 2009, Mason et al. 2017) and this extends to reaction to humans (Aublet et al. 2009, Mason et al. 2017). Understanding that there is a huge difference in the perception of people as a threat between domesticated goats and ibex needs serious consideration in any treatise that attempts to examine differences in space-use between the two species rather than assuming that habitat differences are simply based on feeding preferences.

General competition between Ibex and goats, annual and long-term temperature trends

A prime aim of this work was to investigate spatio-temporal differences in space use by grazing goats and Alpine ibex. Conversely, as the populations were studies in different places and times, the present work could not investigate competition between the two species, except point out that there seems to be appreciable overlap in grazing preferences thus there might be potential for competition if the two species were to occur in sympatry. However, this is only likely to be an issue if goats are allowed to graze in a manner that is not central place foraging, which is the norm in the French Alps (Aublet et al. 2009, Mason et al. 2017). Such a foraging pattern means that the goats will always graze within a defined range (see Chapter 4), with this being limited by the distances that they can roam within the day.

Provided that the distribution of such goat herds leaves appropriate space for the ibex, with their ability to move across the landscape using the environmental resources in a patchy manner (Fig. 6, cf. goat figure from Chapter 4), I believe that potential competition is unlikely to be a problem for the ibex.

Our study, which was conducted in some of the year's warmest months, does, however, point to the confounding effects of temperature in space-use, both at a seasonal level and, in the longer term, as a result of global warming (Aublet et al. 2009, Mason et al. 2017). This ties in with previous work (Aublet et al. 2009, Mason et al. 2017) that suggests that ibex are sensitive to temperature. Higher temperatures presumably reduce the overall time that ibex can spend grazing and could well make large areas of the Alps, the lower, hotter regions, unviable for them. I would expect patterns to vary with season though, and this would have to be factored into any considerations of livestock competition. I suggest that year-long deployments of position and activity-determining tagging technology should be deployed on the ibex to provide the necessary data to examine this. In the meantime, caution with regard to livestock usage of the Alps would seem sensible in order to balance the abundance of introduced with native fauna.

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Chapter 6

Landscape of rage: *Identification and fine-scale mapping of head-butting in domestic goats (Capra aegagrus hircus) and alpine ibex (Capra ibex) using biologging*

Abstract

Head-clashing by ungulates is of high interest to behavioural ecologists because it is costly and is associated with competition for resources (food, minerals, space and access to mates). Although the behaviour is distinctive, it is difficult to study and record, especially in mountain ungulates. This study uses animal-attached loggers to record acceleration and global position system (GPS) data on domestic goats (*Capra aegagrus hircus)* and on Alpine ibex (*Capra ibex)* to develop new methods, and quantify and locate in space, head-clashes in both species. The method used a time-series lowest common denominator (LoCoD) Boolean approach to successfully identify >80% of the observed head-clashes of the goat with no false positives (against verified data from visual observations), and was modified to be used on ibex biologging data. Mapping the behaviour revealed how ten tagged domestic female goats competed for a salt lick and space within their pen. Similar analysis on data from six male ibex showed expected trends, with head-clash frequencies being performed throughout the year but with a sudden increase during the pre-rut and rutting periods. Mapping the behaviour showed the location of the agonistic interactions before and during the rut. It also showed increases in distances travelled at this time, in agreement with the seasonal movements expected during that time, and supporting the theory that the mating season involves a heavy investment by adult male ibex. This study provides hence new approaches to use animal-attached logger data to reveal important, but difficult to observe directly, behavioural changes associated with time and space in ibex life history, with potential to inform conservation management strategies.

Introduction

Head-butting by animals, whereby two individuals clash the fronts of their heads together (Shank 1972), is widespread and has keenly interested ecologists and ethologists for a long time (Darwin 1871). There is evidence that it was used by dinosaurs (Barghusen 1975, Benoit et al. 2017) and that it occurs in extant animals as diverse as insects (Siva-Jothy 1987), fish (Muñoz et al. 2012), cetaceans (Gowans and Rendell 1999) and ungulates, where it occurs very frequently (Shank 1972, Clutton-Brock 1989, Pipia et al. 2008, Willisch and Neuhaus 2010), both in wild animals and their domestic equivalents. In particular, the 'head-clash' is present in both domestic goats (*Capra aegagrus hircus*) as well as the congeneric alpine ibex (*Capra ibex*). In these goats, the behaviour consists of individuals rearing back and surging forward to bang their horns together – a process that can be repeated several times in succession. The display is associated with males showing their dominance while competing for females (Shank 1972, Clutton-Brock 1989, Willisch and Neuhaus 2010, Stanley and Dunbar 2013) but it is also present in female domestic goats competing for resources (Pretorius 1970). This behaviour is energetically costly and dangerous action as animals accelerate rapidly towards one another, finally coming together with a high impact collision characterised by large forces near critical cranial organs (Alvarez 1990). In goats at least it, however, rarely leads to physical damage due to structured heads which absorb the impact (Shackleton and Shank 1984).

Head-butting is a fundamental part of the mating season or the rut (Clutton-Brock 1989, Mysterud et al. 2004, Holand et al. 2006), where particularly males of polygynous ungulate species invest much of their energy in competing for, and defending access to, the females (Mysterud et al. 2004, Villaret and Bon 2010, Willisch and Neuhaus 2010). Agonistic behaviour in general, associated with the rut, aside from head-clashes, is energetically costly and often associated with the males prioritising mating even over grazing, leading to a reduced post-rut likelihood of individual survival during the subsequent winter months. Given that head-clashing, dominance and access to females are all associated, the study of head-clashing is of particular interest because it is one aspect that relates animal effort to chances of reproductive success and survival (Brivio et al. 2010). Alpine ibex display a strategy of established dominance hierarchies, a hierarchy tactic that involves the males competing with one another *via* head-clashes throughout the year to assess each individual dominance. During the pre-rut and rutting period there is a surge in male on male agnostic behaviours, but less than in other ungulate species (Toïgo et al. 2007, Brivio et al. 2010, Tettamanti and Viblanc 2014), with evidence that ibex males may adopt conflict reduction strategies to reduce such energy-intensive interactions during the rut (Willisch and Neuhaus 2010).

Although head-clashes are obvious and striking behaviours to the observer, understanding the full extent of their usage is particularly problematic in cryptic ungulates that adopt this behaviour. This is because the ease with which they can be observed is highly context dependent: Animals that are easily observable from an appropriate distance may engage in head-clashes but inappropriate proximity of the observer changes behaviour. This makes mountain ungulates particularly problematic because, living in their extreme environments, they cannot be observed for much of their day. Even when observable, direct visual observation requires considerable field work effort, with typically only few events observed. For example, Willisch and Neuhasu (2010) conducted 1141 hours of 238 continuous focal observations over three years in the Alps during the rut on a total of 71 different males, recording 76 fights among around 62 different male dyads. This problem can, however, be circumvented by biologging techniques (Brown et al. 2013), if robust approaches are developed to reliably identify the occurrence of such behaviours. The most sophisticated biologgers contain GPS units, accelerometers, magnetometers, pressure and temperature sensors (and more) and record these parameters at infra-second rates (typically tens of Hz) (Holton *et al*. in press). When such tags are placed on a study animal, they can reveal animal movements (Shepard et al. 2008, Handcock et al. 2009), behaviours (Fehlmann et al. 2017, Williams et al. 2017), physiologies (Roper et al. 2001, Carbone et al. 2007, Handcock et al. 2009) and energetics (Qasem et al. 2012, Wilson, Börger, et al. 2020, Dickinson et al. subm.) in relation to environmental factors seamlessly over time without incurring the classic time-consuming, physically limiting and subjective problems of the straightforward observational approach (Canine 1990, Crofoot et al. 2010). This has obvious value for studying head-clashes in mountain goats whereby, in particular, the likely ability of accelerometers to define head-clashes due to the substantial deceleration incurred during the clash can be combined with the fine-scale movement paths of animals using GPS-corrected, magnetometer-derived dead-reckoning (Bidder et al. 2015) (see Chapter 3) to examine social interactions in detail across time and space.

The aims of this study were to; (i) use *Capra hircus* as a model to examine tag-derived accelerometer data of head-clashes to identify specific features that are unique to the behaviour, (ii) create robust classification rules that correctly identify these agonistic interactions in freely roaming goats and wild alpine ibex, (iii) pair the quantified head-clashes with dead-reckoned high resolution paths to find areas of social interest and describe any diurnal patterns in domestic goats, and (iv) adopt the approach for Alpine ibex to reveal where aggressive interactions occur during and outside the rut and to elucidate monthly patterns in the frequency of the aggressive behaviour.

Methodology

Study site

I placed loggers on animals from a herd of domestic goats located in a pasture valley within the Massif du Bauges game and wildlife national reserve (45.60485°N, 6.18295°E) in the French Alps (Fig. 1a). This farmed group consisted of over 40 females and 1 male that browsed a segregated area of approximately 2 km^2 between June and October.

Wild ibex were captured at several field sites the French Alps, in the Belledonne mountains (45.2241°N, 6.0305°E) centred around the village of Allemond (Fig. 1b).

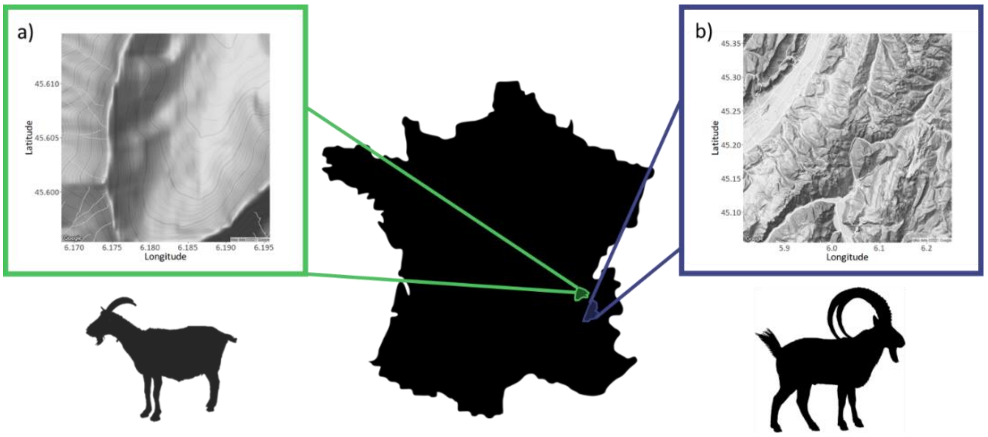


Figure 1 - Maps (google) of (a) the site used for the domestic goat study within the Bauges massif and (b) the site used for the alpine ibex study within the Belledonne massif, both with respect to France.

Further details of the study sites, study species, biologger setups, deployments of collars and focal observations are given in chapters 3 and 4.

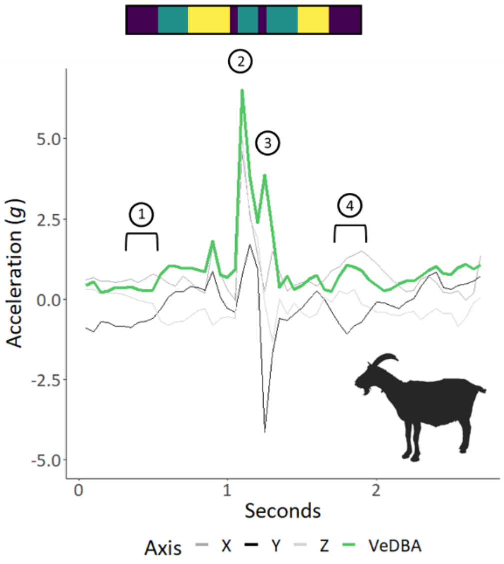
Behavioural observations

Behavioural observations were recorded using the *ab-libitum* focal sampling method (Altmann 1974) noting time carefully so that behaviours could be synchronised with acceleration data to ground-truth all behaviours. A total of 6 hours of observations across six individual goats were taken with any change of behaviour recorded resulting in over 124 observations (appendix, table 7).

Identification of head-clashing behaviour

To quantify the head clash behaviour, 43 recorded observations of the behaviour in animals tagged with biologgers were compared to their corresponding acceleration data and inspected using the Daily Diary Multiple Trace – DDMT software (Wildbyte Technologies 2020). Vectorial dynamic body acceleration (VeDBA – for definition see chapters 3 and 4) was selected as a prime metric for identification of the behaviour as it showed clear peaks in sequential waves during head-clashes while also mitigating against issues associated with tag orientation and noise in the data. VeDBA achieves this by integrating all three (Qasem et al. 2012) acceleration axes. A time-dependent approach, which breaks down the behaviour into time-based segments using a 'lowest common denominator' (LoCoD) (Wilson et al. 2018), was chosen as the behaviour showed regular and predictable waveforms with defined wavelengths in the VeDBA signal. An initial simple 'lowest common denominator' (LoCoD) implementation however classified periods with high VeDBA values but this identified both head-clashing and some cases of running as false positives. Thus, I used a combination of LoCoD rules on multiple interacting elements incorporating time, which allowed head-clashes to be definitely separated from any other behaviours.

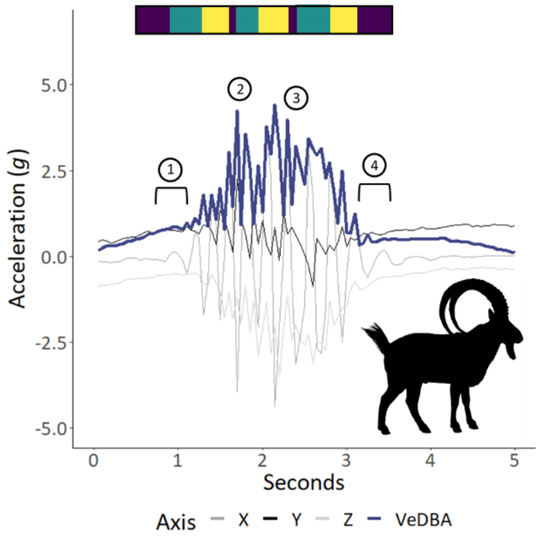
For this, the time series was expanded to create a detection algorithm that incorporated different sequential elements, all of which had to be recognised as TRUE based on their values and their timing for head-clashing to be identified. Timing windows included; the number of sequential data points within the first element for which the rule had to be true, how many sequential data points would then be skipped until the search for the next rule to be true for the second element (i.e. generation of a 'blindspot') and how many sequential data points should be searched within the next element for the next rule to be verified. If the first element was found to be true, the search continued for the second element, this process continuing for all elements to be true in sequence before the behaviour was identified as a positive match (see details of the general method in Wilson *et al.*, 2018). For the domestic goat, a four-element rule was defined to pick out a head-clash (Fig. 2, Table 1). Detailed inspection of the acceleration signals allowed each element to be justified. For example, element 1 needed a period of low activity to initiate the search for the behaviour since head-clashes are always preceded by a pause. Element 2 recognised a defined high acceleration in the VeDBA (surpassing a threshold) associated with the head-clash. Element 3 recognised a second wave of high VeDBA as part of the head-clash resulting from hysteresis in the collar while element 4 was a renewed period of low activity because individuals always paused following head-clashes (Fig. 2, Table 1).



Element	Rule	How many events valid for 🟪	Range to begin next search 🟦	How many events to search for the next element 🟨
1	VeDBA < 1.0	10	10	20
2	VeDBA > 1.5	1	3	10
3	VeDBA > 1.5	1	10	10
4	VeDBA < 1.0	10	NA	NA

Figure 2 - A line plot of how acceleration and VeDBA changes over time during an observed domestic goat head-clash. Each element is numbered on the signal with the time windows colour-coded in the bar above the plot. Table 1- Each element is listed with its corresponding rule and timing.

The time series was then adapted to be used on the alpine ibex (Fig. 3, table 2). Since the domestic goat is so anatomically similar to wild caprids, and head-clashing is so distinct, I believe that the algorithm for detecting clashes can be adapted in a robust and straightforward way. After inspection of the ibex data using the goat head-clash algorithm, I modified the search algorithm for alpine ibex by increasing the threshold for the VeDBA peaks – due to manifestly higher acceleration signatures (the species is heavier, with markedly larger horns, and therefore produces head-clashes with a higher force). The timing of the second VeDBA peak with respect to the first was also increased due to the greater time for the collar hysteresis stemming from the greater size of the alpine ibex (Fig. 3, Table 2).



Element	*Rule*	*How many events valid for* 🟪	*Range to begin next search* 🟩	*How many events to search for the next element* 🟨
1	VeDBA < 1.0	10	10	20
2	VeDBA > 3.0	1	3	40
3	VeDBA > 3.0	1	10	10
4	VeDBA < 1.0	10	NA	NA

Figure 3 - Changes in acceleration and VeDBA over time, during what was believed to be an ibex head-clash (unobserved). Each element of the search algorithm to define head-clashing in ibex is numbered on the signal with the time windows colour-coded in the bar above the plot. Table 2- Each element is listed with corresponding rule and time windows.

Aggressive interactions are often related to efforts to protect, or gain access to, contested resources. To investigate relations between the spatial distribution of head clashing events and the distribution of food resources in goats, I related the distribution of head-clashing events to the distribution of grazing time (with grazing identified and quantified as detailed in chapters 3 and 4).

Dead-reckoning

Dead-reckoning was used to convert low resolution GPS into high resolution estimate locations (Bidder et al. 2015). This process is a series of vectorial calculations on acceleration and magnetometry data from which speed and animal heading are derived (see Chapter 3 for further details and methods). To deal with cumulative error in heading and variation in the relationship between VeDBA and true speed, the periodic GPS fixes were used to correct the dead-reckoned path. This correction aligned the dead-reckoned path with GPS data after correcting for rotation, forcing the dead-reckoned path to fit between the corresponding GPS points. The DDMT programme was used to dead-reckon as well as to GPS-correct to produce

1 Hz locations for each individual animal for periods of up to 30 days, using the method detailed in chapter 3.

Mapping behaviours

Each head-clash was matched to the GPS-corrected dead-reckoned path using time as the common base. This gave a location for each head-clash and allowed the behaviours to be mapped. R (R Core Team, 2019) and R Studio (RStudio Team 2020) and the package "ggmap" was used to access google maps satellite imagery to map out the behaviours.

To assess the head-clash density over space, the R "recurse" package was used. This revisit analysis marked any occasions when two or more head-clashes occurred within a defined proximity of one another. Proximity areas were selected based on the species. I used a 25 m^2 proximity for the ibex and 10 m^2 for the goats since these animals moved as a herd. The mapped behaviours were then coloured according to revisits to give a heat map effect for visual inspection.

Distance travelled

To calculate the distance between adjacent locations, step length was calculated using the "fossil" package within R , based on the following equation;

$$Err = a\cos(\sin Lat_{DR1} \cdot \sin Lat_{DR2} + \cos Lat_{DR1} \cdot \cos Lat_{DR2} \cdot \cos(Lon_{DR2} - Lon_{DR1})) \cdot 6371$$

Where; Lat_{DR1}= Latitude of dead-reckoned step 1, Lat_{DR2}= Latitude of dead-reckoned step 2,Lon_{DR1}= Longitude of dead-reckoned step 1, Lon_{DR2}= Longitude of dead-reckoned step 2

To give total distanced travelled the sum of all step lengths was calculated.

Results

Domestic goats

The time series behaviour identification algorithm was successful in picking out 36 of the 43 observed head-clashes, giving the rule an 84% reliability rate. The ethogram data from the direct visual observations of 6 hours across six goats provided a total of 81 events of other behaviours, none of which elicited false positives in the search algorithm, thus with 0% false positive rate.

Revisit analysis on all individuals with identified head-clashing events, showed an epicentre to the behaviour (Fig. 4), with a maximum of 66 occurrences within the goats' pen. There were also dense patches of head-clashes just north-east and south-west of the pen, with occasional other patches of higher reoccurrences at the outskirts of the goats' herd movement range (Fig. 4a). Correcting this information for time spent in an area however, by considering number of head clashes per hour, showed there was a lower incidence of head clashes per hour around the pen and a higher incidence at the range limits, particularly in the north-east and north-western sectors (Fig. 4b)

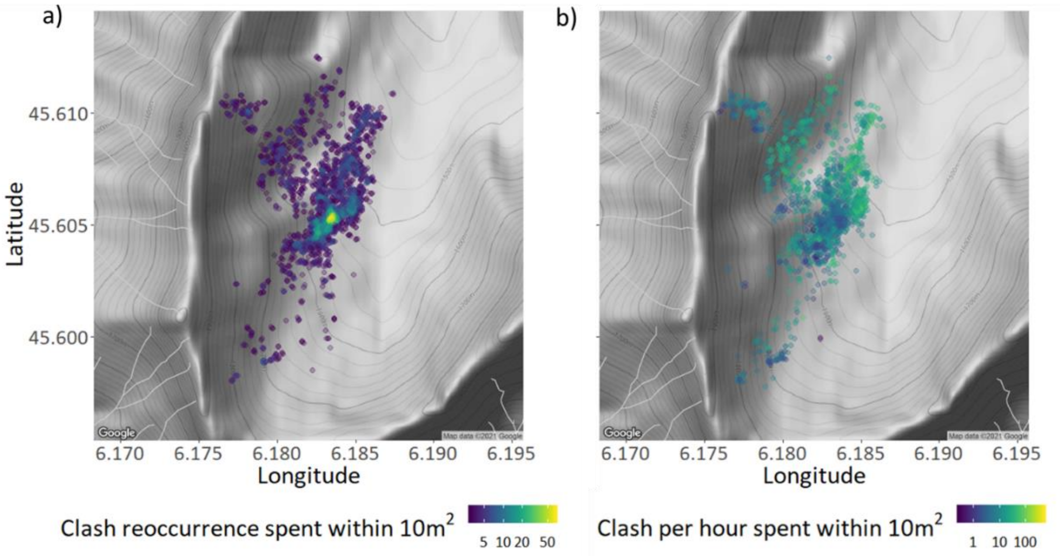


Figure 4 - Mapped head clash behaviours of domestic goats, with each behaviour location coloured by (a) the number of reoccurrences to show density (with reoccurrences being defined as two or more incidences of head-clashing within 10 m^2 of one another) and (b) clashes per hour spent per location (with time spent being defined

from 1 Hz location data within 10 m^2 of one another). Satellite map supplied by google maps. Data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within les Bauges, France.

There was also notable inter-individual variation in the time-corrected incidence of head clashes, reflected both in the absolute values as well as their distribution in space (cf. goats 4 and 9 in Fig. 5).

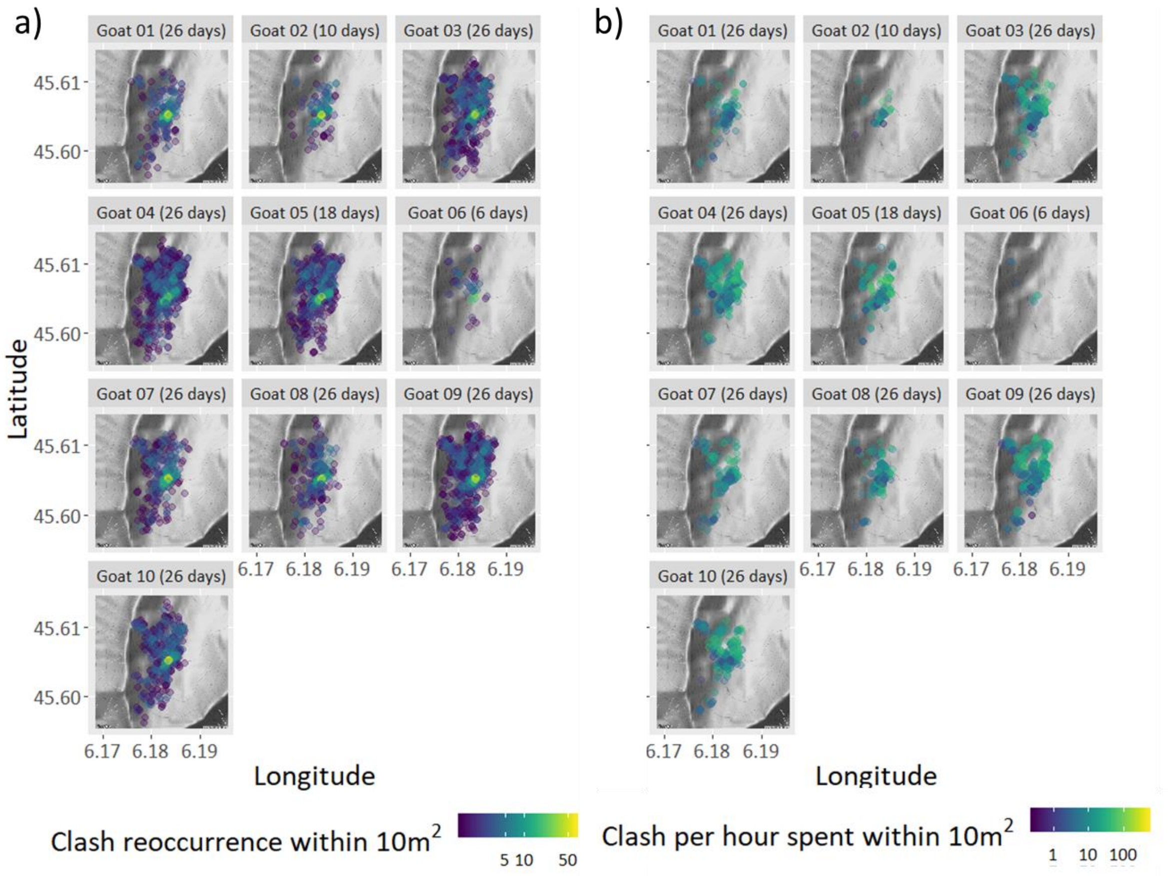


Figure 5 - Mapped head clash behaviours for individual goats, with each behaviour location coloured by (a) the number of reoccurrences to show density (with reoccurrences being defined as two or more incidences of head-clashing within 10 m^2 of one another) and (b) clashes per hour spent (with time spent being defined from 1 Hz location data occurring within 10 m^2 of one another). Satellite map supplied by google maps. Data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within les Bauges, France.

Average daily head-clash frequency showed a 5-fold variation between individuals (Table 3), unrelated to the number of days the goats had been monitored ($\rho = 0.2610$; $p = 0.4663$; Spearman rank correlation). Similarly, VeDBA at impact provides a measure of the force of impact (Table 3) and there was individual variation in the mean VeDBA (force) of head-clashes (CV = 0.0744) and especially the maximum VeDBA (CV = 0.2137). Interestingly (see also Table 3), there was a strong negative correlation between the daily frequency of head-clashes and the mean VeDBA of head clashes (ρ = -0.73; *p* = 0.0163; Spearman rank correlation), whereas there was no consistent relationship with individual variation in the maximum VeDBA of head clashes (ρ = 0.14; *p* = 6992; Spearman rank correlation).

Table 3- List of metrics and frequencies derived from the behaviour and dead-reckoned data for each domestic goat. Data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within les Bauges, France.

Animal ID	*Daily Diary data analysed (days)*	*Daily mean head-clash frequency*	*Daily average distance travelled (km)*	*Mean VeDBA during head-clashes (g)*	*Max VeDBA during head-clashes (g)*
Goat 1	26	12	8.58	0.6	14.44
Goat 2	10	12	8.36	0.57	18.34
Goat 3	26	25	8.29	0.54	16.16
Goat 4	26	39	8.68	0.49	16.72
Goat 5	18	40	8.65	0.48	14.94
Goat 6	6	8	8.65	0.52	8.86
Goat 7	27	13	9.02	0.58	20.98
Goat 8	26	16	8.10	0.55	15.45
Goat 9	26	40	9.43	0.51	16.06
Goat 10	26	24	8.98	0.51	20.92
Mean		23	8.67	0.54	16.29

Average head-clash frequency across all goats over the course of the day showed the same general ungulate activity pattern of high occurrence in the morning after dawn and the evening before sunset – compare the pattern of hourly head clashing frequency in Figure 6 with the very similar pattern of the distance moved per hour.

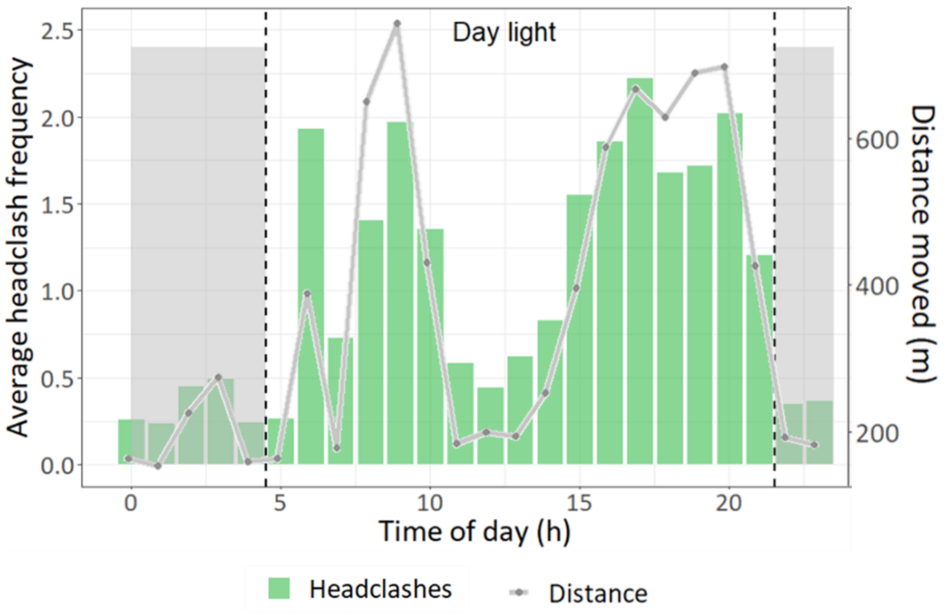


Figure 6- Mean head-clash frequency across of individuals as a function of hour of day. Data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within les Bauges, France.

In accordance with this pattern, the frequency of head-clashing was linked to both distance moved (Fig. 7a) and grazing frequency (Fig. 7b). Specifically, the hourly number of head-clashes across all individuals (y) was related to the average hourly distance travelled across all individuals (x) *via* ($y = x0.003 - 0.467$, P<0.001, R^2= 0.84). Using the behavioural analysis for grazing described in chapter 4, the proportion of each hour spent grazing could be defined across all goats. Average hourly head-clashes across all individuals (y) were significantly positively related to the hourly proportion time spent grazing across all goats (x) *via* ($y = 3.282x + 0.238$, p<0.001, R^2=0.67).

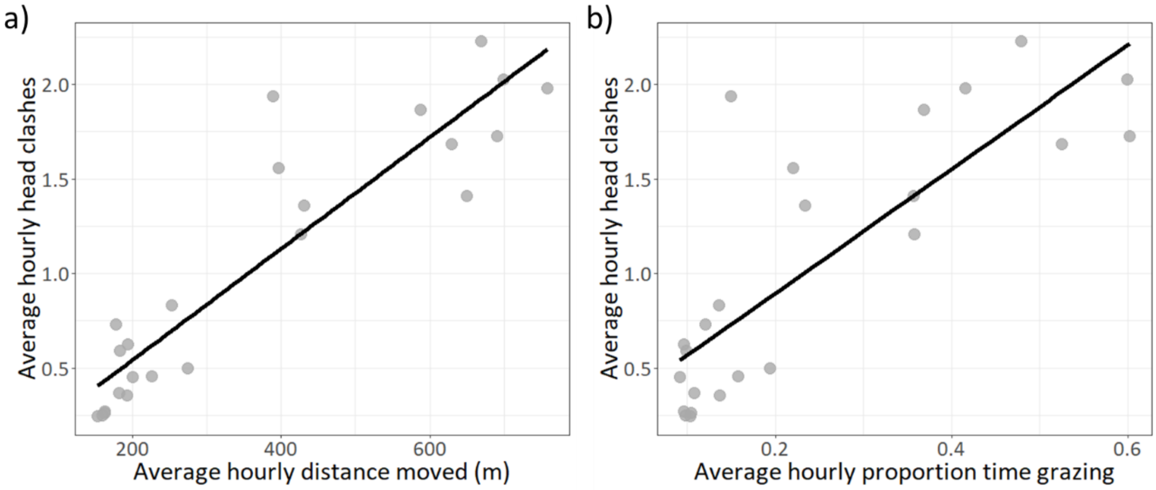


Figure 7- (a) Scatter-plot of mean hourly head-clashes across all individuals against average hourly distance moved across all individuals (calculated from the dead-reckoned path); (b)- Scatter-plot of average hourly head-clashes across all individuals against the average hourly proportion of time spent grazing across all individuals. Data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within les Bauges, France.

Wild ibex

Based on the constructed head-clash algorithm for ibex, clash locations were apparent across the area frequented (Fig. 8a) with what appeared to be hotspots. In particular, a dense patch was revealed close to the capture site with 10 head-clashes/50 m^2, two other locations had maximum occurrences of 30 head-clashes/50 m^2 (Fig. 8a). As with the goats though, the spatial pattern of the frequency of head-clashes per time differed from that of absolute numbers of head-clashes, with hotspots of high head-clashing frequency being widely scattered across the range, with a particularly high incidence in the north-western sector (Fig 8b).

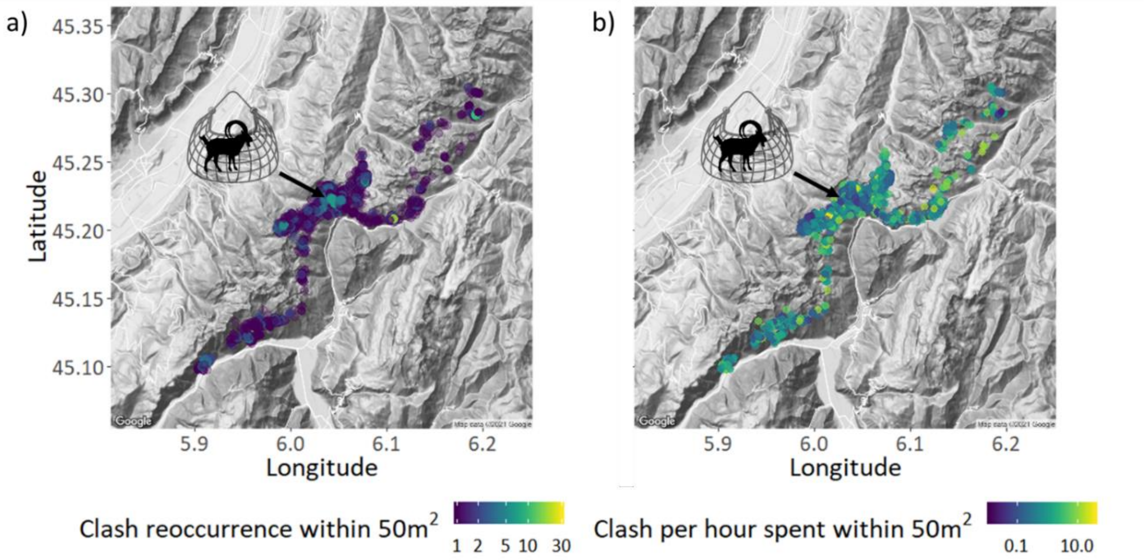


Figure 8 - Mapped head-clash behaviours for alpine ibex, with each clash location coloured by (a) the number of reoccurrences to show density (with reoccurrences being defined as two or more incidences of head-clashing within 50 m^2 of one another) and (b) clashes per hour spent (with time spent being defined from 1 Hz locations within 50 m^2 of one another). The capture site is indicated by arrow with an ibex in a net. Satellite map supplied by google maps. Data from varied logging periods (47 to 217 days) from six male ibex tagged in late May to June 2017 within Belledonne, France.

There was appreciable inter-individual variation in the spatial pattern of occurrence and the frequency of head clashes (part of which was due to very different tagging durations and differences in the time of year (see below) (Fig. 9a). The six individual maps indicate that head-clashes were prevalent around the capture site but also occurred over the other areas used by the animals. Again, the picture of absolute numbers of head-clashes changed substantially for individuals if these values were converted to the incidence of head-clashes per unit time (Fig. 9b). For example, ibex 4 displayed a spot with a high number of head-clashes per unit area close to the limit of its north-east range, with a low prevalence in the south-west corner but this pattern was almost reversed when the data were time corrected: Here, head-clashes per unit time (and area) occurred more frequently in the south-west corner (Fig. 9b).

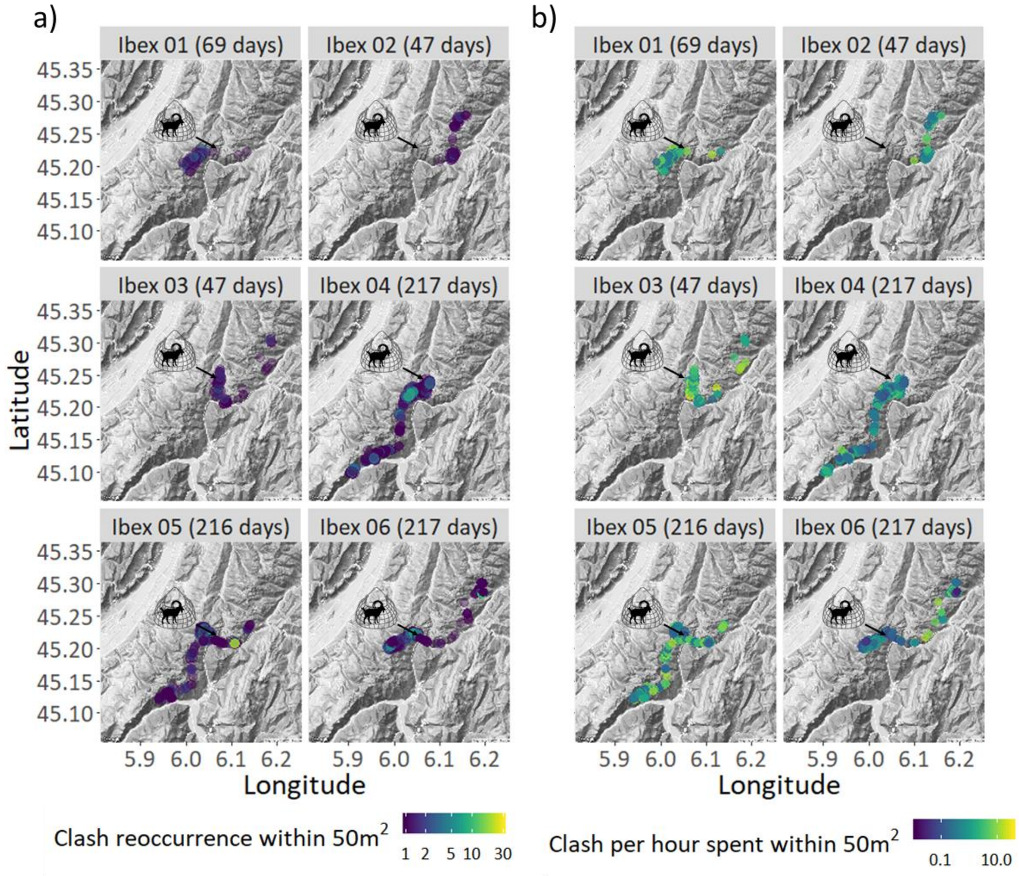


Figure 9 - Mapped head-clash behaviours with behaviour location for each individual, (a) the number of reoccurrences to show density (with reoccurrences being defined as two or more incidences of head-clashing within 50 m^2 of one another) and (b) clashes per hour spent (with time spent being defined from 1 Hz locations within 50 m^2 of one another). The capture site is indicated by arrow with an ibex in a net. Satellite map supplied

by google maps. Data from varied logging periods (47 to 217 days) from six male ibex tagged in late May to June 2017 within Belledonne, France.

The incidence of head-clashes and the distance travelled by the wild ibex varied across the year, with mean daily distance travelled across all individuals decreasing into the winter months into what is considered to be the rutting period – November and December (Fig. 10a). Overall, the total monthly number of head-clashes across all individuals was below 100 clashes until November and December when the incidence more than doubled (Fig. 10a). Closer inspection of the head clashes for just these two months indicated that the three individuals tagged for this time executed this behaviour across their movement range (Fig. 10b).

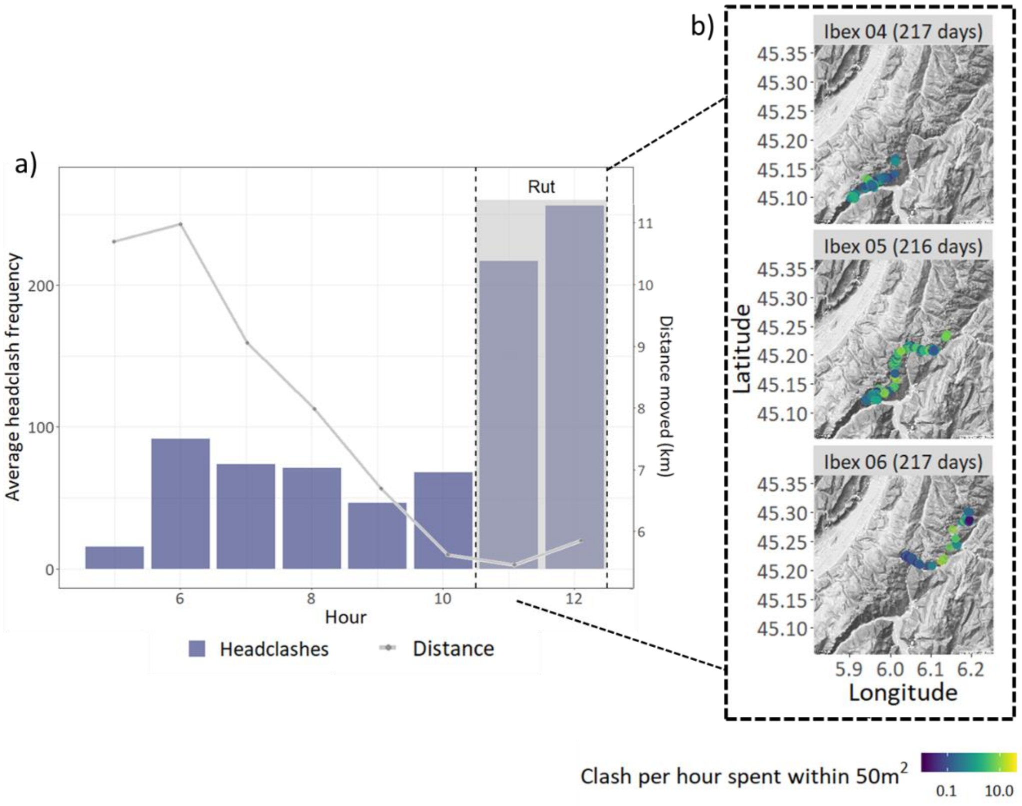


Figure 10- (a) Mean head-clash frequency across individuals with month of year with an interpolated scatter-plot showing how average monthly distance moved across of individuals changes at the same time. (b) shows maps of head-clashes for the three individuals with data available during the rut (November and December). Each head-clash location is coloured by numbers of revisits. Data from varied logging periods (47 to 217 days) from six male ibex tagged late May to June 2017 within Belledonne, France.

Despite the fact that animals outside the rutting period ostensibly travelled more in terms of absolute distance covered per day, all three animals for which I had data of movements and head-clashes both outside and inside the rutting period ranged more widely during the rut than otherwise (Fig. 11), engaging in head-clashes in virtually the entirety of the area covered.

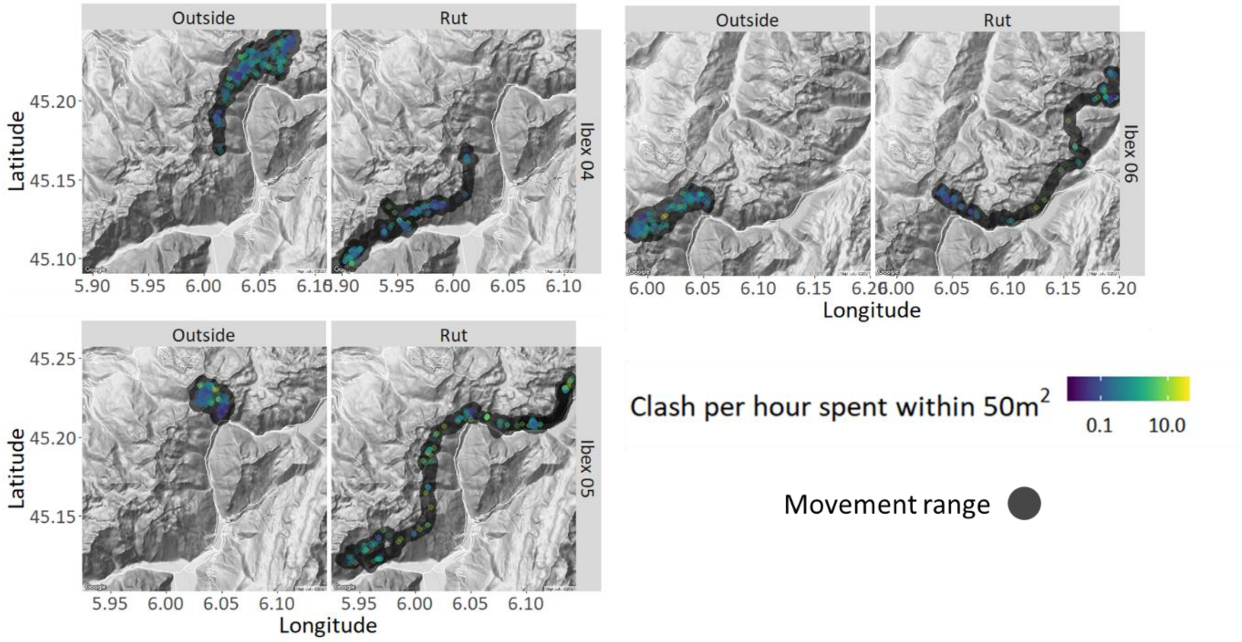


Figure 11 – Comparison of ranging and rutting behaviour for the three individual ibex where data collection covered both rutting and 'non-rutting' periods (cf. Table 4). The total area occupied for the two periods is shown in grey with the time-corrected frequency of head-clashes superimposed. Note the diminutive area exploited outside the rut compared to the rut itself, even though this represented a period that was about 2.6 times longer than the rutting period (ca. 157 days compared to 60). Head-clashing occurred both during the rut and outside it.

In accordance with the very strong increase in head-clashing frequency during the rut (Fig. 11), the daily frequency of head clashing events was higher for the three individuals monitored into the rut, as compared to that of those monitored for shorter periods outside the rut (Table 4). Interestingly, whilst the mean VeDBA of head-clashes did not vary strongly between individuals, the maximum deceleration (VeDBA) recorded was markedly higher for the individuals monitored also during the rut (Table 4).

Finally, comparing the ibex data to the goat data (Table 3 vs. Table 4), given the 2.7 larger average body size of the former (80kg vs. 30 kg), the recorded VeDBA values at impact should be larger, too. Accordingly, the maximum VeDBA recorded across all the individual ibex was 2.9 larger than the maximum VeDBA recorded for the goats; the mean VeDBA was 2.7 times larger.

Table 4- List of metrics derived from the behaviour and dead-reckoned data for each tagged alpine ibex. Data taken from varied logging periods (47 to 217 days) from six male ibex tagged in late May to June 2017 within Belledonne, France.

Animal ID	*Daily Diary data analysed (days)*	*Daily mean head-clash frequency*	*Daily mean distance travelled (km)*	*Mean VeDBA during head-clashes (g)*	*Max VeDBA during head-clashes(g)*
Ibex 1	69	3	12.875	0.9	19.99
Ibex 2	47	2	12.222	1.74	18.37
Ibex 3	47	2	13.306	1.72	16.8
Ibex 4	217	5	8.679	1.11	24.01
Ibex 5	216	4	7.818	1.14	21.54
Ibex 6	217	4	4.437	1.06	24.17
Mean		3	9.890	1.28	20.81

Discussion

Ability to discriminate head-clashes

Head-clashes are distinctive behaviours to observe (Shank 1972, Shackleton and Shank 1984) and, by their nature, are expected to produce a distinctive acceleration signature because an animal (especially the head and neck) moving at an appreciable velocity is suddenly subject to a substantial deceleration (Shank 1972). Indeed, it is hard to imagine any other natural circumstance that would lead to such high deceleration values. This nominally means that it should be simple to search the acceleration data for these high peaks to define head-clashes. However, observations of the domestic goats and examination of their data made it apparent that such interactions vary between relatively gentle 'head-butting' and dramatic head-clashing, where animals may both rear up before descending into a very high force head-clash. Indeed, precursors of what might be construed as head-clashes were also observed, with the head being lowered and an animal surging forward slightly, directing its attention to another, before stopping abruptly before any collision. Even this will produce a low g event. So, what constitutes a head-butt, clash or precursor to this agonistic behaviour (Pretorius 1970)? In some ways, using a threshold, as was done in this chapter, constitutes a solution. According to our definition, a head-clash has taken place when the VeDBA exceeds 1.5*g* (and the other parts of the algorithm are fulfilled; see Methods). I appreciate, in the continuum between a slight movement indicating head-butt intent and a high impact full rearing head-clash, that this process selectively removes the lower intensity agonistic interactions but at least I do not have a filter set to the lower end where there is an argument about whether the data indicate an agonistic interaction at all. Indeed, setting the VeDBA thresholds where I did only led to missing a small percentage of the lower intensity head-clashes. Against this, the process of using high VeDBA thresholds also means that there are unlikely to be other behaviours with which head-clashing can be confused, something that explains why I got no false positives in our domestic goat validation set. I believe achieving the latter is very important.

The distinctiveness of the head-clash signal makes translation of this agonistic behaviour identification rules between one species liable to work well with another (Williams et al. 2015, Jeanniard-du-Dot et al. 2017, Dickinson et al. subm.), which is why I felt it appropriate to search for ibex head-clashes based on the domestic goat data. As with the domestic goats, it is hard to conceive of a situation where such high decelerations could be produced without head-to-head impact. But in a manner similar to the goats, I was obliged to set a threshold, which should be higher in the more massive alpine ibex (see also the strict observed correlation between differences in relative body size and relative mean and max VeDBA at impact – see Table 3 vs. Table 4). Also, on inspection, I noted that the second peak occurred later than in the domestic goats so I altered the algorithm accordingly. I believe that the displaced second VeDBA peak was also mass-related: What happens during the head-clash, is that the animal essentially stops at the moment of impact and the collar continues forward, travelling somewhat up the neck, until it meets the lower rearward-facing part of the animal's skull, which is where (and when) the greatest deceleration in the tag occurs (cf. peak in both the surge axis and the VeDBA in Fig. 2). Note that this occurs a fraction of a second later than the actual head-to-head impact. But, following this initial deceleration, the collar is then also typically bounced back posteriorly, causing it to travel until it reaches the body, at which point it decelerates again, producing a reverse peak in the surge acceleration (cf. Fig. 2) and a second peak in the VeDBA (for which all accelerations are positive). In the larger ibex, the reverse travel of the collar following the initial impact, the hysteresis, is expected to take longer, which is why the time between the two peaks was increased in the search algorithm.

I note, in this, the value of the manual, rather than machine-led, construction of the algorithm to locate head-clashes in the ibex was based on the rule derived and validated for domestic goats. This is specifically because the mechanics of the acceleration signal can be reasoned through and modified taking physical differences between the species, which directly impact differences in the acceleration signal, into account. Although not explicitly tested, I believe that a machine-learning approach would have struggled to detect ibex head clashes with any certainty if the process were based on domestic goats; for similar arguments see also (Viviant et al. 2010, McClune et al. 2014, Wang et al. 2015).

A final point is relevant in discussing the value of acceleration metrics to derive the forces involved in head clashes. As mentioned above, the measured deceleration is only a proxy for the actual deceleration experienced by the skull because the effect is diminished by resistance of the collar to travel up the neck (Dickinson et al. 2020, Wilson, Rose, et al. 2020), with the expectation being that the higher the force of the impact, the higher the recorded VeDBA. However, the highest decelerations in a two animal head-clash will be experienced by the animal that gets pushed back by the impact (albeit individuals are not always pushed back) rather than the individual with the greatest momentum. This is because the pushed-back individual has an acceleration signature resulting from a change of a positive to a negative velocity whereas the animal that does not get pushed back only slows down, thereby experiencing less deceleration. This explains how head-clashes can manifest dominance by larger individuals because their greater mass and therefore momentum (*momentum = mass*

X *velocity*) will tend to displace their opponents, subjecting them to greater deceleration and therefore greater forces (*force* = *mass* X *acceleration*). This is relevant with respect to discussion of the VeDBA values in our studies because, in any given head-clash between two individuals, the weaker (or lighter) animal will record the highest VeDBA values, which seems somewhat counterintuitive. Across the population though, I would expect stronger individuals to generally exert higher forces during their head-clashes, in part by virtue of their mass. The close relationship between relative VeDBA values and relative body size observed between ibex and goats confirms this.

Finally, the value of head-clashing as a metric for determining the success of agonistic encounters has to take into account the frequency of encounters as well as the force developed within each encounter. I noted substantial differences in both of these for the domestic goats (Table 3), with individual values ranging between means of 9 and 40 head-clashes per day and developing maximum VeDBA values of between 9 and 21 g and an interesting close relationship between the VeDBA values and the frequency of head clashes (although there was no obvious relationship between head-clash frequency and maximum VeDBA (Table 3)). Notwithstanding the development of forces referred to above, I propose that this variation could be due to the hierarchical system adopted by goats (Alvarez et al. 2003, Stanley and Dunbar 2013); established dominant individuals and lesser goats compete little with each other but adjacent individuals on the dominance ladder have to compete regularly (Alados et al. 2000), in accordance also with the general idea that animals should weigh carefully the costs and benefits of investment in direct aggressive interactions (Clutton-Brock et al. 1979, Clutton-Brock & Parker 1995). A more comprehensive monitoring of all the individuals in the flock with biologgers would allow such detailed investigation. Specifically, the outcomes of the head-clashes between known individuals could perhaps be judged based on the distribution of the forces developed (see above), potentially revealing details of the dominance hierarchy.

Head clashing in domestic goats

Head-clashing has been well documented in the literature, with it generally being interpreted as an aggressive behaviour to assert dominance with respect to getting access to resources (Miranda-de la Lama and Mattiello 2010, Stanley and Dunbar 2013), which may be mating opportunities (Mysterud et al. 2004, Miranda-de la Lama and Mattiello 2010, Bro-Jørgensen 2011, Tettamanti and Viblanc 2014), food (Helen et al. 2006, Miranda-de la Lama and Mattiello 2010) or space (Fernández et al. 2007, Miranda-de la Lama and Mattiello 2010, Patison et al. 2015). I can use this interpretation to examine where resources were located for the domestic goats because I would expect the frequency of the behaviour to be highest where resources are most coveted. The epicentre of the agonistic behaviour appeared to be the goat pen. In fact, I determined that head-clashes even occurred overnight, albeit at a low intensity (Fig. 6), which I interpret as being competition for optimum space in the densely-packed overnighting area. Hay bags were also hung up on the sides of the pen in a manner that only allowed access to a limited number of animals at a time, which presumably led to further competition within the pen. Around the pen, head-clashing was also frequently observed, and I surmise that this was due to the salt licks. Salt is a limited resource for many ungulate species (Toigo et al. 1999, Marchand et al. 2015) so I expected individuals to compete with one another for regular access. In addition, the domestic goats spent much time ruminating outside the pen over midday where shade was at a premium so I expected some agonistic interactions associated with that. However, all these head-clashes were not time-corrected and so represent absolute numbers of head-clashes per unit area. Time-corrected head-clashes (i.e. number of clashes per unit of time) showed the reverse trend (Fig. 4b, 6b), where animals in the pen had relatively fewer interactions than at the limits of their foraging ranges (Fig. 4b). This implies that whatever factors elicit head-clashing away from the pen were most apparent at these spots. In accordance with the suggestion that these encounters were due to competition for foraging spots/resources, the highest frequencies of head-clashing were often located at the edges of the foraging ranges (Fig. 4b), where the vegetation quality may also be highest, being least grazed (Elliott et al. 2009).

Time of day, and extent of movement were two factors that appeared to have a substantial effect on the incidences of head-clashing (Fig. 6), broadly in accordance with the general dawn/dusk peak of activity in many ungulate species. Furthermore, the peak in head-clashing at around 06h00 corresponded also with an increase in distance moved even before the herd was let out the pen and appeared to be related with agonistic interactions associated with the goats being milked at this time and matches my personal observations that the goats became more aggressive before and during milking. Similar dominance interactions are documented for dairy cows (Crossley et al. 2017) and may be associated with the discomfort of over-full udders and the relief that milking offers, this reprieve specifically being the resource for which the goats are competing (Alados et al. 2000, Alvarez et al. 2003, Miranda-de la Lama and Mattiello 2010).

Head clashing in alpine ibex

Given the accepted paradigm, that head-clashes in ungulates represent agonistic behaviour related to resources (Shackleton and Shank 1984, Clutton-Brock 1989), the head-clashes identified from the ibex dataset revealed some interesting patterns. These can be considered within the presumed model for ibex sociality, that adult males are territorial and hierarchical, defending access to females, but combined with a careful timing of investment in agonistic interactions, such as establishment of hierarchies before the peak of the rut so not to divert resources from the mating itself (Willisch and Neuhaus 2010). Thus, the year-round incidence of head clashing in all the tagged ibex suggests that establishment and maintenance of dominance hierarchies occurs throughout the year, with a dramatic increase in the pre-rut period (Willisch and Neuhaus 2010) and rutting period (Brivio et al. 2010, Tettamanti and Viblanc 2014). In accordance with cost vs. gain considerations, these data show that also the force of head clashes increased dramatically during the rut (see Results and Table 4).

In accordance with the considerable overlap in area use by the tagged animals (Chapter 5) and that head-clashing occurred across all sites, especially during the rut (Figures 8, 9), ibex use mating tactics where multiple males associate with a receptive female (with the latter closely followed (‘tending’) and dominated by the dominant male, but with sub-ordinate males trying to achieve temporary access (‘coursing’) in the case of sudden mating opportunities.

Despite the low sample size, I believe that it was relevant that all three males that were equipped for both the rutting and the non-rutting period, exhibited higher rates of head-clashes during the rut (Fig. 10a) and expanded the areas they occupied and in which they engaged in head-clashing (Fig. 10b), in accordance with tending and coursing mating tactics.

Generalities of head-clashing

This work on head-clashing in goats and in ibex using goat-based acceleration metrics to identify head-clashing illustrates further potential of the application of biologging technologies for behavioural ecology studies. Head-clashing is about dominance, winners and losers, and it is easy to see how, if a whole herd of goats were tagged, the winners and losers of interactions could be defined so as to deduce the herd-wide hierarchy. Within this, because the acceleration metrics allow us to allude to the forces produced during each agonistic interaction, I could also use these as measures of the costs of positional maintenance in the hierarchy. The high resolution of movement and ability to determine precisely when and where grazing occurs could also help us examine the gains of specific interactions – winners in a head-clash over resources are expected to exploit those while losers must move elsewhere. The costs of such movement in the loser (e.g. Chapter 4) together with its presumed lower quality food, can be used to derive a net gain metric (kJ ingested/kJ used (Arnold 1985, Bergman et al. 2001) and this perhaps linked to stature (Toigo et al. 1999, Côté 2000, Büntgen et al. 2014). Thus, with the domestic animals at least, this would start to provide important links between sociality, hierarchy and resource limitation, certainly a reason to advocate the biologging approach.

Wild animals such as the ibex are more problematic because it is probably impossible to tag all the individuals within a given area. Nonetheless, extensive tagging protocols should allow researchers to detail interactions between known individuals and, in the same way as in the goats, identify the winners and losers. The highly resolved dead-reckoning of movement (Chapter 2 and 3) together with identification of behaviour (Chapter 3 and 4) should then allow us to describe the ostensibly much greater consequences of the outcomes of these extraordinary agonistic behaviours.

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Chapter 7

Ungulates as cartographers: *How do topography and habitat affect the movement energetics of ungulates in mountain areas?*

Abstract

Travel is considered to account for a substantial proportion of a species' daily energy expenditure, especially in active, warm blooded animals. The environment through which a species moves can dictate the cost of movement (or transport: COT), including the incline of slopes, substrate penetrability, and superstrate density. I used multi-sensor biologging data from six ungulate species living in the French Alps (3 wild; alpine ibex (*Capra ibex*), mouflon (*Ovis gmelini musimon × Ovis sp.*) and chamois (*Rupicapra rupicapra*) and 3 domestic; cows (*Bos taurus*), sheep (*Ovis aries*) and goats (*Capra aegagrus hircus)*) to estimate and quantify cost of travel by using vectoral dynamic body acceleration (VeDBA) as a proxy for energy expenditure. This information combined with detailed mapping data of the Alps in which theindividuals moved, allowed to identify how slope and habitat affected movement costs and compare this across species. Critically, the straight line slope angles (the steepest incline reported for cartographic data) were not used as such by any of the species. Instead, animals travelled obliquely adopting a "zig-zag" approach so that the angle that any individual experienced was much lower than that of the actual topography. This strategy allowed animals to manage the cost of moving on any slope. Movement modes revealed how COT changed whether species were ascending or descending, with projected descent movement costs being slightly less due to animals taking advantage of potential (gravitational) energy gained. Travel speed affected the VeDBA-based proxy for COT even though most species moved particularly slowly on steep inclines. Models that considered speed, COT, slope and habitat type showed clear relationships between COT and slope with variation across habitat types. Although VeDBA-derived values for energy expenditures cannot be strictly compared across species without appropriate calibration, inter-specific differences in COT for given slopes were so large that, rather than energy landscapes being a fundamental feature of the

environment for animals, the magnitude of any energy landscape may depend strongly on the movement capacity and specific life history and needs of a species, beyond simple differences in body size.

Introduction

Understanding the cost of animal movement and how the environment can alter this cost is fundamental for biologists because movement costs account for a large portion of a species' daily energetics (Garland 1983, Rezende et al. 2009, Scantlebury et al. 2014). Indeed, compared to other metabolic processes, movement costs are so substantial (Speakman and Selman 2003, Halsey et al. 2015) that there is assumed to be a particularly strong selection pressure for animals to move through their environments efficiently (Merker 2005, Fahrig 2007, Shepard et al. 2013). Judicious movement should take into account the many physical attributes of the environment that modulate the energy expenditure associated with travel, including wind and water currents in fluid environments (Riotte-Lambert and Weimerskirch 2013, Elliott et al. 2014) and substrate penetrability (White and Yousef 1978, Crête and Larivière 2003), substrate resistance (Fancy and White 1987, Crête and Larivière 2003, Shepard et al. 2013) and incline (Dailey and Hobbs 1989, Wall et al. 2006, Halsey and White 2017) in terrestrial systems. The cost of movement can be quantified and translated into metabolic costs while considering several confounding variables (e.g. speed, mass) (Dickinson et al., 2021; Shepard et al., 2013).

Within terrestrial energy landscapes (Wilson et al. 2012, Shepard et al. 2013), changes in height are the most energetically onerous (Wall et al. 2006, Parsons et al. 2008, Lees et al. 2013, Halsey and White 2017, Dunford et al. 2020) because of the associated changes in potential energy (PE), which relate to the mass of the animal (M), the height change incurred (ΔH) and the gravitational constant (g) *via* $PE = Mg\,\Delta H$ (cf. chapter 6). This energy is converted into necessary mechanical power to climb a slope (P) *via* $P = PE/t$ so travel speed and degree of incline play key roles in the rate at which energy is expended by an animal moving on slopes. Although it is clear from the formula how energy must be invested by a climbing animal, the apparent potential energy gain from descent is not fully realized because animals have to invest energy to brake downward motion when slopes become steep (Richard Taylor et al. 1972, Armstrong et al. 1983, Fancy and White 1987) which also increases the metabolic cost of travelling down steeper slopes (Dailey and Hobbs 1989, Birn-Jeffery and Higham 2014, Dickinson et al. subm.).

The amount of deformation of substrates can also affect the energy expenditure of travelling animals (Shepard et al. 2013, Halsey 2016). Particularly strenuous substrates in this regard are soft surfaces, such as sand (Pinnington and Dawson 2001, Voloshina et al. 2013), where energy expenditure for a given speed may be higher than movement on a hard substrate (Pinnington and Dawson 2001). Snow is another example (White and Yousef 1978, Fancy and White 1987, Crête and Larivière 2003), but this also includes a component of the third element of terrestrial energy landscapes, which is the energy required to push or pull limbs through a superstrate (Crête and Larivière 2003). Costs are hard to determine but it is obvious that thick vegetation, for example, requires more effort to move through than sparse foliage or open ground (Shepard et al. 2013).

Other factors can dictate the cost of moving across spaces that are not environmental. For example, the metabolic cost to move will differ with species depending how adapted that species is to move efficiently within the surrounding environment (Wall et al. 2006, Dunford et al. 2020). As highlighted in the above equation, mass (M) of the animal which differs with species can dictate the overall power required to move (Garland, 1983; Parsons et al., 2008; Halsey, 2016; Halsey and White, 2017) .

It is well established that animals often move to minimize the costs of transport (COT)(defined as the energetic cost of moving a defined mass of over 1 m (Tucker 1970)), which can explain a suite of movement parameters such as when and where animals move and the details of track tortuosity (Shepard et al. 2013). But the precise costs of energy landscapes depend on the species moving through them. For example, a snowshoe hare (*Lepus americanus*) moving over deep snow may not sink at all and so have no superstrate to push through whereas a moose (*Alces alces*), with its high body mass and relatively small surface area of the hooves producing high pressure points, may have to struggle (Parker et al. 1984, Fancy and White 1987, Murray and Boutin 1991). Therefore, a prime challenge is to understand how animals move ('movement capacity') in association with energy landscapes that are relevant to them and for this energy expenditure should be considered in relation to environmental characteristics across species using that environment. Overall, COT is a quantification for the energy required for an animal to displace itself.COT not only considers'power required' but takes into account the animals speed, standard gravity forces acting on the animal and the individual's mass and indicates how efficiently an animal is moving (Halsey, 2016; Halsey and White, 2017; Shepard et al., 2013).

The Alps offer an area with a great range in habitats and topography making the site a naturally variable environment in terms of classic energy landscapes. It is populated by a number of native ungulate species; alpine ibex (*Capra ibex*), mouflon (*Ovis gmelini musimon × Ovis sp.*) and chamois (*Rupicapra rupicapra*), which are adapted at the challenges of mountain environment, such as extreme seasonal climates, highly variable and steep inclines, including steep dangerous slopes that however may also offer potential protection from predators. During the summer months a very large number of domestic ungulates also graze on alpine grasslands – especially cows (*Bos taurus*), sheep (*Ovis aries*) and goats (*Capra aegagrus hircus)* (Herzog & Seidl 2018).

This study system provides an excellent opportunity to study how contrasting species deal with the challenges of topography and habitat, by using sensor-rich data loggers that allow the calculation of their fine-scale movement paths in relation to habitat (Chapters 2, 3, 4) as well as to allude to their movement energetics (Qasem et al. 2012, Jeanniard-du-Dot et al. 2017).

Thus, the overall aim of this study is to use biologging data from six free-roaming ungulate species, ranging in body mass from 30 to 600 kg, to assess how they respond to defined energy landscapes within a mountainous region and to compare movement strategies between species. There are four principal objectives; (i) to compare how slope affects the movement energetics (using dynamic body acceleration as a proxy) of six ungulate species, (ii) to model the DBA-defined costs of transport against slope for various identified habitat types for each study species, (iii) to identify species-specific paths that appear to minimize movement costs within the area and (iv) to combine the above within an over-arching framework that seeks to construct species-specific energy landscapes in order to understand space use by this ungulate group.

Methods

Study sites

Three study sites were selected for data collection on free roaming ungulate species (Fig. 1, Table 1), all of which were within the French Alps with similar habitat types which, however, varied in their incidence and topography, and all part of long-term wildlife monitoring projects.

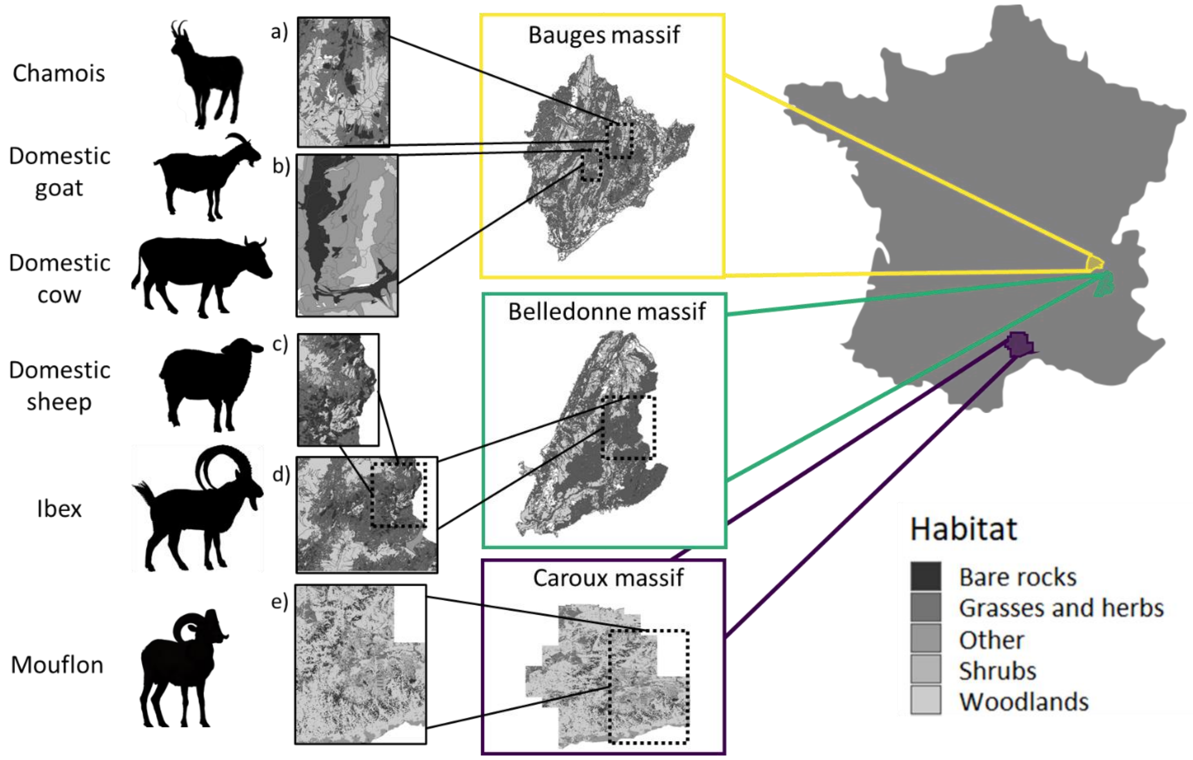


Figure 1 – Illustration of the overall study area and the position of specific relevant sites within France. (a) The Bauges massif was used for studying the chamois, (b) the domestic goat and (c) the domestic cow. The Belledonne massif was used for (c) the domestic sheep and (d) alpine ibex study while (e) the mouflon was studied within the Caroux massif. Each map has polygons outlined and is coloured based on habitat.

The Bauges massif (45.60485°N, 6.18295°E) was used as the study site for three species including wild chamois, which roamed a large area (Fig. 1a), domestic goats and domestic cows , both of which were restricted to 2 km^2 pastures by farmers (Fig.1b), although the goats were in fact free to roam. The Bauges mountain range had a lower average altitude and shallower slopes than the adjacent Bellendonne massif, which resulted in the Bauges having more vegetation cover (see chapter 4 for further details). Belledonne (45.13610°N, 6.04020°E) was the massif used for domestic sheep and wild alpine ibex. These two species were tagged within the same section. As with the Bauges massif study, the ibex roamed widely whereas the sheep used a smaller area, which effectively giving the species two different study sites (Fig 1c, 1d respectively) within the Belledonne massif. The average altitude of the Belledonne massif mountain range was the highest of the three massifs and had the steepest average slopes (see chapter 5 for further details). Mouflon were tagged in the Caroux mountains (43.60854°N, 2.98639°E), situated ~300km away from the other two sites. The individuals tagged used a large part of this game and wildlife national reserve (Fig. 1e). Caroux is a sub-Mediterranean habitat with an appreciably lower average altitude than the other study sites and has the least extreme topography (Marchand et al. 2015). The weather is also correspondingly milder than the other study sites due to the combined influence of Mediterranean, oceanic and mountainous climates (Baudière 1962).

Study species

The numbers of animals used within the six species varied between 2 and 11, with appreciable variation in the sex ratio according to species (Table 1). Despite slight variation in tag deployment durations, and the time of year when most data were collected, most data sets were >20 days and collected during the summer (Table 1).

Table 1- A list of species used in the study and details of the data collected.

Species	*Individuals*	*Sex*		*Logging duration range (days)*	*Mean logging duration*	*Time of year for logging*	*Study site*
		Female	*Male*				
Domestic cow	8	8	0	≈9 to ≈25	≈22	Aug 2017	Bauges
Domestic goats	10	10	0	≈5 to ≈25	≈20	Aug 2017	Bauges
Domestic sheep	11	11	0	≈ 11	≈ 11	Aug 2018	Belledonne
Chamois	2	2	0	≈ 27	≈27	Sept 2017	Bauges
Ibex	6	0	6	≈ 27	≈27	Jun 2017	Belledonne
Mouflon	5	4	1	≈ 27	≈27	Jul 2017 (n=2) Jul 2018 (n=1) Oct 2018 (n=1)	Caroux

Jul 2019 (n=1)

Biologgers

The wild species had commercial Lotek 3300S GPS collars (Lotek 2020) with lab-designed external housing fixed over the existing housing containing “Daily Diary” accelerometer and magnetometer (see chapter 2 and 4 for further details). The domestic species were collared with lab-built collars with a housing containing a Daily Diary and TechnoSMart GiPsy unit (TechnoSMart 2020). The collar was weighted at the bottom to keep the housings containing the above devices on top of the animals’ necks (see chapters 2 and 4 for further details).

Deployment

Wild species were captured using drop nets traps that were remotely activated and baited using salt licks (Toigo et al. 1999, Jullien et al. 2001). Once trapped, the animals were hooded, handled and processed with their weight, hoof length, horn length and sex recorded. Each species was then collared with a device that was calibrated (for details see chapter 4) on site.

For the domestic species, individuals (were caught in their pen, or the milking station, and handled directly. All collars were calibrated at the study site and attached to the animal.

VeDBA

Vectoral dynamic body acceleration (VeDBA) (Qasem et al. 2012) was calculated (for equation and further details see chapter 4) using the DDMT software (WIldbytes Ltd., Swansea, UK) to be used as a proxy for speed (Bidder et al. 2012, 2015) and energy expenditure (Qasem et al. 2012, Jeanniard-du-Dot et al. 2017, Wilson, Börger, et al. 2020, Dickinson et al. subm.) in all species. VeDBA is notorious for its noise as it varies dramatically between periods of footfall (which produces a high deceleration spike) and between footfalls (where the values stabilize for a brief period) (Wilson, Rose, et al. 2020). A recommendation to deal with this is to smooth values over at least a full stride cycle (Wilson et al. 2020). As a consequence, VeDBA values were smoothed (sVeDBA) using a running mean over 40 data points (corresponding to 2 seconds) (Shepard et al. 2008). The high temporal resolution of acceleration data collected, necessitated some sub-sampling to 1 s resolution for some parts of the analysis (see below) to process the information, which was constrained by computational capacity.

Definition of active behaviours

Smoothed VeDBA values were used to define three principal behaviours; resting, grazing and moving for domestic goats with appropriate ground-truthing *via* direct observation (see chapter 4) and adapted for the alpine ibex (see Chapter 5). However, not all species behaviours could be calibrated with observations or adapted (as above) with clear justifications. As a result, grazing and moving could not be separated from each other in some species with certainty, especially since all species move to variable extents while grazing. Instead, I separated behaviours into either ‘active behaviours’ or ‘inactive behaviours’, which were defined by using sVeDBA thresholds (Fig. 2). As noted in Shepard et al. (2008), the difference in acceleration signals over time (including sVeDBA) between activity and inactivity is striking, being effectively stable during inactivity and highly variable the instant an animal moves (Shepard et al. 2008) (Fig. 2).

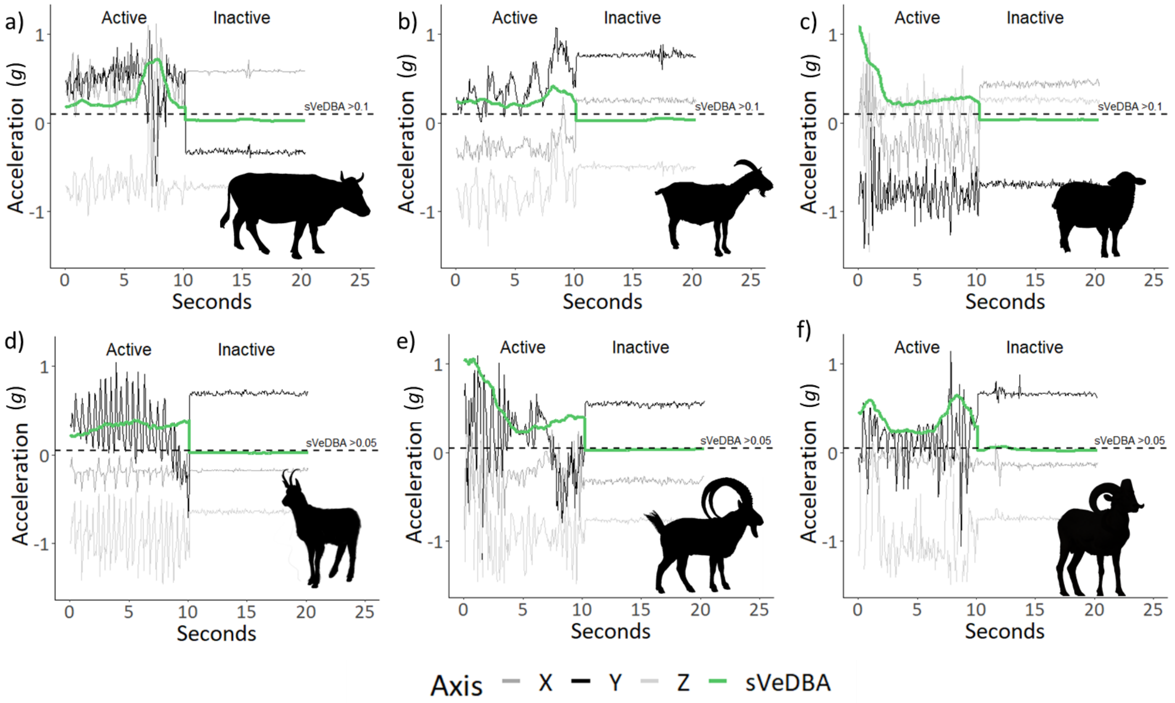


Figure 2- *Examples raw acceleration data from the 3 orthogonal axes (grey lines) and sVeDBA (green line) to show changes over time with changing active and inactive behaviours for; (a) domestic cow, (b) domestic goat, (c) domestic sheep, (d) chamois, (e) ibex and (f) mouflon. The thresholds used to separate these two states are shown using the dashed lines with the thresholds specified.*

By inspecting the data as detailed in chapter 4, I noted that the only appreciable change to sVeDBA thresholds across species was due to the noise in data from the lab-built collars, which were lighter than the Lotek collars used in the wild species. As a result, the lab-built collars were more prone to move during minimal animal movement such as head turning (recorded by the accelerometers). Thus, for the wild species, the behaviour thresholds were reduced by 0.05 *g* compared to their domestic counterparts (Fig. 2; see also chapter 5 and 6). If any period resulted in a sVeDBA value that surpassed the given threshold, the period was marked as ‘active’ behaviour, and if it did not, it was marked as ‘inactive behaviour’. However, once ‘active behaviour’ was recognized, it was considered to have occurred for a minimum time of one second before the data was interrogated again. This behavioural analysis was carried out in the Wildbyte software ‘DDMT’ (Wildbyte Technologies 2020).

Dead-reckoning

The GPS location frequencies were set to provide comparatively low temporal resolution and varied across species (Chapter 3, Table 1), ranging from 1 fix every 15 minutes to 1 fix every 2 hours. To increase the location fix rate and bring all species to the same frequency, dead-reckoning was used to fill the gaps between GPS points (see chapter 3 for further details). In this, VeDBA was used as a proxy for speed (Bidder et al. 2015, Dickinson et al. subm.) with GPS correction being used to offset any error in speed (or heading) by altering the coefficient for the gradient between VeDBA and speed (for definition see chapter 3) so that dead-reckoned pathways led to points that coincided in time and space with the GPS points. This process accounts for differences in the linear relation between VeDBA and true speed which are expected to vary between species (Bidder et al. 2012) and for different substrates and slopes (Dickinson et al. subm.).

Speed

The dead-reckoning process gave a location every second so that speed could be derived by examining the distance between the two locations per second. This was calculated using R-studio using the “fossil” package in R (see chapter 3 for details).

Altitude

The pressure was converted to altitude (*h*) using a formula that incorporates a temperature correction:

$$h = \frac{\left(\left(\frac{P_0}{P}\right)^{\frac{1}{5.257}} - 1\right) \times (T + 273.15)}{0.0065}$$

where the altitude is in metres, P_0 is pressure at sea level, P is pressure reading from the logger (recorded at 2 Hz) and T is temperature.

Mapping

R (R Core Team, 2019) and R studio (RStudio Team 2020) was used, with several packages including “ggmap”, “ggplot2”, “sf”, “raster,” and “rgdal” to map high resolution GPS-corrected dead-reckoned paths with overlayed defined behaviours, VeDBA metrics, step lengths, speeds and changes in altitude. Combing this 1 Hz path with detailed mapping data (supplied by Grenoble University and the National Hunting and Wildlife Agency (ONCFS) management team) (Tronchot 2008) allowed slope (in degrees) and habitat type to be extracted from shape and raster files. The habitats had to be unified (Table 2) with varying habitat definitions and to ensure sufficient data was available to build the desired energy landscape models.

Table 2- List and break-down of how available habitat information was combined to define shared habitats with revised habitat descriptions.

Study habitat ID	*Description*	*Belledonne habitats*	*Bauges habitats*	*Caroux habitats*
Bare rock	Predominately exposed rock in the form of rock face or loose scree. Vegetation can be present including pioneer species, grasses and herb species.	Rock shadow, exposed rock, snow (on assumption bare rock during summer months)	Scree	Rock, bare ground
Grasses and herbs	Grass and herb species making up lawns that have a variety of biodiversity and productivity including Nard,	Diverse lawns, herbs	Nard, Laiche, Seslerie, Dry grass, Forage (mowing meadows), megaphorbiaie species	Lawns, grasses, meadows, mixed open areas (herbs and shrubs)

	Laiche, Seslerie and Megaphorbiaie species			
Shrubs	Mixture of open, fruit baring, closed, low and tall shrub species	Closed shrubs, open shrubs, low shrubs, shrubs with fruits	Shrubs	Broom moors, Heather, Callune moors, fern heaths, blueberry moors
Woodlands	Forest made up of a mix of deciduous and conifer species including open, patchy woodlands	Spruce, Conifers in islets, larch, Beech, Birch, mix of hardwoods, loose forest	Spruce, beech, alder	Hardwood, Holm oaks, Pine forests, Beeches, Chestnut trees, undifferentiated softwood, mixed forests
Other	Not selected for energy landscape model due to lack of abundance	Low swamp, water	None	Farmland, Urban areas, villages and hamlets, water

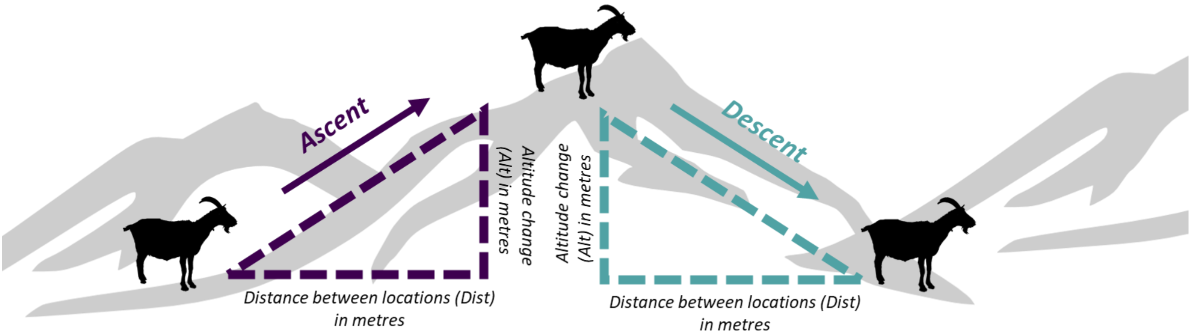
Summary data

Many millions of data points are necessary if 40 individual animals are examined for all the data over >20 days each on a second-by-second basis. To condense this information, summary data were calculated where totals and means were calculated every time the species moved 10 m. From this, the proportion of time spent engaged in active behaviours was derived to remove the extended periods of resting behaviour (since I am only interested in movement here). Altitude change was defined as part of movement using following filters; ‘ascents’ were defined when there was a >0.5 m change over 10 m, ‘descent’ was defined when there was a <-0.5 m change over 10 m, and anything in between was defined as ‘level movement’. From the 10 m summaries, a crude proxy estimate of cost of transport (COT) was calculated by dividing the total sVeDBA by the distance moved to give sVeDBA per metre moved (COT_{sVeDBA}).

Slope data was recorded as a percentage (Tronchot 2008). To better visualize and analyse this and the high number of 10 m summaries, each slope value was rounded to the nearest whole percentage and mean metrics within species were calculated for every slope integer.

Animal chosen slopes against cartographic slopes

The literature is explicit about how animals can moderate their power outputs for moving up steep inclines by adopting a zig-zag path, moving upward at much shallower slopes but increasing distance travelled (Llobera and Sluckin 2007). To examine the extent to which the study ungulates did this, I examined the rate at which animals moved up slopes defined by the digital elevation model data by calculating their vertical velocity or change in altitude. I did this by subtracting altitude estimates at time t = 1 from the altitude at time t = 0 every time the animal moved 10 metres. Knowing the altitude change and the distance moved by the animals from the change in the individual's location, I used simple trigonometry to provide an estimate of the slope taken by the animal as a function of the cartographic slope (fig 3). The slope was then converted to slope as a percentage to match the mapping data.



$$Animal\ angle\ for\ ascent\ (\%) = \left(\tan^{-1}\frac{Alt}{Dist}\right) \times 0.278 \qquad Animal\ angle\ for\ descent\ (\%) = \left(\tan^{-1}\frac{(Alt\ \times -1)}{Dist}\right) \times 0.278$$

Figure 3 – Schematic figure to show data from the 10 metre distance summaries and trigonometry was used to calculate an estimate animal angle of travel.

Building energy landscapes using random fixed effects models

To construct the proxy energy landscapes, the relationship between COT_{sVeDBA} with slope incline for each habitat had to be predicted. A linear mixed effect model was used, fitted in R using the lme4 package, with random intercept by animal ID and slope also as random slope, with a different model for every species for both ascent and descent. By filtering each habitat on the map, the slope and intercept could be derived from the model and for giving a COT_{sVeDBA} value for, finally, each 25 metre sector (the change in resolution from 10 m was dictated by the available map resolution) of any given cartographically-defined slope.

Results

Speed with slope

All 6 species showed little change in general travel speed across slopes although mean speeds were lowest during ascent, highest during level travel and intermediate during descent in all species (although in the chamois, the incline movement occurred at similar speeds) (Fig. 4).

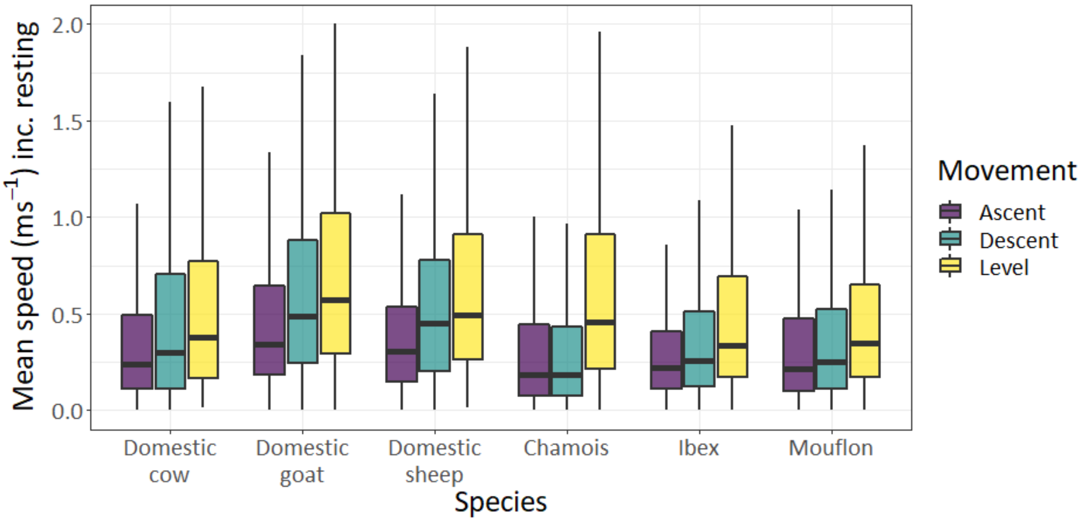


Figure 4- Boxplot (horizontal bars show medians, box limits show quartile limits and whiskers indicate range limits not including outliers) showing the relationship between speed and whether each of the 6 different study species was ascending, descending or travelling on level ground. Ascent is represented by purple, descent by

green and level travel by yellow. The mean speed was taken including resting periods, in other words the speed of the animal (0 ms^{-1}) was considered when the animal was not moving.

Detailed consideration of speed with respect to slope showed though, for animals moving up slope, speed decreased approximately linearly with incline for all species except the chamois, where speed actually increased with incline steepness (Fig. 5).

Fig. 5

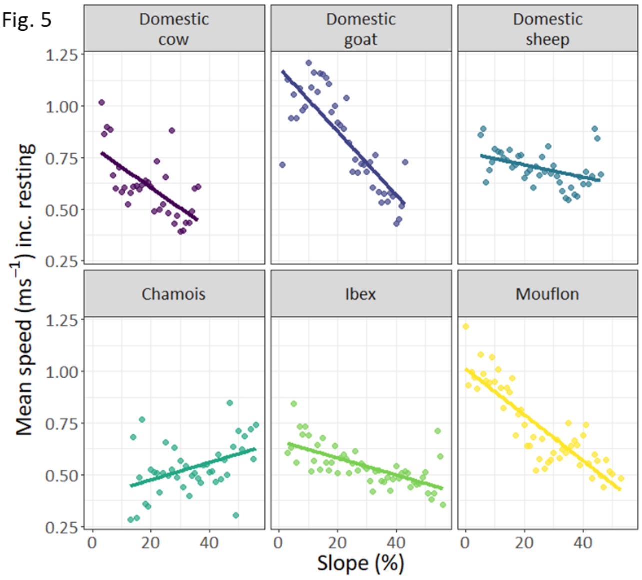


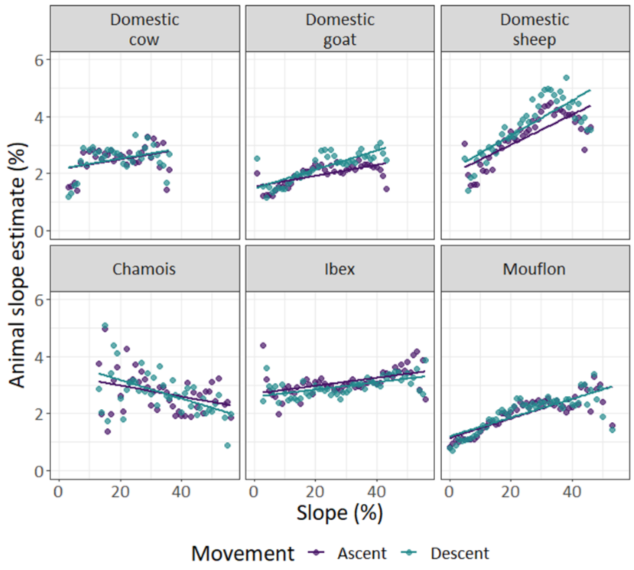
Table 3 - Slope vs mean speed (ms^{-1}) inc. resting coefficients from linear regression analyses

Species	*Coeff.*	*Intercept*	*R^2*	*P value*
Domestic cow	-0.010	0.803	0.414	<0.001
Domestic goat	-0.015	1.185	0.678	<0.001
Domestic sheep	-0.003	0.773	0.170	<0.001
Chamois	0.004	0.390	0.178	<0.05
Ibex	-0.004	0.663	0.442	<0.001
Mouflon	-0.011	1.014	0.759	<0.001

Figure 5 – Scatter-plots for each study species showing how mean travel speed changes with slope. Table 3 shows the simple linear regression results for the data displayed.

Animal slope estimates as a function of cartographic slopes

Animals travelled up and down slopes at much shallower angles than the maximum incline indicated by cartographic data for those slopes (Fig. 6).



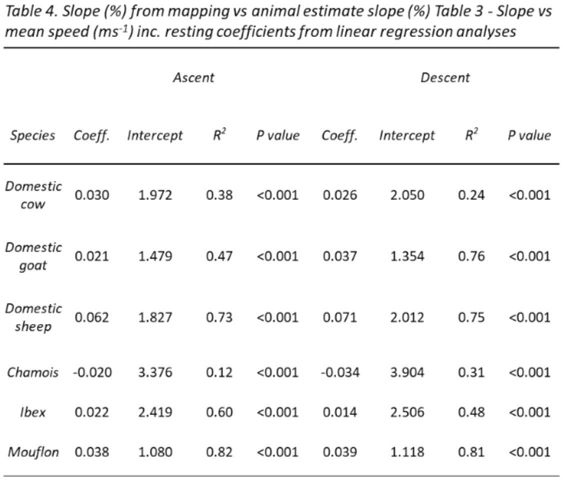


Table 4. Slope (%) from mapping vs animal estimate slope (%) Table 3 - Slope vs mean speed (ms^{-1}) inc. resting coefficients from linear regression analyses

	Ascent				Descent			
Species	Coeff.	Intercept	R^2	P value	Coeff.	Intercept	R^2	P value
Domestic cow	0.030	1.972	0.38	<0.001	0.026	2.050	0.24	<0.001
Domestic goat	0.021	1.479	0.47	<0.001	0.037	1.354	0.76	<0.001
Domestic sheep	0.062	1.827	0.73	<0.001	0.071	2.012	0.75	<0.001
Chamois	-0.020	3.376	0.12	<0.001	-0.034	3.904	0.31	<0.001
Ibex	0.022	2.419	0.60	<0.001	0.014	2.506	0.48	<0.001
Mouflon	0.038	1.080	0.82	<0.001	0.039	1.118	0.81	<0.001

Figure 6 – Estimates of the slope angle taken by the 6 study species of ungulates in relation to the cartographic inclines for both ascending and descending animals. Points show species-specific grand means across all datasets and 10 m travel lengths.

There were notable species-specific differences in slopes chosen (i.e. the observed incline of the path) according to incline of the terrain, with domestic goats, sheep, ibex and mouflon all increasing their chosen slope angles with increasing incline (Table 4; Figure 6). Although cows showed the same trend, it was far less marked while chamois actually decreased both ascent and descent angle with the slope of the terrain (Fig. 6, Table 4), which accords with the previous result that they are the only species to increase speed in steeper terrain (Figure 5; Table 3).

Cost of travel with slope

Our proxy for cost of transport (COT_{sVeDBA}) showed the reverse of the speed estimates according to whether animals ascended, descended or moved on level ground (Fig. 7).

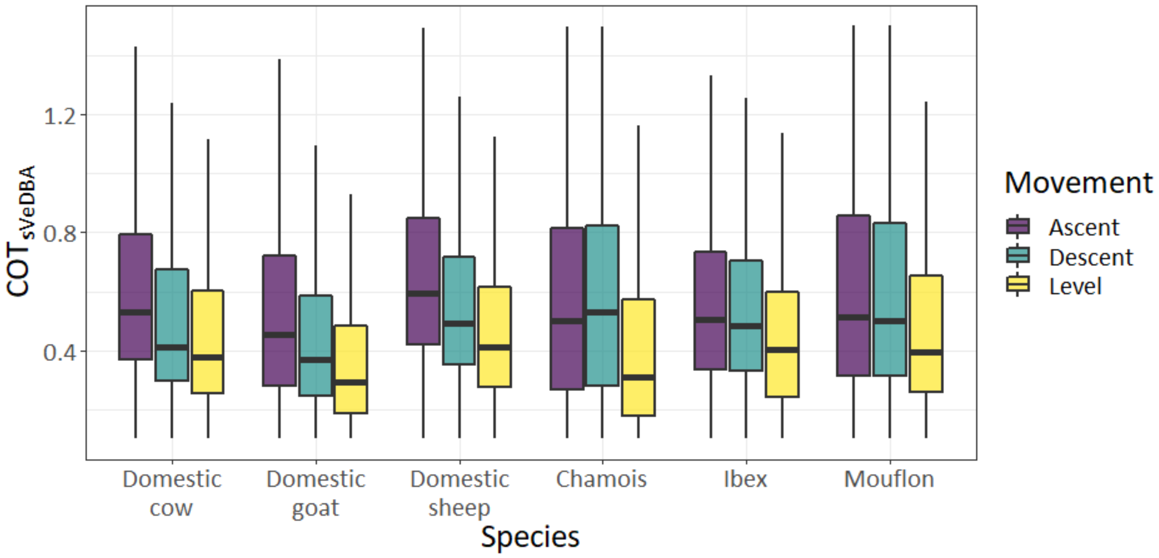


Figure 7 - Boxplot (horizontal bars show medians, box limits show quartile limits and whiskers indicate range limits not including outliers) showing the relationship between COT_{sVeDBA} *and whether animals were ascending, descending or travelling on level ground. Ascent is represented by purple, descent by green and level travel by yellow.*

Detailed examination showed how the slope of COT_{sVeDBA} increased with respect to terrain slope for all species apart from chamois (Fig. 8), in accordance with the precious results (Table 3; Table 4). The chamois also had a higher average VeDBA value per metre travelled. The gradients of this relationship differ also between other the five species with the positive trend with the domestic sheep, goats and ibex COT being affected less compared to the Mouflon and notably the cow with a high coefficient estimate and R-squared value.

Fig. 8

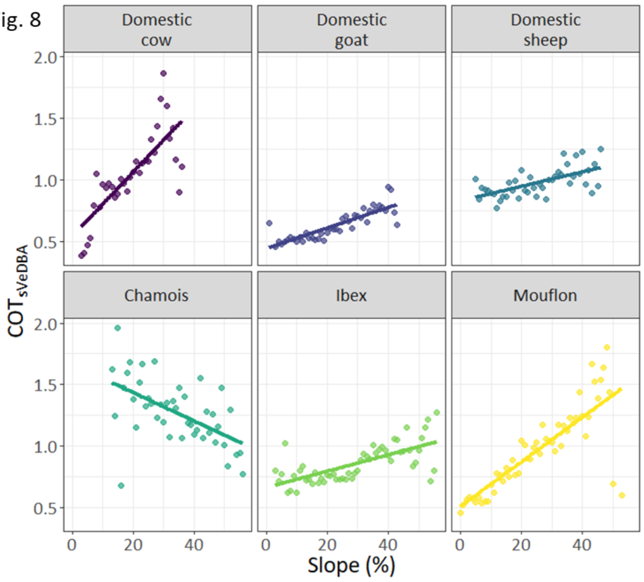


Table 5 - Slope vs $\text{COT}_{\text{sVeDBA}}$ (sVeDBA per metre)) coefficients from linear regression analyses

Species	*Coeff.*	*Intercept*	*R^2*	*P value*
Domestic cow	0.026	0.538	0.613	<0.001
Domestic goat	0.008	0.440	0.708	<0.001
Domestic sheep	0.006	0.827	0.396	<0.01
Chamois	-0.012	1.669	0.307	<0.001
Ibex	0.007	0.661	0.473	<0.001
Mouflon	0.018	0.507	0.654	<0.001

Figure 8 – Scatter-plots for each study species showing how mean $\text{COT}_{\text{VeDBA}}$ changes with cartographic slope. Table 5 shows the simple linear regression results for the data displayed.

The map of the study site for the domestic goat is an example of the combined habitat and slope data available (Fig. 9a). The combination of both slope and habitat for these animals on $\text{COT}_{\text{VeDBA}}$ in shown in Fig. 9b, exemplifying the substantial variation. This approach was supported with simple linear models which showed significant relations between the two variables but with notably low R^2 values (max <0.02) (see appendix, Table 6 for the full statistical table).

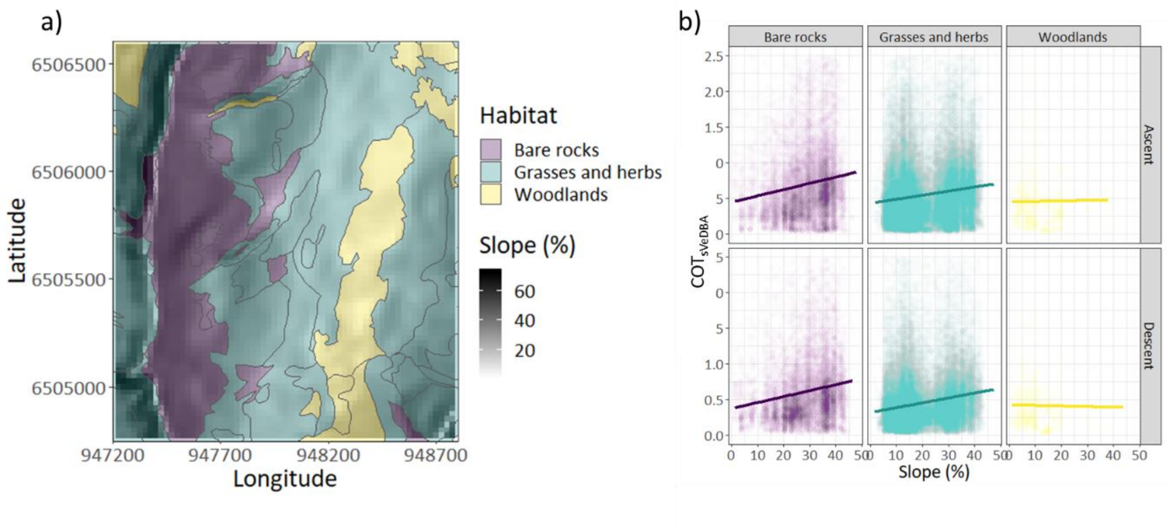


Figure 9- (a) Map of the domestic goat study site with poly shapes representing habitats and pixels showing how slope (%) changes across 25 m^2 areas. (b) Scatter-plots of VeDBA per metre moved against slope for both

movement mode and all habitats present, coloured to match the mapped habitats with simple liner regression lines to represent the trend. Domestic goat 10 m summary data, filtering out level movement, was used for this analysis.

These patterns are confirmed by the results from the linear mixed effects models of how $\text{COT}_{\text{VeDBA}}$ is affected by slope and habitat. Within almost all species an increase in $\text{COT}_{\text{VeDBA}}$ with slope across habitats for bare rocks, and a consistent change of slope in vegetated habitats (Table 6).

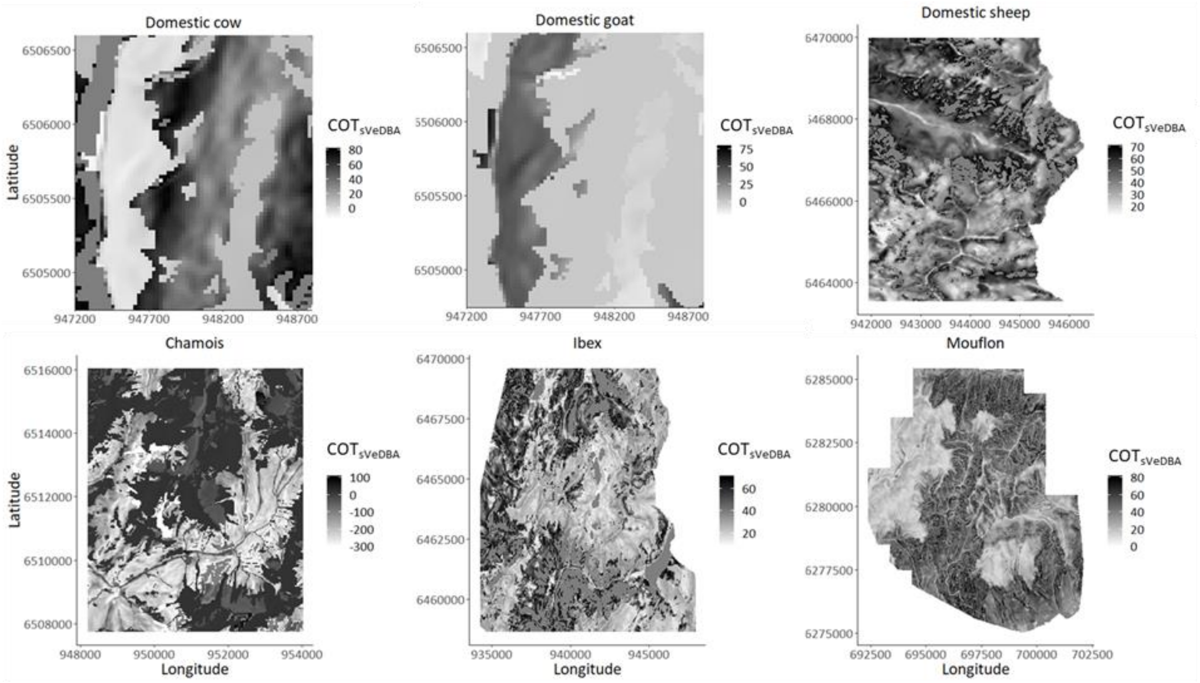
Table 6- Habitat-specific cost of transport ($\text{COT}_{\text{VeDBA}}$) against slope – coefficient estimates form a linear mixed effects model with animal ID as random intercept and terrain slope as random slope, controlling for speed and the speed by slope interaction. Models were fitted separately for ascent and descent for each species.

		Domestic cow			Domestic goat			Domestic sheep		
		Slope	Intercept	P value	Slope	Intercept	P value	Slope	Intercept	P value
Bare rock	Ascent	-0.430	13.229	0.280	0.991	7.253	<0.01	0.794	12.139	0.084
	Descent	-1.175	13.007	0.150	0.501	6.238	<0.01	0.202	10.287	0.647
Grasses and herbs	Ascent	1.632	12.321	<0.001	-0.002	6.685	<0.001	0.297	11.769	0.244
	Descent	0.615	10.905	<0.001	0.013	5.646	<0.001	0.717	10.377	0.125
Shrubs	Ascent	No Data			No Data			-0.406	12.548	0.020
	Descent							0.288	9.974	0.830
Woodlands	Ascent	0.080	7.499	0.240	-0.326	5.963	<0.001	-0.833	12.529	0.108
	Descent	0.416	6.588	<0.001	-0.494	4.894	0.010	-1.143	11.207	0.131

		Chamois			Ibex			Mouflon		
		Slope	Intercept	P value	Slope	Intercept	P value	Slope	Intercept	P value
Bare rock	Ascent	-1.278	10.666	0.462	0.491	10.040	0.074	1.193	10.451	0.005
	Descent	-1.218	9.710	0.345	0.697	9.132	<0.001	0.721	10.967	0.139
Grasses and herbs	Ascent	0.158	15.587	0.012	0.519	9.711	0.902	1.676	10.067	0.035
	Descent	0.223	15.342	0.028	0.577	8.843	0.488	1.016	9.280	0.391
Shrubs	Ascent	2.970	18.995	0.021	1.472	10.143	0.001	2.270	10.909	<0.001
	Descent	-5.391	14.891	0.020	1.643	9.073	<0.001	1.180	9.961	0.298
Woodlands	Ascent	-7.216	23.948	<0.001	1.864	10.628	0.012	1.239	10.240	0.816
	Descent	-0.856	9.132	0.821	0.883	12.524	0.681	0.604	9.366	0.690

Based on the above work, the predicted COT_{VeDBA} per $25m^2$ could be superimposed on the mapped areas used by each species, effectively correcting for both slope and habitat type (Figure 10). This showed the marked variation in COT_{VeDBA} across areas for some species linked, in part, to the variation in the habitat (slope and superstrate types). Of note are the high costs of, for example, shrubs for ascending chamois and for woodlands for ascending ibex (cf. Table 5) and the extremely low values for ascending chamois in general. The reduced area of the study site for cows and goats with the reduced habitat types makes the much higher COT_{VeDBA} for the cows compared to the goats particularly obvious.

Ascent:



Descent:

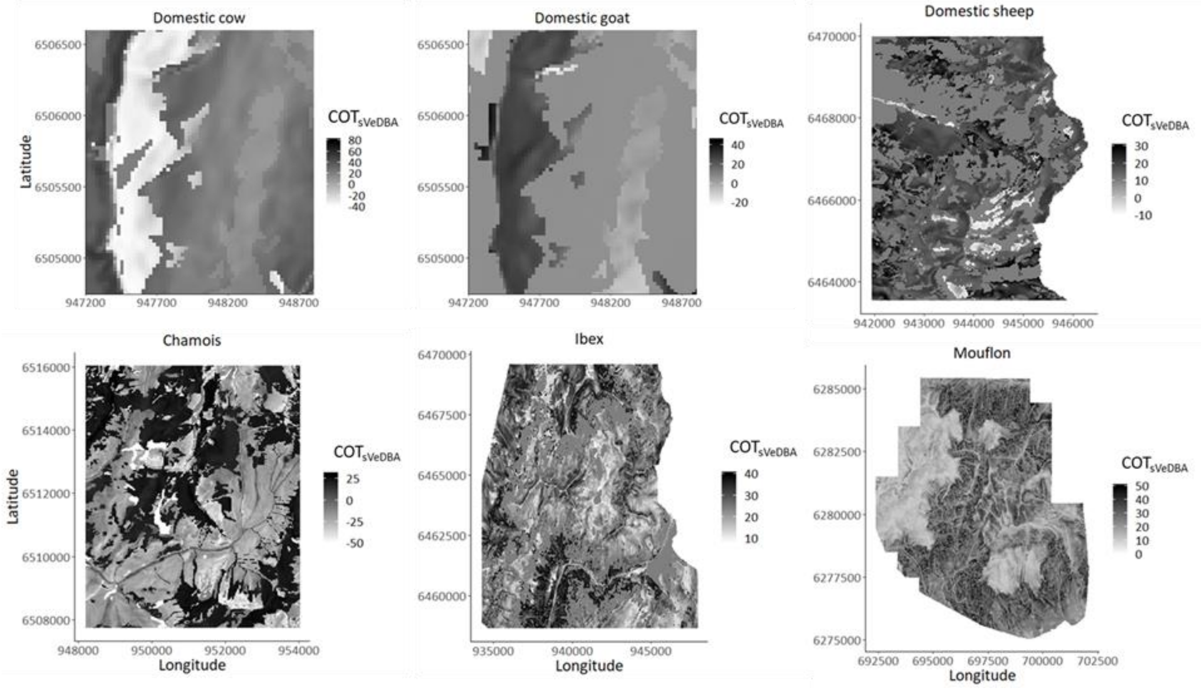


Figure 10 – Energy landscapes constructed using COT$_{VeDBA}$ against slope and vegetation following mixed effect linear models which took into account ID as a fixed random effect on intercept, and speed as a random effect on slope. Both ascent and descent is shown for each species.

Discussion

The robustness of VeDBA-based metrics to define behaviour

My ability to determine behaviours, and most specifically when animals are moving depends critically on how well VeDBA codes for behaviour. Since the pioneering work of Ken Yoda (Yoda et al. 1999), it has been well established that tri-axial acceleration can be used to help identify behaviours, with numerous authors following suite and describing many complex manners, including machine learning (Martiskainen et al. 2009, Fehlmann et al. 2017) and Boolean-based algorithms (Lush et al. 2018, Wilson et al. 2018), by which acceleration can be interpreted to identify specific behaviours (Shepard et al. 2008, Moreau et al. 2009, Campbell et al. 2013, McClune et al. 2014). However, most of these studies work with data from tags fixed firmly to their animals and so the acceleration data properly reflect movement of the animal's trunk (Moreau et al. 2009, Kölzsch et al. 2016, Dickinson et al. 2020). Collars can rotate and, to an extent, pitch forwards and backwards independently of the animal during movement, making identification of behaviours appreciable more problematic (Wilson, Rose, et al. 2020). Vectorial metrics, using all three acceleration axes, such as VeDBA (Qasem et al. 2012), negate some of these issues because all three dimensions of space are covered but they are still compromised in their discriminatory capacity because the specific information from individual axes is missing. My approach of using a VeDBA-based threshold was chosen as a broad-brush approach to defining behaviour into either 'inactive' or 'active' because it eliminates the need to examine individual axes that are, by themselves, poor indicators of state. Against this, I have only aspired to resolve behaviours into one of two states. This is conservative, but there is no doubt that it will work in a general sense because a fully inactive animal produces no VeDBA. The crucial detail, however, lies in where the threshold is set to define the two states, not least because even resting animals produce some limited VeDBA signal. My choice of VeDBA thresholds to differentiate between 'active' and 'inactive' behaviours (Fig. 2) was minimally different between species and seemed appropriate based on observations of the domestic species and examining the corresponding raw and VeDBA acceleration signals (see Chapter 4, 5). Certainly, there is normally a step change in sVeDBA when animals transition between the two states (Fig. 2). However, potential slight inaccuracies in our choice of the threshold will do little to change the basic pattern, that the more active an animal is, the higher its VeDBA (McClune et al. 2014, Fehlmann et al. 2017, Dickinson et al. subm.).

The robustness of VeDBA-based metrics for interspecies comparisons of power use

The value of VeDBA as a proxy for energy expenditure has been validated many times, with the relationship being linear (Qasem et al. 2012, Jeanniard-du-Dot et al. 2017, Wilson, Börger, et al. 2020) but it is not perfect across conditions. For example, Dickinson et al (subm.), working with pigmy goats (*Capra aegagrus hircus*) on a treadmill, demonstrated a tight linear relationship between VO_2 and VeDBA for animals walking on the flat, and on both positive and negative slopes of 15°. However, the relationship going up the slope was significantly different to that of the flat or downhill walking, with more oxygen consumed per VeDBA unit. Although my animals did not walk up anything like such steep slopes as the test conditions used by Dickinson et al (subm.), (15° is equivalent to a slope of 26.8% while our species ascended using maximum slopes of about 5%, or *ca.* 3°), there is likely to be an effect on the robustness of the VeDBA proxies for metabolic rate according to slope. Specifically, VeDBA-values would tend to underestimate metabolic rate, and therefore COT_{VeDBA}, on steeper inclines. I could use the goat data within Dickinson et al (subm.) to correct for this effect but the domestic goats were not typical in our data set (see below) and the difference would in any event be minimal.

To date, to my knowledge, there has been no study that has examined how VeDBA changes according to animal body form, lifestyle and mass. In this study, the body forms of our study ungulates are broadly similar, as is general lifestyle (but see below), but mass varies between about 30 kg for the domestic goats (McKean and Walker 1974, Alados et al. 2000) and roughly 600-700 kg for a cow (Bouissou 1972, McMorris and Wilton 1986), well over an order of magnitude. Of relevance to movement capacity, within ungulates, the most notable consequence of increasing mass, and body size, is that the legs are longer (Alexander et al. 1981, Hildebrand and Hurley 1985) so that stride length increases (Hildebrand and Hurley 1985, Garland et al. 1990). This is important because it is the specifics of the strides that produce the VeDBA signature. In particular, the VeDBA is derived from the difference between the smoothed and raw acceleration values for all 3 axes whereby peaks in this difference are apparent in each stride (Fig. 11). As stride frequency decreases so too does the sVeDBA (Fig. 11).

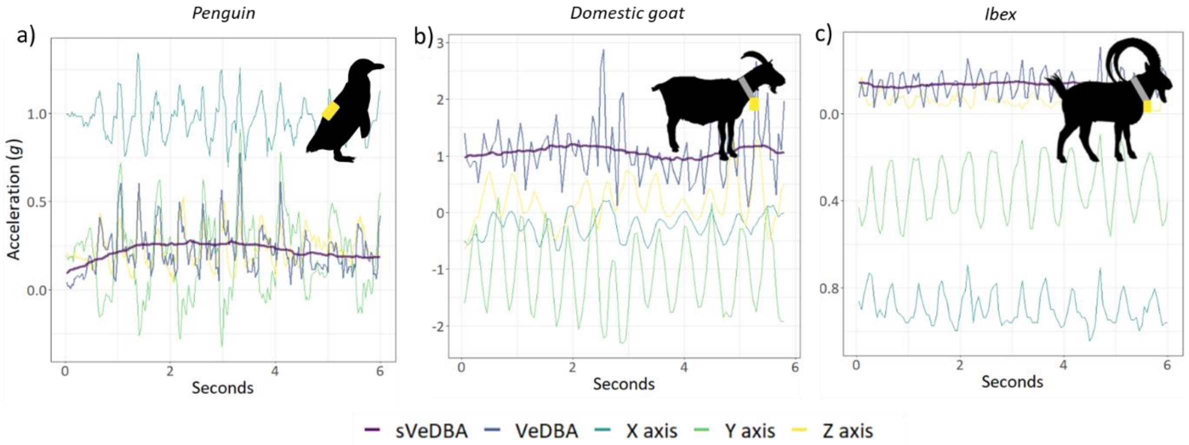


Figure 11 – Translation of a raw acceleration signature from walking into VeDBA (purple line) and sVeDBA (dark purple – smoothed over 1 s) using (a) an example of an animal where the tag was firmly affixed to the body (a penguin – data from RPW), (b) a collar-mounted tag on a domestic goat (this chapter) and (c) a collar-mounted tag for an ibex that is weighted to emulate the animal's movement more appropriately. Note that the penguin begins to walk from stationary (left hand-side) and how peaks and troughs in the sway axis (green line), due to the lateral movement in the waddling gait, coincide with peaks in both heave (blue line), as the bird momentarily rises during each step, and surge (yellow line), as the bird accelerates forward with each stride. In the production of VeDBA, the differences between all these values and the smoothed accelerations for each of the axes (lines running through the raw acceleration traces) are made positive and added vectorially. This produces very distinct peaks in the VeDBA with each stride. These relate to the dynamism of the strides and the step frequency (both of which decrease on the right-hand side of the graph) and shows clearly how step frequency affects the production of VeDBA and sVeDBA. The goat and ibex examples show a similar, though more complex, quadruped pattern but greatly obscured due to collar roll. Nonetheless, the same patterns regarding VeDBA and sVeDBA hold true.

The expectation is, therefore, all other things being equal, that my cows should have broadly lower VeDBA values than the goats, for example, because they have lower stride frequencies for a given speed. This is not obviously the case (at least as reflected in the COT$_{\text{VeDBA}}$ estimates (e.g. Fig. 8). However, it is difficult to make robust comparisons because I did not have controlled conditions (such as a treadmill – cf. Dickinson et al. subm.). Instead, my data show

how COT_{VeDBA} varies with slope (Fig. 8) at times where the animals were controlling their own speed (Fig. 5) and indeed, the extent to which they walked continuously. Nonetheless, I tentatively suggest that the expectation is that the larger ungulates should have lower VeDBA values for given speeds on level ground at least. I therefore propose to bear this in mind as I examine how animals of different masses deal with slopes and habitat under the null hypothesis that there is no difference in VeDBA (or mass-specific VeDBA) *versus* power-use across species so that any disproportionate increase in VeDBA with performance (speed and slope) in cows in particular (being substantially larger than all other species), genuinely reflects power investment.

Species-specific movement tactics

Perhaps the most striking feature of the way the study animals moved on slopes is the difference between animal slope angles, which are determined by the angle at which animals move up or down the cartographic (maximum) slope, and the slope of the terrain itself (Fig. 6). Indeed, these animal angles were a fraction of the maximum angle of the slope. I believe that there are two elements to this. Firstly, animals were often moving and grazing (cf. Chapter 4, 5) rather than just moving, and grazing, in itself, is not expected to relate to slope. Secondly, I have no indication of the extent to which these animals intended to walk directly up or down the slopes. Such considerations are easily dealt with when examining human trails up mountains where people wish to reach a peak (Rees 2004) so that the energetics of zig-zag tracks can be examined (Llobera and Sluckin 2007, Lempidakis et al. 2018). However, in the case of my mountain ungulates, animal-chosen slope angles are a complex mixture of the energetics of slope movement and accessing resources. In this respect, I am unable to make definitive statements except to note the speeds selected and the animal-chosen slopes as a function of the cartographic slopes.

Within our dataset, I have information on both uphill and downhill movement, and note that animal-selected slopes in relation to cartographic slopes are strikingly similar for both uphill and downhill movement (Fig. 6). Although it is clear that uphill locomotion is most energetically onerous, followed by downhill movement and finally movement on the flat (Fig. 6) for reasons discussed earlier, for convenience, I concentrate in the following discussion on uphill movement, understanding that patterns will be similar for downhill movement, if less extreme.

In order to understand species-specific tactics for dealing with inclines, it is important to merge animal slopes with respect to the slope of the terrain (Fig. 6) with animal-chosen speeds as a function of terrain slopes (Fig. 5) to give us the species-specific relationship between animal-chosen speed and animal-chosen slope (Fig. 12).

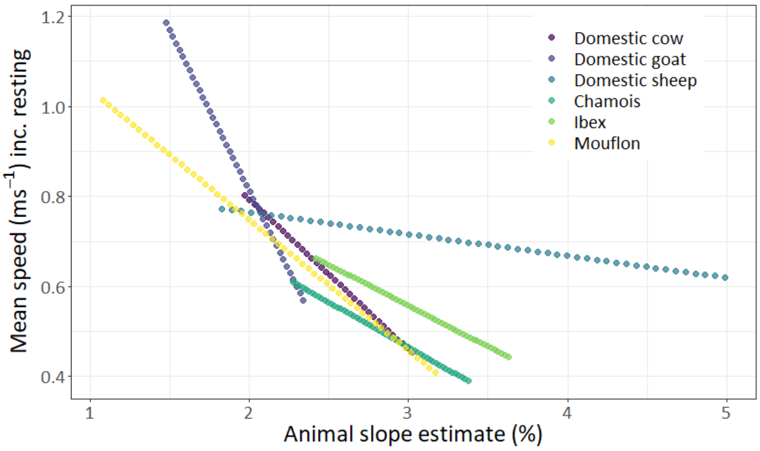


Figure 12 – Relationship between the mean maximum speed travelled by 6 species of ungulate on inclines (cf. Fig. 4) and the incline chosen by the ungulates (cf. Fig. 6) derived by combining regressions.

A number of aspects are apparent in this representation. First, both the ibex and the chamois ascended with constrained slopes (Fig. 11), even though they move in terrains that are both steep and extensive (20-50% for the chamois and 10-60% for the ibex) (Fig. 6). The power consequences for them are apparent in Fig. 8, which shows that the ibex has the lowest positive COT_{VeDBA} *versus* slope coefficient of all species except for the sheep, while the chamois has a negative coefficient, although by the time this is converted to a COT_{VeDBA} *versus* animal-chosen slope (by combining COT_{VeDBA} *versus* animal-chosen slope and animal-chosen slope against terrain slope), it is positive (Fig. 12). The power consequences are also the result of the fairly minimum change in speed over that range and, together, this translates into minimized dynamic range in power, assuming power can be equated linearly to VeDBA (and the evidence for this is compelling, even for ungulates - (Dailey and Hobbs 1989, Parsons et al. 2008, Halsey and White 2017, Dickinson et al. subm.). A consequence of this minimized power range is that the potential for overheating (cf. Chapter 5) is also less variable and perhaps more controllable and this may be a reason why the animals choose to move up slopes at the angles they do.

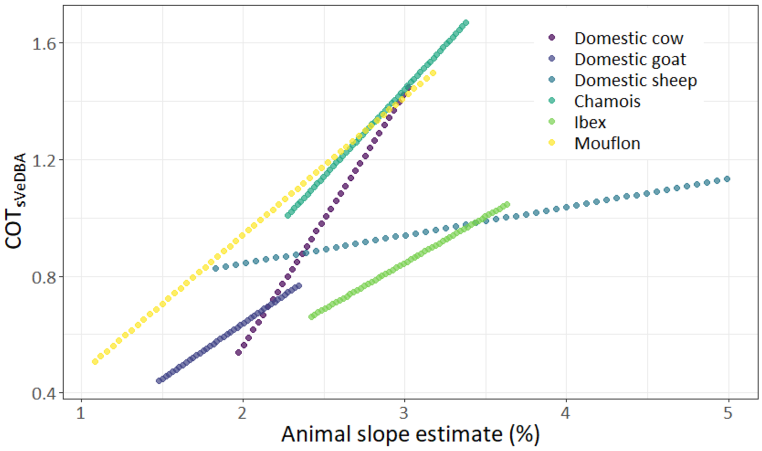


Figure 13 - Relationship between COT_{VeDBA} (cf. Fig. 8) and the mean incline chosen by animals to ascend for 6 species of ungulate on inclines (cf. Fig. 6) derived by combining regressions. Note that both the positions of the lines as well as their gradients are important, with lines closest to the left hand side being proxies for power use (although COT_{VeDBA} also needs to be seen within the context of travel speed (cf. Fig. 12)).

The rate of speed drop with (chosen) slope in goats is notably high (Fig. 12), and it is also clear that these animals move so that their trajectories take them predominantly up shallow slopes (Fig. 12), irrespective of the cartographic slopes (Fig. 6). This strategy leads to a minimization in the rate of potential energy change during ascent (because their effective climb rate is reduced), which will keep power requirements low and is presumably the reason why their gradient of their COT_{VeDBA} *versus* terrain slope is also particularly shallow (Fig. 8) and why they operate at low COT_{VeDBA} values overall (Fig. 13).

The mouflon tended towards climbing slopes that were between 1 and 3.5%, which applied to mapped slopes of 0 to 55% (Fig. 6), with the highest gradient of all species bar the sheep (Table 4, Fig. 6). So, despite them adopting an appreciable reduction in speed drop over the range (Fig. 12), they had one of the highest absolute values of COT_{VeDBA} across slopes and highest rates of increase in COT_{VeDBA} with animal slope of the species examined (Fig. 13).

Although cows adopted relatively low speeds (Fig. 12) and travelled so as to move up low slope angles, with little variation according to terrain slope (Fig. 6), they had the highest rate of increase of COT_{VeDBA} against animal slope of all the species (Fig. 13). If my earlier null hypothesis, that VeDBA is a suitable proxy for power (and therefore COT_{VeDBA} for cost of transport) irrespective of size is to be adopted, it would seem as if moving up slopes is most onerous for cows. This is likely to be further emphasized because, as projected earlier, there are reasons to think that cows, by virtue of their size, should have lower COT_{VeDBA} values that the other species. An explanation for this is provided by Wall *et al*. (2005), who point out that slope-climbing is more onerous for larger animals because of muscles being ~33% less efficient when climbing compared to flat surface travel and the shifting of extra body weight against gravitational forces. That this restricts cow movement on slopes is also indicated by the high COT_{VeDBA} values at low animal-chosen slopes (Fig. 13), despite the reduced speed at which they operate (Fig. 12).

The most surprising result of this study concerns, though, the sheep. The data indicate that sheep reduce their mean travelling speed the least in relation to slope of all the species (Fig. 13) and also have the lowest COT_{VeDBA} values while doing this (Fig. 14) and exploiting an appreciable range of slopes, both in their chosen slopes and the cartographic slopes (Fig. 8). This makes sheep real outliers and this is particularly apparent if the COT_{VeDBA} values, the speeds and the animal-chosen slopes are placed within one three-dimensional graph (Fig. 14).

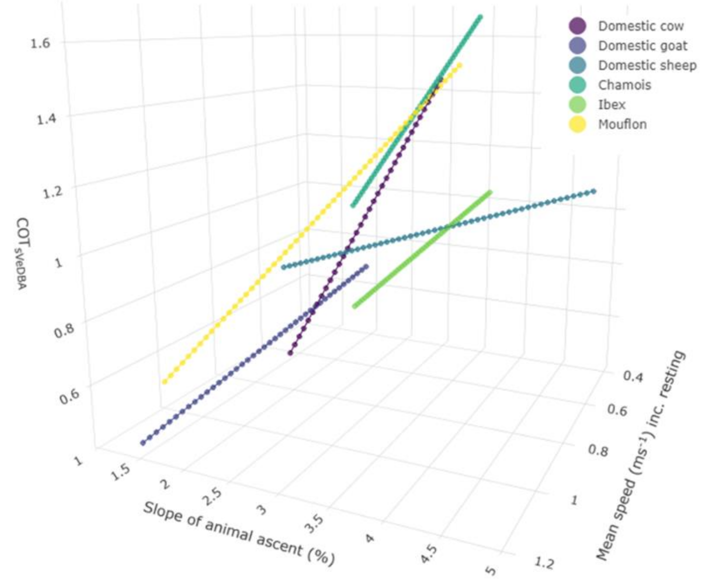


Figure 14 – 3d plot linking the VeDBA-derived costs of transport with travelling speed and ascent angles (combining Figs 12 and 13) adopted by the 6 species of ungulates used in this study.

It is not clear why the sheep are so efficient and, in any event, a proper calibration of oxygen consumption *versus* VeDBA (Dickinson et al. subm.) would be needed for all species for this to be confirmed. However, assuming the VeDBA proxy for power to be true (Qasem et al. 2012, Jeanniard-du-Dot et al. 2017, Wilson, Börger, et al. 2020), this movement efficiency may explain why sheep have been adopted as the animal of choice for mountainous regions across the globe (Zeuner 1963, Ryder 1983). The wild ancestor of the domestic sheep was the Asian mouflon (*Ovis gmelini musimon × Ovis sp.*), a mountain-dwelling species, which was domesticated around 11,000 years ago (Meadow et al. 1989). What is notable though is that, within our 6 study species, the mouflon had the most dissimilar strategic and energetic profile to the sheep, having the highest $\mathrm{COT}_{\mathrm{VeDBA}}$-linked performance of the group (cf. Figs 6, 8, 12, 13, 14). If the Asian mouflon behaves in a manner similar to this species, and I assume that there are survival-linked advantages to their strategy, the process of domestication has changed this dramatically. As a result, the domestic sheep seems well adapted, both behaviourally and physiologically, to exploit a wide variety of slopes within mountain regions.

As expected, the COT_{sVeDBA} decreased with speed adopted by each species, and the rate of energy expenditure increases with speed. Higher speeds offer a more efficient way to traverse an environment but the speed the species travelled at decreased with slope possibly explaining the inefficient travel.

Energy landscapes for sympatric ungulates

A prime aim of this study was to construct and compare the energy landscapes of 6 different ungulate species living in the same area, positing that although conditions such as topography are fixed, that the costs of movement will vary according to animal type. In fact, although my study areas were similar, most of our species were not truly sympatric.

Nonetheless, inspection of the energy landscapes for ascending and descending ungulates across their respective areas shows huge variability in the costs of moving over the terrain they exploit (Fig. 10). Here, it is also notable that patterns of high costs, primarily associated with cartographic incline, are similar for both ascents and descents because steep inclines necessitate energy to negotiate, but for different reasons (see above). In a general sense, the proposed energy landscapes should highlight the areas that are energetically onerous for the different species. Future work could consider integrating that with the presumed benefits of different areas, such as food quality, access to mates and likelihood of predation. Especially interesting is the difference according to substrate, especially the difference between bare rocky ground and the vegetated habitats (Table 6).

There was, however, a case where two animals, the goats and the cows, exploited exactly the same environment. Here, the data indicate that they had, as hypothesized, very different energy landscapes to one another, both for ascending and descending behaviours (Fig. 10). Notwithstanding the lack of a proper calibration between oxygen consumption and VeDBA with which to ground-truth the data, the inter-specific differences are dramatic, with cows having substantially higher COT_{VeDBA} values for most of the exploited regions, only comparing to goats in a tongue of land rising northwards, starting in the south-east, and having lower COT_{VeDBA} values in a tongue of land rising northwards, starting in the south-west (Fig. 10). At once, this illustrates that energy landscapes do indeed seem to vary between species exploiting the same environment but it also points to the competitive advantage that one species may have over another according to the habitat. In my study, slope turned out to be the major modulator of COT_{VeDBA}, but habitat type, by virtue of the animals having to push through superstrate (Murray and Boutin 1991, Crête and Larivière 2003, Shepard et al. 2013) or expend energy by having a more tortuous track (Wilson et al. 2013) , will also play a role. The precise behaviours adopted by the animals, such as how their chosen ascent slope changes with terrain slope and how they modulate speed with slope will affect their power use, but will also affect the extent to which they can move up and down mountain slopes to exploit resources (including access to females for males). Species that climb up steeper gradients will access benefits linked to variable altitudes better but they will pay a high energetic cost and so net sum gains will determine the success of this strategy. Included in the potential deficits are temperature which, as examined in chapter 5, may constrain high energy behaviour which might have had benefits in the past, when global warming was not an issue (Aublet et al. 2009).

Most importantly, although this work is a first step towards understanding space-use in mountain ungulates, it does, at least, show the breadth of factors that are likely to impact population wellbeing. Faced with such complexity, conservationists have a daunting task if they are to ensure species success in such as fast-changing world.

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Chapter 8

Synopsis

Naively into the thesis

When the project and my PhD started, I had great ambitions to collect and collate high resolution (20 Hz) multiple sensor tagging data on six ungulate species for periods of between 30 days and a whole year, and for up to 20 individuals for each species across two field seasons. Certainly, by working with Grenoble University and the 'French National Office for Hunting and Wild Fauna' (ONFCSs), and within the Swansea Lab for Anima Movement (SLAM), this seemed highly achievable. But my post-graduate optimism fostered naivety and, although part of the work capitalised on commercial GPS collars, I was in for some serious lessons.

I suppose that the most important of those was that wild animals have no regard for the expense, construction time or utility of tags that I attach to them. I have heard of researchers talking of this but the special qualities of my ungulates (simple brute force) and the environment in which they live (freezing to hot temperatures with drastic precipitation – chapter 2) make for a particular brand of hopelessness. With hindsight, the idea that I might construct and deploy such hi-tech, lab-built tags for periods that, at that point, were an order of magnitude longer than ever done before, was crazy. SLAM tag deployments using Daily Diaries (DDs) are typically a few days (Wilson et al. 2008, Sala et al. 2012, Scantlebury et al. 2014, Williams et al. 2015) although, exceptionally, there had been deployments of up to 3 weeks (Fehlmann et al. 2017, Gunner et al. 2020). Finally, of course, many of the species on which I was to work are effectively invisible – they cannot normally be observed - so the idea that I could sit on a sunny mountain slope sipping coffee from a flask and watch what the wild ungulates did with my tags through binoculars was fanciful in the extreme.

My MRes, which involved tagging tortoises on a tropical island for a few days at most, did little to prepare me for the storm of possibilities that long-term tagging of wild ungulates would produce. And finally, the one thing that would undoubtedly have helped me with general housing design, the deployment of tags on domestic ungulates (sheep, cows and goats – chapter 3, 4, 5), did not happen until the deployments on the wild species (mouflon, ibex and chamois) had taken place. A chance that I was supposed to have for a second deployment on the wild ungulates, was cancelled after the French researchers discovered that the commercially available collars were malfunctioning. This was depressing as a PhD student but demonstrates that even the might of industry is not guaranteed to deal with the vagaries of wild animals, especially, it would seem, alpine ungulates.

As time into my thesis progressed, eroding the time I had left to finish the job, it became clear that great thought and consideration was needed into the design of the housing for Swansea's DD that would complement the Lotek collar (being used by our partners), including force measurements and the weatherproofing for the internal electronics of the tag. The simple truth about long-term deployments (~12 months) is that they are high risk, because any failure that occurs within that extended time can effectively result in catastrophic failure (no data at all) and all that time is lost in such a short-term project that can ill-afford it. Indeed, the framework proposed by Bidder et al. (Bidder et al. 2014) about tagging failures kept nagging me: That, even if the probability that a tag fails per unit time is constant (for whatever reason), the overall probability of failure increases with deployment period according to simple probabilistic rules – like shaking a 12 with two dice. Throw the dice for long enough and you will get 12!

So, the material of the DD housing, how it should be waterproofed and then attached to the housing, haunted my start into this thesis for much longer than I thought possible, and is now hidden in chapter 2 in a few short words. The construction of the housing was made all the more difficult by the understandable ethically motivated restrictions on tag mass (e.g. (Vandenabeele et al. 2015, Kölzsch et al. 2016, Wilson et al. 2019)). Batteries alone took up a large portion of tag weight because recording for long periods requires greater energy reserves (Holton et al. in press) so I also spent much time testing power consumption and the effect of this on various batteries (not all batteries are created equal).

And finally, having decided on the best design for my DDs, I had the deployments in the Alps on wild animals that are elusive, difficult to manage, and for which there were limited opportunities to catch. To say this the whole process was extremely stressful (for me as well as them) was putting it mildly. But I did it. After all that, I was not to know whether my ministrations had paid off until months, almost years, later.

Many unforeseen failures occurred that affected the end data set, although even these experiences will be valuable for any future tagging projects. Some housings were destroyed by the mouflon, presumably from head-butting (Fig. 1) and all data were lost because the smashing was so complete that even the circuit board of the DDs could not be found. A tagged chamois was also found dead after falling into a ravine (with the data irretrievable).

Figure 1- (a) Acceleration trace of possible high impact (>10 g), agnostic social interaction causing destruction of "daily diary" housing units. (b) Image of collar attached to mouflon with daily diary housing intact. (c) Collar collected following deployment in the field with ABS plastic missing, bolts holding the housing in place still intact but showing the housing fragmented off. Data and images of collars taken from mouflon tagged in Caroux, France, during the rutting season in 2017.

Two mouflon were killed by a wolf (there was apparently only one in the region). The data from the tags showed the drama of the last seconds of these animal's lives (e.g. Fig. 2), emphasizing the value of such systems for elucidating transient, but critical, moments in animals' lives – for predators as well as prey (Cooke et al. 2013, Wilson et al. 2015). Given the effective scarcity of this predator, that so 'many' of my equipped animals were caught, raises questions about whether the tags did not contribute to the process. Other, more mundane but more common, reasons for data loss, included SD cards that seemed unable to function for long periods under the deployment conditions without incurring data corruption. This was particularly frustrating because the tags were successfully retrieved (no small matter) and then, despite asking specialist companies to try and extract the data from the cards, it was to no avail. If there is one key message about deployment of tags that use memory cards, it is that card quality is critical, whatever the manufacturers tell you.

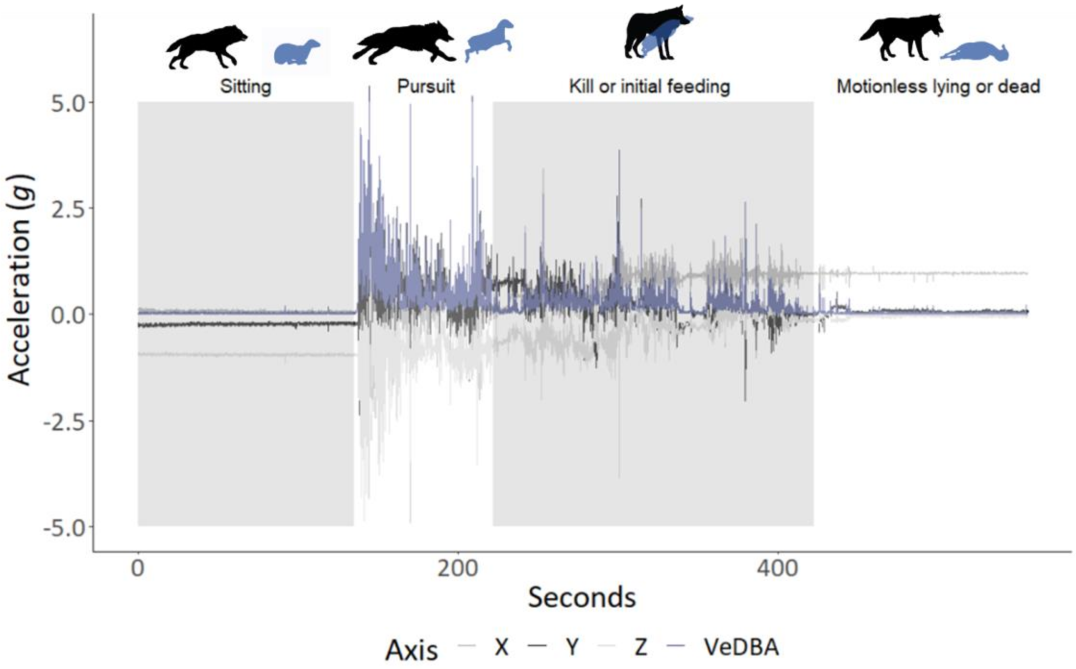

Figure 2- Line graph to visualise acceleration and VeDBA across time during the final movement of mouflon's life. Changes in acceleration signify changes in posture and activity leading to four proposed phases of mouflon and wolf interaction, sitting, pursuit, kill and dead. Mouflon death was confirmed to be caused by wolf by post-mortem.

The benefits of starting with domestic animals extend beyond housing/collar design

Although I was unable to benefit from the domestic livestock in designing my housings, they proved critical in helping me understand my data from wild animals because I could observe them and inspect the acceleration and magnetometer signals with respect to behaviour and movement. In fact, livestock has been well studied in this respect within the literature (e.g. Miranda-de la Lama and Mattiello n.d., Alvarez et al. 2003, Sanon et al. 2007, Chapinal et al. 2009, Lush et al. 2018), not least because these animals have high economic value within the farming industry (Miranda-de la Lama and Mattiello n.d., García-Martínez and Bernués 2009). Nonetheless, I had to bear in mind that farmed animals (are bred to) undertake less dynamic movements than wild animals, and also display a much simplified array of behaviours (Campbell et al. 2013) under 'gentler' environmental conditions, such as slope angle (because no farmer wants to have to retrieve her/his livestock from a cliff!). Nonetheless, a step taken by a domestic goat is functionally much the same as a step taken by a wild ibex so, given the questions I was attempting to answer within the thesis, my domestic animals served as excellent surrogates for the wild species (e.g. Chapter 5, 6), as well as being interesting in their own right (chapters 4, 7).

Dealing with behaviours

This process of matching data to behaviours was not easy, even though many publications imply that it is (Shepard et al. 2008). This was primarily because my animals all wore collars, onto which the DDs were attached, whereas literature examples of deriving behaviour from accelerometer data tend to use examples where the tags are affixed tightly to the trunk of the animal (Yoda et al. 1999, Williams et al. 2015, Kölzsch et al. 2016). Collars rotate (Moreau et al. 2009, Dickinson et al. 2020), so that acceleration axes become confused, most particularly because the heave and sway axes are effectively interchangeable. And the degree of rotation depends on the weighting of the collar (another challenging element that I have glossed over in this thesis) and the movement of the animal because, for example, the faster an animal travels, the more the collar tends to rotate (pers. obs). One potential way around this, would have been to have used machine-learning, such as random forests (Martiskainen et al. 2009, Fehlmann et al. 2017, Rast et al. 2020), to allow some 'black box' approach to classify behaviours. This is wonderfully convenient, but the machine can only learn from what it is given, and if the test data do not represent the full suite of conditions to which that animal is exposed, it cannot be expected to perform to the level it does under the controlled conditions. This particularly germane for animals in mountains where, in acceleration terms, the data change radically according to slope. A good example of this is apparent in the sheep literature: Lush *et al*. (2018) cite a success of detection of sheep urination of 87% in precision and 62% in recall using machine-learning on animals with behaviours calibrated in a flat paddock. But this method detected only a fraction of examples of exactly the same animals on a mountainside (Marsden et al. 2021). In fact, following this, Marden et al. (in press) changed their approach to identify urination using a Boolean approach (Wilson et al. 2018). This was based on identifying particular signatures within the data set that were slope-independent, such as differentials and vectorial sums in the acceleration signals, and showed 100% success for the paddock trials and expected urination rates for the mountainside sheep (Marsden *et al*., in press).

For reasons such as this, I opted for the Boolean approach (Wilson et al. 2018), but also because I could see what was happening at every stage, which is empowering and sometimes very necessary. The Boolean approach capitalised on the SLAM lab-built programme, Daily Diary Movement Trace (DDMT), which is extraordinarily powerful, although challenging to learn to use. As a consequence, I spent many hours visually inspecting, practising, and understanding acceleration data, for what they meant themselves in terms of animal movement as well as how they are represented in the DDMT visualisation tool. During this time, I was successfully able to define behaviours using acceleration data employing both Boolean rules as well as adding a time element to help identify different 'LoCoD' aspects of behaviours (Chapter 4, 5). The trade-off in accuracy, reliability, adaptability and efficiently (analysis time and computer power) in my algorithms was not specifically assessed. However, a general trend emerged wherein the more complex the rule and the stricter the time series windows associated with it, the greater the accuracy of the algorithm for finding specific behaviours. However, it is easy to over-specify the rules so that the behaviours, if they do not accord exactly to the conditions set, will be missed. A thorough examination of this process, including the time invested by the computer to search through the data to detect events, would be useful to define realistic expectations for people using this method.

During my behavioural meanderings, I was aware of many ideas that I could have pursued. These included broad areas associated with accelerometery, such as how animal mass affects acceleration signals. But it also touched on fleeting behaviours that are relevant for a suite of behavioural issues, such as how post-agnostic behaviours could reveal winners and losers after head-clashes (the winner would hold ground, the loser mover away) and perhaps allow me to build a dominance hierarchy of populations or depict individual personality. These concepts were entertained and discarded due to the workload associated with data handling and analysis. This was somewhat frustrating, but in the interests of the specific tasks associated with my chapters, the right decision. Maybe I can visit them later? In any event, I have a very thorough grounding in acceleration and magnetometry data now, which will facilitate analyses that I might undertake using this sort of data in the future, irrespective of the animal on which it is collected.

Dealing with data

In a manner similar to my naivety with respect to the tag construction, I was unprepared for the task of dealing with billions of data points, even from single animals. A quick calculation of deployment lengths and sampling rates would have told me what I should have known. With 8 channels recording at 20 Hz, a DD attached to an animal for 200 days will record over 2.7 billion data points, and although my tags sampled at lesser rates for the pressure and temperature readings, for example, it illustrates the point. So, I discovered that utilizing billions of data points to produce 20 Hz dead-reckoned paths for >200 days on multiple individuals soon cut my wings. I embraced my (hi-specification) computer limitations and produced dead-reckoned paths at 1 Hz (and for some figures sub-sampled further to produce visualisations). This is defendable given that I needed to resolve relatively ‘broad’ space-use and movement (e.g. Chapter 4), but it did mean that the details in the movement of some of the ungulate behaviour, such as head-clashing (Chapter 6), were lost on me.

Similarly, I could not over-indulge in examining other ‘interesting’ behaviours, such as how individual goats move according to the movement and behaviour of adjacent conspecifics (O’Bryan et al. 2019, Pérez-Solano et al. 2020). The data are now available, however, a precious and hard-won resource that can be examined at any point in the future. Indeed, animal ethics considerations would advocate this strongly, rather than instigating more studies if the questions being asked can be answered with existing data. Importantly, even during the analysis, I was acutely aware of the value of my high-resolution data. The ‘norm’ in studies on wild animals is for people to have comparatively ‘rare data’, for example GPS data every hour, to which they have to apply hidden Markov maths to try and define ‘states’. Such approaches are superfluous in DD information-rich datasets, where the sub-second details are available, seamlessly for the whole tag operation period. So, I have the treasure and do not have to speculate if I want to know what is in the box. But I decided in the end that I did not have the time to sift through it; thesis duration limitations are unforgiving.

Expanding our understanding of energies

The literature reminds us repeatedly of the value of energetics in animal behaviour (Aublet et al. 2009, Scantlebury et al. 2014, Wang et al. 2015), movement (Pearson et al. 1995, Wilson et al. 2013), reproduction (Holand et al. 2006, Brivio et al. 2010, Willisch and Neuhaus 2010), in fact almost everything (Patton 1962), so it seemed appropriate to visit this in my thesis. Dynamic body acceleration (DBA) has been shown to be extremely valuable with respect to helping define animal energetics with a linear relationship between power and DBA across taxa, although the gradients and intercepts vary (Wilson et al. 2020). My tags allowed me to determine DBA, and so, in a general sense, I could allude to changing power costs within species and this proved important for assessing animal reactions to incline. However, I had no calibration, such as was done by Dickinson et al (subm.), so it is important for me to be circumspect in how far I could push the issue. Determination of costs of transport (COT) might seem a step too far in this regard. However, the calculated speed seemed appropriate (chapter 3) so, given that the COT is given by the power to move divided by the speed (Taylor and Rowntree 1973, Taylor et al. 1974), the derived COT-values are likely to be no more subject to variation than DBA itself. Importantly though, calculation of COT allowed me to effectively remove speed in my application of COT to slope-travelling behaviour (Chapter 7). The value is this is obvious from chapter (*last chapter*), where I could allude to differing energy landscapes (Shepard et al. 2013) according to species for the same topography. This indicates that slope *per se* is not enough in our construction of energy landscapes but that precisely how the species approach a given energy landscape defines how onerous it is for them. In that respect, for me, dead-reckoning really came into its own, demonstrating that none of the ungulates apparently ever climbed directly up or down the slope, instead travelling obliquely at shallow angles, something that was independently confirmed by the rate of change of pressure with respect to speed. So, although I tend to consider mountains by virtue of how steep they are (the incline specifically being defined by the maximum gradient), this is not applicable to the animals that inhabit these slopes. Instead, the slopes impose a constraint for gentle angular climbing but nothing more. This, in turn, means that I should perhaps be considering access to resources by animals on slopes according to contours rather than altitudinal accessibility (Dunford et al. 2020, Dickinson et al. subm.).

Energy expenditure to move is particularly relevant for ungulates with regard to foraging because these animals have to invest such a high percentage of their time grazing, which involves movement, so it was relevant for me to consider resource availability. However, although I could determine with reasonable certainty that animals were feeding, and in what habitat type, I could not determine precisely what they favoured. The literature shows that food plant choice in ungulates is complex (Pokorná et al. 2013, Iussig et al. 2015, Pittarello et al. 2017) with, for example, sheep preferring some foodstuffs in the morning and others in the afternoon (Pulliam and Pyke 2008, Pittarello et al. 2017). The principle behind optimal foraging is not just that animals should chose when to leave food patches (Krebs 1980, Pyke 1981) but also, particularly when applied to herbivores, what they choose to eat (Zweifel-Schielly et al. 2009, Mason et al. 2017, Pittarello et al. 2017). This makes perfect sense. They are surrounded by food but some plants within the matrix of vegetation are better for them (more nutritious or contain more energy) than others and there must be considerable selection pressure for them to choose carefully. So my attempts at determining habitat preferences as a measure of determining foodstuff preferences are primitive seen in this light.

Techniques such as video collars may provide more detailed answers (Newmaster et al. 2013) for future work but it is hard to see how this complex issue will be resolved satisfactorily in the short term. Nonetheless, linking animal pathways to behaviour to vegetation types is a first step in this direction.

Marrying dead-reckoning with behaviour

The work within this thesis that identifies feeding habitat, illustrates what I consider to be a critically important feature of the DD technology for understanding the spatial ecology of animal behaviour. This is the ability to marry observations of behaviour with locality by inspecting the behaviour deduced from accelerometers with the time-synchronised GPS-corrected dead-reckoned tracks. Recent ecological work has emphasized that animal landscapes can be considered as 'landscapes of fear' (Laundré et al. 2001, Hernández et al. 2005, Kohl et al. 2018), 'energy landscapes' (Shepard et al. 2013) or even 'accident landscapes' (Wheatley et al. 2021), which is another way of saying that the 'value' of the landscape for animals varies, with positive and negative effects according to locality. In accordance with this, authors have noted, for example, that animals avoid 'landscapes of fear', selecting to use areas where predators are less likely to be present (Laundré et al. 2001, Hernández et al. 2005). This avoidance changes over time, including within the daily cycle (Kohl et al. 2018). While this area-switching is useful, not least for conservation reasons (Bleicher 2017), it gives no clue as to what behaviours animals exhibit in the different landscapes that might indicate why they choose their particular paths. The ability of accelerometers and magnetometers to resolve behaviour, including e.g. vigilance (Wilson et al. 2020), in detail (Shepard et al. 2008, Williams et al. 2017) means that it should be possible to determine the onset of behaviours, such as vigilance, that indicate why animals choose the pathways that they do. Indeed, ultimately, it should be possible to ascribe a full suite of behaviours to time and space within all the areas used by animals which would go a long way to illustrating how a species fits within its environment.

Ecological questions

With so much of my PhD being dedicated to solving methodological issues, there has been an inevitable bias towards the ‘technical’ side of biology. Our data is only as good as our research protocols, however, so I believe this aspect is critically important. Indeed, a recent submission by Garde et al. (2021) makes clear how blind acceptance of the apparent capacity of technology (specifically accelerometers) can lead to fundamental errors in interpretation. But my concentration on technology has come at the expense of dealing with biological matters so it is worthwhile pointing to biological questions that may be addressed using this technology. In 2012, Sutherland et al. (2012) published a paper in the Journal of Ecology entitled ‘Identification of 100 fundamental ecological questions’, which was compiled using data from 388 participants who sought to identify the 100 (presumably most) important questions in pure ecology. These questions understandably reflected technical and conceptual issues in ecology and were wide-ranging across scales of time, space and populations. Many of these questions will perplex researchers for years to come but a few of them may now be addressed using animal-attached technology. For example, one question asks ‘*How do organisms make movement decisions in relation to dispersal, migration, foraging or mate search?*’. Although this is obviously a very big and multifaceted question, the extraordinarily high temporal and spatial resolution of GPS-enhanced dead-reckoning means that decisions that occur on any scale can be examined. This ranges from the rapid twists and turns as animals try to outmanoeuvre predators, with strategy depending on relative predator and prey masses (Wilson, Griffiths, et al. 2015), through decisions to avoid or favour certain areas of the landscape for energetic reasons (Shepard et al. 2013 Energy landscapes Am Nat) –including the rate at which animals might negotiate slopes (see chapter 7) - to general dispersal metrics (Lidicker 1992), which can be coached in terms of instantaneous speeds and track tortuosities as well as their means over periods equating to months or even years of dispersal. Indeed, I note that biologgers can now operate over years (chapter 6) and have even been demonstrated to do so by a research group in Prague working on red deer (*Cervus elaphus*) and boar (*Sus scrofa*) who have data spanning over two years. This is a significant proportion of the lifespan of these animals and it is extraordinary to think that the hierarchy of movement decisions taken by animals can now be considered over seconds or months.

With respect to ‘when’ and ‘where’ movement decisions occur, recent work by Potts et al. (2018) argues that movement decisions are apparent by a change in movement metrics, most common of which is a change in direction. So GPS-enhanced dead-reckoning can show where turn points occur (Potts et al. 2018) and these can be considered with respect to potential elicitors of the turns. These might be details of how an ungulate walks around a marsh to minimize its costs of transport (Shepard et al. 2013), uses a mountain path to minimize the risk of slipping (Wheatley et al. 2021) or decides to curtail its outward movement from its central place (as exemplified in chapter 4). Indeed, the high resolution of movement tracks now allows us to examine tracks with respect to (the high resolution of) the environment (google earth or digital elevation models) to see the effects of topography and substrate across scales. Similarly, the ability to examine movement with respect to high resolution data on vegetation (e.g. chapter 4) shows how biologgers can contribute to elucidating another one of the 100 questions in ecology ‘*How do resource pulses affect resource use and interactions between organisms*?’. Put simply, we expect animals to respond to changing food resources by moving to exploit them as they become available (chapter 4) and biologgers should show when and where this occurs. The technology might even give clues as to the cues the animals respond to: consistent movement upwind to hone in on a food resource may show the influence of odour plumes in food-finding (Nevitt et al. 1995, Keller et al. 2001, Dove 2015).

Resource pulses are driven, in part, by meteorological conditions, the importance of which also presumably led the Sutherland et al. (2012) consortium to ask ‘*How do natural communities respond to increased frequencies of extreme weather events predicted under global climate change?*’. A prime strength of biologging tags is that they can record for long periods, which increasingly incorporates extreme weather events (Barnes 2013, Tippett 2018). As with any behaviour- and movement elicitors, the more finely tuned the data collection system, the more precisely responses to specific elicitors can be determined. Thus, sub-second resolution in biologging sensors in tandem with synoptic weather data promises to allow us to understand how animals respond to the specifics of weather better than at any point in the past and my work on the importance of temperature in chapter 5 on modulating movement speed and power has looked specifically at this. A charming reference to how animals respond to environmental variation in ‘extreme events’ has been proposed by the Max Plank Institute, who have equipped domestic goats *(Capra hircus)* grazing the mountain of Vesuvius with biologgers designed to transit data indicating when the animals respond to volcanic activity (Maier 2021). Work has indicated that goats are far more sensitive to imminent eruptions than recording apparatus, possibly because they respond to infra-sound (Maier 2021), so they may save lives as well as reveal how animal sensory capacities and responses have survival value to the animals themselves.

A final question posed by Sutherland et al. (2012); '*What is the relative importance of direct (consumption, competition) vs indirect (induced behavioural change) interactions in determining the effect of one species on others?*', also illustrates that biologgers have an important role to play in helping understand animal/animal interactions. Competition is considered a major driver of animal movement and behaviour strategy although precisely how competition is manifest and resolved is not always easy to quantify. As chapter 5 (head butting) showed with the work on head-clashes, biologgers are not only able to quantify the extent and intensity of competitive interactions, they can also show where these occur. This is relevant because competition is associated with resources. Detailed studies of resource quality and 'winners' and 'losers' (the loser in a head clash will likely be the animal with the lowest acceleration signature but also, as apparent in the dead-reckoned trace, the animal that retreats) can help identify the rules by which competitive games are played and the likely outcome. In goats, for example, what role does mass play in success in competitive interactions and, bearing in mind that mating attempts should be readily identifiable by biologgers, how might this affect lifetime reproductive success? In this case, as with the other questions posed above, it may be that, as Ludwig Mies van der Rohe said, the 'devil is in the details' but if that is the case, then biologging would seem set to deal with that, allowing us to move towards answering some of the fundamental questions in ecology.

The final word

This thesis began as an attempt to try and better understand how the alpine ungulates behave according to space and time in their extraordinary landscape and the discussion above makes it clear that my best efforts have just scratched the surface. Indeed, one of the reasons for this was that I was so focussed on the many technical problems, both in terms of hardware and software, that I failed to see many of the exciting avenues of investigation until it was too late. Then again, if I had not dedicated so much time to problem solving, I might have no data or analysis at all. Frank Delarny, in *The Matchmaker of Kenmare'* wrote “Start with the difficult and when it gets easy, everything else is easier”. I think that I started with the difficult, but I would like to believe that I have maybe made it easier for others for the future. There is certainly a lot of data in the bank as well as tips on how to examine it. Surely that is cause for celebration?

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Appendix

Appendix Supplementary Information for ‘**Chapter 3 - Step in the right direction for dead-reckoning terrestrial animals: Using behavioural definition analysis to improve the accuracy of dead-reckoned locations’**, ‘**Chapter 4 - Move. Eat. Rest. Repeat: Habitat preferences and space-use of a herd of domestic goats (*Capra aegagrus hircus*) in the French Alps’** and ‘**Ungulates as cartographers: How do topography and habitat affect the movement energetics of ungulates in mountain areas?’**

Table 1 – List of GPS units used in study with corresponding batteries and logging times to calculate weight per day for GPS taking 1 fix every second.

Animal and unit ID	*Sample frequency*	*Battery type*	*Battery capacity (mAh)*	*Battery weight (g)*	*Logging days*	*Total Data points*	*Power drawn every day (mAh)*	*Weight of battery required to log for 1 day*
Cow 9 week 1 GiPSy 5	1Hz	A-cell 3.6v	3600	25.15	1.8	132693	533.33	3.73
Cow 9 week 2 GiPSy 5	1Hz	A-cell 3.6v	3600	25.15	2.16	193533	444.44	3.10
Cow 9 week 3 GiPSy 5	1Hz	A-cell 3.6v	3600	25.15	1.84	177001	521.74	3.64
				Mean	1.93	167742.33	499.84	3.49

Table 2 – List of each behaviour and how Daily Diary Movement Trace (DDMT) was used to quantify each one across for each species.

	Domestic cow	*Domestic goat*	*Domestic sheep*
Behaviour	*Simple rule used to quantify behaviours using acceleration*	*Simple rule used to quantify behaviours using acceleration*	*Simple rule used to quantify behaviours using acceleration*
Resting/inactive	If VeDBA smoothed (across 40 events) <0.07	If VeDBA smoothed (across 40 events) <0.1	If VeDBA smoothed (across 40 events) <0.1
Grazing	If VeDBA smoothed (across 40 events) >0.07 AND VeDBA smoothed (across 40 events) <0.3	If VeDBA smoothed (across 40 events) >0.1 AND VeDBA smoothed (across 40 events) <0.23	If VeDBA smoothed (across 40 events) >0.1 AND VeDBA smoothed (across 40 events) <0.27
Moving	If VeDBA smoothed (across 40 events) >0.3	If VeDBA smoothed (across 40 events) >0.23	If VeDBA smoothed (across 40 events) >0.27
Steps	If difference in the y axis acc. (differential across 3 events) >0.2 AND VeDBA smoothed (across 40 events) <0.6	If difference in the y axis acc. (differential across 3 events) >0.11 AND VeDBA smoothed (across 40 events) <0.5	None

	Chamois	*Ibex*	*Mouflon*
Behaviour	*Simple rule used to quantify behaviours using acceleration*	*Simple rule used to quantify behaviours using acceleration*	*Simple rule used to quantify behaviours using acceleration*
Resting/inactive	If VeDBA smoothed (across 40 events) <0.05	If VeDBA smoothed (across 40 events) <0.05	If VeDBA smoothed (across 40 events) <0.05
Grazing	If VeDBA smoothed (across 40 events) >0.05 AND VeDBA smoothed (across 40 events) <0.23	If VeDBA smoothed (across 40 events) >0.05 AND VeDBA smoothed (across 40 events) <0.18	If VeDBA smoothed (across 40 events) >0.05 AND VeDBA smoothed (across 40 events) <0.22
Moving	If VeDBA smoothed (across 40 events) >0.23	If VeDBA smoothed (across 40 events) >0.18	If VeDBA smoothed (across 40 events) >0.22
Steps	None	If difference in the y axis acc. (differential across 5 events) >0.19 AND VeDBA smoothed (across 40 events) <0.4	If difference in the y axis acc. (differential across 5 events) >0.1 AND VeDBA smoothed (across 40 events) <0.4

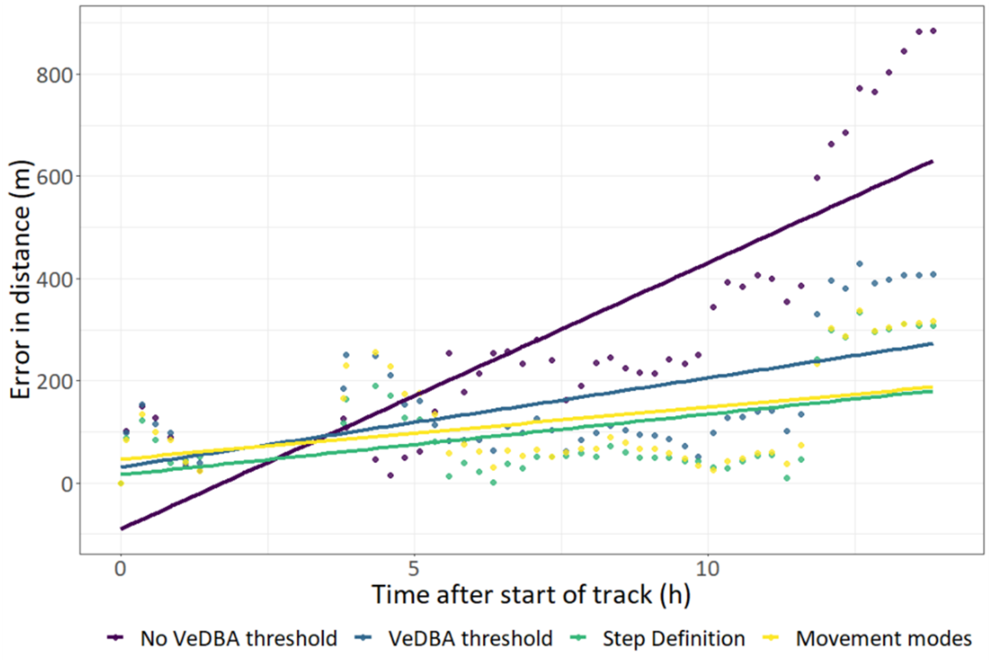

Figure 1 – Accumulation of error over time (cf. chapter 3, Fig. 8) during 14 hours of dead-reckoning implemented for data from a domestic goat (tagged in August 2017 within the Bauges, France) according to travel determined

using four different criteria (see text) (cf. chapter 3, Fig. 8). The error refers to the distance between GPS- and dead-reckoning fixes for each shared dead-reckoned and GPS location where positions were not superimposed (see text).

Table 3 - Results of mean total error for each sampling method across all species across their tested periods (14-24h). Simple linear model output showing gradient of the amount of error per hour and the R-squared value. Asterixis show the significance level of the relationship (p<0.05, ** p<0.01, **p<0.001)*

Species	*DR method*	*Mean error (m)*	*Coefficient (m error per hour)*	*R^2 (error per hour)*
Domestic goat	No VeDBA threshold	475.41	92.27***	0.40
	VeDBA threshold	349.13	54.25***	0.31
	Step definition	302.59	47.55***	0.24
	Movement modes	274.76	44.83***	0.40
Domestic cow	No VeDBA threshold	294.21	38.95* **	0.16
	VeDBA threshold	186.03	23.28***	0.43
	Step definition	187.82	27.12***	0.37
	Movement modes	160.93	20.01***	0.28
Ibex	No VeDBA threshold	596.46	37.34***	0.51
	VeDBA threshold	372.84	24.70***	0.43
	Step definition	326.21	22.89 ***	0.37
	Movement modes	307.76	20.22***	0.27
Mouflon	No VeDBA threshold	370.45	18.77***	0.12
	VeDBA threshold	153.79	11.93***	0.26
	Step definition	155.65	8.64*	0.21
	Movement modes	176.08	15.71***	0.28

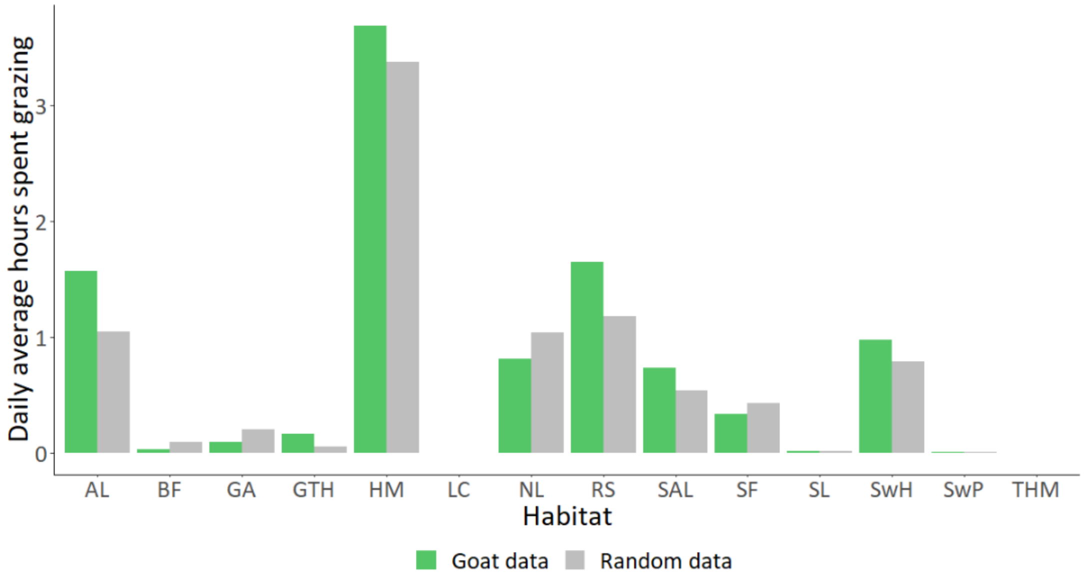

Figure 2 - The daily hours grazed for random modelled data and average real goat data for each habitat. Data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within les Bauges, France.

*Table 4 - List of selection coefficients for each habitat compared to the rock slab habitat, giving data for each data collection period as well as an overall coefficient (*** = p<0.001). Data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within les Bauges, France.*

Habitat	*03rd to 07th August*	*08th to 12th August*	*13th to 17th August*	*18th to 23rd August*	*23rd to 29th August*	*Overall*
Alpine lawns	1.033***	-0.0698***	0.588743***	0.40218***	-0.30574***	0.550403***
Beech forest	-2.56641***	None	10.51628	-4.13682***	-1.17484***	-2.72497***
Grazing tall herb formations	0.60008***	0.756318***	1.184982***	1.233181***	1.025152***	1.299811***
Green alder	0.120506***	None	-0.06512***	-1.85001***	-0.84121***	-1.49511***
Limestone cliffs	None	None	None	None	-10.6513	-9.66675
Nardus lawns	-0.41761***	-3.80961***	-0.39637***	-0.94168***	-0.33268***	-0.70112***
Rock slabs	0.644431***	-0.65558***	-0.52764***	0.029938***	0.248457***	-0.28213***
Scree with herbs	0.796234***	0.072037***	-0.37334***	-0.17553***	0.096949***	0.217175***
Scree with petasites	0.520096***	-0.24384***	0.204754***	-0.59817***	-3.65837***	0.104217***

Sedge lawns	0.586863***	-0.29698***	1.621108***	-11.6494***	-1.0148***	-0.1922***
Semi-arid lawns	0.418021***	0.21499***	0.466087***	-0.08441***	-1.20598***	0.155925***
Spruce forest	0.09452***	-1.04508***	-0.69586***	-2.5481***	None	-1.34163***
Tall herb meadows	None	None	None	None	-10.6513	-9.66675

Table 5- List of selection coefficients for each habitat compared to the bare rock habitat and slope (%) giving data for each data collection period as well as an overall coefficient. Ibex data from 30 days for each of six wild ibex tagged in June 2017 within Belledonne, France. Goat data from varied logging periods (5 to 25 days) from ten domestic goats tagged in August 2017 within the Bauges, France.

	Grasses		*Herbs*		*Woodland coniferous*		*Woodland Deciduous*		*Shrubs*		*Snow*		*Woodland open*		*Slope*	
Study ID	*Goat*	*Ibex*	*Goat*	*Ibex*	*Goat*	*Ibex*	*Goat*	*Ibex*	*Goat*	*Ibex*	*Goat*	*Ibex*	*Goat*	*Ibex*	*Goat*	*Ibex*
1	0.17	0.21	1.50	0.31	-1.25	-5.48	-2.27			0.11		0.12		0.56	0.013	0.006
2	-0.17	0.83	0.86	0.98	-1.07		-11.74	0.74		1.51		-0.95		-0.34	0.004	-0.001
3	0.07	-0.36	1.27	0.16	-1.29		0.89	1.55		0.39		-0.51		0.25	0.009	0.019
4	0.29	0.24	1.55	0.23	-1.16	-1.31	-2.34	-1.51		0.35		-0.27		0.03	0.007	0.017
5	0.36	-1.26	1.61	-0.68	-0.52		-4.12	-12.87		-0.64		-0.25		-1.39	0.015	0.036
6	-0.49	-0.12	0.19	-0.20	-0.61	0.51	-11.64	-0.40		1.10		-0.66		0.30	0.019	0.046
7	0.13		1.52		-1.41		-14.57								0.009	
8	0.20		1.23		-1.48		-2.13								-0.002	
9	0.06		1.49		-1.49		-2.88								0.009	
10	0.08		1.53		-1.60		-2.28								0.003	
Mean	0.07	-0.08	1.28	0.13	-1.19	-0.40	-2.16	0.09		0.47		-0.42		-0.10	0.009	0.021

Table 6 - VeDBA per metre moved against slope for both movement mode and all habitats present, coloured to match the mapped habitats with simple liner regression lines to represent the trend. Domestic goat 10 m summary data, filtering out level movement, was used for this analysis.

		Domestic goat		
Habitat	*Intercept*	*Estimate*	*P value*	*R^2 value*
Bare		0.415	0.003 <0.001	0.004
Grasses		0.367	0.004 <0.002	0.005
Woodlands		0.401	-0.004 <0.003	0.002

Table 7- List of observations taken to comprise focal data. Behaviours obtain from observing goats during study week 1 and 2, tagged in August 2017 within the Bauges, France.

Goat Study ID	*Behaviour*	*Date*	*Time*	*Notes*
G9W1	Walking	20/07/2017	09:45:51	Across rocks
G6W1	Walking	20/07/2017	15:13:40	
G6W1	Salt lick	20/07/2017	15:13:52	
G6W1	Head clash	20/07/2017	15:14:18	With G4
G6W1	Head clash	20/07/2017	15:14:52	
G6W1	Salt lick	20/07/2017	15:16:21	
G6W1	Walking	20/07/2017	15:17:24	
G6W1	Standing	20/07/2017	15:17:33	
G6W1	Head clash	20/07/2017	15:22:10	
G6W1	Salt lick	20/07/2017	15:22:15	
G6W1	Walking	20/07/2017	15:22:11	
G6W1	Drinking	20/07/2017	15:22:15	
G6W1	Walking	20/07/2017	15:25:27	
G6W1	Standing	20/07/2017	15:25:46	
G6W1	Walking	20/07/2017	15:25:51	
G6W1	Walking	20/07/2017	15:30:20	
G6W1	Head clash	20/07/2017	15:30:36	
G6W1	Head clash	20/07/2017	15:31:18	
G1W1	Salt lick	20/07/2017	15:34:47	
G4W1	Walking	23/07/2017	11:40:16	Uphill
G4W1	Standing	23/07/2017	11:42:09	
G4W1	Walking	23/07/2017	11:43:30	
G3W1	Walking	23/07/2017	11:56:51	
G9W1	Browsing	23/07/2017	12:03:26	Some grazing
G9W1	Browsing	23/07/2017	12:04:07	Stretching
G9W1	Standing	23/07/2017	12:04:25	Chewing
G9W1	Standing	23/07/2017	12:04:45	Chewing
G9W1	Standing	23/07/2017	12:05:43	Alert head up
G9W1	Shuffle	23/07/2017	12:06:29	
G9W1	Browsing	23/07/2017	12:07:05	Stretching
G9W1	Standing	23/07/2017	12:07:29	Chewing
G9W1	Shuffle	23/07/2017	12:07:38	
G9W1	Flinch	23/07/2017	12:08:00	
G9W1	Flinch	23/07/2017	12:09:09	
G9W1	Grazing	23/07/2017	12:10:35	
G9W1	Standing	23/07/2017	12:11:06	Chewing
G9W1	Shuffle	23/07/2017	12:13:19	
G9W1	Head clash	23/07/2017	12:13:43	Listed as social interaction
G9W1	Standing	23/07/2017	12:14:21	Head up
G1W1	Browsing	23/07/2017	12:21:47	
G1W1	Walking	23/07/2017	12:23:47	180 turn
G1W1	Standing	23/07/2017	12:24:13	

G1W1	Grazing	23/07/2017	12:24:31	
G1W1	Walking	23/07/2017	12:25:03	
G1W1	Standing	23/07/2017	12:25:20	
G1W1	Flinch	23/07/2017	12:25:33	
G1W1	Walking	23/07/2017	12:25:46	
G1W1	Standing	23/07/2017	12:25:54	
G1W1	Grazing	23/07/2017	12:26:16	
G1W1	Walking	23/07/2017	12:27:15	
G1W1	Grazing	23/07/2017	12:27:30	
G1W1	Grazing	20/07/2017	16:58:24	
G1W1	Walking	20/07/2017	16:59:04	
G1W1	Browsing	20/07/2017	17:00:17	
G1W1	Browsing	20/07/2017	17:09:46	
G1W1	Walking	20/07/2017	17:11:07	
G1W1	Standing	20/07/2017	17:11:23	
G1W1	Walking	20/07/2017	17:11:31	
G1W1	Running	20/07/2017	17:19:16	All goats running
G4W1	Head clash	20/07/2017	15:12:18	
G4W1	Head clash	20/07/2017	15:13:09	
G4W1	Head clash	20/07/2017	15:14:18	With G6
G4W1	Salt lick	20/07/2017	15:15:30	
G4W1	Walking	20/07/2017	15:16:08	
G4W1	Drinking	20/07/2017	15:16:29	
G4W1	Lying	20/07/2017	15:17:24	Under milking station
G2W1	Salt lick	20/07/2017	15:23:20	
G2W1	Salt lick	20/07/2017	15:24:28	
G2W1	Walking	20/07/2017	15:24:59	
G2W1	Salt lick	20/07/2017	15:26:28	
G2W1	Head clash	20/07/2017	15:28:38	Light head clash
G2W1	Walking	20/07/2017	15:29:10	
G2W1	Flinch	20/07/2017	15:29:25	
G2W1	Walking	20/07/2017	15:30:30	