Mobile link functions in unpredictable agricultural landscapes

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Abstract

Animal movement is a crucial aspect of life, influencing ecological and evolutionary processes. It plays an important role in shaping biodiversity patterns, connecting habitats and ecosystems. Anthropogenic landscape changes, such as in agricultural environments, can impede the movement of animals by affecting their ability to locate resources during recurring movements within home ranges and, on a larger scale, disrupt migration or dispersal. Inevitably, these changes in movement behavior have far-reaching consequences on the mobile link functions provided by species inhabiting such extensively altered matrix areas. In this thesis, I investigate the movement characteristics and activity patterns of the European hare (*Lepus europaeus*), aiming to understand their significance as a pivotal species in fragmented agricultural landscapes. I reveal intriguing results that shed light on the importance of hares for seed dispersal, the influence of personality traits on behavior and space use, the sensitivity of hares to extreme weather conditions, and the impacts of GPS collaring on mammals' activity patterns and movement behavior.

In Chapter I, I conducted a controlled feeding experiment to investigate the potential impact of hares on seed dispersal. By additionally utilizing GPS data of hares in two contrasting landscapes, I demonstrated that hares play a vital role, acting as effective mobile linkers for many plant species in small and isolated habitat patches. The analysis of seed intake and germination success revealed that distinct seed traits, such as density, surface area, and shape, profoundly affect hares' ability to disperse seeds through endozoochory. These findings highlight the interplay between hares and plant communities and thus provide valuable insights into seed dispersal mechanisms in fragmented landscapes.

By employing standardized behavioral tests in Chapter II, I revealed consistent behavioral responses among captive hares while simultaneously examining the intricate connection between personality traits and spatial patterns within wild hare populations. This analysis provides insights into the ecological interactions and dynamics within hare populations in agricultural habitats. Examining the concept of animal personality, I established a link between personality traits and hare behavior. I showed that boldness, measured through standardized tests, influences individual exploration styles, with shy and bold hares exhibiting distinct space use patterns. In addition to providing valuable insights into the role of animal personality in heterogeneous environments, my research introduced a novel approach demonstrating the feasibility of remotely assessing personality types using animal-borne sensors without additional disturbance of the focal individual.

While climate conditions severely impact the activity and, consequently, the fitness of wildlife species across the globe, in Chapter III, I uncovered the sensitivity of hares to temperature, humidity, and wind speed during their peak reproduction period. I found a strong response in activity to high temperatures above 25°C, with a particularly pronounced effect during temperature extremes of over 35°C. The non-linear relationship between temperature and activity was

characterized by contrasting responses observed for day and night. These findings emphasize the vulnerability of hares to climate change and the potential consequences for their fitness and population dynamics with the ongoing rise of temperature.

Since such insights can only be obtained through capturing and tagging free-ranging animals, I assessed potential impacts and the recovery process post-collar attachment in Chapter IV. For this purpose, I examined the daily distances moved and the temporal-associated activity of 1451 terrestrial mammals out of 42 species during their initial tracking period. The disturbance intensity and the speed of recovery varied across species, with herbivores, females, and individuals captured and collared in relatively secluded study areas experiencing more pronounced disturbances due to limited anthropogenic influences.

Mobile linkers are essential for maintaining biodiversity as they influence the dynamics and resilience of ecosystems. Furthermore, their ability to move through fragmented landscapes makes them a key component for restoring disturbed sites. Individual movement decisions determine the scale of mobile links, and understanding variations in space use among individuals is crucial for interpreting their functions. Climate change poses further challenges, with wildlife species expected to adjust their behavior, especially in response to high-temperature extremes, and comprehending the anthropogenic influence on animal movements will remain paramount to effective land use planning and the development of successful conservation strategies.

This thesis provides a comprehensive ecological understanding of hares in agricultural landscapes. My research findings underscore the importance of hares as mobile linkers, the influence of personality traits on behavior and spatial patterns, the vulnerability of hares to extreme weather conditions, and the immediate consequences of collar attachment on mammalian movements. Thus, I contribute valuable insights to wildlife conservation and management efforts, aiding in developing strategies to mitigate the impact of environmental changes on hare populations. Moreover, these findings enable the development of methodologies aimed at minimizing the impacts of collaring while also identifying potential biases in the data, thereby benefiting both animal welfare and the scientific integrity of localization studies.

Zusammenfassung

Die Bewegung von Tieren ist ein entscheidender Aspekt des Lebens, der ökologische und evolutionäre Prozesse beeinflusst. Sie spielt eine wichtige Rolle bei der Gestaltung der biologischen Vielfalt und verbindet Lebensräume und Ökosysteme miteinander. Anthropogene Landschaftsveränderungen, z.B. in der Landwirtschaft, können die Bewegung von Tieren behindern, indem sie ihre Fähigkeiten beeinträchtigen, Ressourcen innerhalb ihres täglichen Bewegungsradius zu lokalisieren und im größeren Maßstab, ihre Wanderung oder Ausbreitung limitieren. In dieser Thesis untersuche ich die Bewegungsmerkmale und Aktivitätsmuster des Feldhasen (*Lepus europaeus*), um seine Bedeutung als Schlüsselart in fragmentierten Agrarlandschaften zu verstehen. Ich lege faszinierende Ergebnisse vor, die die Bedeutung des Hasen für die Verbreitung von Saatgut, den Einfluss von Persönlichkeitsmerkmalen auf das Verhalten und die Raumnutzung, die Sensibilität des Hasen gegenüber extremen Witterungsbedingungen und die Auswirkungen von GPS-Empfängern auf die Aktivitätsmuster und das Bewegungsverhalten der Säugetiere beleuchten.

In Kapitel I führte ich ein kontrolliertes Fütterungsexperiment durch, um den potenziellen Einfluss von Hasen auf die Samenausbreitung zu analysieren. Durch die zusätzliche Verwendung von GPS-Daten von Hasen in zwei kontrastierenden Landschaften konnte ich nachweisen, dass Hasen eine wichtige Rolle spielen, da sie in kleinen und isolierten Habitatfeldern als effektive mobile Verbindungsglieder für viele Pflanzenarten fungieren. Die Analyse der Samenaufnahme und des Keimungserfolgs zeigte, dass verschiedene Eigenschaften der Samen, wie Dichte, Oberfläche und Form, die Fähigkeit der Hasen, Samen durch Endozoochorie zu verbreiten, stark beeinflussen. Diese Ergebnisse verdeutlichen die Wechselwirkung zwischen Hasen und Pflanzengemeinschaften und liefern somit wertvolle Erkenntnisse über die Mechanismen der Samenverbreitung in fragmentierten Landschaften.

Durch den Einsatz standardisierter Verhaltenstests in Kapitel II konnte ich konsistente Verhaltensreaktionen bei in Gefangenschaft lebenden Hasen aufdecken und zeitgleich den komplexen Zusammenhang zwischen Persönlichkeitsmerkmalen und räumlichen Mustern in Wildhasenpopulationen untersuchen. Diese Analyse bietet Einblicke in die ökologischen Interaktionen und die Dynamik von Hasenpopulationen in landwirtschaftlichen Lebensräumen. Indem ich das Konzept der Tierpersönlichkeit untersuchte, stellte ich eine Verbindung zwischen Persönlichkeitsmerkmalen und dem Verhalten von Hasen her. Ich habe gezeigt, dass die durch standardisierte Tests gemessene Kühnheit den individuellen Erkundungsstil beeinflusst, wobei schüchterne und kühne Hasen unterschiedliche Raumnutzungsmuster aufweisen. Meine Forschung liefert nicht nur wertvolle Einblicke in die Rolle der Tierpersönlichkeit in heterogenen Umgebungen, sondern stellt auch einen neuartigen Ansatz vor, der die Durchführbarkeit einer Fernbeurteilung von Persönlichkeitstypen mithilfe von am Tier angebrachten Sensoren ohne zusätzliche Störung des Zielindividuums demonstrierte.

Da die Klimabedingungen die Aktivität und folglich die Fitness von Wildtierarten auf der ganzen Welt stark beeinflussen, habe ich in Kapitel III die Sensibilität von Hasen gegenüber Temperatur, Luftfeuchtigkeit und Windgeschwindigkeit während ihrer Hauptfortpflanzungszeit ermittelt. Ich stellte fest, dass die Aktivität stark auf hohe Temperaturen über 25 °C reagiert, wobei die Auswirkungen bei extremen Temperaturen von über 35 °C besonders ausgeprägt sind. Die nicht lineare Beziehung zwischen Temperatur und Aktivität war durch gegensätzliche Reaktionen bei Tag und Nacht gekennzeichnet. Diese Ergebnisse unterstreichen die Anfälligkeit der Hasen für den Klimawandel und die möglichen Folgen für ihre Fitness und Populationsdynamik bei einem anhaltenden Temperaturanstieg.

Da solche Erkenntnisse nur durch Fangen und Besendern von Wildtieren ermöglicht werden können, habe ich in Kapitel IV die potenziellen negativen Auswirkungen auf das Individuuum, sowie den Erholungsprozess nach dem Anlegen des Halsbandes untersucht. Hierfür analysierte ich die zurückgelegten täglichen Entfernungen in Verbindung mit der Aktivität von 1451 terrestrischen Säugetieren aus 42 verschiedenen Arten während ihrer anfänglichen Verfolgung. Die Intensität der Störung sowie die Geschwindigkeit der Erholung variieren je nach Art, wobei Pflanzenfresser, Weibchen und Individuen, die in relativ abgelegenen Untersuchungsgebieten gefangen und mit Halsbändern versehen wurden, aufgrund bisher begrenzter anthropogener Einflüsse stärkere Störungen erfahren.

Mobile Verbindungsglieder sind essentiell für die Erhaltung der Biodiversität, indem sie eine wichtige Rolle in der Dynamik und Resilienz von Ökosystemen spielen. Weiterhin macht ihre Fähigkeit, sich durch zerstückelte Landschaften zu bewegen sie zu wichtigen Schlüsselkomponenten bei der Wiederherstellung von zerstörten Landschaften. Individuelle Bewegungsentscheidungen bestimmen den Maßstab der mobilen Verbindungen und die Schwankungen der Raumnutzung unter Individuen zu verstehen ist unerlässlich, um deren Funktion zu interpretieren. Der Klimawandel stellt eine weitere Herausforderung dar, indem Wildtiere dazu gezwungen werden, sich zu adaptieren, insbesondere an Hochtemperatur-Extreme. Den anthropogenen Einfluss auf Tierbewegungen aufzudecken bleibt von größter Bedeutung in der Landnutzungsplanung und die Entwicklung von erfolgreichen Strategien zum Schutz der Natur.

Diese Thesis liefert ein umfassendes ökologisches Verständnis von Feldhasen in Agrarlandschaften. Die Ergebnisse meiner Forschung unterstreichen die Bedeutung von Hasen als mobile Bindeglieder, den Einfluss von Persönlichkeitsmerkmalen auf Verhalten und räumliche Muster, die Anfälligkeit von Hasen gegenüber extremen Wetterbedingungen und die unmittelbaren Folgen der Halsbandanbringung auf Tierbewegungen. Damit leiste ich einen wertvollen Beitrag zum Schutz und zur Bewirtschaftung von Wildtieren, indem ich die Entwicklung von Strategien zur Abschwächung der Auswirkungen von Umweltveränderungen auf Hasenpopulationen unterstütze. Darüber hinaus ermöglichen diese Erkenntnisse die Entwicklung von Methoden, die darauf abzielen, die Folgen der Halsbandanbringung zu minimieren und gleichzeitig potenzielle Verzerrungen in den Daten zu identifizieren, was sowohl dem Tierschutz als auch der wissenschaftlichen Integrität von Lokalisierungsstudien zugutekommt.

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General Introduction

1.1 Movement ecology

The ability of organisms to move is a fundamental aspect of life and plays a vital role in various ecological and evolutionary processes. Throughout history, the diverse array of movement patterns observed among microorganisms, plants, and animals sparked human curiosity (Swingland and Greenwood 1983). Nowadays, movements are important to consider when addressing issues such as habitat fragmentation, climate change, invasive species, or the dissemination of pests and diseases (Nathan et al. 2008a). Studying animal movement can be both intriguing and challenging. Movement patterns of animals play a crucial role in various biological phenomena, and understanding them is essential for conservation, human health, and food-related applications (Nathan et al. 2008b, Kays et al. 2015). In the past, researchers used to rely on field biologists and their antennas, performing complex triangulation to track a limited number of locations per animal and day, which provided only a basic understanding of the animal's use of space (Kays et al. 2015). Recently, significant advances in tracking technology have led to the development of smaller and more advanced tracking devices. These devices are now capable of recording millions of movement steps at high temporal resolution and over long periods in progressively smaller animals (Wilmers et al. 2015).

1.1.1 The golden age of bio-logging

Advances in technology (i.e., animal-borne sensors) made it possible to track the movement and behavior of a wide range of animals with high accuracy, consequently referring to the current epoch as "The golden age of bio-logging" (Wilmers et al. 2015). While recent reviews have described the different types of sensors (Cooke et al. 2004, 2013, Rutz and Hays 2009) and how they are used on different taxa (Cooke et al. 2004), animal-borne sensors have become a popular tool in ecological and wildlife research due to their ability to provide valuable data on animal behavior, movement, and environmental conditions (Hussey et al. 2015). These sensors are typically attached to the animals via collars, backpacks, or implanted devices and can collect various types of data, including GPS location, temperature, and activity levels (Cagnacci et al. 2010). Animal-borne sensors are being used to study a range of species, from marine mammals and terrestrial mammals to birds, reptiles (Block et al. 2011), and insects (Daniel Kissling et al. 2014).

Tri-axial accelerometers measure static and dynamic acceleration (i.e., the animals' movement) in three dimensions (Hughey et al. 2018). These measurements can be used to remotely identify acceleration patterns and assign them to defined behaviors (Scheibe and Gromann 2006, Watanabe et al. 2008) or calculate proxy values for activity levels (Wilson et al. 2006, Qasem et al. 2012). Data obtained from these sensors is crucial to enhance our understanding of animal behavior, migration patterns, habitat preferences, and responses to environmental changes (Kays et al. 2015). Beyond research purposes, animal-borne sensors have the potential to strongly contribute to conservation efforts. They can be used to inform conservation efforts and help to develop management strategies for threatened or endangered species (Cooke 2008). By providing consistent insights into the focal species, these sensors empower us to make informed decisions to support their well-being and ensure conservation efforts.

Advancements in technology have revolutionized animal tracking, transforming it into a domain of big data. This shift is attributed not only to high-resolution GPS data but also to incorporating additional sensors and integrating remote sensing data pertaining to the focal landscape. These developments have broadened our capabilities to collect comprehensive information and gain deeper insights into numerous animal species and their respective habitats. (Kays et al. 2015). While more comprehensive methods for measuring environmental variables (e.g., LiDAR or satellite imaginary) exist, it is undeniable that animal-borne sensors have crucially advanced our understanding of natural and physical processes as well as ecosystem functioning (Wilmers et al. 2015). Moreover, future directions suggest utilizing tracked animals as free-roaming sensors of environmental change. For example, they can document ocean currents (Shamoun-Baranes et al. 2011) or monitor arctic temperature and vegetation changes due to climate change (Wijk et al. 2011)

1.1.2 The movement ecology paradigm

Animal movement plays a pivotal role in shaping biodiversity patterns and can occur for a variety of reasons (e.g., mating, defending a territory, foraging, migrating, dispersing) (Nathan 2008a, Clobert et al. 2012, Jeltsch et al. 2013). The movement ecology framework, formulated by Nathan et al. (2008a), is a useful tool for understanding the processes and behaviors that drive animal movement. Here, the authors distinguish between three basic components related to the focal individual: the internal state - *why move?*, the motion capacity - *how to move?*, and the navigation capacity - *where to move?*, resulting in an individual's movement path. Jeltsch et al. (2013) refined this concept by integrating Chessons' (2000) established theory on the maintenance of species as well as the concept of mobile links (Fig. 1.1). Animals can be classified as a resource, process, or genetic linker based on the primary function they serve in terms of transporting and relocating resources between areas (Lundberg and Moberg 2003, Jeltsch et al. 2013).

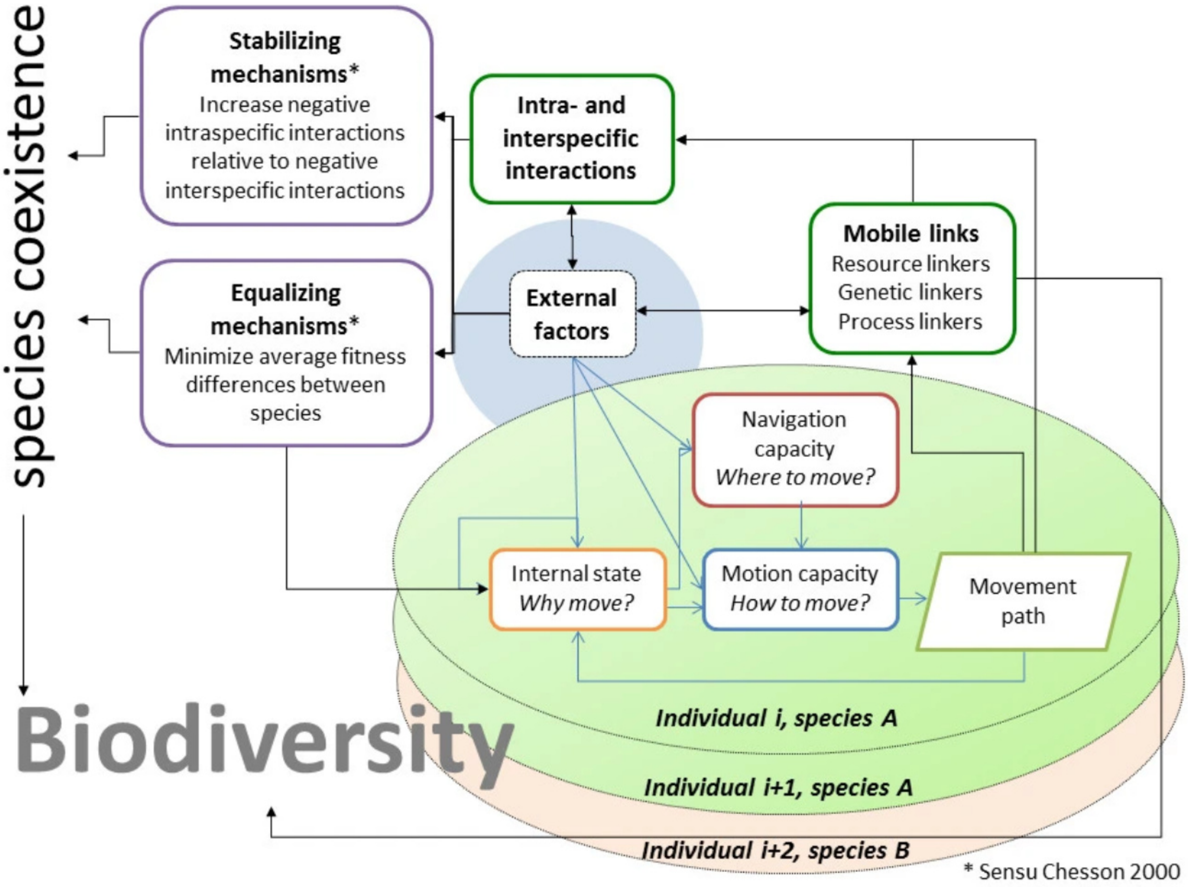

Fig. 1.1 From Jeltsch et al. (2013): Integrative conceptual framework for the linkage of movement ecology with biodiversity research. The movement ecology framework for individuals (after Nathan et al. 2008a) is linked to the concept of mobile links and the concept of equalizing and stabilizing mechanisms for species coexistence (Chesson et al. 2000). An individual moves according to its internal state, its navigation capacity and its motion capacity, all of which are shaped by external environmental conditions. The resulting movement path, in turn, creates a feedback loop with the individuals' internal state. Via the movement path, animals provide a link between communities and ecosystems that are otherwise separate.

The movement ecology framework is a holistic approach that aims to understand the dynamics of animal movement at different scales, from the individual to the population level. This framework is based on the idea that a complex interplay of internal and external factors influences animal movement. Understanding these factors is essential for understanding the ecology and evolution of animal populations.

The importance of mobile linkers for biodiversity

While moving, animals provide links between habitats and otherwise separated ecosystems (Lundberg and Moberg 2003, Jeltsch et al. 2013). By relocating seeds to distant habitats, they play a vital role as genetic linkers in population dynamics of various plant species across different ecosystems (Jordano et al. 2007, Pakeman 2001, Sasal and Morales 2013).

In intensively managed farmlands, where remaining habitats are often small and isolated, dependence on animal-mediated seed dispersal makes plant species particularly vulnerable to extinction (Rogan and Lacher 2018), highlighting its ecological relevance. Other mobile link functions are provided by process linkers, i.e., organisms that provide or support an essential process (e.g., grazing), and resource linkers, which transport energy between trophic levels (e.g., defecating) (Lundberg and Moberg 2003). However, knowledge about the quali- or quantification of such mobile link processes, especially in agricultural landscapes, is still limited. Moreover, although existing studies primarily concentrate on long-distance seed dispersal by large herbivores, particularly ungulates (Albert et al. 2015, Baltzinger et al. 2019), smaller mammals have received relatively less attention despite their considerable potential for dispersal (e.g., Fischer and Türke, 2016, Lessa et al. 2019, Naoe et al. 2019).

Individual movement decisions

Earlier studies on hares show high variability in movement responses to specific environmental conditions. Such variable responses in behavior may be attributed to animal personalities. Animal personality, defined as consistent individual differences in behavior across different contexts (for a more detailed definition, see chapter 3), can play a crucial role in shaping movement characteristics: Studies have shown that personality traits such as boldness (Ward et al. 2004), activity level (Eccard and Herde 2013), and exploration tendency (Réale et al. 2007) can impact an animal's ability to navigate through complex environments (Conrad et al. 2011), to respond to potential threats (Krause and Ruxton 2002, Leclerc et al. 2017), and to exploit resources effectively (Patrick et al. 2017, Gharnit et al. 2020). Consequently, personality traits affect key ecological processes such as predator-prey interactions (Leclerc et al. 2017), competition (Farine and Whitehead 2015), coexistence (Schlägel et al. 2020), and dispersal (Dingemanse et al. 2003). Only a few studies established links between personality and local movements in free-ranging animals, and thus a key question remains, how personality traits relate to movement strategies in the wild (Nilsson et al. 2014). Yet, these small-scale movements are of key importance for identifying ecological interactions and forming individual niches. In this regard, differences in space use among individuals might reflect different exploration styles between behavioral types along the shy-bold continuum.

Changing climate - changing behavior

Altered weather conditions due to climate change can strongly affect the activity, movement behavior, and energy expenditure of wildlife, which are crucial for an individual's fitness (Brown et al. 2004). Wildlife can respond to changing climatic conditions through local genetic adaptation, migration to more favorable habitats, or phenotypic plasticity (Walther et al. 2002, Hetem et al., 2014). However, human-induced changes in climate and landscape connectivity occur at a rapid and severe pace, limiting opportunities for local genetic adaptation and migration (Meester et al. 2018). Habitat loss and landscape fragmentation further restrict climate-induced migration and dispersal patterns (Collingham and Huntley, 2000, Walther et al. 2002, Travis, 2003). In fragmented landscapes, phenotypic plasticity, which encompasses changes in phenology, physiology, and behavior (Boutin and Lane, 2014; Hetem et al. 2014), is likely the most immediate response of wildlife to mitigate the adverse effects of rapidly changing climatic conditions on their activity and energy budgets (Noonan et al. 2018). Unfavorable conditions such as cold and humid weather can increase the energy investment required for thermoregulation in homeothermic animals (Seltmann et al. 2009, Lenis Sanin et al. 2016), promote the development of pathogens, potentially increasing the spread of diseases (Altizer et al. 2006; Rödel and Dekker 2012), and increase the risk of predation (Rödel and Dekker 2012). The European hare, recognized as an important umbrella species in agricultural landscapes, serves as an indicator of ecological threats to a diverse array of species within ecological communities (Schai-Braun et al. 2020). However, hare populations have been experiencing a decline over the past few decades, primarily attributed to agricultural intensification (Tapper and Barnes 1986, Vaughan et al. 2003). Moreover, unfavorable weather conditions during certain seasons contribute to this decline, as increased energy demands may not be met, potentially leading to mortalities (Tapper and Barnes, 1986).

The understudied effects of GPS-collaring

Understanding wildlife movements is crucial to comprehend behavioral responses to global environmental changes, ecosystem functioning, and nature conservation (Hebblewhite and Haydon 2010). The application of collars or similar devices on animals is a commonly used approach and involves capturing, handling, and releasing animals (Powell and Proulx 2003, Iossa et al. 2007). The capturing process or the collar itself may lead to behavioral modifications, which are largely understudied in wildlife species (but see: Brooks et al. 2008, Stabach et al. 2020). These modifications may affect animal welfare but also the interpretation of research findings (Morellet et al. 2009, Northrup et al. 2014, Brogi et al. 2019). Additionally, there is a lack of well-defined ethical guidelines for applying such devices (Wilson and McMahon 2006), and protocols for handling data from the initial tracking days after release are non-existent. One reason for this knowledge gap is the uncertainty regarding the duration of impairment caused by animal-borne tracking devices in different species. The impacts of tags and deployment procedures can vary significantly depending on the species, logger type, tag size, deployment duration, and specific attachment method (Hawkins 2004, Ropert-Coudert and Wilson 2004, Wilson and McMahon 2006). Hence, a cross-taxa study regarding the effects of tagging would be highly beneficial to adjust ethical guidelines accordingly and to help uncover potentially biased movement data.

1.2 Mammalian movements in the Anthropocene

In the Anthropocene, approximately 50 to 70% of the Earth's terrestrial surface has already been modified by humans (Rowcliffe et al. 2012), consequently leading to significant shifts in global biodiversity and ecosystem functioning (Hein et al. 2012). Beyond habitat destruction and loss of biodiversity, anthropogenic landscape modifications are also known to affect the movement patterns of animals (Tucker et al. 2018) and hence, habitat use (Ciach and Pęksa 2019). Especially human infrastructure can induce various behavioral responses in animals, including avoidance (Howe et al. 2013), shifts in movement speed or altered habitat preference in response to road density (Scrafford et al. 2018), or a shift in activity patterns (e.g., from diurnal to nocturnal [Neumann et al. 2013]). Moreover, animals can alter their behavior in response to the presence and activity of humans (Corradini et al. 2021, Wilmers et al. 2021). Animal movements, however, play a pivotal role in ecosystem functioning because they can serve as mobile links (Lundberg and Moberg 2003) and influence critical ecosystem processes such as seed dispersal, food web dynamics, as well as population and disease dynamics (Bauer and Hoye 2014, Jeltsch et al. 2013, Lundberg and Moberg 2003). Hence, it remains critical to understand how animal movement patterns are affected by anthropogenic influences (quantified by, e.g., the human footprint), as restricted movement processes will affect ecosystem functioning and consequently directly impact human well-being by affecting important ecosystem services (Tucker et al. 2018).

1.3 Unpredictable agricultural landscapes

From an animal's perspective, agricultural landscapes are unpredictable for several reasons. One factor is the constant change and manipulation of the landscape as fields with different crops are plowed, planted, and harvested at different times of the year. This can make it difficult for animals to find food and shelter and disrupt their breeding and migration patterns (Fischer et al. 2006, Fahrig 2007, Öckinger and Van Dyck 2012, Lange et al. 2013). In addition, human activities such as machinery or hunting can cause noise and disturbance that exacerbate the landscape's danger to wildlife (Sunde et al. 2009, Mayer et al. 2021). Further, the fragmentation of natural habitats by roads, fences, and other barriers restricts the movement of terrestrial species, consequently influencing metapopulation dynamics (Gebauer et al. 2013) and gene flow (Banks and Lindenmayer 2014), possibly leading to population declines (Schtickzelle et al. 2006, Bonelli et al. 2013, Awade et al. 2017).

Hence, animals living in such unpredictable landscapes may have to use various adapted strategies to survive. *Migrating*: Some animals may be able to switch to different types of habitats depending on the season or the availability of resources (Viana et al. 2018); *Movement corridors*: Some animals may use specific routes or corridors to move between different habitats, such as wildlife underpasses or overpasses to cross roads or move through fields (Smith et al. 2015); *Adapting*: Some animals may be able to tolerate or avoid human disturbance, such as noise or traffic, and still use the area for food or breeding (Samia et al. 2015). Movement is essential for survival and intrinsically linked with individual fitness (Andreassen and Ims 1998). Not all species have the same ability to adapt to the unpredictable agricultural landscapes' changes and pressures, consequently leading to population declines or even extinction (Thompson and Fronhofer 2019).

1.4 The European hare

The European hare (*Lepus europaeus* (Schai-Braun et al. 2020), hereafter referred to as 'hare') is a typical medium-sized (3.5–5 kg, [Zachos 2016]) mammalian herbivore that is found in a wide range of habitats, and an important umbrella species in agricultural landscapes (Schai-Braun et al. 2020). They feed on various herbs, grasses, and field crops (Tapper and Barnes 1986, Schai-Braun et al. 2013). Hares are born precocial, i.e., fully furred, with open eyes and the ability to move around (Schai-Braun et al. 2021). Juvenile hares begin to eat vegetation at around three weeks old and become independent at around four weeks (Schai-Braun et al. 2021). As hares approach adulthood, they disperse from their natal home ranges and establish their territories (Schai-Braun and Hackländer 2014). Hares are generally solitary animals, although they may form temporary mating bonds during the breeding season. Being territorial, they will defend their territory against intruders of the same sex. They are active both day and night but are mainly crepuscular and nocturnal (Chapman and Flux 1990). European hares are known for their strong reproductive potential. They can breed all year round, but the peak of breeding activity is in spring (Frylestam 1980). Female hares have a short gestation period of 42 days, are capable of superfetation (Kozdrowski et al. 2011), and can produce several litters per year, with an average of 4-5 leverets per litter (Pepin 1989). Further, they are fast runners and can reach speeds of up to 20 $\frac{m}{s}$ (Garland 1983, Williams et al. 2007), which successfully helps them to avoid predators in open agricultural landscapes. Hares rely on richly structured open areas that provide year-round cover and food. In such favorable habitats, the rate of population increase is less affected by predation, adverse weather, or diseases (Hackländer 2023).

Nonetheless, one challenge faced by hares roaming in such landscapes is the ongoing loss of natural habitats. The conversion of grasslands and other natural habitats to croplands (Tscharntke et al. 2005) can make it difficult for hares to find food and shelter. With modern machinery and fragmentation, agricultural measures are probably the leading cause of hare population decline (Berny and Sup 2000). To mitigate these challenges, conservation strategies that protect remaining natural habitats and create wildlife corridors can help animals move and successfully find forage in unpredictable agricultural landscapes.

1.5 Thesis structure

The overarching objective of this thesis is to enhance our understanding of how specific animal-landscape conditions (internal status of the mobile linker, abiotic conditions, or landscape complexity) influence space use and, thus, the amount and frequency of mobile links critical for biodiversity. In the following, I investigate the efficiency of hares as mobile linkers and the impact of animal personality, rising temperatures, and the collaring process *per se* on space use and activity patterns. Through these investigations, I aim to contribute valuable insights into the dynamics of animal movements and their implications for biodiversity conservation.

The following chapters present empirical case studies, focusing on specific research questions that have garnered significant attention in current scientific research. Each chapter represents a thematically distinct article that can be read independently. Three of the studies (**chapter 1: *Seed traits matter - Endozoochoric dispersal through a pervasive mobile linker***, **chapter 2: *Personality drives activity and space use in a mammalian herbivore***, and **chapter 3: *The Heat is On: Impacts of Rising Temperature on the Activity of a Common European Mammal***) are published in international peer-reviewed journals *Ecology and Evolution*, *Movement Ecology*, and *Frontiers in Ecology and Evolution*, respectively. The fourth study (**chapter 4: *Tracking of mammals - Quantifying the impact of collaring***) will soon be submitted to a peer-reviewed journal. These thematically stand-alone chapters are prefaced with a general introduction followed by a general discussion. All manuscripts are written in the first person plural, as multiple co-authors contributed to them. I am the main author in the studies in chapters 1, 2, 3, and 4 and was primarily responsible for study design, fieldwork, data collection, analysis, and writing of the respective manuscripts.

Seed traits matter - Endozoochoric dispersal through a pervasive mobile linker

In the first chapter, I present the first controlled feeding experiment with hares, in which both the ratio of seed intake and germination success after digestion were recorded. I disentangle the effects of seed morphological traits on germination success after digestion while controlling for phylogenetic relatedness by generating phylogenetic trees with extracted genomic DNA and consequently calculating the phylogenetic signal based on model draws. Further, I measure the habitat connectivity in two contrasting agricultural landscapes in Brandenburg (homogeneous, large field sizes) and Bavaria (heterogeneous, small field sizes) using GPS-based movement data of GPS-collared hares. Our findings suggest that, for hares, the most critical seed characteristics for successful endozoochorous seed dispersal minimize seed exposure to the digestive system (i.e., dense seeds with a small surface area and an elongated shape). Furthermore, I show that a hare's retention time is long enough to interconnect different habitats, especially grasslands, and crop fields. Besides alternative seed dispersal mechanisms, this most likely allows hares to act as effective mobile linkers contributing to ecosystem stability during times of agricultural intensification. This study combines plant ecology, phylogenetics, and movement ecology to help understand the mechanisms of recolonization through seed import from off-site patches where the resources for natural succession are impoverished. Moreover, it facilitates mechanistic understanding of mobile link processes (i.e., genetic links), especially in agricultural landscapes.

Personality drives activity and space use in a mammalian herbivore

In the second chapter, I tested whether personality, measured as a level of boldness, is associated with space use in hares. Furthermore, I postulate that activity can be used as a universal proxy for classifying animal personalities along the bold-shy continuum. Combining standardized behavioral tests with acceleration measurements of hares in enclosures and from a wild population, I introduce a novel approach demonstrating how remote assessment of personality types is achievable without additional disturbance of the focal individual. I show that overall dynamic body acceleration (ODBA), measured by acceleration sensors in GPS collars, was positively related to bold behavior in European hares. Further, space use varied with boldness, with shy individuals having larger home range sizes than bold conspecifics. These results help explain variation in state-dependent behavior (e.g., risk-taking) and space use and further facilitate understanding of underlying processes that drive spatial, ecological, and evolutionary dynamics in heterogeneous environments.

The Heat is On: Impacts of Rising Temperature on the Activity of a Common European Mammal

In the third chapter, I analyze how changing extreme weather conditions affect the activity of European hares in a central part of their distribution range. Extreme weather periods, such as heat waves or exceptional precipitation events, are increasingly observed in recent summers across Europe and are predicted to occur more frequently and last longer as climate change continues. Undoubtedly, this will directly affect animals' fitness and hence population dynamics. Wildlife can respond to new climatic conditions, but the pace of human-induced change limits opportunities for adaptation or migration. Thus, it remains unclear how these changes will affect behavior, movement patterns, or activity levels. I investigate how ambient weather affects the activity of hares during their peak reproduction period. I found that temperature, humidity, and wind speed influence their activity. Extreme climatic events show the strongest effect: Activity increases with rising temperatures during the inactive period (daytime) and vice versa during their active period (nighttime). This was especially pronounced during tropical nights with outstanding high temperatures. Females were found to be even more sensitive to hot conditions than males. This might be crucial, as they must substantially invest in reproduction during this stage of life. The study highlights the importance of understanding the relationship between (extreme) weather conditions and mammal behavior, crucial for conservation and management purposes.

Tracking of mammals - Quantifying the impacts of collaring

In the fourth chapter, I quantify and qualify the consequences of GPS-collaring on the movement behavior (GPS-derived) and the energy budget (ACC-derived) of mammals. Collaborating with 101 researchers worldwide, I compiled a dataset of 1451 individuals out of 42 mammal species from North America, Europe, Asia, and Africa. Through a comparative analysis of changes in daily distances covered and activity spent during the first ten days versus days 11-20, I found that the process of collaring influences both the activity and movement behavior of mammals. The immediate activity level of individuals immediately after release significantly differs from that observed in the subsequent days, with a gradual stabilization particularly evident in omnivorous species. Additionally, most species travel longer daily distances following the collaring procedure compared to their average daily long-term distances. During the initial days, both omnivores and carnivores had reduced activity, while herbivores showed ambivalent, species-specific reactions. Herbivores, particularly males, recover most quickly. Furthermore, irrespective of species, individuals captured and collared in remote areas require a longer period of recovery. In conclusion, mammals show distinct reactions, such as increased or decreased activity and distances moved, evident in their movement behavior during the initial tracking days. This study provides ethics committees with more useful evidence than is currently available to decide on the allowance of studies involving animal biotelemetry and further enables researchers to develop methods that minimize collaring effects but also to identify possibly biased data, to benefit both animal welfare and the science bolstered by localization studies.

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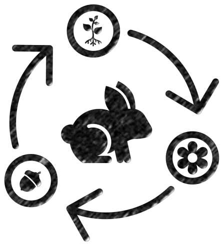
Chapter 1

Seed traits matter — Endozoochoric dispersal through a pervasive mobile linker



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Abstract

Although many plants are dispersed by wind and seeds can travel long distances across unsuitable matrix areas, a large proportion relies on co-evolved zoochorous seed dispersal to connect populations in isolated habitat islands. Particularly in agricultural landscapes, where remaining habitat patches are often very small and highly isolated, mobile linkers as zoochorous seed dispersers are critical for the population dynamics of numerous plant species. However, knowledge about the quali- or quantification of such mobile link processes, especially in agricultural landscapes, is still limited. In a controlled feeding experiment, we recorded the seed intake and germination success after complete digestion by the European brown hare (*Lepus europaeus*) and explored its mobile link potential as an endozoochoric seed disperser. Utilizing a suite of common, rare, and potentially invasive plant species, we disentangled the effects of seed morphological traits on germination success while controlling for phylogenetic relatedness. Further, we measured the landscape connectivity via hares in two contrasting agricultural landscapes (simple: few natural and semi-natural structures, large fields; complex: high amount of natural and semi-natural structures, small fields) using GPS- based movement data. With 34,710 seeds of 44 plant species fed, one of 200 seeds (0.51% with seedlings of 33 species germinated from feces. Germination after complete digestion was positively related to denser seeds with comparatively small surface area and a relatively slender and elongated shape, suggesting that, for hares, the most critical seed characteristics for successful endozoochorous seed dispersal minimize exposure of the seed to the stomach and the associated digestive system. Furthermore, we could show that a hare's retention time is long enough to interconnect different habitats, especially grasslands, and fields. Thus, besides other seed dispersal mechanisms, this most likely allows hares to act as effective mobile linkers contributing to ecosystem stability in times of agricultural intensification, not only in complex but also in simple landscapes.

Keywords: *Lepus europaeus, Mobile links, Endozoochory, Seed dispersal, Seed dispersal syndrome, Agricultural landscapes.*

2.1 Introduction

In recent decades, we are witnessing a massive loss of biodiversity in flora and fauna (Pimm et al. 1995, Sala et al. 2000, Cardinale et al. 2012, Chase et al. 2020), with habitat loss and fragmentation as two major drivers (Tscharntke et al. 2005, Estreguil et al. 2013, Rogan and Lacher 2018). Habitat fragmentation may lead to movement or dispersal barriers not only for animals (Andren 1994, Steffan-Dewenter and Tscharntke 1999, Crooks et al. 2011, 2017) but also for plants (Malcolm et al. 2002, Tscharntke et al. 2005, Estreguil et al. 2013, Rogan and Lacher 2018). Although many seeds are dispersed by wind and can travel long distances across unsuitable matrix areas, a large proportion relies on co-evolved zoochorous seed dispersal (Cousens et al. 2010) to connect populations from isolated habitat islands. The animals carrying seeds to distant habitats function as mobile linkers (Lundberg and Moberg 2003, Jeltsch et al. 2013) and are critical for the population dynamics of numerous plant species in various ecosystems (Pakeman 2001, Jordano et al. 2007, Sasal and Morales 2013), leading at best to a restoration of disturbed sites (Lundberg and Moberg 2003). Especially in intensively used agricultural landscapes where remaining habitat islands are often very small and highly isolated, dependence on zoochorous seed dispersal makes plant species particularly vulnerable (Rogan and Lacher 2018). Hence, seed dispersal has become a major constraint on establishing plant communities and restoring isolated habitat patches (Pywell et al. 2002).

In endozoochorous systems, seed dispersal success is often explained through the respective suite of seed traits (i.e., seed dispersal syndrome, but see Green et al. (2021) that may influence ultimate germination after gut passage (Pakeman et al. 2002, Johnson et al. 2019). For example, comparatively small and light seeds were found to enhance dispersal success via sheep *Ovis gmelini aries*, rabbits *Oryctolagus cuniculus* (Pakeman et al. 2002), fallow deer *Dama dama* (Mouissie et al. 2005a), or waterfowl (Soons et al. 2008, Lovas-Kiss et al. 2020). Also, denser seeds (mass/volume ratio) show increased dispersal rates when digested by cattle (Simao Neto and Jones 1987, Gardener et al. 1993) and sheep (Russi et al. 1992). Further, seed shape (e.g., rounder seeds, as measured by, e.g., the Flatness- or the Eccentricity index (Cervantes et al. 2016), were shown to positively influence germination success after dispersal by ungulates (Heinken et al. 2002, Pakeman et al. 2002, Mouissie et al. 2005a).

Recently, studies on the dispersal syndrome integrate phylogenetic relatedness of plant species (D'hondt and Hoffmann 2011, Boedeltje et al. 2015, Lovas-Kiss et al. 2020) and found that not only morphological seed traits but also the taxonomic relatedness of plant species needs to be considered when determining seed survival rates after complete digestion. In general, the species are seen as non-independent since phylogenetically close species tend to be similar (Grafen 1989). The closer two plant species are phylogenetically, the more similar their seed composition is, therefore, their resistance to the digestive system of the animals (Burns and Strauss 2012). Moreover, since closely related species share similar traits, it is unclear whether phylogenetic relatedness promotes the patterns attributed to a particular trait or whether there is a causal relationship with the trait *per se* (Lovas-Kiss et al. 2020).

While current research mainly focuses on long-range epi- and endozoochorous seed dispersal by large herbivores (especially ungulates, see Albert et al. 2015b, Baltzinger et al. 2019), smaller mammals seem to be rather understudied despite their dispersal potential (e.g., Fischer and Türke 2016, Lessa et al. 2019, Naoe et al. 2019). For example, the European brown hare (*Lepus europaeus*, hereafter referred to as 'hare') is a typical medium-sized herbivorous mammal (body mass 3.5-5 kg [Zachos 2016]) in agricultural landscapes feeding on various wild herbs, grasses, and field crops (Tapper and Barnes 1986, Vaughan et al. 2003, Schai-Braun et al. 2013). Seeds are part of their natural diet and are eaten actively or passively during foraging (Sokos et al. 2015). Due to their spacious home ranges (in complex agricultural landscapes: e.g., 4-day range size = 8 ± 7.8 ha, in simple agricultural landscapes: 23.9 ± 18.2 [Ullmann et al. 2020]), hares move across different habitat types, disperse seeds within their fecal pellets (Tapper and Barnes 1986, Schai-Braun et al. 2015), and can overcome plant dispersal barriers (Reitz et al. 1994, Eycott et al. 2007, Schai-Braun and Hackländer 2014). Indeed, feces samples of European hares from different ecosystems contain various germinable seeds of many plant species, indicating their capacity as effective mobile linkers (Mediterranean: Izhaki and Ne'eman 1997; Forest habitats: Heinken et al. 2001, Panter and Dolman 2012; Mountainous landscapes: Henríquez et al. 2014).

Our study aims to disentangle the effects of the most common morphological seed traits (i.e., seed mass, seed density, seed shape) as well as seed surface area and its ratio to mass on germination success while controlling for phylogenetic relatedness. We present the first controlled feeding experiment with hares in which both the ratio of seed intake and the germination success after digestion were recorded. Including common, rare, and invasive plant species as well as common field crops, we selected 44 plant species of open landscapes fed to captive hares. We hypothesize that taking the phylogenetic relatedness into account, high density and a comparatively small surface are advantageous for the seed survival after digestion by hares.

Further, we assessed the potential of hares as mobile linkers (i.e., seed dispersers), measured by the connectedness of distinct habitat types through hares in two contrasting agricultural landscapes (simple landscapes with large field sizes vs. complex landscapes with comparatively small field sizes), using GPS-based movement data. We expect that as field size increases, the potential for hares as mobile linker decreases, i.e., hares connect fewer habitats in simple compared to complex landscapes.

2.2 Methods

Seed characteristics

For our feeding experiment, we selected 44 arable plant species with different morphological seed traits. Seed traits (length^a, width^a, height^a, volume^a, mass^b) were available on the CC- BY^a (Ganhão and Dias 2019, 38 of 44 species) database, the SID^b (SID Database, 2021, 43 of 44 species) or the LEDA^{a,b} (Kleyer et al. 2008, mass: 1 of 44 species, volume: 6 of 44 species) database (Tab. S3). For species with multiple entries, we calculated the respective mean values. No data regarding seed height were available for 6 species (14%); therefore, we completed the dataset through supplementary searches in different grey literature sources following Picard et al. (2016). To qualify seed morphology, we calculated the Eccentricity index ($EI = \frac{length}{width}$) and the Flatness index ($FI = \frac{length + width}{2 \cdot height}$) following Cervantes et al. (2016), as well as seed density, i.e., mass per volume. Additionally, we calculated shape type (variance in dimensions: $V_s = \sum \frac{(x_i - \bar{x})^2}{3}$, with $x_1 = \frac{length}{length}$, $x_2 = \frac{width}{length}$, $x_3 = \frac{height}{length}$) following Bekker et al. (1998) to establish a proxy for seed surface area. For rather spheric seeds ($V_s < 1$), we used the formula for elliptical and for rather slender elongated seeds ($V_s > 1$), the formula for cylindrical objects, as well as the seed surface area to seed mass ratio.

Hare feeding experiment

We assessed the endozoochorous seed dispersal potential in a controlled feeding experiment with hares. Therefore, we tested the influence of seed morphological traits while considering phylogenetic relatedness on the germination success of the 44 plant species after intestinal passage. Germination rates were assessed twice before the feeding experiment to determine the seeds' germination capacity and once to assess seedling survival after being digested by hares.

In two consecutive years, during May−July 2019 & 2020, a defined number of seeds (depending on availability: 685−1500, Tab. 1, Tab. S3) were fed to captive hares in Niederfinow (Brandenburg), at the field station of the Leibniz Institute for Zoo and Wildlife Research (IZW), Berlin, around 40 km north of Berlin. During the feeding experiment, hares were housed in 2 m^2 cages. The floors of the cages consisted of a plastic grid with a mesh size large enough for the fecal pellets to fall through and be collected from a wooden collector mounted underneath but small enough to allow comfortable sitting and walking. The upper part of the cages was closed with a metal mesh and a roof, whereas the lower part with the collector was covered with a cotton cloth to avoid contamination of the samples with anemochoric dispersed diaspores. Food and water were offered *ad libitum.* Prior to the experiment, we carefully cleaned the cages and the fecal collector, covering the latter with thick paper to obtain a clean surface.

The feeding experiment was performed as an incomplete randomized block design due to the availability of hare individuals (2019: n = 8, 2020: n = 7; one hare was omitted because it refused to ingest the seeds). All hares received the same number of seeds of all plant species, but seed feeding was blocked in time, and not all plant species were offered simultaneously to a particular hare. Instead, different species combinations were fed to ease seedling identification by mixing them with regular hare food (nutritious pellets & oats). Seeds of respective 1 to 4 species (n per species = 100) were fed with a minimum in-between break of 4 days to ensure all seeds were being entirely excreted or digested (retention time: 7 ± 1.4 h; Stott 2008). During the following three days, feces were carefully collected daily and air-dried in closed paper bags. Then, feeding was repeated 8 times, with each hare receiving different combinations until all seeds were fed (Tab. 1, Tab. S3).

Germination capacity of offered seeds

The germination capacity of the seeds was determined in a control group germination test. *A priori*, the seed samples were stratified at 4°C for six weeks to break seed dormancy. 100 seeds of each species were counted and, following Heinken et al. (2001), placed in plastic boxes (180x133x87mm), pre-filled with a 2 cm layer of Seramis® (clay granules) substrate, and 1 cm of germination soil. Boxes were covered with perforated lids and put into RUMED® and Fitotron® light cabinets for six weeks. The cabinets were set to a day/night rhythm of 12 hours each, including 12 hours of maximum lighting of 100%. Species were separated into two groups according to their preferred germination temperatures (SID Database, 2021: 5°C/15°C and 15°C/25°C, day/night, respectively, Tab. 1). The humidity was visually controlled in a daily manner, and germination progress was recorded every 3 days. We used the germination capacity (control) results to calculate the standardized germination success of each plant species after gut passage ($Standardized\ germination\ success$ [%] = $\frac{100 \cdot germinated\ seeds\ (feces)}{(germinated\ seeds\ (control\ group) \cdot \frac{seeds\ fed}{100})}$). Dry fecal samples were stratified in the same way as the seed samples in the control group. Prior to germination, pellets were soaked in distilled water and carefully opened with rounded glass sticks; then, they were planted analogously to the control group. Germination was recorded every three days, and seedlings were marked and identified as soon as they showed distinct characteristics.

Phylogeny

We extracted genomic DNA from our 44 different plant species (Tab. 1) from 100-150 mg of fresh plant tissue with a modified CTAB plant DNA extraction protocol following Inglis et al. (2018). During the elution process, the amount of TE buffer was reduced to 60 µl to ensure a sufficient final concentration of DNA. After a quantity check of the concentration and pureness via a spectral photometer (NanoDrop ND-1000, Thermo Scientific®), the DNA was stored at -20°C.

We amplified a 633 bp fragment of the nuclear ribosomal internal transcribed spacer 1 (ITS1) 5.8S and ITS2 to assess the species level and phylogenetic relationship. Polymerase chain reactions (PCRs) were performed according to previously published protocols (White et al. 1990, Cheng et al. 2016). We cleaned the amplified products using an ExoAP procedure followed by a sequencing reaction and Sanger sequencing (Applied Biosystems™ 3500 Genetic Analyzer). The ITS1 – ITS2 region sequences were aligned with ClustalW (Thompson et al. 2003, Larkin et al. 2007) as implemented in Geneious v8.1.9 (Kearse et al. 2012).

Phylogenetic trees were generated of 35 amplified ITS1 – ITS2 region sequences and nine additional ITS1 – ITS2 region sequences from GenBank (Clark et al. 2016) as the respective species had not grown sufficiently to extract enough DNA (*Anthriscus sylvestris, Crepis capillaris, Taraxacum officinale, Tripleurospermum inodorum, Artemisia vulgaris, Onobrychis viciifolia, Lythrum salicaria, Armeria maritima, Poa annua*; GenBank: GQ379320.1, AJ633381.1, AJ633290.1, JF907423.1, AM398927.1, AB854512.1, AY035750.1, AJ225574.1, GQ324485.1). The phylogenetic relationship was established with RAxML (version 8.0.0, Stamatakis 2014) using the Maximum likelihood algorithm as well as the GTRGAMMAI substitution model (Yang 1993) with 10000 bootstrap replicates. The resulting best tree (Fig. 1) given by RAxML was used in all downstream analyses.

Hares as mobile linkers in contrasting agricultural landscapes

To investigate the potential of seed dispersal by hares throughout the landscape, we explored the connectedness of distinct habitat types (grassland, forest, field, wetland, quarry, and urban) with movement data of 63 GPS-collared hares in two contrasting landscapes. One study site represented a simple landscape in North-East Germany, Brandenburg, about 100km north of Berlin, with an average field size of 27.5 ± 1.1 ha, covered up to 62% by arable land (study site hereafter referred to as "simple landscape"). The second study site was located in South Germany, Bavaria, about 50km north of Munich, with comparatively small field sizes of 2.9 ± 0.04 ha, covered by 66% of arable lands (study site hereafter referred to as "complex landscape"). We created a dataset using GPS data of 48 hares from Ullmann et al. (2018, 2020), caught in 2014 and 2015 (27 in the simple landscape, 21 in the complex landscape) combined with additional 15 individuals caught during 2019 and 2020 in the simple landscape. The 63 hares were caught and handled according to Ullmann et al. (2018), and the corresponding data was stored in the Movebank data repository (Wikelski et al. 2020). All individuals used for our analysis were tracked for a minimum of 10 days. The GPS resolution was adjusted to hourly GPS fixes, resulting in a total of 62,528 GPS locations. For further description of the study sites, GPS collaring, and data storage, see Ullmann et al. (2018) and Mayer et al. (2018). Land-use types and GPS data were used from published data (Mayer et al. 2018, Ullmann et al. 2018, 2020). Animal tracking was obtained in accordance with the Federal Nature Conservation Act (§ 45 Abs. 7 Nr. 3) and approved by the local nature conservation authority (reference numbers: 2347-6-2019, LUGV V3- 2347-22-2013 and 55.2-1-54-2532-229-13).

Generally, we were interested in the potential of hares to connect habitats of differing or similar land-use types in the two contrasting landscapes. Hence, we first calculated distances between all habitat patches with at least one GPS location as follows. We used QGIS (QGIS Development Team 2021) to calculate the centroids of all visited habitat patches and derived a distance matrix using the R packages sf (Pebesma 2018) and rgeos (Bivand and Rundel 2020). Then, we compared the centroid distances of differing land-use types and similar land-use types to the mean Euclidian distances hares traveled within their retention time interval of 7 ± 1.4 h (Stott 2008) between the two contrasting landscapes. More specifically, we performed the analysis for retention times of mean – CI: 5.6 h, mean: 7 h, and mean + CI: 8.4 h, respectively, and report the overall mean values. The distances were estimated using the R package amt (Signer et al. 2019).

Particularly, we were interested in the amount of realized connections of patches through hares. Therefore, we calculated how many differing land-use types and unique patches of the same land-use type each hare visited on average during the retention time intervals. For this purpose, we first assigned the land-use type (grassland, forest, crop field, wetland, quarry, and urban) and the unique patch id to all GPS locations. Second, we generated initial tracks of consecutive GPS locations lasting 5.6 h, 7 h, and 8.4 h for each individual and counted the number of land-use types and single, unique patches of the same land-use type visited. Third, we shifted these tracks to subsequent GPS locations and repeated counting until the end of the observation time (moving window). Finally, we averaged the number of visited land-use types for each retention time interval and unique patches per land-use type for each individual and compared those between the two different landscapes.

Statistical Analysis

All analyses were conducted in R version 4.0.2 (R Core Team 2020), R Studio version 1.2.5019 (R Studio Team 2019), and QGIS (QGIS Development Team 2021). We used the R package dplyr (Wickham et al. 2021) for data management and ggplot2 (Wickham 2016) for figure generation.

Germination success

A priori, we excluded *Anthriscus sylvestris* from further analysis as it did not germinate in the control group. Subsequently, we excluded seed traits that correlated with each other (Flatness index, mass, volume, surface/mass ratio; Pearson correlation coefficient > 0.7, Fig. S1) from further analysis (Dormann et al. 2013) and performed a PCA to select the variables for subsequent analysis, which explained most of the variance (Fig. S2). We used a general linear mixed model to investigate how standardized germination success was related to seed traits (seed density, Eccentricity index, and seed surface area). Markov chain Monte Carlo (MCMC) was implemented to estimate the influence of predictor on response variables using the R package MCMCglmm (Hadfield 2010) with germination rate as the dependent variable and the seed traits included as fixed effects (n iterations = 5,000,000, burnin = 50,000, thin = 500). To identify the model that explained most of the variance, we performed model selection (Appendix: Tab. S1) based on the deviance information criterion (DIC) using the dredge function implemented in the R package MuMIn (Barton 2016). Following the studies of Burnham and Anderson (1998), we used the model with the highest DIC score (lowest DIC value) to explain our data. All models within 2 DIC units were considered as competing models (Spiegelhalter et al. 2002).

We repeated the analysis using Bayesian MCMCglmm, including phylogenetic inertia (i.e., a measure of branch length from each species) as a random effect in the model n iterations = 5,000,000, burnin = 50,000, thin = 500). We used the same dependent and explanatory variables combined with a correlation structure based on the phylogenetic tree (Fig. 1) for subsequent model selection (Appendix: Tab. S2). To evaluate whether the inclusion of the phylogenetic data improved our model, we compared their DIC values. Following others, we calculated Lynch's phylogenetic heritability as a phylogenetic signal measure and report the posterior mean heritability and the 95% interval of highest posterior density (HPD) based on MCMC draws from the marginal posterior distribution (Lovas-Kiss et al. 2020). The response variable was log (x+1)-transformed (to include zeros) for both models to obtain a distribution approximate to normal (Mangiafico 2017); predictor variables were log-transformed to reduce heteroscedasticity.

Table 1: Plant species and their corresponding seed characteristics

Genus	Species	Seeds fed[s]	GT [°C][b]	GC [%]	GS [%][d]	FI	EI	Mass [mg]	Volume [mm^3]	Density [mg/mm^3]	Area[d] [mm^2]	Area/Mass [$\frac{mm}{mg}$]	Seed origin *e	Neo-ophyte[f]	Sta-tus[g]
Achillea	*millefolium*	700	15/25	87	4.76	2.12	2.67	0.0002	0.3805	0.0005	5.6116	28058	TK	no	-
Anthriscus	*sylvestris*	685	15/25	0	-	7.11	6.17	0.0037	2.7061	0.0014	23.7055	6372	RH	no	-
Armeria	*maritima*	800	15/25	7	0	2.48	1.99	0.0014	0.6603	0.0021	7.9176	5655	RH	no	V
Arnoseris	*minima*	800	5/15	81	0.77	1.95	2.15	0.0004	1.7114	0.0002	5.2934	13966	SC	no	2
Artemisia	*vulgaris*	700	15/25	3	4.76	1.87	2.58	0.0002	0.3565	0.0004	4.4369	27730	TK	no	-
Berteroa	*incana*	700	15/25	38	0	1.83	1.18	0.0005	0.844	0.0006	6.301	12911	TK	yes	-
Brassica	*napus*	800	15/25	99	0.13	3.7	1.13	0.0033	1.6999	0.0019	10.5926	3209	PP	yes	-
Bupleurum	*rotundifolium*	800	5/15	84	0	3.59	2.15	0.0025	1.9856	0.0012	14.9075	6011	SC	no	2
Capsella	*bursa-pastoris*	700	15/25	13	2.2	1.08	1.85	0.0001	0.0902	0.0011	1.6695	16695	TK	no	-
Crepis	*capillaris*	685	15/25	65	0.22	1.93	3.52	0.0002	0.1633	0.0015	3.3544	13976	RH	no	-
Dactylis	*glomerata*	800	15/25	75	0.33	5.27	4.77	0.0008	1.9152	0.0004	17.354	21692	RH	no	-
Daucus	*carota*	800	15/25	88	0.14	3.7	1.85	0.0012	2.2454	0.0005	14.1852	11890	RH	no	-
Elymus	*repens*	685	15/25	35	3.34	8.07	4.52	0.0037	4.5846	0.0008	40.264	10754	RH	no	-
Epilobium	*hirsutum*	685	15/25	80	0.73	0.93	2.31	0.0001	0.037	0.0027	1.2335	12335	RH	no	-
Festuca	*rubra*	800	15/25	88	0.14	6.77	5.85	0.0012	2.2288	0.0005	24.1146	20095	RH	no	-
Legousia	*speculum-veneris*	800	5/15	97	0	1.11	1.33	0.0002	0.1727	0.001	2.3562	14058	SC	no	-
Lithospermum	*arvense*	800	5/15	96	0.13	5.19	1.58	0.0058	3.7585	0.0015	22.0733	3793	SC	no	V
Lolium	*perenne*	1500	15/25	87	0.92	6.82	4.32	0.002	4.1263	0.0005	31.7648	15882	RH, TK	no	-
Lotus	*corniculatus*	800	15/25	74	0.51	1.9	1.2	0.0009	0.4686	0.0019	4.0355	4623	RH	no	-
Lupinus	*polyphyllus*	800	15/25	52	1.44	9.21	1.33	0.0212	25.5254	0.0008	58.9049	2778	SV	yes	-
Lythrum	*salicaria*	700	15/25	9	9.52	0.43	2	0.0001	0.0048	0.0147	0.3142	4487	TK	no	-
Malva	*sylvestris*	800	15/25	93	0.13	3.38	1.17	0.0055	11.3008	0.0005	12.3484	2245	RH	no	-
Matricaria	*chamomilla*	700	15/25	62	2.76	3.19	4.39	0.0001	0.4556	0.0002	7.6111	84568	TK	no	-
Matricaria	*discoidea*	700	15/25	80	0.18	1.22	2.66	0.0001	0.3247	0.0004	1.8081	12823	TK	yes	-
Medicago	*sativa*	800	15/25	95	0.53	3.94	1.72	0.0024	4.3937	0.0005	16.8454	7159	RH	yes	-
Neslia	*paniculata*	800	15/25	7	0	3.54	1.26	0.0026	9.7147	0.0003	11.4291	4395	SC	no	3
Oenothera	*biennis*	700	15/25	77	1.11	2.14	1.75	0.0004	0.5551	0.0007	4.7397	11849	TK	yes	-
Onobrychis	*viciifolia*	800	15/25	52	0	8.26	1.65	0.0178	13.1685	0.0014	39.3092	2208	RH	yes	-
Papaver	*argemone*	800	5/15	71	1.76	0.96	1.9	0.0002	0.0546	0.0027	1.2504	8336	SC	no	-
Poa	*annua*	685	15/25	1	218.98	2.99	3.48	0.0003	0.5983	0.0005	7.827	26089	RH	no	-
Poa	*trivialis*	700	15/25	33	4.76	2.78	4.46	0.0001	0.3283	0.0003	5.4201	54200	TK	no	-
Scabiosa	*columbaria*	800	15/25	11	0	7.55	3.05	0.0021	34.1292	0.0001	41.2797	19617	RH	no	-
Silene	*latifolia*, subsp. alba	700	15/25	97	0.29	2.03	1.26	0.0009	0.8296	0.0011	5.7118	6222	TK	no	-
Sorghum	*bicolor*	800	15/25	100	0.25	9.6	1.31	0.0132	12.1953	0.0011	45.7504	3465	AS	yes	-
Stellaria	*media*	700	15/25	27	1.06	1.43	1.11	0.0004	0.3814	0.001	3.7335	9333	TK	no	-
Taraxacum	*officinale*	800	15/25	69	0	4	3.86	0.0007	1.4092	0.0005	12.6786	18112	RH	no	-
Teesdalia	*nudicaulis*	800	5/15	93	0.13	1.58	1.56	0.0003	0.6136	0.0005	3.9584	13509	SC	no	-

Table 1: continued

Genus	Species	Seeds fed^s	GT [°C]^b	GC [%]	GS [%]^d	FI	EI	Mass [mg]	Volume [mm^3]	Density [mg/mm^3]	Area^d [mm^2]	Area/Mass [$\frac{mm}{mg}$]	Seed origin *e	Neo-ophyte^f	Sta-tus^g
Trifolium	*hybridum*	800	15/25	99	0.13	1.62	1.16	0.0007	0.4587	0.0015	4.0134	5733	RH	yes	-
Trifolium	*pratense*	1500	15/25	74.5	0.54	4.11	1.38	0.0013	4.6064	0.0003	21.097	16228	RH, TK	no	-
Trifolium	*repens*	800	15/25	89	0.7	1.99	1.21	0.0007	0.992	0.0007	6.2471	8924	RH	no	-
Tripleurospermum	*inodorum*	685	15/25	30	0	2.51	2.55	0.0004	2.5916	0.0001	7.1673	19153	RH	no	-
Valerianella	*dentata*	800	5/15	83	0.15	2.13	1.84	0.0009	0.6676	0.0013	5.2229	5803	SC	no	V
Valerianella	*rimosa*	800	5/15	68	2.57	3.54	1	0.0012	3.0434	0.0004	12.5664	10385	SC	no	3
Viola	*arvensis*	700	15/25	46	0	2.01	1.75	0.0006	0.4877	0.0012	4.7892	8402	TK	no	-

GT: Germination temperature; GC: Germination capacity; GS: Standardized germination success; FI: Flatness index; EI: Eccentricity index.

Morphological seed traits were obtained from the SID (SID Database 2021), LEDA (Kleyer et al. 2008), and CC-BY Database (Ganhão and Dias 2019). The seed trait "height" to calculate area and FI was additionally obtained through supplementary searches in different grey literature sources for *M. chamomilla, M. discoidea, N. paniculata, Scabiosa columbaria, and Tripleurospermum inodorum.*

[a] Number of seeds overall fed, numbers < 700 result from limited availability of the respective seeds.

[b] seeds were sown below or above ground depending on their preferences with a day/night cycle of 12h/12h.

[c] Calculated in relation to "Germination capacity [%]" as $\frac{100 \cdot germinated\ seeds\ (feces)}{(germinated\ seeds\ (control\ group) \cdot \frac{seeds\ fed}{100})}$.

[d] Seed surface area was calculated with the formula for elliptical objects for seeds with ($V_s < 1$), and cylindrical objects for seeds with ($V_s > 1$). Variance in dimensions was calculated as: $sum\ \frac{(x_i - \overline{x})^2}{3}$, with $x_1 = \frac{length}{length}$, $x_2 = \frac{width}{length}$, $x_3 = \frac{height}{length}$, formula from Bekker et al. (1998).

[e] Seeds were ordered at RH (Rieger-Hofmann, https://www.rieger-hofmann.de), TK (Templiner Kräutergarten, https://templiner-kraeutergarten.de), AS (Asklepios Seeds, https://www.asklepios-seeds.de), PP (Pflanzen- Pflanzen, https://www.pflanzen-pflanzen.de), or SC (self-collected in the field, Bavaria, Germany).

[f] Status as a Neophyte in German, data from: https://www.floraweb.de/, retrieved: 22.07.2021.

[g] Conservation status in Germany (red list), data from https://www.floraweb.de/, retrieved: 22.07.2021.

2.3 Results

Out of 34,710 seeds from 44 plant species fed, 177 seedlings of 33 species emerged from feces (0.51%). Considering the species-specific germination capacity, the standardized germination success was 6% in total. Standardized germination success varied largely among species (max: 219% for *P. annua*) and was higher for non-neophytes (mean: 1.27%) than for neophytes (mean: 0.42%) and for endangered species (mean: 1.21%) compared to non-endangered ones (mean: 0.52%) without *P. annua* into account (Tab. 1).

Phylogenetic reconstruction

The maximum likelihood tree calculated from a 633 bp long fragment containing ITS1, 5.8S, and ITS2 shows a well-separated phylogeny of the 15 different families, supported by generally fairly high bootstrap values (65%-95% indicated by grey dots, >95%-100% indicated by black dots; Fig. 1). The division between monocotyledons (here grasses) and dicotyledons was confirmed with a bootstrap value of 100%. Furthermore, within the dicotyledons, the maximum likelihood tree reflects a clear separation according to the family's origin, supporting the robustness of the data analysis.

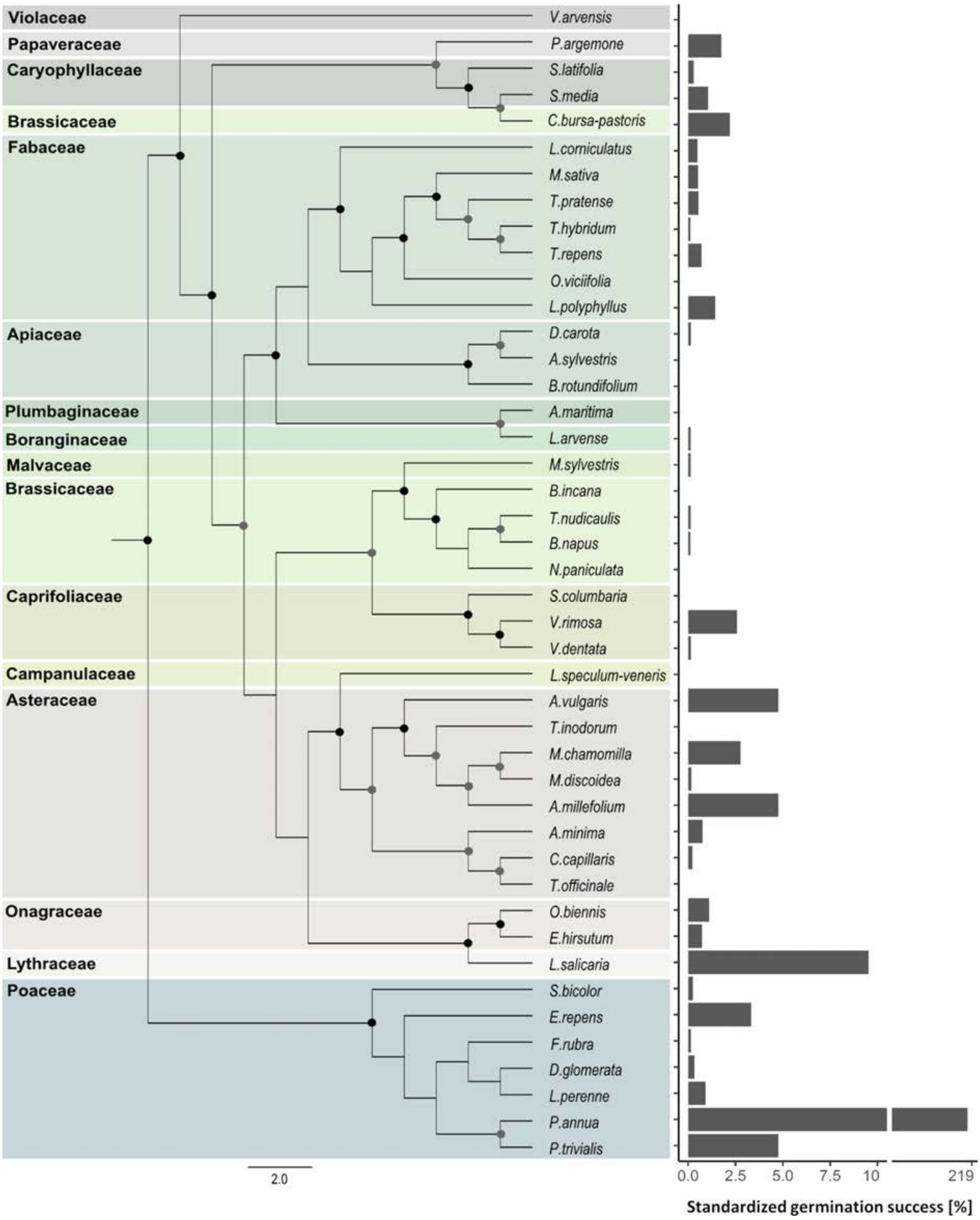

Fig. 2.1 Left: Phylogenetic Maximum Likelihood tree based on full ITS1 – ITS2 region (including ITS1, 5.8S and ITS2) sequences of 44 selected plants species. Dots indicate bootstrap values ≥ 65, while grey dots indicate bootstrap support of 65%-95%, and black dots indicate bootstrap support of 95%-100% of the branch splits. Right: Standardized germination success of seeds [%] after being digested by hares. The X-axis is split at 10% to obtain a better perspective.

Seed traits and their influence on germination success

Seed's germination was linked to the three covariates: seed density, Eccentricity index (EI), and seed surface area (Fig. 2), as shown by all competing models within 2 DIC units. Rather long, elongated seeds (increasing EI), an increasing seed density, and a decreasing seed surface area were positively related to standardized germination success after gut passage. Using an MCMCglmm with phylogeny as a random effect significantly increased model convergence compared to the models without phylogeny (best-fit models: Δ DIC = 3.8, Tab. S1 & Tab. S2). Heritability as measured by Lynch's signal (mean = 0.046, 95%, HPD interval 0.0014 – 0.14) significantly influenced the model outcome.

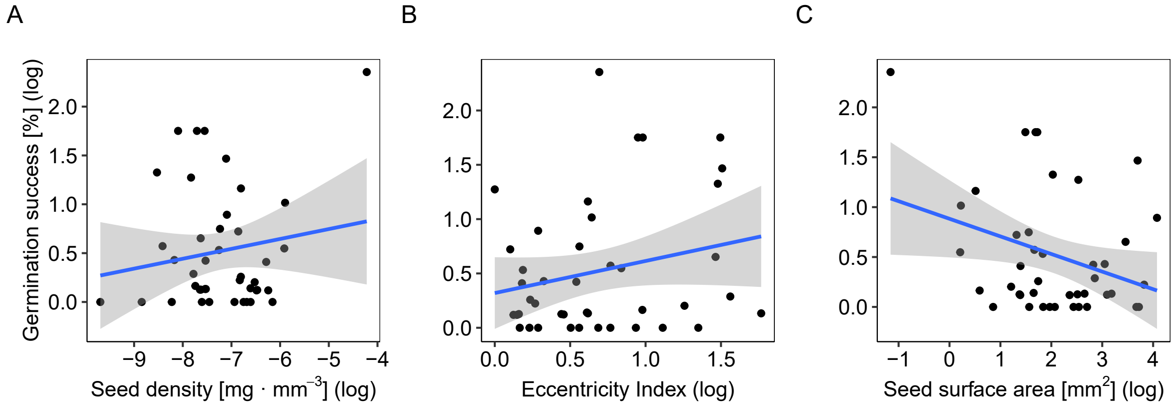

Fig. 2.2 Dependence of standardized germination success on (A) seed density, (B) seed shape as measured by the Eccentricity index and seed surface area (n = 43). Observed values (circles), predicted values (blue line), and confidence intervals (gray shading) for the MCMC-GLMMs. Graphs are shown without the outlier *P. annua* to obtain a better perspective.

Mobile link potential of hares in agricultural landscapes

The distance to differing land-use types (simple: 376 ± 241 m; complex: 192 ± 97 m), the distance from crop field to crop field (simple: 579 ± 302 m; complex: 365 ± 149 m), and the distance from grassland to grassland (simple: 289 ± 151 m; complex: 163 ± 47 m) was larger in simple versus complex landscapes, while that from forest to forest (simple: 193 ± 36 m; complex: 232 ± 125 m), was smaller (Fig. 3A). Hares in simple landscapes moved 1.30 ± 0.28 km per 7 ± 1.4 h retention time interval (i.e., potential dispersal distance), while those in complex landscapes traveled 0.77 ± 0.17 km during the same period. Comparing both study sites, hares connected on average slightly more differing land-use types in simple landscapes (1.30 ± 0.16 m) than in complex landscapes (mean: 1.10 ± 0.15) within a 7 ± 1.4 h period. Hares in complex landscapes connected more fields, fewer isolated grassland patches and a similar amount of forest than in simple landscapes (Fig. 3B, C).

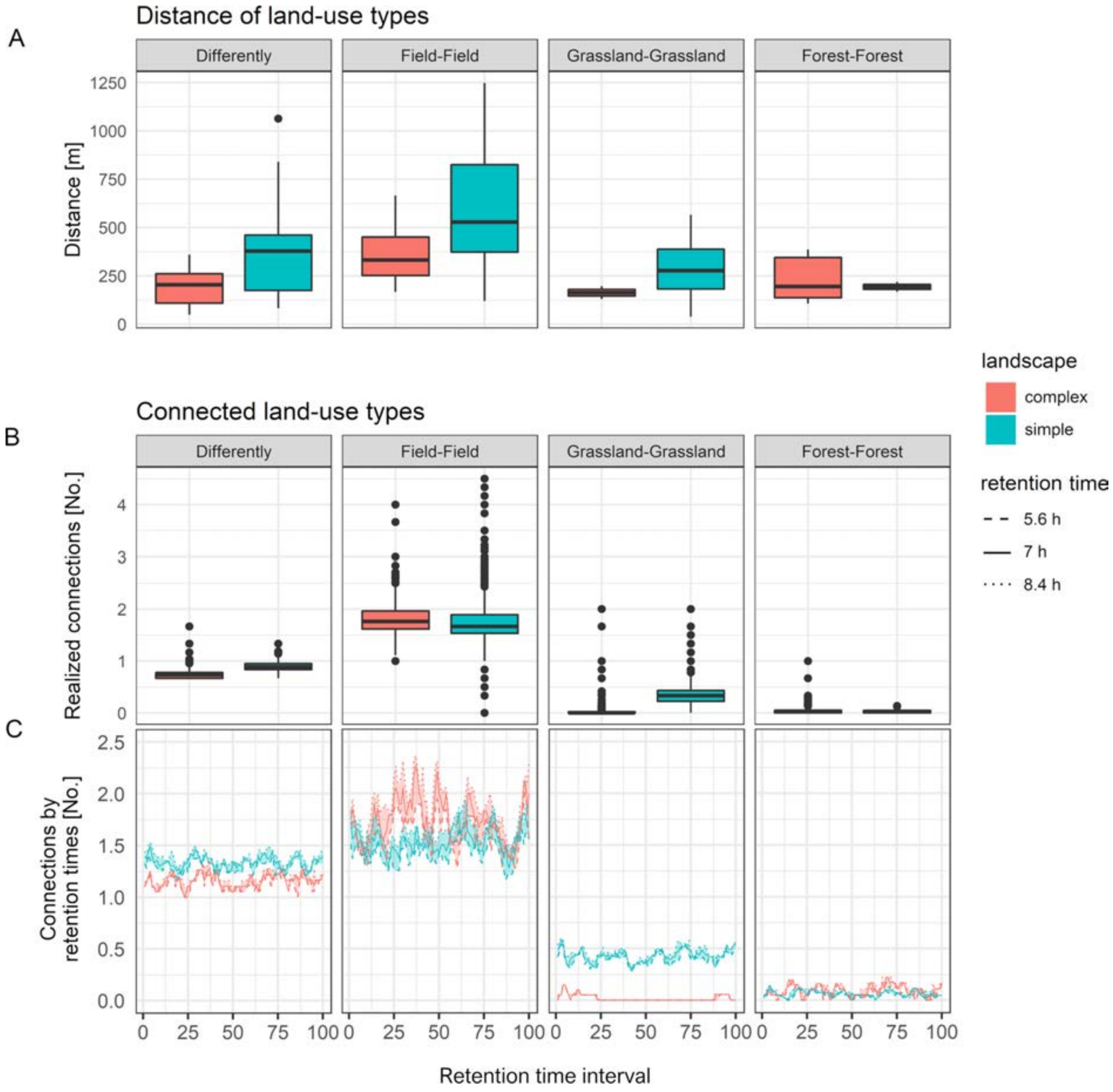

Fig. 2.3 Average distances between land-use types in complex and simple landscapes. Fig. 3B: Average number of connected land-use types of hares within the retention time of 7 ± 1.4 hours (moving window approach) in complex and simple landscapes. Fig. 3C: Number of connected land-use types of hares within the retention time intervals of 5.6, 7, and 8.4 hours (moving window approach) in complex and simple landscapes. Left to right: Differing habitat types include distances (A), realized connections (B), and connections by retention time (C) between grassland, crop field, wetland, forest, quarry, or urban; between fields; grasslands; and forest patches. Land use types were recorded from 62,528 GPS locations of 63 individual hares (42 in simple, 21 in complex landscapes).

Across both regions, hares connected mainly various crop fields (70.78 ± 1.96%). To a lesser extent, they connected crop fields with grasslands (12.72 ± 1.25%), grasslands with grasslands (4.34 ± 0.53%), and crop fields with forests (2.95 ± 0.55%).

2.4 Discussion

Seed characteristics

With this controlled feeding experiment, we provide fundamental advances in understanding the potential impacts of mobile linkers as seed dispersers. Hitherto our understanding of the efficiency of smaller mammals and their potential impacts on plant communities and recruitment was limited, as most of the literature focuses on rather large mammals with more extensive home ranges (Mouissie et al. 2005b, Albert et al. 2015b, Karimi et al. 2020; but see, e.g., Lessa et al. 2019, Naoe et al. 2019, Yang et al. 2019. Our feeding experiment demonstrates that 32 out of 42 species that germinated in the control group also survived the gut passage of hares and germinated afterward. However, with one exception (*P. annua*), all species showed lower germination rates after gut passage in relation to the control group. Indicated by the range of germination rates and similar to findings from Milotić and Hoffmann (2016), germination success was clearly taxon-dependent. To understand the mechanisms behind successful germination, most endozoochoric studies consider seed traits and their influence on dispersal rates exclusively (e.g., Pakeman et al. 2002, Cosyns et al. 2005, Mouissie et al. 2005b). According to our study, germination success depends both on such morphological traits and on taxon-specific additional factors, such that neglecting phylogenetic affinity of the observed species may compromise our understanding of endozoochoric seed dispersal – and, ultimately, germination success – by mobile linkers (D'hondt and Hoffmann 2011, Boedeltje et al. 2015, Lovas-Kiss et al. 2020).

Our best-fit model revealed that, consistent with our hypotheses, denser seeds with comparatively small surface areas are positively related to germination success. Contrary to our expectations, not rounder but rather long, elongated seeds show higher germination rates after being digested by hares. Consistent with our findings, increasing seed hardness was identified as the most critical factor for gut passage survival in mallards (*Anas platyrhynchos*) in a study of waterbirds (Lovas-Kiss et al. 2020) after controlling for phylogeny. Kleyheeg et al. (2018a, b) demonstrated that harder seeds are more likely to survive the gizzard of mallards, where mechanical digestion occurs before the seeds are further released into the intestine. Therefore, harder seeds are more likely to survive intestinal passage and are egested over a more extended range of time, increasing the maximum putative dispersal distance (Farmer et al. 2017, Kleyheeg et al. 2019). Although the digestive systems of birds and mammals are very different, it stands to reason that specific characteristics of seeds determine their survival after digestion, irrespective of the respective mobile linker. The importance of such seed traits seems evident as, e.g., birds and ungulates often disperse the same plant species. (Soons et al. 2008, Albert et al. 2015a, Lovas-Kiss et al. 2019, 2020).

Furthermore, we found a decreasing seed surface area as a significant driver for successful germination. Thus, we assume that dense and heavy seeds with relatively small surface areas enhance seed dispersal via hares as such seeds seem to be better protected from the milieu prevailing in the stomach. Hence, we conclude that most seeds will lose their germination capacity inside the digestive system. This is consistent with the findings that dense and small seeds are superior in endozoochoric seed dispersal by mammals (Williams et al. 2000, Bourgeois et al. 2005, D'hondt and Hoffmann 2011, Shiels and Drake 2011, Albert et al. 2015a, b, Lepková et al. 2018) or waterbirds (Lovas-Kiss et al. 2020). We did expect rounder, more spheric seeds to show higher germination rates as found, e.g., as shown for ungulates (Heinken et al. 2002, Pakeman et al. 2002, Mouissie et al. 2005a). The finding that elongated seeds are superior in surviving digestion might be reasoned through the digestive system of hares. However, this is purely speculative. Besides, in a feeding experiment by Cosyns et al. (2005), more elongated seeds were also shown to be positively related to germination success after digestion by rabbits, cattle (*Bos taurus*), donkeys (*Equus asinus*), and horse (*Equus cabbalus*). Another explanation might be that for our selection of plants, the Eccentricity index was interdependent with the surface-to-mass ratio, and therefore, similar to seeds with less area, digestion processes have less contact area to break down the seeds. In summary, the most critical seed characteristics for successful endozoochorous seed dispersal minimize exposure of the seed to the stomach/gut and their associated digestive fluids (i.e., dense seeds with less seed surface area). In addition, supported by the inclusion of phylogeny and that some seeds with similar traits show different germination rates, we argue that specific compositions of the seed coat are better adapted to survive digestion than others.

Hares as mobile linkers

Connecting fragmented habitat patches is essential for zoochorous plant species as it helps to stabilize biodiversity in fragmented landscapes (Lundberg and Moberg 2003, Damschen et al. 2019), where many animal species provide effective functional connectivity and seed dispersal via endozoochory (Williams et al. 2008, Pellerin et al. 2016).

We could show that hares connect different habitats in simple and complex agricultural landscapes within their species-specific retention time and, therefore, can act as mobile linkers. Despite the relatively low germination rates after hare's digestion, we emphasize that long-distance dispersal through endozoochory might have disproportional large effects on plant community composition and species persistence (Nathan et al. 2008, Schurr et al. 2009). Considering the number of seeds produced per plant, ingested by individual hares throughout the year, and subsequently transported to sites that may be more favorable for germination, the total amount may be quite significant. Contrary to our prediction, the number of interconnected habitats with different land-use types was similar in both landscapes. Although hares moved twice the daily distance in simple compared to complex landscapes, they connected more crop fields with crop fields in the latter landscape, probably because field sizes were about 10% of those in simple landscapes. Surprisingly though, more grasslands were connected in simple landscapes. We argue that hares need to travel more often to such high-quality foraging habitats. Both grasslands and field margins contain a higher plant species diversity than their arable surroundings (Marshall and Moonen 2002, Rosado and de Mattos 2017) but are simply less available in a landscape with comparatively large fields. A higher plant diversity, found in field margins and grasslands, is associated with health benefits for hares, and there is a substantial selection for a highly diverse diet (Reichlin et al. 2006). Moreover, the observed loss of high-quality habitat patches with wild herbs may be related to decreasing hare populations (Hackländer 2002). The non-existent difference in forest patch connections seems justified, as the distance of such habitats is similar in both areas.

Conclusively, hares seem to be well adapted to both simple and complex landscapes and connect several habitats while foraging. Thus, hares as mobile linkers seem to play an important role in determining local plant communities (Lundberg and Moberg 2003). These mobile linkers, especially on human-disturbed land such as agricultural landscapes, might be critical acting as mediators of recolonization through seed import from off-sites (i.e., grasslands or field margins) to patches where the resources for natural succession are impoverished (Duncan and Chapman 1999, Lundberg and Moberg 2003). In this sense, many mobile linkers are essential factors determining the direction of ecosystem development following a disturbance (Cox and Elmqvist 2000, Nyström and Folke 2001).

Our results suggest that management plans in agricultural landscapes should consider the functional role of mobile linkers in maintaining ecosystems and contributing to ecosystem resilience. This is even more evident as especially rare and non-neophytic species achieved higher germination rates in our study. For the support of hares, this would imply maintaining a high plant diversity at the field margins, e.g., through the establishment of flowering strips or the temporary set-aside of fields.

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2.6 Declarations

Data availability statement

Data files to perform the analyses are supplied as supplementary materials at the Dryad data repository at https://doi.org/10.5061/dryad.98sf7m0k6. The sequence data used to build the phylogenetic tree are openly available on GenBank of NCBI at https://www.ncbi.nlm.nih.gov/ under the accession numbers GQ379320.1, AJ633381.1, AJ633290.1, JF907423.1, AM398927.1, AB854512.1, AY035750.1, AJ225574.1, GQ324485.1, and OL415903 - OL415937.

Conflict of interest

The authors declare no conflict of interest.

Author contributions

Jonas Stiegler: Conceptualization (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing-original draft (lead). **Katrin Kiemel**: Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Visualization (supporting); Writing-review & editing (supporting). **Jana Eccard**: Writing-review & editing (supporting). **Christina Fischer**: Writing-review & editing (supporting). **Robert Hering**: Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Visualization (supporting); Writing-review & editing (supporting). **Sylvia Ortmann**: Writing-review & editing (supporting). **Lea Strigl**: Investigation (supporting); Methodology (supporting); Writing-review & editing (supporting). **Ralph Tiedemann**: Writing-review & editing (supporting). **Wiebke Ullmann**: Data curation (supporting); Writing-review & editing (supporting). **Niels Blaum**: Conceptualization (equal); Methodology (equal); Writing-review & editing (lead).

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2.8 Supporting information

Table S1: Model selection table without phylogeny, ranked by DIC#

model	(Int)	log(density)	log(EI)	log(seed surface area)	df	logLink	DICc	delta	weight
6	0.632	0.612		-0.207	4	-57.632	119.147	0	0.295
2	0.248	0.554			3	-58.425	119.76	0.613	0.217
4	1.239	0.636	0.146		4	-58.535	120.961	1.815	0.119
8	0.877	0.631	0.041	-0.19	5	-58.168	121.182	2.035	0.106
1	0.634				2	-59.682	121.276	2.129	0.102
5	0.997			-0.177	3	-59.306	121.531	2.385	0.089
3	1.002		0.051		3	-60.162	123.209	4.062	0.039
7	0.615		-0.06	-0.2	4	-59.796	123.477	4.33	0.034

The initial model was calculated with the 3 covariates ’density’, ’EI’ and ’seed surface area’ as $y \sim N(\mu,\sigma^2 I)$ with $\mu=\beta_0+ \beta_1 \cdot x_1+ \beta_2 \cdot x_2+\beta_3 \cdot x_3$.

Table S2: Model selection table including phylogeny, ranked by DIC#

model	(Int)	log(density)	log(EI)	log(seed surface area)	df	logLink	DICc	delta	weight
5	1.196			-0.242	4.000	-52.316	115.389	0.000	0.283
1	0.682				3.000	-53.210	116.171	0.782	0.192
6	0.973	0.320		-0.248	5.000	-53.366	117.128	1.739	0.119
7	0.863		-0.055	-0.267	5.000	-52.859	117.137	1.748	0.118
3	1.313		0.088		4.000	-53.154	117.234	1.845	0.113
2	0.483	0.271			4.000	-54.172	117.830	2.441	0.084
8	0.885	0.306	-0.017	-0.254	6.000	-53.852	118.880	3.491	0.049
4	1.363	0.339	0.130		5.000	-54.372	119.220	3.831	0.042

The initial model was calculated with the 3 covariates ’density’, ’EI’ and ’seed surface area’ as $y \sim N(\mu,\sigma^2 I)$ with $\mu=\beta_0+ \beta_1 \cdot x_1+ \beta_2 \cdot x_2+\beta_3 \cdot x_3$.

Table S3: Plant species and their initially considered seed characteristics

Family	**Genus**	**Species**	**Year**$^{\alpha}$	$V_s{}^{\beta}$	**Length**$^{\gamma}$ **[mm]**	**Width**$^{\gamma}$ **[mm]**	**Height**$^{\gamma}$ **[mm]**	**Mass**$^{\gamma}$ **[mg]**
Apiaceae	*Anthriscus*	*sylvestris*	2020	1.376	6.562	1.063	1.022	0.0037
Apiaceae	*Bupleurum*	*rotundifolium*	2019	1.045	2.879	1.338	1.057	0.0025
Apiaceae	*Daucus*	*carota*	2019	0.972	2.894	1.56	1.034	0.0012
Asteraceae	*Achillea*	*millefolium*	2020	1.137	2.003	0.751	0.3	0.0002
Asteraceae	*Arnoseris*	*minima*	2019	1.045	1.717	0.797	0.587	0.0004
Asteraceae	*Artemisia*	*vulgaris*	2020	1.124	1.749	0.677	0.35	0.0002
Asteraceae	*Crepis*	*capillaris*	2020	1.235	1.814	0.515	0.45	0.0002
Asteraceae	*Matricaria*	*chamomilla*	2020	1.299	3.089	0.704	0.29	0.0001
Asteraceae	*Matricaria*	*discoidea*	2020	1.136	1.136	0.427	0.41	0.0001
Asteraceae	*Taraxacum*	*officinale*	2019	1.263	3.712	0.963	0.6	0.0007
Asteraceae	*Tripleurospermum*	*inodorum*	2020	1.118	2.205	0.865	0.71	0.0004
Boranginaceae	*Lithospermum*	*arvense*	2019	0.887	3.331	2.109	1.767	0.0058
Brassicaceae	*Berteroa*	*incana*	2020	0.713	1.538	1.304	0.44	0.0005
Brassicaceae	*Brassica*	*napus*	2019	0.687	1.954	1.726	2.027	0.0033
Brassicaceae	*Capsella*	*bursa-pastoris*	2020	0.972	0.993	0.535	0.336	0.0001
Brassicaceae	*Neslia*	*paniculata*	2019	0.753	2.14	1.7	1.65	0.0026
Brassicaceae	*Teesdalia*	*nudicaulis*	2019	0.878	1.4	0.9	0.393	0.0003
Campanulaceae	*Legousia*	*speculum-veneris*	2019	0.788	1	0.75	0.297	0.0002
Caprifoliaceae	*Scabiosa*	*columbaria*	2019	1.186	5.863	1.925	1.75	0.0021
Caprifoliaceae	*Valerianella*	*dentata*	2019	0.969	1.75	0.95	0.8	0.0009
Caprifoliaceae	*Valerianella*	*rimosa*	2019	0.608	2	2	1.537	0.0012
Caryophyllaceae	*Silene*	*latifolia*	2020	0.756	1.516	1.199	0.85	0.0009
Caryophyllaceae	*Stellaria*	*media*	2020	0.673	1.148	1.036	0.545	0.0004
Fabaceae	*Lotus*	*corniculatus*	2019	0.722	1.24	1.036	1.279	0.0009
Fabaceae	*Lupinus*	*polyphyllus*	2019	0.788	5	3.75	2.247	0.0212
Fabaceae	*Medicago*	*sativa*	2019	0.932	3.035	1.767	1.025	0.0024
Fabaceae	*Onobrychis*	*viciifolia*	2019	0.912	4.55	2.75	2.698	0.0178
Fabaceae	*Trifolium*	*hybridum*	2019	0.702	1.217	1.05	0.765	0.0007
Fabaceae	*Trifolium*	*pratense*	2019, 2020	0.81	3.048	2.203	0.968	0.0013
Fabaceae	*Trifolium*	*repens*	2019	0.726	1.548	1.285	0.688	0.0007
Lythraceae	*Lythrum*	*salicaria*	2020	1.01	0.4	0.2	0.308	0.0001
Malvaceae	*Malva*	*sylvestris*	2019	0.71	2.148	1.83	1.343	0.0055
Onagraceae	*Epilobium*	*hirsutum*	2020	1.077	0.864	0.374	0.328	0.0001
Onagraceae	*Oenothera*	*biennis*	2020	0.943	1.626	0.928	1.1	0.0004
Papaveraceae	*Papaver*	*argemone*	2019	0.985	0.87	0.458	0.395	0.0002
Plumbaginaceae	*Armeria*	*maritima*	2019	1.007	2	1.007	0.96	0.0014
Poaceae	*Dactylis*	*glomerata*	2019	1.32	4.882	1.024	0.766	0.0008
Poaceae	*Elymus*	*repens*	2020	1.306	7.221	1.598	1.057	0.0037
Poaceae	*Festuca*	*rubra*	2019	1.365	6.433	1.099	0.614	0.0012
Poaceae	*Lolium*	*perenne*	2019, 2020	1.295	6.26	1.448	0.779	0.002
Poaceae	*Poa*	*annua*	2020	1.231	2.754	0.791	0.601	0.0003
Poaceae	*Poa*	*trivialis*	2020	1.303	2.631	0.59	0.494	0.0001
Poaceae	*Sorghum*	*bicolor*	2019	0.776	4.363	3.338	3.14	0.0132
Violaceae	*Viola*	*arvensis*	2020	0.942	1.633	0.933	0.81	0.0006

$^{\alpha}$Experiments were conducted either in 2019, 2020, or during both years.

$^{\beta}$Variance in dimensions was calculated as: $sum\ \frac{(x_i-\bar{x})^2}{3}$, with $x_1 = \frac{length}{length}$, $x_2 = \frac{width}{length}$, $x_3 = \frac{height}{length}$, formula from Bekker et al. (1998).

$^{\gamma}$Seed traits (length, width, height, mass) were available on the CC- BY (Ganhão and Dias 2019) database, the SID (SID Database, 2021) or the LEDA (Kleyer et al. 2008) database. The trait height was obtained through supplementary searches in different grey literature sources for *M. chamomilla, M. discoidea, N. paniculata, Scabiosa columbaria, and Tripleurospermum inodorum.*

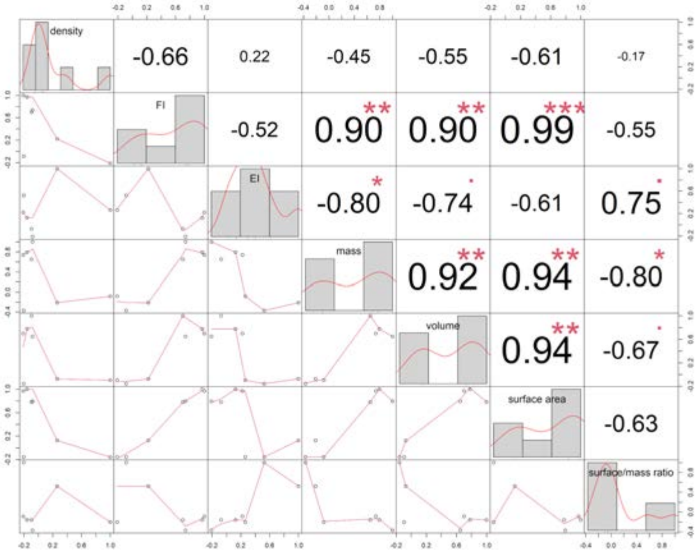

Fig. 2.4 S1: Chart of the Pearson correlation matrix of all variables initially considered for statistical modeling (variables with correlation coefficient > 0.7 were excluded from subsequent analysis. The distribution of each variable is shown on the diagonal. On the bottom of the diagonal, the bivariate scatter plots with a fitted line are displayed. On the top of the diagonal, the value of the correlation plus the significance levels is shown as asterisks. p-values (≤ 0.001 *** , ≤ 0.01 ** , ≤ 0.05 * , > 0.05 *n.s.*).

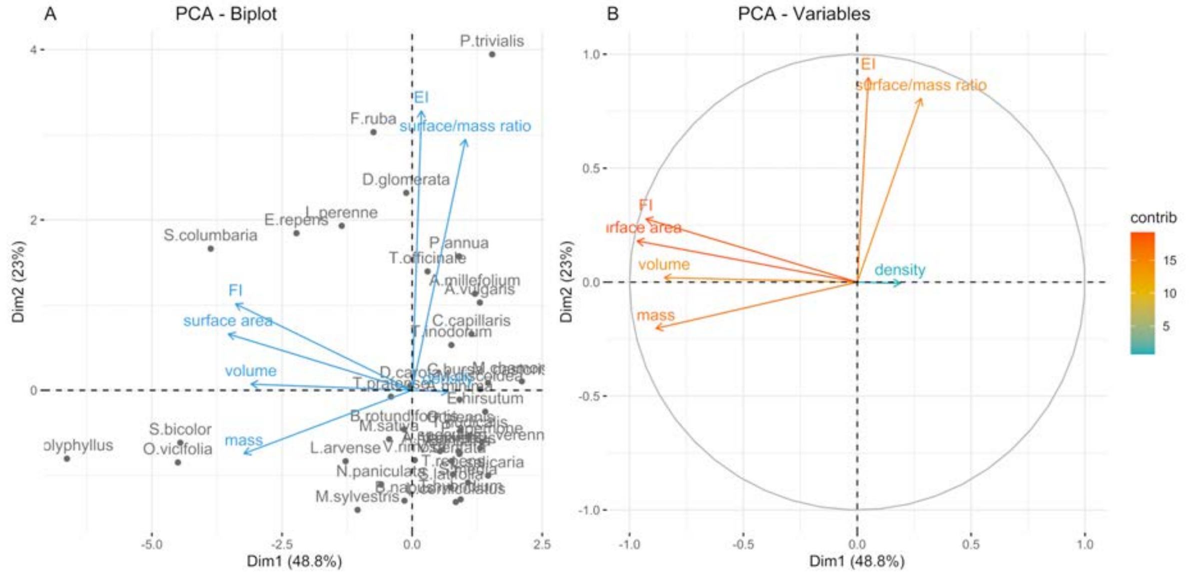

Fig. 2.5 S2: Biplot of individual plant species and all variables initially considered for statistical modeling (A). Graph of variables (B), positively correlated variables point towards the same side of the plot. Negatively correlated variables point to opposite sides of the graph. We used variables with the highest contribution per dimension (EI, density, and surface area), illustrated by the length and color of the arrow, for subsequent analysis.

Chapter 2

Personality drives activity and space use in a mammalian herbivore

read @Movement Ecology

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Abstract

Background

Animal personality has emerged as a key concept in behavioral ecology. While many studies have demonstrated the influence of personality traits on behavioral patterns, its quantification, especially in wild animal populations, remains a challenge. Only a few studies have established a link between personality and recurring movements within home ranges, although these small-scale movements are of key importance for identifying ecological interactions and forming individual niches. In this regard, differences in space use among individuals might reflect different exploration styles between behavioral types along the shy-bold continuum.

Methods

We assessed among-individual differences in behavior in the European hare (*Lepus europaeus*), a characteristic mammalian herbivore in agricultural landscapes using a standardized box emergence test for captive and wild hares. We determined an individual's degree of boldness by measuring the latencies of behavioral responses in repeated emergence tests in captivity. During capture events of wild hares, we conducted a single emergence test and recorded behavioral responses proven to be stable over time in captive hares. Applying repeated novel environment tests in a near-natural enclosure, we further quantified aspects of exploration and activity in captive hares. Finally, we investigated whether and how this among-individual behavioral variation is related to general activity and space use in a wild hare population. Wild and captive hares were treated similarly and GPS-collared with internal accelerometers prior to release to the wild or the outdoor enclosure, respectively. General activity was quantified as overall dynamic body acceleration (ODBA) obtained from accelerometers. Finally, we tested whether boldness explained variation in (i) ODBA in both settings and (ii) variation in home ranges and core areas across different time scales of GPS-collared hares in a wild population.

Results

We found three behavioral responses to be consistent over time in captive hares. ODBA was positively related to boldness (i.e., short latencies to make first contact with the new environment) in both captive and wild hares. Space use in wild hares also varied with boldness, with shy individuals having smaller core areas and larger home ranges than bold conspecifics (yet in some of the parameter space, this association was just marginally significant).

Conclusions

Against our prediction, shy individuals occupied relatively large home ranges but with small core areas. We suggest that this space use pattern is due to them avoiding risky and energy-demanding competition for valuable resources. Carefully validated activity measurements (ODBA) from accelerometers provide a valuable tool to quantify aspects of animal personality along the shy-bold continuum remotely. Without directly observing - and possibly disturbing - focal individuals, this approach allows measuring variability in animal personality, especially in species that are difficult to assess with experiments. Considering that accelerometers are often already built into GPS units, we recommend activating them at least during the initial days of tracking to estimate individual variation in general activity and, if possible, match them with a simple novelty experiment. Furthermore, information on individual behavioral types will help to facilitate mechanistic understanding of processes that drive spatial and ecological dynamics in heterogeneous landscapes.

Keywords: *Animal personality, Movement ecology, Inter-individual differences, ODBA, Energy expenditure, European hare*

3.1 Introduction

In the paradigm of movement ecology, an animal's space use is explained as a consequence of the influence of external factors on three movement processes: internal state, navigation, and motion capacity (Nathan et al. 2008). An increasing number of studies show high among-individual differences in movement characteristics that cannot be explained by the paradigm alone (Spiegel et al. 2017, Shaw 2020). Spiegel et al. (2017) refined this paradigm by including personality-dependent spatial ecology and suggested that among-individual differences in behavioral types are a predictor for space use. Consistent among-individual variation of behavior over time is referred to as animal personality (Réale et al. 2007), a key concept in behavioral ecology (Wolf and Weissing 2012, Dingemanse and Dochtermann 2013, Koski 2014, Shaw 2020).

Although animal personality is widely recognized as a critical intrinsic component of behavior, its quantification under field conditions remains a challenge for two main reasons. First, extensive species-specific standardized tests need to be developed and performed repeatedly to measure consistency in among-individual differences in behavior (Uher et al. 2013). Under such test conditions, restraining individuals could interfere with the procedures and objectives of the intended field study, and direct observation of individuals could be impossible. Second, observed among-individual differences in behavior need to be ecologically validated (Réale et al. 2007). In most field studies, this would result in a prolonged handling time of individuals, which contrasts with minimizing effects on trapped animals or maximizing sample size (Webster and Rutz 2020).

Réale et al. (Réale et al. 2007) summarized the fundamental personality traits as activity, boldness, exploration behavior, aggressiveness, and sociability. While most of them are difficult to quantify in the wild, the personality trait activity – defined as an individual's general level of activity - can be recorded using accelerometers. Hence, such derived measurements may allow for a remote classification of behavioral types. The main aim of this study was to assess whether and how aspects of animal personality (quantified in standardized and repeated emergence and novel environment tests) and general activity (quantified via accelerometers) are related and whether they are correlated with space use. Moreover, our novel approach shows a feasible way to combine experiments in a controlled environment with ones in the wild. Thus, we contribute to answering a fundamental question in personality research and movement ecology, namely how behavioral traits covary with movement strategies in the wild (Nilsson et al. 2014).

Previous research highlights that among-individual differences in behavior, i.e., animal personality, are a key aspect of variation in "internal states" underlying movement and space use (Hertel et al. 2020a), with individuals varying consistently in how, where, and when they move (Found and St. Clair 2016, Spiegel et al. 2017). Variation, particularly along the shy-bold continuum (Archer 1973, Gosling 2001), is suggested to affect crucial ecological processes, e.g., predation rates (Leclerc et al. 2017) or population structure (Clobert et al. 2009, Found and St. Clair 2016), and to generate spatio-temporal variability that influences individuals' interactions with biotic and abiotic factors (Bolnick et al. 2011, Chapman et al. 2011, Wolf and Weissing 2012, Best et al. 2015, Holtmann et al. 2017). For example, boldness and exploration have been shown to correlate with variation in foraging patterns (Patrick et al. 2017, Gharnit et al. 2020) or habitat use (Spiegel et al. 2017, Hertel et al. 2019). However, only a few studies focused on local movement types [but see: 32–34], even though small-scale movements are of crucial importance for ecological interactions (Stamps 1995, Conner et al. 1999, Powell 2000, Mettke-Hofmann et al. 2005, Morris 2005), the formation of individual niches (Schirmer et al. 2019, 2020), and hence the community dynamics and species coexistence (Kobler et al. 2009, Pearish et al. 2013, Best et al. 2015, Farine and Whitehead 2015, Spiegel et al. 2015, Schlägel et al. 2020). In addition to movement data derived from GPS devices, tri-axial accelerometers measure static and dynamic acceleration (i.e., the animals' movement) in three dimensions (Hughey et al. 2018). These measurements can be used to remotely identify acceleration patterns and assign them to defined behaviors (Scheibe and Gromann 2006, Watanabe et al. 2008) or calculate proxy values for activity levels (Wilson et al. 2006, Qasem et al. 2012, López et al. 2015, Gunner et al. 2020). One well-established example is the overall dynamic body acceleration (ODBA), allowing us to estimate free-ranging animals' activity-related energy expenditure after careful validation (Wilson et al. 2006, Gleiss et al. 2011). Accelerometers are increasingly implemented in studies of animal behavior, ecology, or physiology (Fahlman et al. 2008, Shepard et al. 2008, Green et al. 2009, Halsey et al. 2009, 2011, Halsey and White 2010, Nathan et al. 2012, Mosser et al. 2014, Noonan et al. 2014, Chimienti et al. 2016, Hicks et al. 2017) and may be a promising tool to assess animal personalities remotely (Gharnit et al. 2020).

In the present study, we experimentally identify and link behavioral types of a mammalian herbivore (*Lepus europeaus*) to their general activity recorded by accelerometers. After relating the individuals' degree of boldness to its' activity in both captive and wild hares, we ultimately test for their association with space use in a wild population. Recent studies on space use of the European hare found high among-individual variation in movement patterns that remained hitherto largely unexplained (Ullmann et al. 2018, 2020). Here, we present a 3-step approach in which we (i) quantify and test the repeatability of among-individual differences in behavior along the bold-shy continuum of captive hares with repeated standardized emergence and novel environment tests in an open-field arena, (ii) link the degree of boldness to a captive individual's general activity in the arena derived from accelerometers and assessed via ODBA, and (iii) investigate the association of wild hares activity and space use with their degree of boldness, estimated from behavioral responses along the shy-bold continuum, proven to be temporarily stable in captive hares. In this final step, we explore the relation of repeatable metrics of behavior linked to animal personality with space use in a disturbance-mediated agricultural landscape described by Ullmann et al. (Ullmann et al. 2018, 2020). More specifically, we relate home range size and core area size to an individual's position along the shy-bold continuum.

We hypothesize that similar to findings in small [36, 75, 77] and medium-sized mammals [76], general activity (i.e., ODBA) and boldness are positively linked in hares. Further, we expect that boldness predicts space use with bolder individuals allocating both a larger home range and a larger core area.

3.2 Methods

Step 1 - Animal personality tests in captive hares

Captive European hares were studied at the field station of the Leibniz Institute for Zoo and Wildlife Research (IZW), located about 40 km north of Berlin (Brandenburg, Germany, 52°51'06.5"N, 13°54'57.2"E; WGS84). There, hares are kept and bred for reproduction studies [e.g., 79]. All individuals used in this study are housed singly in small cages of 2 m2 or arenas with concrete floors (5 m x 10 m, where two individuals share the enclosure).

In July and August 2019 and 2020, we conducted repeated novel environment tests with 14 captive hares in an enclosure, that is an open field arena (8 m x 27 m) surrounded by a transparent metal mesh fence with a height of 180 cm. The area was freshly mowed and equipped with a 2 m^2 housing box as a familiar retreat site, a small shelter on the opposite side, and two troughs containing food and water *ad libitum*.

The individual was weighed and transferred to the new enclosure in a wooden box (60 cm x 25 cm x 30 cm). This box was placed in the front right corner inside the enclosure, carefully opened, and remained untouched. Each hare was individually tested while remaining in the enclosure for three consecutive days. In total, we tested 14 individuals in the novel environment test; 12 of them provided GPS/ACC recordings. All experiments were continuously videotaped with a GPS-synced digital camera (Woodmann et al. 2002) during periods of sufficient daylight (i.e., 06:00 – 22:00). Repetition trials were conducted after two weeks. Latencies of specific behaviors (Latency look, Latency leave, and Delta look-leave; definitions in Table 1) were determined from video recordings by one observer (AL).

Step 2 - ODBA in captive hares

Prior to testing, each individual was collared with a GPS device with an internal 3-axial accelerometer (ACC) weighing 69 g (< 2% of a hares' body mass, model 1AA, e-obs GmbH). Acceleration was recorded at 33 Hz (byte count 495) every 2 min, and ODBA values were calculated with the R package moveACC (Scharf 2018) as $ODBA=|A_x|+|A_y|+|A_z|$, where A_x, A_y, and A_z are the derived dynamic accelerations corresponding to the three perpendicular axes of the sensor (Qasem et al. 2012) (Tab. 1).

Step 3 - ODBA and home range of free-ranging wild hares

The field study site was located in an agricultural landscape 100 km northeast of Berlin (53°21'22.8"N, 13°48'03.0"E; WGS84) within the "AgroScapeLab Quillow" catchment, the research platform of the Leibniz Centre for Agricultural Landscape Research (ZALF) and the BioMove research training group. The climate is described as continental/Atlantic transition with long dry phases in spring and cold winters. The mean annual precipitation is 486 mm, and the mean annual air temperature is 8.4 °C. The landscape is dominated by loamy soils and intensive cultivation of winter cereals, rape, and maize. The field sizes are on average 27.5 ± 1.1 ha (Schirmer et al. 2019, Ullmann et al. 2020).

Wild hares (n = 14, Tab. S1) were trapped by chasing them into woolen nets [for details, see 76,83], weighed, sexed, and equipped with GPS/ACC collars (model 1AA, e-obs GmbH). While all hares were adults, the exact age was not determined to reduce the duration of time the animals were exposed to handling stress. An acceleration-informed GPS frequency was programmed as follows: GPS locations were recorded every 4 min during normal and high activity. When no activity was recorded, GPS fixes were logged every hour (Ullmann et al. 2020). Tracking data were stored in the Movebank data repository (Wikelski et al. 2020). Acceleration recordings were programmed as for the captive hares. After collar fitting, hares were moved inside a wooden transport box (60 cm x 25 cm x 30 cm) to an open area in the field. At the release point, the top plate of the box was opened, and latencies for looking out of the box and leaving the box were recorded according to the novel environment test (Tab. 1). From untangling the hare from the net until releasing it from the box, the handling procedure lasted between 30 to 45 min. Remote data download was triggered whenever an individual was within range of a base station (model basis 5, e-obs GmbH) deployed near the trap location. Hares were tracked for a varying duration, depending on the coverage of the receiver antennas and the battery life of the collar (Tab. S1).

TABLE 1: Definitions, min-max range, and units of behaviors observed during novel environment tests with captive European hares (*Lepus europaeus*) in an open field arena and on the release of captured free-ranging hares. ODBA data are based on acceleration loggers applied in collars.

Behavior	**Definition**	**Unit**	**Range**$^{\gamma}$	**Location**$^{\beta}$
Latency look$^{\alpha}$	Latency until the eyes were above the edge of the box for the first time.	[s]	1 - 3,951	both
Latency leave$^{\alpha}$	Latency until the hare was outside the box with its full body for the first time.	[s]	1 - 3,961	both
Delta look-leave$^{\alpha}$	Delta between Latency look & Latency leave	[s]	0 - 3482	both
Exploring the first 3 m$^{\alpha}$	Latency from Latency leave until the hare crossed the first 3 meters of the enclosure with its entire body.	[s]	40 - 7,817	enclosure
Exploring the enclosure$^{\alpha}$	Latency from Latency leave until the hare reached the opposite end of the enclosure with its full body (27m).	[s]	66 - 12,000	enclosure
3-day activity	Mean ODBA value for three successive days, calculated after the release of the individual (72 hrs).	$[\frac{m}{s^2}]$	0.10 - 0.51	both
10-day activity	Mean ODBA value for 10 successive days, calculated after the release of the individual. (240 hrs).	$[\frac{m}{s^2}]$	0.16 - 0.30	field
20-day activity	Mean ODBA value for 20 successive days, calculated after the release of the individual (480 hrs).	$[\frac{m}{s^2}]$	0.18 - 0.31	field
30-day activity	Mean ODBA value for 30 successive days, calculated after the release of the individual (720 hrs).	$[\frac{m}{s^2}]$	0.17 - 030	field

$^{\alpha}$ behaviors were recorded for both the initial & repetition trials of the captive-bred hares.

$^{\beta}$behaviors were recorded at the **enclosure** site, in the **field**, or at **both** locations.

$^{\gamma}$12,000 was used as a maximum value.

Statistical analyses

First, we estimated adjusted repeatability of behaviors in captive hares (Latency look, Latency leave, Delta look-leave, Exploring first 3m, Exploring enclosure; Tab. 1) using linear mixed effect models and bootstrapping (number of parametric bootstraps for interval estimation: 10,000; number of permutations to calculate asymptotic p-values: 10,000; p-values shown refer to repeatability) with the individual as a random factor and adjusting for housing type as a fixed effect with the R package rptR (Nakagawa and Schielzeth 2010, Stoffel et al. 2017).

Second, we tested whether repeatable among-individual differences in behavior explain variation in recorded ODBA. As "Delta look leave" (Tab. 1) is derived from both Latency leave, and Latency look and the latter correlated among each other (Pearson correlation coefficient > 0.7), we considered Latency look and Latency leave in separate models for subsequent analyses. We calculated a linear mixed effect model with the latency as a response variable, housing type, and the number of the respective trial (i.e., first or second measure of the latency) as fixed effects and individual as a random effect. Following Hertel et al. (Hertel et al. 2020b), we derived the best linear unbiased predictor (BLUP) by extracting the conditional modes of the random effect (individual) from the fitted model. Then, we calculated a generalized linear model with activity (mean ODBA over the 3 days in the exclosure) as a response variable, Gamma error distribution, and predictor variables BLUP, body mass, and housing type. Then, we related the latencies of wild hares to the mean ODBA during the first 3, 10, 20, and 30 days of tracking per individual (Tab S1). Body mass was included in both models as a fixed effect. As captive hares experienced two types of housing conditions (small cages of 2 m² with one individual; small arenas of 50 m² with two individuals), we additionally included housing as a fixed effect in the models. Subsequently, for captive hares, we performed a step-wise backward model selection based on the information criterion Akaike (AICc, corrected for small sample size) using the dredge function implemented in the R package MuMIn (Barton 2016). Following the studies of Anderson and Burnham (Anderson and Burnham 2004) and Pinheiro and Bates (Pinheiro and Bates 2000), we selected the model with the highest Akaike score (lowest AICc value) to best explain our data. All models within 2 AICc units were considered as competing models (Tab. S2, S3).

Third, we tested if among-individual differences in behavior, i.e., boldness expressed as short latencies, predict space use in wild hares. We first calculated the cumulative home range sizes of consecutive days (days 1 to 32, Fig. S1) to assess how many tracking days are needed to reach home range size saturation. After visual inspection (Fig. S1), we decided to calculate home range sizes of the initial 20 and 30 (n = 12, Tab. S1) days after releasing the captured hares. Then, we calculated home range sizes based on 95% (home range) and 50% (core area) of the kernel utilization distribution while considering autocorrelation for continuous time (akde; R package move [Kranstauber et al. 2020] and ctmm [Fleming and Calabrese 2020]).

Finally, we related the logarithmized home range and core area sizes to the predictor variables “body mass” and Latency look or “Latency leave” with Gaussian error distribution (quantile residuals were checked using the DHARMa package [Hartig 2022]). Due to the low sample size of captive hares (repeatability: n = 14, 4 females, 10 males; ODBA: n = 12, 4 females, 8 males) and wild hares (see Tab. S1), we did not further analyze the effects of sex. All analyses were performed in R version 4.0.2 (R Core Team 2020) and R Studio version 1.2.5019 (R Studio Team 2019).

3.3 Results

Among-individual differences in behavior and their linkage to acceleration data

We found temporal consistency in three of the five behavioral variables (n = 14, all $R \geq 0.5$, all $p < 0.05$): Latency look ($R = 0.62 \pm 0.18$, $p = 0.014$), Latency leave ($R = 0.59 \pm 0.18$, $p = 0.021$) and Delta look-leave ($R = 0.49 \pm 0.20$, $p = 0.021$). All other behavioral variables were not repeatable over time (Tab. 1, Fig. 1).

Consequently, we considered hares that took a comparatively long time to look out or leave the box as shy and hares that left the box quickly as bold individuals. The bolder an individual (i.e., the shorter Latency look and Latency leave), the higher the individual’s activity (ODBA) during the first three successive days it roamed freely in the novel environment without effects of body mass (Fig. 1 A, B, Tab. 2).

We found a similar pattern for free-ranging hares (single measurement of the latencies while releasing the individual). Hares that quickly looked out of the release box (Latency look) or left it (Latency leave) were also more active throughout the first 3, 10, 20 and 30 tracking days (Fig. 1 C, D, Tab. 2).

Personality effects on space use of wild hares

Behavioral responses were shorter in wild hares (Latency look: 27 s ± 18 s and 26 s ± 18s, Median ± SD; Latency leave: 37 ± 18 s and 26 s ± 19s, Median ± SD) compared to captive hares (72 s ± 1017 s and 135 s ± 1276s; Median ± SD). Bold behavioral types (i.e., individuals with fast behavioral respones) had smaller 20-day home ranges with larger 20-day core areas (Fig. 3, Tab. 3). The same pattern was found for 30 days and Latency look, whereas the link with Latency leave was almost marginally significant (Fig. 3, Tab. 3).

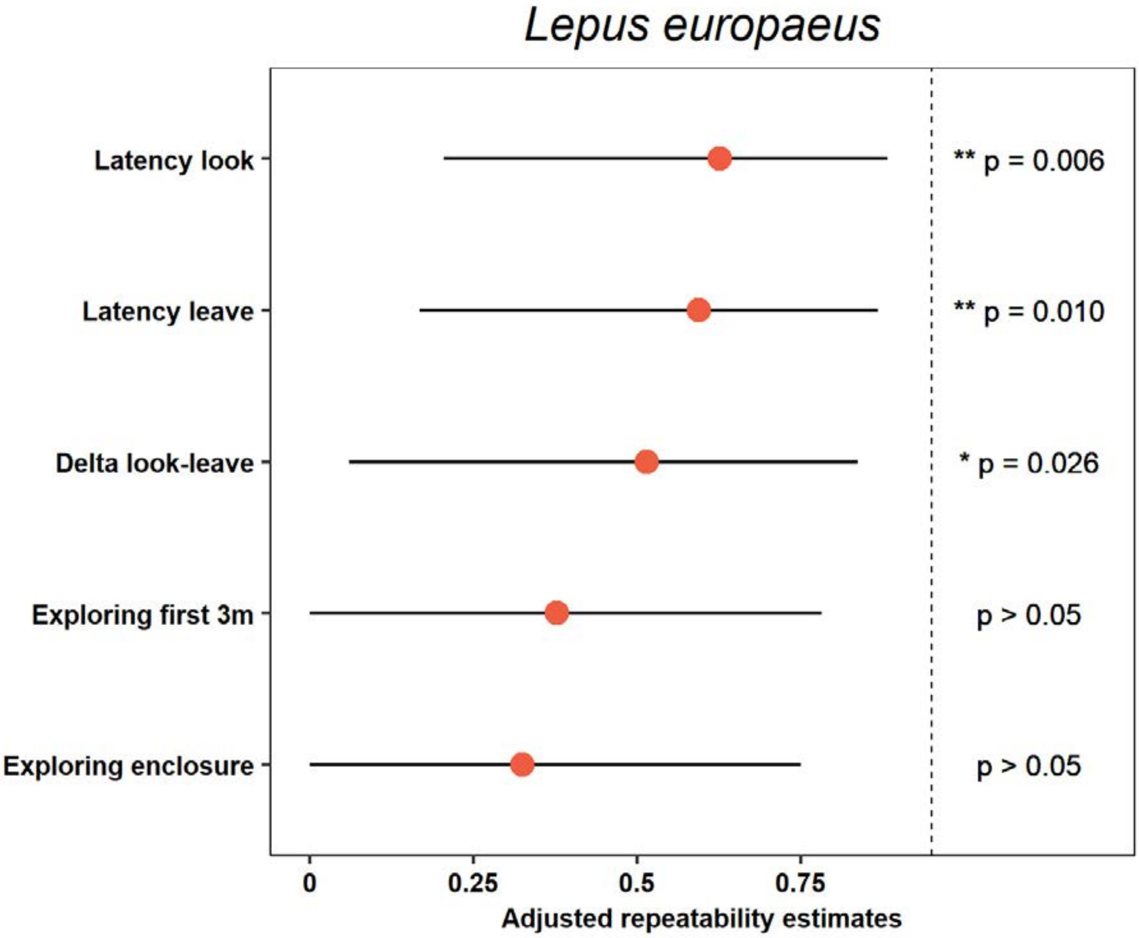

Fig. 3.1 Adjusted repeatability (i.e., fixed effect for enclosure type, 10 hares were kept in cages, 4 hares were kept in arenas) of behavioral variables quantified in repeated novel environment tests of 14 captive European hares (Lepus europaeus) in an open field arena. Latency look: p (LRT) = 0.006, p (permutation) = 0.009; Latency leave: p (LRT) = 0.010, p (permutation) = 0.014; Delta look-leave: p (LRT) = 0.026, p (permutation) = 0.030; Exploring first 3 m: p (LRT) = 0.093, p (permutation) = 0.124; Exploring enclosure: p (LRT) = 0.135, p (permutation) = 0.183. Shown are repeatability estimates (red dots) and their 95% confidence intervals (lines) estimated via parametric bootstraps (n = 10,000 simulations); p-values are based on permutations (n = 10,000).

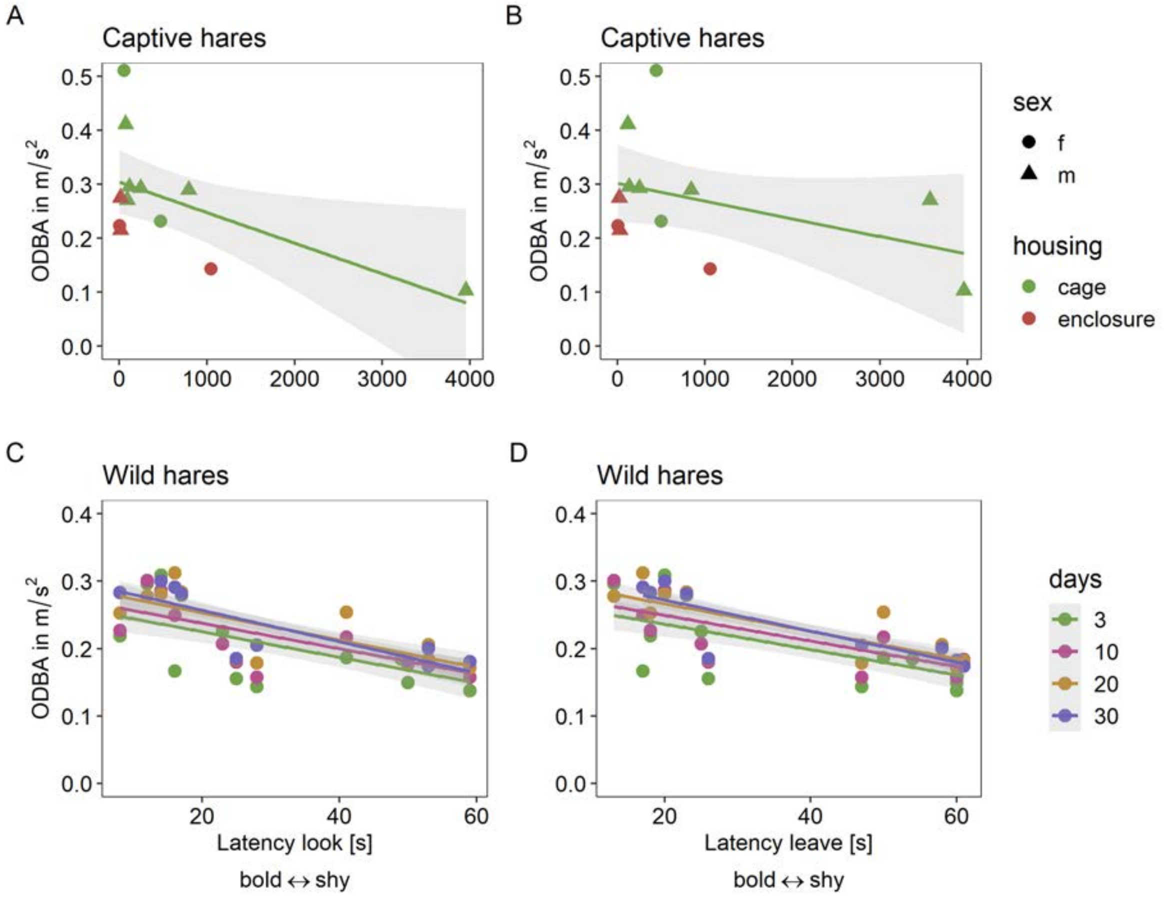

Fig. 3.2 Observed values (circles and triangles), predicted values (connected by the black line), and SE (gray shading) for (A) The latency to first look out of a safe retreat; p = 0.003 and (B) the latency to leave a safe retreat in relation to general activity (mean ODBA measured in $[\frac{m}{s^2}]$) during the three consecutive days in a novel environment in 12 captive hares; p = 0.045. The behavioral trait (C) Latency-look and (D) Latency leave (small latencies equal to a high score on the bold-shy continuum) of wild hares (*Lepus europaeus*) and their relationship with general activity (mean ODBA) for the first 3 (n = 14), 10 (n = 13), 20 (n = 12) and 30 (n = 12) days of tracking; all p < 0.026.

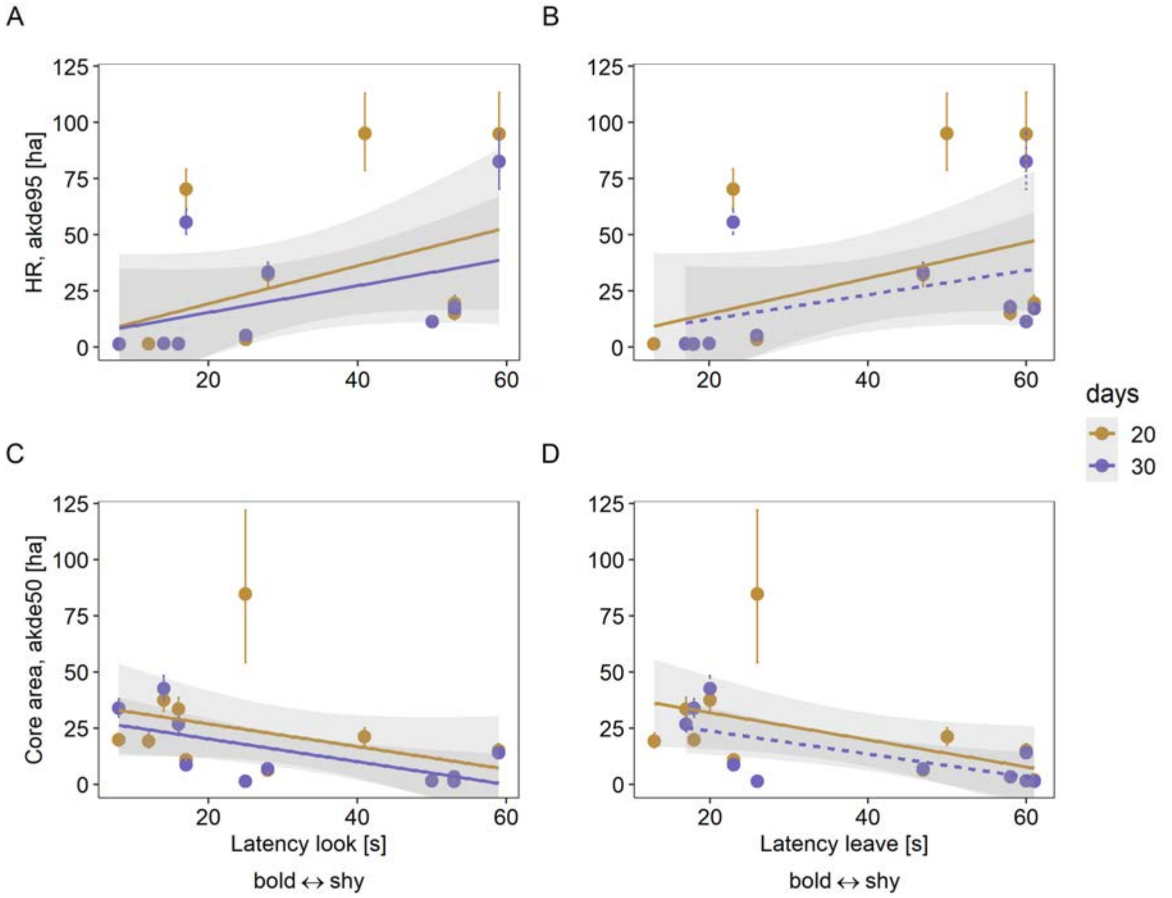

Fig. 3.3 Observed values (circles) with low-high error bars (95% CI), predicted values (connected by lines, dashed lines show non-significant regressions), and SE (gray shading) of wild hares (*Lepus europaeus*) for relationships between behavioral variables (A) Latency look and (B) Latency leave with home range size (akde95) of the first 20- and 30 days after release; (C) Latency Look and (D) Latency leave with core area size (akde50) of the first 20- and 30 days after release. n = 12.

TABLE 2: Model results: Activity measurements in relation to the BLUP (derived from *Latency look* ~ housing type + number of trial + (1|individual) and *Latency leave* ~ housing type + number of trial + (1|individual) for captive hares, and to *Latency look* and *Latency leave* for wild hares.$^{\alpha}$

Hares	Activity period		Latency look				Latency leave			
		Coefficients	Estimate	Std. Error	t value	Pr(>|t|)	Estimate	Std. Error	t value	Pr(>|t|)
captive	3 days	(Intercept)	4.796	0.476	10.071	<0.001	3.804	0.383	9.938	<0.001
		BLUP	0.056	0.014	4.13	0.003	0.097	0.042	2.292	0.045
		housing	-1.099	0.535	-2.053	0.07	-	-	-	-
wild	3 days	(Intercept)	0.363	0.172	2.106	0.059	0.341	0.162	2.107	0.059
		Latency	-0.002	0.001	-2.564	0.026	-0.002	0.001	-2.717	0.020
		mass	-0.024	0.038	-0.619	0.548	-0.016	0.036	-0.447	0.664
wild	10 days	(Intercept)	0.443	0.135	3.286	0.008	0.410	0.125	3.289	0.008
		Latency	-0.002	0.001	-3.276	0.008	-0.002	0.000	-3.492	0.006
		mass	-0.039	0.030	-1.307	0.221	-0.029	0.028	-1.044	0.321
wild	20 days	(Intercept)	0.515	0.128	4.028	0.003	0.471	0.120	3.939	0.003
		Latency	-0.002	0.001	-3.779	0.004	-0.002	0.000	-3.884	0.004
		mass	-0.051	0.028	-1.795	0.106	-0.038	0.027	-1.416	0.191
wild	30 days	(Intercept)	0.477	0.141	3.397	0.011	0.371	0.138	2.676	0.032
		Latency	-0.002	0.000	-4.714	0.002	-0.002	0.000	-4.613	0.002
		mass	-0.040	0.030	-1.302	0.234	-0.013	0.031	-0.408	0.695

$^{\alpha}$ For our dependent variable, the mean ODBA, we assumed a Gamma error distribution.

TABLE 3: Model results: Home range sizes in relation to *Latency look* and *Latency leave*.[α]

Home range type		Latency look				Latency leave				
		Estimate	Std. Error	t value	Pr(>|t|)	Estimate	Std. Error	t value	Pr(>|t|)	Pr(>|t|)
20 days, akde50	Coefficients	11.28	3.38	3.34	0.01	10.279	3.135	3.279	0.010	<0.001
		-0.04	0.01	-2.86	0.02	-0.041	0.012	-3.310	0.009	0.045
		-1.71	0.76	-2.24	0.05	-1.416	0.719	-1.969	0.080	-
		-2.130	5.578	-0.382	0.711	-0.622	5.336	-0.117	0.910	0.059
20 days, akde95	(Intercept)	0.060	0.023	2.628	0.027	0.060	0.021	2.887	0.018	0.020
		0.579	1.259	0.460	0.656	0.145	1.224	0.118	0.909	0.664
		14.45	4.56	3.16	0.02	12.874	5.107	2.521	0.040	0.008
30 days, akde50	(Intercept)	-0.04	0.02	-2.57	0.04	-0.034	0.017	-2.003	0.085	0.006
		-2.49	1.01	-2.46	0.04	-2.125	1.158	-1.835	0.109	0.321
		-8.590	5.948	-1.444	0.192	-6.547	6.193	-1.057	0.326	0.003
30 days, akde95	(Intercept)	0.047	0.020	2.376	0.049	0.046	0.021	2.194	0.064	0.004
		2.076	1.320	1.573	0.160	1.567	1.404	1.116	0.301	0.191
		(Intercept)	0.477	0.141	3.397	0.011	0.371	0.138	2.676	0.032
wild	30 days	Latency	-0.002	0.000	-4.714	0.002	-0.002	0.000	-4.613	0.002
		mass	-0.040	0.030	-1.302	0.234	-0.013	0.031	-0.408	0.695

[α] For our dependent variable, the logarithmic HR size, we assumed a Gaussian error distribution.

3.4 Discussion

By combining standardized behavioral tests under open field arena conditions and biologging of activity and space use of free-ranging individuals, we found that among-individual differences along the shy-bold continuum are consistent over time and related to overall activity and space use in European hares. Furthermore, we demonstrated how remote assessment of personality types without additional disturbance of the focal individual is achievable.

The variation in boldness of the hares was associated with short- and long-term differences in overall activity (ODBA) calculated from accelerometer measurements, with shy individuals having lower activity scores than bold individuals. Interestingly, this pattern was observed for both hares under experimental conditions in an open field arena and hares in a wild population in an agricultural landscape in north-eastern Germany. In wild hares, heavier individuals were also less active. We can not exclude that this might also be partly related to an individual's age, which was not determined during handling; however, all individuals were adults (> 3800g, roughly above 2 years).

Notably, wild hares generally responded faster than captive hares. We suspect that this is due to captive hares being more used to handling and are, therefore, not as naive to humans as wild hares. Due to the relatively small sample sizes, we did not follow a covariance partitioning approach and did not account for differing habitat prerequisites (e.g., multivariate mixed models to study correlations between behavioral traits on various hierarchical levels (Brommer 2013). Despite the limited sample size, the repeatability of behaviors compares well with findings from other taxa (e.g., meta-analysis: 91). Further, we showed how behavioral traits covary with movement behavior leading to the dichotomy in space use patterns in a wild hare population. The positive correlation between general activity and boldness is consistent with previous findings using standardized behavioral tests, for example, in common voles, *Microtus arvalis* (Lantová et al. 2011), bank voles *Myodes glareolus* (Schirmer et al. 2019), gray mouse lemurs, *Microcebus murinus* (Dammhahn and Almeling 2012), and Siberian chipmunks, *Tamias sibiricus* (Boyer et al. 2010). This consistency highlights that the correlation also persists beyond short behavioral tests to longer-term and natural conditions. Our approach extends existing observations and shows that activity in relation to animal personality can be measured using animal-borne accelerometers in combination with simple novelty experiments.

Similarly, in eastern chipmunks, dawn activity and percentual activity per day (measured as ODBA via accelerometers) were positively related to exploration speed, although overall activity patterns varied according to temporal variability in food availability (Gharnit et al. 2020). Behavioral variation along the shy-bold continuum could reduce intraspecific competition as individuals with varying levels of boldness likely also differ in their risk-taking or exploration behavior (Dammhahn and Almeling 2012, Schirmer et al. 2020). Particularly in agricultural landscapes, bolder individuals may also be more resilient to disturbance from agricultural measures like soil tillage or harvest.

Boldness (and associated activity) was correlated with space use of hares in the wild population. Previous studies have shown that bolder individuals occupy more extensive home ranges, as found for bank voles (*Myodes glareolus*) (Schirmer et al. 2019), sleepy lizards (*Tiliqua rugosa*) (Spiegel et al. 2015), or common brushtail possums (*Trichosurus vulpecula*) (Wat et al. 2021). Contrary to our expectation, bold hares had smaller home ranges during the initial 20 and 30 days after release but with larger core areas.

Dissimilarity in space use and movement of bold and shy individuals might reflect different exploration styles between behavioral types along the shy-bold continuum. In general, resources are dispersed across a landscape (Silver et al. 2000, Macdonald and Johnson 2015), but parts of a home range with higher resource density should be more important than those with fewer. Particularly bold individuals might successfully defend larger portions of these high-value areas, whereas shy individuals might be more likely to roam in search of less contested habitats, resulting in larger home ranges with smaller core areas. Hence, we suggest that bold hares are more successful in competing for valuable areas against shy individuals, forcing them to continue moving to find an unoccupied, suitable habitat.

This interpretation is tentatively supported by the energy expenditure of hares in our study, being negatively associated with body mass (non-significant trend only), which is consistent with findings of great tits *Parus major* (Moiron et al. 2019) and Asian particolored bats *Vespertilio sinensis* (Wang et al. 2020). Since bold animals tend to take more risks (Sih et al. 2004, Carter et al. 2013, Zwolak and Sih 2020) and have higher energy costs, we suggest that occupying and defending a smaller area of higher forage quality might further allow bolder individuals to outweigh an increased risk of being detected by predators. This suggestion is in line with home range sizes varying largely among individuals. Although shy individuals in the present study presumably avoided risky situations, they occupied large home ranges with low habitat quality, i.e., they needed to move further to meet their energy demands and had lower feeding rates, possibly negatively affecting their fitness (Sih et al. 2004, Luttbeg and Sih 2010, Zwolak and Sih 2020). However, boldness has been shown to scale positively with (basal) metabolic rate in many species, and individuals with faster rates require more or higher-quality resources to meet their energetic demands (Biro and Stamps 2008, Careau et al. 2008, 2009, Réale et al. 2010, Mathot and Dingemanse 2015). Thus, for bold hares, dealing with risky situations and defending their home range against competitors could also be seen as a trade-off between energy expenditure versus habitat quality. Nevertheless, such behavioral variation might eventually facilitate the coexistence of individuals with varying behavioral phenotypes within the same population (Wolf and Weissing 2012).

The link between movement ecology and animal personality is still in its infancy (Spiegel et al. 2017, Hertel et al. 2020a), and the vast majority of studies on animal space use have been conducted without the inclusion of personalities, interpreting their variability mainly in terms of external factors or simple, measurable state variables, such as differences in sex or age. As wild animal populations are naturally composed of individuals differing in behavioral traits (Bolnick et al. 2003, 2011), these inter-individual differences equip populations with a set of variable behavioral responses that could increase their resilience to fluctuating environmental conditions (Atwell et al. 2012, Chimienti et al. 2016, Merrick and Koprowski 2017).

Considering animal personalities in space use studies might be crucial, as there is increasing evidence that sampling bias may inevitably influence the composition of animal personalities within a drawn sample and, therefore, the results of the respective study (Réale et al. 2007, Morton et al. 2013). Behavioral and ecological studies of various species may be affected, as the test subjects may not represent larger populations whose ecological patterns the researchers seek to understand. For example, due to well-established sampling protocols, bolder individuals are more likely to be trapped. In a study with pumpkinseed sunfish, *Lepomis gibbosus*, Wilson and others (Wilson et al. 1993) noted that some fish were so shy that it was impossible to catch them even once, whereas bolder specimens were caught repeatedly (Wilson et al. 1993). Further studies have drawn attention to this personality-related sampling bias (Tuyttens et al. 1999, Réale et al. 2000, Cooke et al. 2007, Biro and Post 2008, Boon et al. 2008), suggesting that the assumption of random sampling might have been violated in many studies (Biro 2013). Although we do not know to what extent we could represent the extent of the shy-bold continuum in hares, we found substantial variation along its axis and demonstrated related differences in activity and space use.

Conclusions

Carefully validated under standardized conditions, activity measurements via accelerometers, such as ODBA, could be a valuable tool to contribute to assessing behavioral types remotely. Considering that accelerometers are often already built into GPS units, we recommend activating them at least during the initial days of tracking to estimate individual variation in general activity and, if possible, match them with a simple novelty experiment. This additional information on individual behavioral types will help to explain variation in state-dependent behavior (e.g., risk-taking) and space use and further facilitate mechanistic understanding of processes that drive spatial and ecological dynamics in heterogeneous environments.

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3.6 Declarations

Ethics approval

All experiments were conducted in accordance with the German Federal Nature Conservation Act (§ 45 Abs. 7 Nr. 3) and approved by the animal ethics committee of the University of Potsdam and by the local nature conservation authority (AZ: 2347-6-2019).

Consent for publication

Not applicable.

Availability of the data

GPS and acceleration data sets generated and analyzed during the current study are stored in the Movebank Data Repository (study IDs: 933567888, 1138520346). Together with the measured behavioral responses, these are available upon reasonable request from the corresponding author.

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Authors' contributions

J.S., **M.D.** and **N.B.** conceived the idea. **J.S.** carried out most of the fieldwork, analyzed the data, and led the manuscript writing. **A.L.** participated substantially in the fieldwork. **N.B.** and **M.D.** led the initial revision of the manuscript. **S.O.** and **S.KS.** participated in manuscript revision and supervised throughout the process. All authors gave final approval for the publication.

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3.8 Supporting information

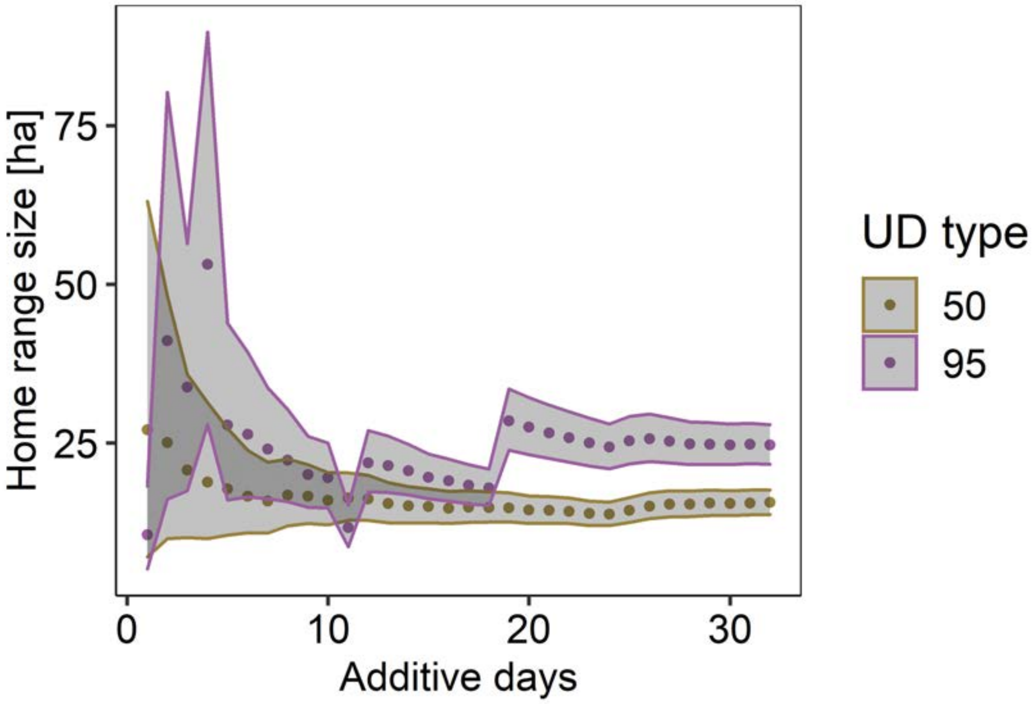

Fig. 3.4 S1: Home range (akde95) and core area (akde50) sizes for additive tracking days (1 - 32) of European hares (*Lepus europaeus*) in a disturbance-mediated landscape (Uckermark, Germany, 2020). Mean values (dots) and 95% confidence interval (grey filled area) for 10 individuals.

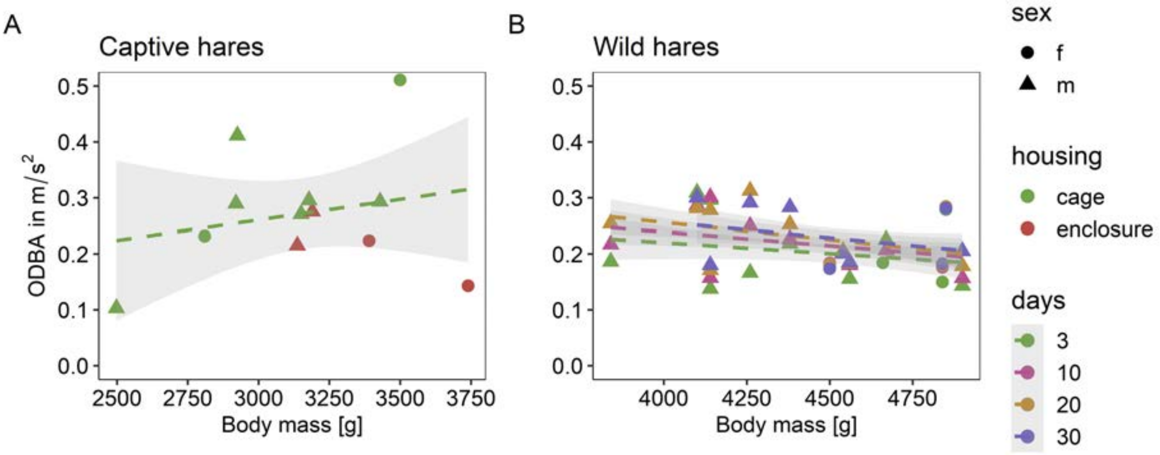

Fig. 3.5 S2: Activity and its relation to body mass of (A) captive hares and (B) wild hares. Measured values (dots and triangles) and non-significant regression lines for 3-days activity of captive and 3, 10, 20 and 30-days activity of wild hares. For sample size see Tab. S1.

Table S1: Overview of the tracking data and the respective sample size per analysis.

ID	days tracked	body mass [g]	sex	analysis	n
7427	4	4660	f	*3-day activity*	*14*
7398	19	4670	m	*10-day activity*	*13*
5581	20	4140	m	*20-day activity*	*12*
5559	22	3840	m	*30-day activity*	*12*
7393	32	4540	m	*20-day HR (akde50)*	*12*
7394	37	4100	m	*20-day HR (akde95)*	*12*
7396	54	4380	m	*30-day HR (akde50)*	*12*
7399	66	4850	f	*30-day HR (akde95)*	*12*
7400	72	4840	f		
7392	74	4900	m		
7397	77	4260	m		
7395	78	4140	m		
7391	95	4500	f		
7428	97	4560	m		

Table S2: Model selection table of captive hares with BLUP derived from *Latency look* ~ housing type + number of trial + (1|individual), tracking data of 3 days, ranked by AIC[α]

model	(Int)	housing	BLUP	mass	df	logLik	AICc	delta	weight
4	4.796	+	0.056		4	20.406	-27.097	0	0.512
3	4.018		0.062		3	17.848	-26.695	0.402	0.419
7	3.038		0.063	<0.001	4	17.902	-22.09	5.007	0.042
8	5.793	+	0.055	<-0.001	5	20.482	-20.965	6.132	0.024
1	3.678				2	10.57	-15.806	11.292	0.002
2	4.666	+			3	11.628	-14.255	12.842	0.001
5	6.868			-0.001	3	10.881	-12.761	14.336	<0.001
6	11.764	+		-0.002	4	13.133	-12.553	14.545	<0.001

[α] For our dependent variable, the mean ODBA of the first 3 tracking days of captive hares, we assume a Gamma distribution: $y_i \sim Gamma(\mu_i, v)\ with\ \mu_i = exp(\beta_0 + \beta_1 \cdot mass_i + \beta_2 \cdot housing + \beta_3 \cdot BLUP_i)$. Here v is a dispersion parameter in which we have no particular interest.

Table S3: Model selection table of captive hares with BLUP derived from *Latency leave* ~ housing type + number of trial + (1|individual), tracking data of 3 days, ranked by AIC$^{\alpha}$

model	(Int)	housing	BLUP	mass	df	logLik	AICc	delta	weight
3	3.804		0.097		3	14.089	-19.178	0	0.511
4	4.7	+	0.087		4	15.713	-17.711	1.467	0.245
1	3.678				2	10.57	-15.806	3.372	0.095
7	4.462		0.095	<-0.001	4	14.106	-14.497	4.681	0.049
2	4.666	+			3	11.628	-14.255	4.923	0.044
5	6.868			-0.001	3	10.881	-12.761	6.417	0.021
6	11.764	+		-0.002	4	13.133	-12.553	6.625	0.019
8	8.001	+	0.076	-0.001	5	16.191	-12.381	6.797	0.017

$^{\alpha}$For our dependent variable, the mean ODBA of the first 3 tracking days of captive hares, we assume a Gamma distribution: $y_i \sim Gamma(\mu_i, v)\ with\ \mu_i = exp(\beta_0 + \beta_1 \cdot mass_i + \beta_2 \cdot housing + \beta_3 \cdot BLUP_i)$. Here v is a dispersion parameter in which we have no particular interest.

Chapter 3

The Heat is On: Impacts of Rising Temperature on the Activity of a Common European Mammal

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Abstract

Climate conditions severely impact the activity and, consequently, the fitness of wildlife species across the globe. Wildlife can respond to new climatic conditions, but the pace of human-induced change limits opportunities for adaptation or migration. Thus, how these changes affect behavior, movement patterns, and activity levels remains unclear. In this study, we investigate how extreme weather conditions affect the activity of European hares (*Lepus europaeus*) during their peak reproduction period. When hares must additionally invest energy in mating, prevailing against competitors, or lactating, we investigated their sensitivities to rising temperatures, wind speed, and humidity. To quantify their activity, we used the overall dynamic body acceleration (ODBA) calculated from tri-axial acceleration measurements of 33 GPS-collared hares. Our analysis revealed that temperature, humidity, and wind speed are important in explaining changes in activity, with a strong response for high temperatures above 25°C and the highest change in activity during temperature extremes of over 35°C during their inactive period. Further, we found a non-linear relationship between temperature and activity and an interaction of activity changes between day and night. Activity increased at higher temperatures during the inactive period (day) and decreased during the active period (night). This decrease was strongest during hot tropical nights. At a stage of life when mammals such as hares must substantially invest in reproduction, the sensitivity of females to extreme temperatures was particularly pronounced. Similarly, both sexes increased their activity at high humidity levels during the day and low wind speeds, irrespective of the time of day, while the effect of humidity was stronger for males. Our findings highlight the importance of understanding the complex relationships between extreme weather conditions and mammal behavior, critical for conservation and management. With ongoing climate change, extreme weather events such as heat waves and heavy rainfall are predicted to occur more often and last longer. These events will directly impact the fitness of hares and other wildlife species and hence the population dynamics of already declining populations across Europe.

Keywords: *Activity, ODBA, Animal tracking, European hare, Extreme weather events, Climate change.*

4.1 Introduction

Global changes in climate and landscape structure can have severe ecological consequences for wildlife across organizational levels (genes, individuals, populations, communities, Møller, 2013; Lau and terHorst, 2020; Ruland and Jeschke, 2020; Theodoridis et al. 2021). Wildlife is capable of responding to new climatic conditions with local genetic adaptation, migration to more favorable conditions, or phenotypic plasticity (Walther et al. 2002; Hetem et al. 2014).

However, human-induced changes in climate and landscape connectivity are rapid and severe, thereby limiting local genetic adaptation and opportunities for migration (Meester et al. 2018). Genetic adaptations are likely to fail in the case of wildlife species that have long generation times and low reproductive output (and therefore low population sizes), making it difficult to keep up with the pace of climate changes (Boutin & Lane, 2014; Hoffmann et al. 2017). With increasing habitat loss and ongoing landscape fragmentation, climate-induced migration and dispersal movements are often limited (Collingham & Huntley, 2000; Walther et al. 2002; Travis, 2003). In fragmented landscapes, phenotypic plasticity including changes in phenology, physiology, and behavior (Boutin and Lane, 2014; Hetem et al. 2014), is likely the most immediate response of wildlife to counter the negative effects of rapidly changing climatic conditions on their activity and energy budgets (Noonan et al. 2018). One of the most fragmented landscapes worldwide are agricultural landscapes in Europe where changes in climate affect the temperate seasonal weather conditions: summers tend to cover a more extended period accompanied by higher temperatures and less rainfall, and winters get shorter with more precipitation and increasing temperatures (Klein Tank et al. 2002; Ergon et al. 2018). In Nordic regions, the annual average temperature increased by more than 2°C since the middle of the 19th century, and a prolongation of the growing season by more than a month is predicted by the end of the 21st century (Ruosteenoja et al. 2011; Ruosteenoja et al. 2016). Increases in rainfall events and precipitation intensity have been observed for locations across northern and middle Europe (Widmann and Schär, 1997; Hanssen-Bauer and Førland, 1998; New et al. 2001). Further, wind speeds are predicted to increase slightly (Pryor et al. 2006) and extreme weather events like heat waves or heavy rain events are predicted to increase in frequency (Coumou and Rahmstorf, 2012; IPCC, 2014).

For wildlife, changing weather conditions due to climate change can strongly affect their activity, movement behavior, and energy expenditure, crucial for an individual's fitness (Brown et al. 2004). Unfavorable conditions like cold and humid weather increase the energy investment necessary for the thermoregulation of homeothermic animals (Seltmann et al. 2009; Klüg-Baerwald et al. 2016; Lenis Sanin et al. 2016) and may enhance the development of pathogens, thereby possibly increasing the spread of diseases (Altizer et al. 2006; Rödel and Dekker, 2012) and the risk of predation (Mech et al. 1987; Rödel and Dekker, 2012). A large proportion of energy is required for movements to reach and explore resources for foraging, finding mates, or withstanding adverse situations that might lower survival probability (Alexander, 2006). Depending on the internal state of an individual (e.g., whether it is hungry or not) and the environmental conditions, movements vary in speed, acceleration, or maneuverability (Nathan et al. 2008; Spiegel et al. 2017). Hence, energy investments differ even between recurring behaviors (e.g., foraging, mating) (Börger et al. 2020; Shaw, 2020; Wilson et al. 2020) in relation to the context-specific environmental condition with the prevailing weather as an important factor. For example, red deer (*Cervus elaphus*) in Europe increase their home range sizes with rising temperatures during winter and vice versa during summer (Rivrud et al. 2010). In addition, behavior and activity adjustments have been shown for different species globally. Japanese macaques (*Macaca fuscata*) decrease their movement activity during rainfall (Hanya et al. 2018), and North American passerines adjust their daily movement distances depending on wind speed and temperature (Grubb, 1978). Also, unfavorable weather conditions like cold or wet conditions decreased activity and shifted the temporal peaks of activity in tropical bats (Appel et al. 2019). With changing weather conditions, the activity and, consequently, the energy expenditure of animals can change to adapt to favorable or adverse conditions (Vickery and Bider, 1981; Hanya et al. 2018; Noonan et al. 2018; Appel et al. 2019).

A widespread species in Europe and parts of Asia is the European hare (*Lepus europaeus*, Pallas, 1778) (Hackländer and Schai-Braun, 2019). Its range covers the temperate zones of Europe from the Mediterranean zones in the south to the cold zones in the north (Fig. 1). The European hare, a common umbrella species in agricultural landscapes, can indicate threats to a variety of species in ecological communities (Schai-Braun et al. 2020). However, hare populations have declined for the last few decades, mainly attributed to the intensification of agriculture (Tapper and Barnes, 1986; Vaughan et al. 2003). In addition, seasonally unfavorable weather conditions are yet another reason for the decline, as energy demand inevitably increases and, if not met, can even cause mortalities (Tapper and Barnes, 1986). Hares, especially the leverets, experience higher mortality rates under wet and cold conditions (Hackländer et al. 2002; Smith et al. 2005; Van Wieren et al. 2006), while warm temperatures lead to longer breeding seasons and higher pregnancy rates (Hewson and Taylor, 1975). On the other hand, high temperatures can also increase the risk of spreading diseases (Smith et al. 2005), and, extremely high temperatures may exacerbate food shortages during drought periods (Baudach et al. 2021). Hares' native habitat is steppe landscapes (Baudach et al. 2021), which are usually warm and dry. We, therefore, assume that rising temperatures are not necessarily disadvantageous for hares and that they adjust their activity accordingly. They do not have to spend as much energy on thermoregulation and can consequently invest more in increased activity or fighting off pathogens (Lenis Sanin et al. 2016). Conditions like high humidity, known for its adverse effects on leveret survival (Hackländer et al. 2002), and the cooling effect at high wind speeds, could be detrimental by further decreasing an individual's body temperature. We assume that they will negatively affect hares' activity, while the activity increases with lower humidity and lower wind speed. On the other hand, the cooling effect of wind at high temperatures can be beneficial and support thermoregulation.

In this study, we analyze how extreme weather conditions affect the activity of European hares in a central part of their distribution range. We were particularly interested in their sensitivities to rising temperatures, wind speed, and humidity during the reproduction period, when hares have to additionally invest energy in mating, prevailing against competitors (males), or lactating (females) (Lincoln, 1974). 1,237,176 acceleration measurements of 33 GPS-collared individuals were used to calculate overall dynamic body acceleration (ODBA), a proxy for hare activity (Wilson et al. 2006; Halsey et al. 2009). Changes in hare activity in response to ambient weather were analyzed separately for their active period at night and the resting period during the day. We hypothesize they react more strongly to extreme weather conditions during the active period at night, with males being more active than females due to larger home ranges and longer daily distances traveled (Rühe and Hohmann, 2004; Mayer et al. 2019). Further, since females must care for and feed their offspring irrespective of prevailing weather conditions, they are less capable of adapting their behavior accordingly. Thus, we expect sex-specific responses to extreme weather events.

4.2 Material and Methods

Study area

The study area is located in an agricultural landscape 100 km northeast of Berlin (53°21’22 N, 13°48’03 E; WGS84) within the "AgroScapeLab Quillow" catchment, the research platform of the BioMove research training group and the Leibniz Centre for Agricultural Landscape Research (ZALF). The landscape is characterized by arable land with relatively large fields of an average size of 27.5 ± 1.1 ha, dominated by intensive cultivation of winter cereals, rapeseed, and maize (Ullmann et al. 2020). Agricultural land covers approximately 74% of the area. The remaining area consists of patchy grasslands, several small water bodies, small forest areas, a few small villages, and single houses. The climate is described as continental-Atlantic transition with long dry phases in spring and cold winters. The mean annual precipitation is 486 mm, and the mean annual air temperature is 8.4 °C (Ullmann et al. 2020; Stiegler et al. 2022).

Animal tracking data

We used accelerometer data of 33 hares (11 females, 22 males, all adults) recorded in 2014, 2015, 2019, and 2020 containing 1,237,176 measurements (Tab S1). Individuals were tagged with e-obs GPS collars containing internal tri-axial accelerometers (model 1AA, 69g, e-obs GmbH, Germany) (Ullmann et al. 2018; Stiegler et al. 2022). Trapping, collaring, and data collection are described in detail in Rühe and Hohmann (2004), and Ullmann et al. (2018). Tri-axial acceleration bursts were recorded every four minutes in 2014 and 2015 (n = 20, Tab. S1), and every 2 minutes in 2019 and 2020 (n = 13, Tab S1). Bursts were recorded at a frequency of 33 Hz for 3.3 sec (resulting in 110 acceleration samples per axis and burst). For each burst, we then calculated the overall dynamic body acceleration (ODBA) as a proxy for hare activity (Stiegler et al. 2022), using the R package moveACC (Scharf, 2021) with

$ODBA = |A_x| + |A_y| + |A_z|$, where A_x, A_y, and A_z are the derived dynamic accelerations corresponding to the three perpendicular axes of the sensor (Qasem et al. 2012). Activity data (ODBA values measured in g-force) were subsequently averaged over 10−minute intervals (i.e., 2 to 5 measurements) and merged with corresponding weather data. For our analysis, we only considered hares with more than 30 consecutive tracking days within the peak reproduction period (May – August, Tab. S1) (Hewson and Taylor, 1975), where approximately 75% of the annual leverets are born and nursed (Hansen, 1992).

Weather data

Weather data originated from a local (within 14 km of the collared hares) weather station (56 m a.s.l., 53°31'53 N, 13°93'38 E, WGS84) managed by the DWD (Deutscher Wetterdienst, opendata.dwd.de). Weather data contained 10-minute measurements of temperature (°C), precipitation (mm), relative humidity (%), and wind speed (m/s) over a period of 27 years (1993−2020).

Statistical analyses

All analyses were conducted in R version 4.0.3 (R Core Team, 2020) and R-Studio version 1.4.1103 (R Studio Team, 2021). We applied generalized additive models (GAM) with the R package mgcv, version 1.8-40 (Wood, 2011) to estimate the effects of weather conditions (temperature, wind speed, and humidity; Pearson correlation coefficient < 0.7) on the activity of hares (ODBA). As an extension to generalized linear models, GAMs use smooth functions to account for non-linear relationships between response and explanatory variables. Thus, a flexible description of the dependency between the response variable and predictors is possible (Wood, 2011). In our case, it is natural to expect a different movement behavior under extreme temperatures than under "average" weather conditions. Therefore, a simple linear model would not explain as much of the variation of the ODBA as the GAM approach.

ODBA values were log-transformed in order to assume normality. The explanatory variables in the model were the three aforementioned weather variables for the combinations of the levels of sex (female/male) and time of the day (day/night), as well as sex and month as fixed effects. As random effects, we included hour of the day, day of the year, and individual id. The day (7 AM – 6 PM) reflects the resting period with the lowest activity, and the night (6 PM − 7 AM) reflects the time with higher activity (Fig. 2). In addition, we included the pairwise combined effects of our weather variables as bivariate smooth functions to account for interaction effects.

We used our weather covariates in combination with the time of day and sex, respectively as smooth functions. This way, we could understand the effect of the weather variables more profoundly rather than understanding the overall effect of the weather variables on

ODBA. As a smoothing basis, penalized splines were used for the weather variables to avoid overfitting. In addition, the hour of the day, the day of the year, and the individual ID were included as random effects since we expected them to influence ODBA. We used the lagged logarithmized ODBA as a smooth effect to respect the error terms independence assumption. In other words, we used the log(ODBA) at time t-1 to also explain the log(ODBA) at time t. Ignoring the independence assumption could lead to underestimating the uncertainty of the estimated effects and therefore provide false significant effects. Subsequently, we performed model selection (Appendix: Tab. S2) based on the deviance information criterion (AIC) using the dredge function implemented in the R package MuMIn (Barton, 2022), with the best-fit model including all variables. A possible pairwise correlation between the three continuous weather variables (10-min measurements) was tested and ruled out. Model validation was conducted with diagnostic residual plots and the ACF of the residuals. Thus, the estimated error terms were much less temporally autocorrelated, as observed in the autocorrelation function (ACF, which displays how consecutive data points are correlated to each other in a time series [Turchin and Taylor, 1992]).

Our final model was specified as follows:

$$\begin{aligned}\log(\mathrm{ODBA}_{t,id}) &\sim \mathcal{N}(\eta_{t,id}, \sigma^2)\\ \eta_{t,id} &= \beta_0 + \beta_{\mathrm{sex}}\mathrm{sex}_{id} + \beta_{\mathrm{month}}\mathrm{month}_t + s(\mathrm{temperature}_t, \mathrm{humidity}_t) + s(\mathrm{temperature}_t, \mathrm{wind\ speed}_t)\\ &\quad + s(\mathrm{wind\ speed}_t, \mathrm{humidity}_t) + s(\mathrm{temperature}_t, \mathrm{by} = c(\mathrm{time\ of\ day}_t, \mathrm{sex}_{id}))\\ &\quad + s(\mathrm{humidity}_t, \mathrm{by} = c(\mathrm{time\ of\ day}_t, \mathrm{sex}_{id})) + s(\mathrm{wind\ speed}_t, \mathrm{by} = c(\mathrm{time\ of\ day}_t, \mathrm{sex}_{id}))\\ &\quad + u_{\mathrm{hour}} + u_{\mathrm{day\ of\ year}} + u_{\mathrm{id}} + s(\log(\mathrm{ODBA}_{t-1,id})),\end{aligned} \tag{4.1}$$

where id indicates the animal identifier and t the corresponding time point. In addition, $s()$ indicates smooth functions. At last, u indicates the usage of random effects. As likelihood for the logarithmized ODBA, we assume a Gaussian distribution. The lagged logarithmized ODBA accounts for the temporal autocorrelation, which was clearly present for this kind of data.

4.3 Results

General activity

Based on our recollected data, hares were on average more active in the night $\left(\overline{\mathrm{ODBA}}_{\mathrm{night}} = 0.33\right)$ than during the day $\left(\overline{\mathrm{ODBA}}_{\mathrm{day}} = 0.14\right)$. Thus, hares were, on average, 136% more active during the night (Fig. 2). Highest activity peaked around dawn and dusk and was still comparatively high at night between dusk and dawn. In contrast, during the day, between dawn and dusk, hares spent most of the time resting or doing other non-energy-demanding activities (e.g., grooming or moving slowly). The lowest activity was recorded around noon, between 11 AM and 2 PM (Fig. 2) In addition, our data show that males $\left(\overline{\mathrm{ODBA}}_{\mathrm{males}} = 0.25\right)$ were on average more active than females $\left(\overline{\mathrm{ODBA}}_{\mathrm{females}} = 0.19\right)$. This represents an average activity difference of 32% (Fig. 2). This pattern was also supported by our model, which indicated that male individuals are likely to have a larger activity (coefficient = 0.15, p-value < 0.001) compared to females (Table. 1).

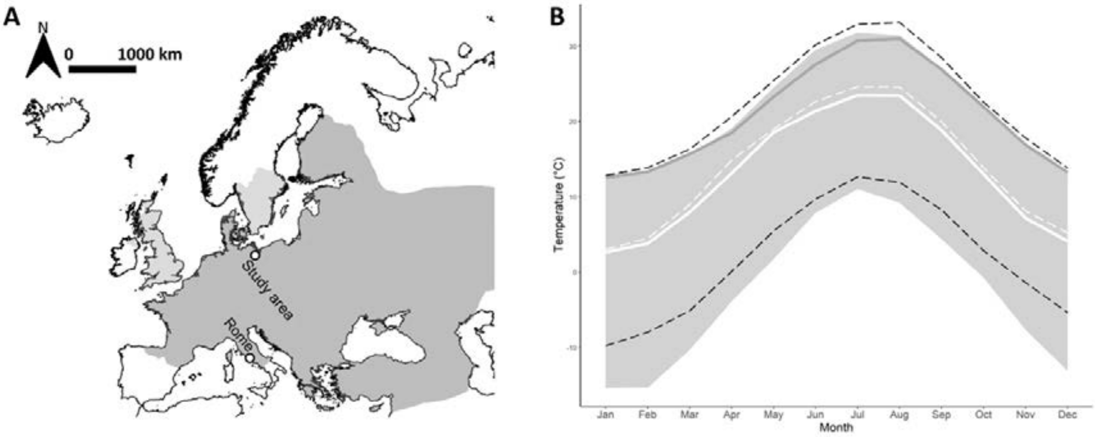

Fig. 4.1 Distribution range of European hares (A) with the respective temperature range (B). **A**: Native distribution area (dark grey) and areas where hares were introduced (light grey) (GBIF 2023). Dots indicate the AgroScapelabQuillow study area north of Berlin (Germany) and Rome (Italy) as an example of the southern edge of the distribution range. **B**: Temperature range within the distribution area (grey) calculated from monthly temperature values of 10 European cities, the AgroScapelabQuillow study area (solid white line), and Rome (dark grey line) between 1970 and 2010. The dashed lines indicate the warming of the last decade and show the mean temperatures of the study area (white dashed line) and the hottest and coldest places in the distribution area between 2010 and 2020.

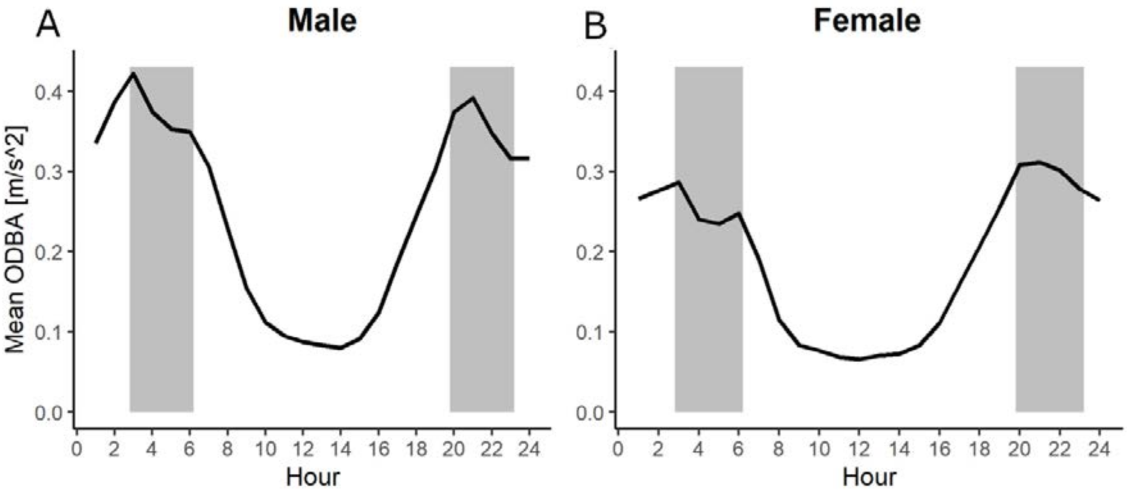

Fig. 4.2 Change of hare activity over a day for males (A) and females (B). Shown is the mean hourly activity (ODBA [$\frac{m}{s^2}$]) for each hour of the day during the reproduction period (May–August) of males (n=22) and females (n=11). The grey areas indicate the approximate times of dawn and dusk (exact times depending on the time of the year).

Table 1: Estimates (Est.), standard deviation (SD), t values, and p values are shown for the model's fixed effects. The model contained the fixed effects sex (f, m) and the month (May, June, July, August). Effective degrees of freedom (edf), reference degrees of freedom (ref.df), F values, and p values are shown for the smooth effects that contained the variables: temperature (temp), humidity (humid), wind speed (wind speed), each in interaction with sex and time of the day, the combined effects of the weather variables (temperature & humidity, temperature & wind speed, wind speed & humidity), and the random terms hour, day of the year (doy), the individual (ID), and the lagged ODBA to account for temporal autocorrelation (ODBA $_{t-1}$).

Parametric coefficients	*Estimate*	*Std. Error*	*t value*	*Pr(>|t|)*
(Intercept)	-2.326	0.084	-27.594	<0.001
sex (male)	0.151	0.036	4.171	<0.001
month (July)	0.090	0.011	8.307	<0.001
month (June)	0.104	0.011	9.251	<0.001
month (May)	0.103	0.013	7.900	<0.001
Smooth effects	*edf*	*ref.df*	*F value*	*p value*
temperature, humidity	6.448	8.009	1.418	0.207
temperature, wind speed	7.662	9.299	6.665	<0.001
wind speed, humidity	5.671	7.127	4.810	<0.001
temp (day, f)	4.015	5.138	5.491	<0.001
temp (night, f)	5.320	6.697	2.730	0.01
temp (day, m)	10.247	12.266	6.401	<0.001
temp (night, m)	7.249	8.963	4.833	<0.001
humid (day, f)	4.345	5.488	4.127	0.001
humid (night, f)	1.066	1.122	26.587	<0.001
humid (day, m)	10.731	12.986	11.542	<0.001
humid (night, m)	3.673	4.664	6.392	<0.001
wind (day, f)	2.587	3.307	13.667	<0.001
wind (night, f)	1.065	1.127	77.276	<0.001
wind (day, m)	5.791	7.271	31.868	<0.001
wind (night, m)	3.226	4.145	31.225	<0.001
hour	21.988	22.000	872.612	<0.001
doy	94.816	123.000	4.645	<0.001
id	30.612	31.000	121.897	<0.001
ODBA $_{t-1}$	11.389	13.456	4432.523	<0.001

Impacts of weather on activity during peak reproduction period

While considering the interactions of sex and time of day; temperature, humidity, and wind speed influenced the activity of hares. Our model shows evidence that the ambient weather conditions likely affect their activity during the peak reproduction period (GAM $R^2 = 0.429$, Tab. 1).

Based on our model, hares are likely to have the strongest reactions to extreme temperatures (Fig. 3) compared to humidity and wind speed. We found a non-linear relationship between the temperature and activity of both males and females at day and nighttime. During the daytime, when hares mostly rest, both males and females increase activity at temperatures above 20 °C, while females generally increase their activity with rising temperatures. For both sexes, the highest increment occurred during temperature extremes of over 35 °C. In contrast, at night, when hares are usually active for foraging and other purposes, both sexes decrease activity at temperatures above 20°C (Fig. 3). However, the absolute effect is larger for females than males during both night- and daytime temperatures. When warm temperatures (> 25 °C) are accompanied by rather low wind speeds (< 3 m/s), activity is likely to decrease, while comparatively higher wind speeds combined with warmer temperatures result in increased activity of hare. When humidity is rather low (< 40 %), our model indicates that hares are expected to increase their activity at particularly low (≤ 10 °C) and high (> 35 °C) temperatures (Fig. S1).

Our model indicates that the main effect of humidity on movement activity is stronger during the day (Fig. 3). During this resting period, males are expected to increase their activity drastically compared to females when humidity is above 80%, especially in combination with higher wind speeds (> 8 m/s) (Fig. S1). While the males decrease their activity towards lower humidity levels, females seem to remain more stable compared to males when humidity is below 40%. During the night in their active time, increasing humidity has a small negative effect on activity. This effect is similar for both sexes.

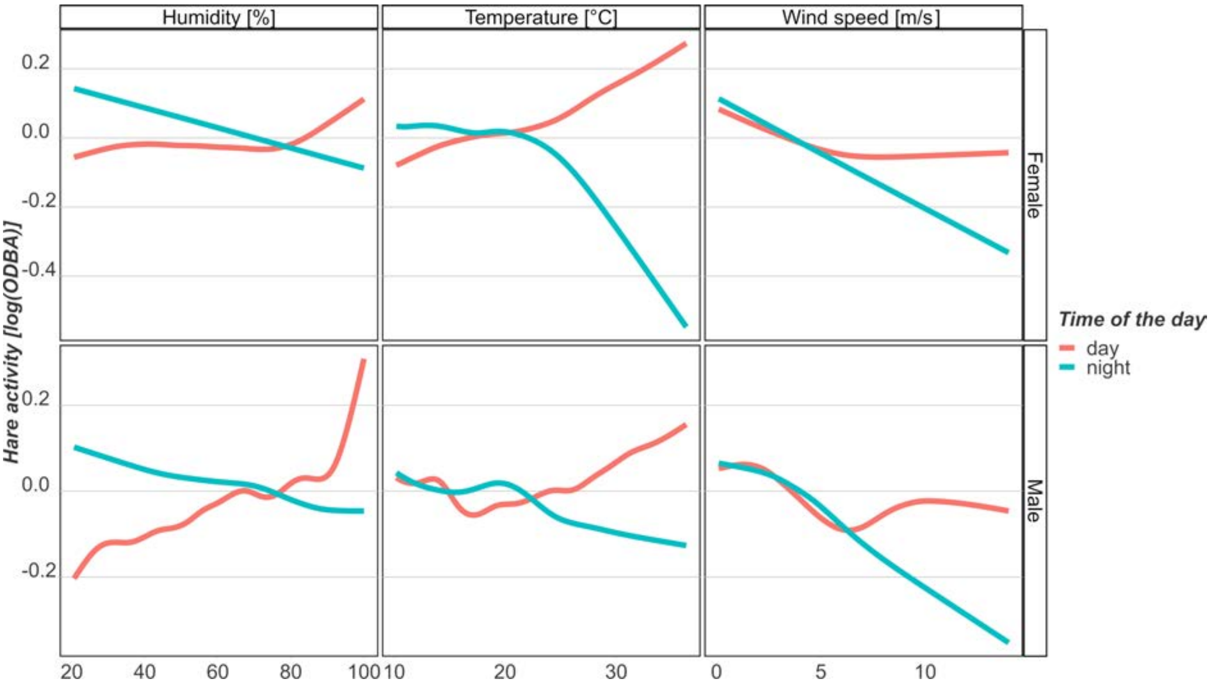

Fig. 4.3 Impacts of temperature, humidity, and wind speed on changes in hare activity $\left(\log\left(\text{ODBA}[\frac{m}{s^2}]\right)\right)$ during peak reproduction period (May–August) for females (above) and males (below). Red lines represent activity changes for the resting period during the day, and blue lines for the active period during the night. Smooth plots show the average effects on the logarithmized ODBA of hares.

With increasing wind speeds, males and females are likely to decrease their activity similarly during both day and night (Fig. 3), except for particularly high wind speeds accompanied by humidity values above 80 % (Fig. S1). The relationship between the activity of females and the wind speed during the night was almost negative linear (edf: night = 1.06, Tab. 1). In addition, males start to decrease their activity to wind speeds at approximately 3 m/s. This effect was negative up to a threshold of 6 m/s. Above the threshold, the effect on activity levels out during the day. At night, it still decreases above 6 m/s but more decelerated.

4.4 Discussion

Temperature, humidity, and wind speed were all important in explaining changes in the activity of hares, a widespread wildlife species occurring in a range of climatic zones across Europe and Asia. At temperatures above 20 °C, hares decreased their activity during the night but showed an increase during the day. While tropical nights are still rare in Central Europe, hot daytime temperatures well above 25 °C combined with high solar radiation occur frequently, and extremes in both are increasing due to climate change (IPCC, 2014). Such elevated temperatures, as well as high humidity and high wind speeds, were most important for immediate and distinct adjustments in activity during both the active period at night and the resting period during the day. However, we also found that high wind speeds have a regulating effect when temperatures are particularly hot, presumably supporting thermoregulation. While earlier studies suggest prevailing weather to have little influence on habitat selection and daily home range size of hares (Mayer et al. 2019), we show clear impacts of extreme weather conditions on hare activity during peak reproduction time. Activity adjustments were similar in both sexes, and males were, on average, more active than females corresponding to generally larger home ranges of males recorded in earlier studies (Rühe and Hohmann, 2004; Ullmann et al. 2018; Mayer et al. 2019). Remarkably, we observed contrary reactions in activity between day and night.

Many mammals cope with the effects of rising temperatures associated with climate change by seeking out cooler microclimates and shifting their activity towards more suitable times of the day (Berry et al. 2023, Hetem et al. 2012; McFarland et al. 2014). The decreasing activity of hares during tropical nights could, therefore, also be a mechanism to avoid overheating, as observed in many wildlife species (Hill, 2006; Rivrud et al. 2010; Lenis Sanin et al. 2016). For example, the subterranean rodent coruro (*Spalacopus cyanus*) was found to fully adjust its activity rhythm to the ambient temperature by switching from diurnal to nocturnal behavior with high temperatures (Rezende et al. 2003). However, in the animal kingdom, there is considerable variation in the ability of endotherms to tolerate high environmental temperatures (Boyles et al. 2011); hence, the rationale for the behavior of the hares remains speculative. The increasing activity of hares during extremely warm daytime temperatures seems counterintuitive, yet high wind speeds also had an antagonistic effect, presumably by supporting thermoregulation. We explain this increase by the resting habits of hares. They usually rest in depressions with good visibility to detect and allow escape movements from potential predators (e.g., Baudach et al. 2021). Therefore, these critical microhabitats are often exposed to direct sunlight without any cover from protective vegetation. Extremely elevated temperatures during the resting period shift the trade-off between predator detection and prevention of overheating. On days with extremely hot temperatures and intense insolation, hares need to search and move to shady depressions with more favorable microclimatic conditions for resting (Lenis Sanin et al. 2016), possibly at the cost of a reduced predator detection capacity. Mayer et al. (2019) showed that the habitat selection of hares changed with increasing temperatures towards areas containing a vegetation height above 50 cm. That suggests that hares react to thermal stress by looking for shelter. Although we did not quantify how temperature affects hares' reproduction success, earlier studies show that the litter size of hares is generally larger under warmer temperatures (Hewson and Taylor, 1975). However, from the observed responses in the activity of the adult hares, we speculate that extremely hot temperatures reduce the survival of leverets. While hares are adapted to warm temperatures, there might be a temperature threshold where it gets too hot for them. A model by Acevedo et al. (2012) shows that *L. europaeus* as well as two other hare species native in Europe (*L. timidus, L. granatensis*) are likely to shift their ranges northward to escape increasing temperatures predicted by the IPCC A2 emission scenarios.

Wet conditions, such as extended rainfall or high humidity periods, reduce leveret survival. The higher energy expenditure for thermoregulation during wet conditions and higher susceptibility to infections through pathogens and parasites (Smith et al. 2005; Rödel and Dekker, 2012) will consequently lead to increased leveret mortality (Hackländer et al. 2002). Adult hares in our study slightly decreased activity with increasing humidity at night, indicating that hares try to avoid activities such as exploration movements to search for high-quality food sources when they get wet. Indeed, the thermal loss of wet fur through evaporation requires additional energy investments for thermoregulation (Jennings et al. 2006). Further thermal losses through convection when moving may explain the observed reduction in the activity of hares under humid conditions and may be an energy-saving mechanism. In contrast, hares increased their activity during the daytime resting period when air humidity exceeded 80%, with the latter possibly also being related to rain events. While wet fur leads to a higher energy consumption due to heat loss (Seltmann et al. 2009), hares might also have started moving to get dry by producing body heat. High humidity during the resting period may be better countered with movement than during the active periods at night because muscular work to produce body heat is costly (Terrien et al. 2011).

Wind can have a cooling effect by increasing heat dissipation from the body due to higher airflow. (Chappell, 1980). Hence, hares slightly reduced their activity in response to high wind speeds. The reduction was observed in both sexes and was slightly more pronounced during the active period at night. During the day, the small but distinct depressions in the ground used for resting most probably already provided a protective wind shelter. A decrease in activity with increasing wind speeds has been observed for many different wildlife species (e.g., the red squirrel (*Tamiasciurus hudsonicus*), or the alpine chamois (*Rupicapra rupicapra*) (Williams et al. 2014; Brivio et al. 2016). Wind affects an animal's visual, olfactory, and auditory senses (Ruzicka and Conover, 2012; Cherry and Barton, 2017), which often influences the detection probability of predators by their prey and vice versa. For prey species like hares, the best strategy with increasing wind speeds is to hide rather than move around and increase the probability of encountering predators. Terrestrial predators like red foxes (*Vulpes vulpes*) or raccoons (*Procyon lotor*) are most active with moderate wind speeds that provide the optimal conditions to detect prey's odor and decrease their activity with low and high wind speeds (Ruzicka and Conover, 2011). Hence, with increasing wind speeds, hares select shelters containing a low vegetation cover, enabling them to detect predators as early as possible. However, when high wind speeds were accompanied by particularly high temperatures, hares increased their activity, presumably due to the cooling effect of the wind.

Conservation challenges under extreme climate conditions and climate change

In the future, extreme weather periods, such as heat waves or extreme precipitation events witnessed during the recent summers in Europe, are predicted to occur more often and last longer with ongoing climate change (IPCC, 2014). Our study area is located in one of the driest regions of Germany, with the fewest days of precipitation and already high temperatures in summer. For those parts, more days with heavy rain, an increasing temperature in summer, and more heat days are predicted towards the middle of the 21st century (IPCC, 2014). In Europe, the study area is in the middle of the temperature range of the current hare distribution (Fig. 1). where the temperature has significantly increased in the last decade (2010-2020) compared to 1970−2010. Although temperature is considered less important than precipitation for short-term hare population fluctuations (Rödel and Dekker, 2012), we found strong evidence that hares immediately change their activity when confronted with high-temperature extremes (decreases in activity during hot tropical nights, increase in activity during the resting period at day). Particularly, the substantial decrease in activity during the night is lost time for essential activities such as foraging or mating. Extended heat waves in summer with dry conditions will additionally affect hares by decreasing food availability (Baudach et al. 2021) or limiting reproductive output due to aggravated heat dissipation (Kearney et al. 2013). With less forage to find, hares may have to increase their daily activity to cover larger distances for finding necessary resources. Badgers (*Meles meles*) have been shown to adapt their activity to the optimum food intake by avoiding non-essential energy expenditure. Considering the scenario of increasing weather extremes, they are predicted to compensate for milder and drier conditions with behavioral plasticity, i.e., an increase in night activity (Noonan et al. 2018). While hares may also have the potential to encounter weather extremes with behavioral plasticity, there might be limitations. Especially females can be affected by food limitations and additional movements during the resting period on hot summer days when hares are forced to search for depressions with more suitable microclimatic conditions. Females must produce highly nutritious milk to satisfy the energy demands of the leverets.

The predicted increase in the number of days with heavy rainfall and the linked increase of extended conditions with high air humidity will likely additionally negatively affect the energy budgets of hares. Hares will have to adjust their activity under these conditions to save energy or get wet and presumably must invest more energy in thermoregulation. In both scenarios, either lost foraging time or foraging with higher energetic demands will directly affect the fitness of lactating females and the leverets (Hackländer et al. 2002; Rödel and Dekker, 2012), and hence population dynamics of many already threatened hare populations across Europe (Hackländer and Schai-Braun, 2019).

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4.6 Declarations

Ethics statement

All experiments were conducted in accordance with the German Federal Nature Conservation Act (§ 45 Abs. 7 Nr. 3) and approved by the animal ethics committee of the University of Potsdam and by the local nature conservation authority (reference numbers: AZ 2347-6-2019, LUGV V3-2347-22-2013, and 55.2-1-54-2532-229-13).

Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

NB and JS conceived the idea. WU and JS carried out most of the fieldwork, JP analyzed the data and contributed strongly to manuscript writing, while RAG led the statistic approach. NB and JS led the revisions of the manuscript while NB supervised throughout the process. All authors gave final approval for the publication.

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Supplemental Data

The online version contains supplementary material available here.

Data Availability Statement

Acceleration data sets generated and analyzed in the scope of this study are stored in the Movebank Data Repository (study IDs: 1138520346, 43360515, 73514179, 918554628). These are available upon reasonable request from the corresponding author. The weather data is managed by the DWD (*Deutscher Wetterdienst*) and is available at http://opendata.dwd.de.

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4.8 Supporting information

Supplementary Figure

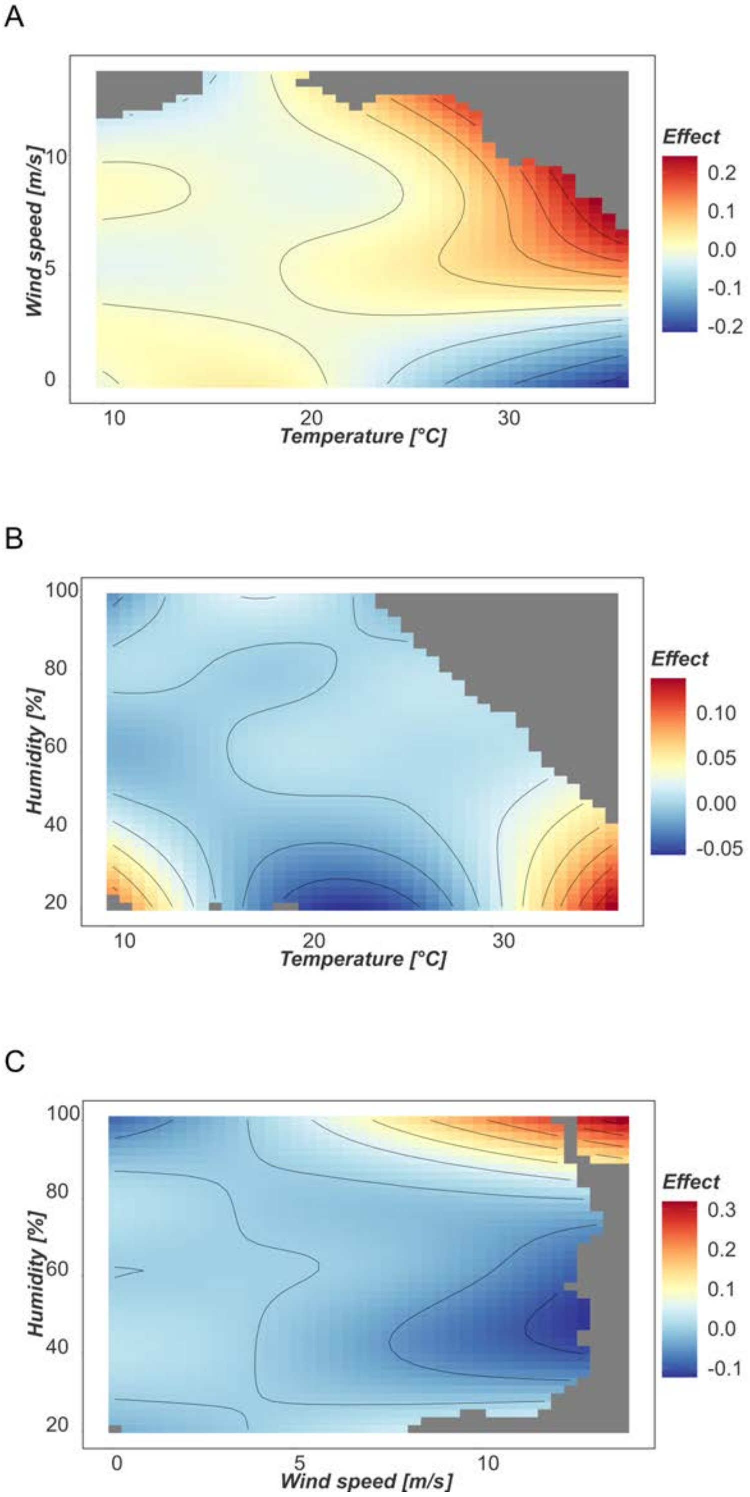

Fig. 4.4 Combined effect of (A) wind speed and temperature, (B) humidity and temperature, and (C) humidity and wind speed on hare activity [log(ODBA)]. The gray areas indicate missing data. Effect size is derived from the best-fit model (Tab. 1, Tab. S2).

Supplementary Tables

Table S1: Tracking data (acceleration) overview.

id	*first timestamp*[α]	*last timestamp*[α]	*movebank study id*	*deployment days*[α]	*sample size*[α,β]	*sex*
1	2020-05-15 19:26:12	2020-08-19 13:02:00	1138520346	95	68871	f
2	2020-05-26 18:12:48	2020-08-07 11:10:00	1138520346	72	51880	f
3	2020-05-25 14:29:45	2020-08-31 10:22:00	1138520346	97	70397	m
4	2020-05-29 12:49:12	2020-08-15 13:26:02	1138520346	78	54902	m
5	2020-06-01 11:22:32	2020-08-18 00:30:00	1138520346	77	55689	m
6	2020-05-08 18:09:24	2020-07-22 15:50:00	1138520346	74	52082	m
7	2020-05-03 19:13:18	2020-07-09 09:30:00	1138520346	66	114011	m
8	2020-05-16 14:22:32	2020-07-10 03:08:00	1138520346	54	39233	m
9	2020-05-16 19:46:00	2020-06-23 11:08:00	1138520346	37	27081	m
10	2020-05-28 17:41:18	2020-06-30 00:10:00	1138520346	32	23236	m
11	2014-05-01 00:00:47	2014-08-09 23:56:00	43360515	100	36358	f
12	2014-05-24 08:32:01	2014-08-31 23:56:00	43360515	99	35872	f
13	2014-06-02 00:00:56	2014-08-31 23:56:00	43360515	90	32760	f
14	2014-06-22 00:00:56	2014-08-31 23:56:00	43360515	70	25560	f
15	2014-06-23 00:00:57	2014-08-31 23:56:00	43360515	69	25120	f
16	2014-05-01 00:00:47	2014-08-31 23:56:00	43360515	122	44278	m
17	2014-05-01 00:01:01	2014-08-31 23:56:00	43360515	122	44278	m
18	2014-05-04 00:00:50	2014-08-31 23:56:00	43360515	119	43200	m
19	2014-06-01 00:00:25	2014-08-31 23:56:00	43360515	91	33119	m
20	2014-06-08 12:56:01	2014-08-31 23:56:00	43360515	84	28852	m
21	2014-06-16 00:00:43	2014-08-31 23:56:00	43360515	76	27720	m
22	2014-05-17 00:00:25	2014-07-15 23:56:00	43360515	59	21600	m
23	2014-05-01 00:00:56	2014-06-16 23:56:00	43360515	46	16920	m
24	2014-07-27 00:00:49	2014-08-31 23:56:00	43360515	35	12960	m
25	2015-05-28 00:01:01	2015-08-30 23:56:00	73514179	94	34189	f
26	2015-06-06 00:00:39	2015-08-31 23:56:00	73514179	86	31320	f
27	2015-05-22 00:00:21	2015-08-31 23:56:00	73514179	101	36720	m
28	2015-05-29 16:56:01	2015-08-31 23:56:00	73514179	94	33848	m
29	2015-06-19 14:04:00	2015-08-31 23:56:00	73514179	73	26429	m
30	2015-07-02 00:00:27	2015-08-31 23:56:00	73514179	60	21960	m
31	2019-08-01 18:54:00	2019-08-31 23:58:00	918554628	30	17431	f
32	2019-08-01 18:38:00	2019-08-31 23:58:00	918554628	30	17437	f
33	2019-07-18 17:54:00	2019-08-31 23:58:00	918554628	44	31863	m

[α] within the main reproduction period (May–August).

[β] frequency of accelerometry was 2 min for the studies 1138520346 & 918554628, and 4 min for the studies 43360515 & 73514179.

Table S2: Model selection based on the AIC information criterion.

The final model was specified as follows:

$$
\begin{aligned}
\log(\mathrm{ODBA}_{t,id}) \sim \mathcal{N}(\eta_{t,id}, \sigma^2)& \\
\eta_{t,id} = \beta_0 + \beta_{\mathrm{sex}}\mathrm{sex}_{id} + \beta_{\mathrm{month}}\mathrm{month}_t& \\
+ s(\mathrm{temperature}_t, \mathrm{humidity}_t) + s(\mathrm{temperature}_t, \mathrm{wind\ speed}_t)& \\
+ s(\mathrm{wind\ speed}_t, \mathrm{humidity}_t) + s(\mathrm{temperature}_t, \mathrm{by} = c(\mathrm{time\ of\ day}_t, \mathrm{sex}_{id}))& \\
+ s(\mathrm{humidity}_t, \mathrm{by} = c(\mathrm{time\ of\ day}_t, \mathrm{sex}_{id})) + s(\mathrm{wind\ speed}_t, \mathrm{by} = c(\mathrm{time\ of\ day}_t, \mathrm{sex}_{id}))& \\
+ u_{\mathrm{hour}} + u_{\mathrm{day\ of\ year}} + u_{\mathrm{id}} + s(\log(\mathrm{ODBA}_{t-1,id})),&
\end{aligned}
$$

where id indicates the animal identifier and t the corresponding time point. In addition, $s()$ indicates smooth functions. At last, u indicates the usage of random effects. As likelihood for the logarithmized ODBA, we assume a Gaussian distribution. The lagged logarithmized ODBA accounts for the temporal autocorrelation, which was clearly present for this kind of data.

model	*s(temp)*	*s(humid)*	*s(wind)*	*s(lag)*	*sex, tod, month, doy*$^{\alpha}$*, hour*$^{\alpha}$*, id*$^{\alpha}$	*ti(temperature, wind speed)*$^{\gamma}$*, ti(temperature, humidity)*$^{\gamma}$*, ti(wind speed, humidity)*$^{\gamma}$	*Δ AIC*	*Δ dev. explained*$^{\beta}$
1	x	x	x	x	x	x	0	0
2	x	x	x	x	x	0	103.2	< 0.1
3	-	x	x	x	x	0	505.5	0.1
4	x	-	x	x	x	0	869.7	0.1
5	x	x	-	x	x	0	630.4	0.1
6	x	x	x	-	x	0	54679.7	10.5
7	x	x	x	x	-	0	49389.3	2.4
8	-	-	-	x	x	0	1717.3	0.3
9	-	-	-	-	x	0	58279.7	11.3

abbreviations: tod = time of day; doy = day of year, i.e., Julian day.

$^{\alpha}$ implemented as a random effect.

$^{\beta}$ dev. explained full model (1) = 42.9%.

$^{\gamma}$ implemented as a combined effect.

Chapter 4

Tracking of mammals – Quantifying the impact of collaring

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Abstract

Attaching GPS collars to study wild mammal movement behavior depicts an extremely stressful event for many species. Immediate effects of catching, immobilizing, collaring, and releasing individuals can affect locomotion processes or activity that may not evidently be detectable in recorded movement patterns. While established animal welfare guidelines and regulatory requirements that allow for such invasive studies exist, many of these are based on findings from isolated case studies. Using GPS- and tri-axial accelerometer data, we compared movements and overall dynamic body acceleration as a proxy for the activity of 1451 terrestrial mammals (42 species) during the initial days of tracking. We hypothesize that there are not only species but also overarching responses, with the dietary type (i.e., herbivore, omnivore, carnivore), sex, and body mass having a significant influence on an individual's duration of the impairment. Further, we were particularly interested in whether the effect size of the impact changes along a gradient of anthropogenic influences (human footprint). By comparing the change in moved distances and an individual's activity of the first ten days with successive days 11-20, we found that activity and movement behavior is influenced by collaring. Mammals showed distinct reactions (increased or decreased activity/movement), which were also reflected in their movement behavior during the initial days of tracking. The activity level immediately after their release differed substantially from that of the following days, with a gradual stabilization particularly evident in omnivores. Further, most species travel larger distances after collaring (days 1-10) than in successive days. Omnivores and carnivores were less active during the initial days, while herbivores showed ambivalent, species-specific reactions. Herbivores, particularly males, recovered most quickly. Further, we found a slower recovery process for individuals caught and collared in areas with high remoteness across all species, indicating that animals in urban areas display enhanced tolerance and adaption to human presence and disturbances. Although disturbances caused by the collaring procedure are clearly visible in animal telemetry data, their intensity diminishes within the initial days of tracking. This, however, raises challenges when tracking individuals over a highly limited duration.

Keywords: *Animal Tracking, GPS, ACC, Activity, Mammals, Collaring Impacts*

5.1 Introduction

Studying wildlife movements is essential for understanding the responses of animal behavior to global environmental changes, ecosystem functioning, and nature conservation (Hebblewhite and Haydon 2010). They play a pivotal role in shaping biodiversity patterns or connecting habitats (Nathan et al. 2008, Jeltsch et al. 2013), and comprehending the far-reaching anthropogenic influence on animal movements is paramount to effective land use planning and conservation strategies (Allen and Singh 2016). In wildlife research, satellite telemetry is increasingly applied, with more animals and species than ever fitted with GPS units (Handcock et al. 2009). Current devices can track individual animal movements at unprecedented fine spatial and temporal resolutions. In addition to high-resolution motion tracking, modern technology has allowed for a variety of sensors to be attached to animals, pushing animal-tracking into the realm of Big Data (Kays et al. 2015) by providing researchers with information not only of the animals' whereabouts but also, e.g., their activity, heart rate or temperature.

Behavioral stages or the activity associated with movement can be readily derived from devices having high-resolution accelerometer (ACC) integration (Wilmers et al. 2015). Such accelerometers measure static and dynamic acceleration (i.e., the animals' movement) in three dimensions (Hughey et al. 2018) and allow to calculate proxy values for activity levels (Wilson et al. 2006, 2020, Qasem et al. 2012, López et al. 2015, Gunner et al. 2020). One well-established proxy is the overall dynamic body acceleration (ODBA), which estimates activity-related energy expenditure of free-ranging animals (Wilson et al. 2006, Gleiss et al. 2011). With high enough resolution data, changes in energetic patterns are not only detectable throughout relatively short time intervals but also reliable and comparable.

Collars or similar devices deployed on animals involve capturing, handling, and releasing the focal individual (Powell and Proulx 2003, Iossa et al. 2007). Capturing can cause behavioral modifications that are largely understudied in wildlife species and may affect the welfare of animals and the interpretation of the studies (but see: Morellet et al. 2009, Northrup et al. 2014, Brogi et al. 2019). The capture and handling process involves several stressful and physically demanding events. They are attributable to the presence of humans and involve sudden and/or loud noises, social isolation, limited movement, and impaired vision capability, which all represent different sources of stress (Theil et al. 2004, Grandin and Shivley 2015, Bergvall et al. 2021). For many species, immobilization also requires the application of specific drugs. In the same way that other threatening events in an animal's life, such as prey chased by a predator, can affect its behavior and movement for several days, each capture and release encounter evokes physiological responses (Iossa et al. 2007, Cattet et al. 2008), ultimately triggering behavioral changes (Alibhai et al. 2001, Harcourt et al. 2010). These behavioral changes can negatively impact the body condition and vital rates, possibly affecting mating success and fitness (Pelletier et al. 2004, Cattet et al. 2008, Brivio et al. 2015). In the worst case, an increased activity as a result of an attached device may affect life-history traits and even survival (Arnemo et al. 2006, Jacques et al. 2009).

In long-term deployments of several months or even years (e.g., satellite tags), the initial days may simply be omitted to be more confident of obtaining unbiased results if the animals will get "used" to the attached sensor afterward, yet no clear guidelines exist. In contrast, in short-term deployments of several days (e.g., bats or flying foxes), the effects of stress from the deployment procedure on animal behavior and activity, in addition to the physical impairment effects due to the weight of tags (Wilson et al. 2021), may result in biased findings through the limited days of animal tracking. In addition, the tags can have further cumulative impacts on animals' welfare and data quality (Ropert-Coudert and Wilson 2004) and can lead to an increased risk of injury (e.g., inflammations or strangulation, Cid et al. 2013) or mobility restriction resulting from changes in an individual's balance (Healy et al. 2004). Conclusively, the capture and the associated manipulation of wild species can cause behavioral changes and may affect not only the welfare of the animal but also the outcome of the intended study. However, the determination of "normal" behavior is challenging to evaluate since the assessment that an animal is behaving "normally" may not be objectively judged and thus be the weakest point in the overall study design (Ropert-Coudert and Wilson 2004).

Clearly, there is a lack of research regarding the effects of the deployment procedure and the tags *per se* on animal behavior (but see, e.g., Brooks et al. 2008, Stabach et al. 2020). Moreover, the ethics of acceptable practices for attached devices are poorly defined (Wilson and Mcmahon 2006), and no protocols for dealing with data of the initial tracking days exist. This is primarily because we do not know for how many days individuals from the focal species are impaired by such animal-borne tracking devices. Yet, findings of limited case studies exist: In captive scimitar-horned oryx (*Oryx dammah*), Stabach et al. (2020) showed clear effects on individuals fitted with GPS collars with elevated stress hormone levels for up to 5 days and behavioral changes (increased headshaking) for up to 3 days. Van de Bunte (2021) found that captive-collared red pandas (*Ailurus fulgens*) reduced daily activity levels and food intake compared to non-collared individuals. Free-ranging red deer (*Cervus elaphus*), Becciolini et al. (2019) increased movement rates and avoided the center of their activity for up to 10 days, probably reflecting the recovery from the chemical immobilization and the GPS tagging procedure and their habituation to the animal-borne device. In Eurasian beavers (*Castor fiber*), the body mass of dominant individuals decreased considerably with the number of repeated capture events (Mortensen and Rosell 2020). In Black bears (*Ursus americanus*), a generally higher tendency to avoid humans after capture events has been observed (Chi et al. 1998). Similarly, post-collar attachment, roe deer (*Capreolus capreolus*) reacted with displacement towards near woodland by avoiding sources of human disturbance combined with reduced activity. These behavioral changes sharply decreased during the first 10 days, with females being less sensitive than males (Morellet et al. 2009).

The effects of tag and the deployment procedure on animal behavior can vary widely across species, logger type, tag size, deployment duration, or the specific attachment methodology (Hawkins 2004, Ropert-Coudert and Wilson 2004, Wilson and Mcmahon 2006). Different species show differing stress responses, especially throughout the initial days of tracking, and further take varying durations to return to their normal state behavior. Moreover, recent research demonstrated ecosystem-wide consequences from changes in animal movement due to human disturbance (Tucker et al. 2018, Doherty et al. 2021) with mammals in highly anthropogenic-influenced areas having smaller home ranges (Wilson et al. 2019) or moving shorter distances (Main et al. 2020) than those in remote areas. In the scope of a meta-analysis, Samia et al. (2015) found disturbed populations of lizards, mammals, and birds more tolerant to human disturbance than less disturbed populations. Consequently, since movement (Tucker et al. 2018) and behavior (Ciuti et al. 2012, Gaynor et al. 2018) change with human proximity, we expect altered responses to human-made capture and immobilization.

In our study, we used GPS tracking- and acceleration data of 1451 terrestrial mammals out of 42 species to quantify the effects of being trapped and handled. As animals were tracked across different ecosystems, we explored if animals in remote areas with fewer anthropogenic influences recover slower, where individuals are less exposed to non-human disturbances. By looking at the activity (ACC) and movement (GPS) patterns of multiple mammal species considering life history traits, we calculated disturbance intensity and explore how fast individuals of different species recover. On this basis, we provide recommendations regarding data analysis for the initial days of tracking. We hypothesize that there are not only species-, but also overarching responses, with females due to their reproductive responsibilities and lighter species being more sensitive, accompanied by a slower recovery. We assume that carnivores are evolutionarily less adapted to being hunted, and therefore also, the type of diet influences the duration and intensity of an individual's impairment.

5.2 Methods

Data collection & preparation

Animal tracking data (GPS and ACC) from multiple data providers were either directly received or downloaded from the Movebank data repository (Wikelski et al. 2020) with the help of the R package move (Kranstauber et al. 2020). The number of individuals ranges from 3−672 out of 42 (GPS, n = 1451), respectively 39 (ACC, n = 1243) mammal species (Fig. 1).

We divided the data into two parts, the first 10 days after the release of the individual and the days 11−20. We took days 11−20 as a "long-term" mean, expecting that most of the reaction towards the collaring/handling process has leveled off within initial 10 days as shown in previous studies (e.g., *Alces alces*: ≤ 4.5 days [Neumann et al. 2011], *C. capreolus*: ≤ 10 days [Morellet et al. 2009], *C. elaphus*: ≤ 10 days [Becciolini et al. 2019]). Subsequently, we related daily averaged values (daily distances, daily activity) to the respective mean during days 11−20 to obtain daily percentage deviation (Fig. 2).

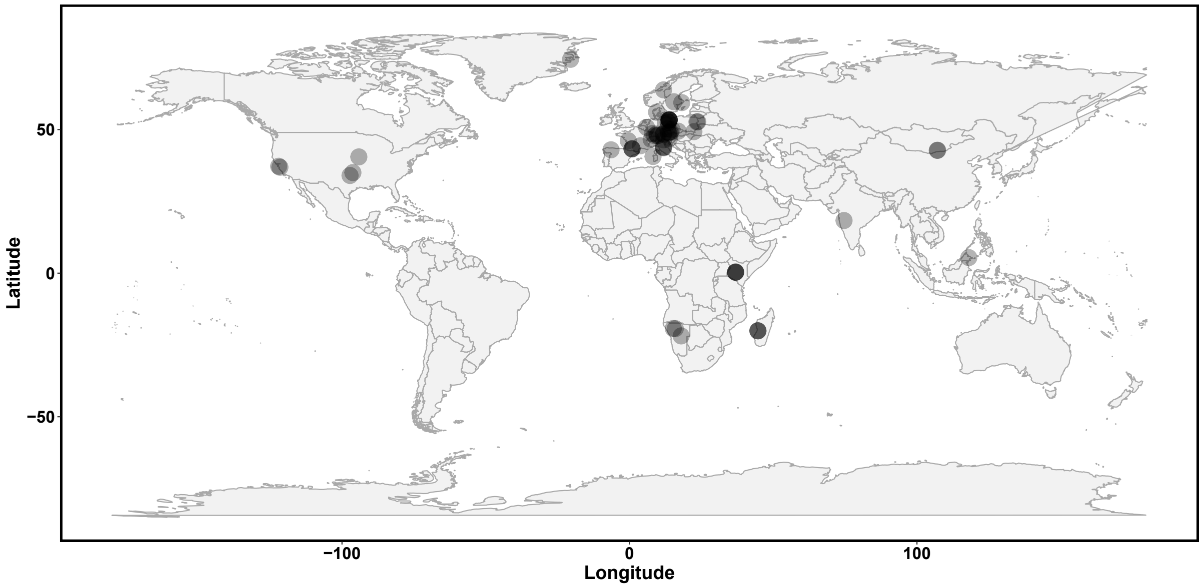

Fig. 5.1 Locations of tracking studies obtained from North America, Europe, Asia, and Africa. Each dot represents one study site, and the darkness of the dot represents the number of individuals (3−672 individuals per species).

In the first step, we omitted individuals with missing data throughout the initial 20 days. We defined data as missing if any discontinuation resulted in less than 1 GPS fix per hour and less than 1 activity measurement per 30 minutes. In total, we compiled a dataset of 1451 individuals from 42 mammal species (ACC), and 1243 individuals from 39 mammal species (GPS). Consequently, we calculated mean daily ODBA values for each individual with the R package moveACC (Scharf 2018) as ODBA = $|A_x| + |A_y| + |A_z|$ for tri-axial measurements; and as ODBA = $|A_x| + |A_y|$ for bi-axial measurements, where A_x, A_y, and A_z are the derived dynamic accelerations corresponding to the three perpendicular axes of the sensor (Qasem et al. 2012). Acceleration records obtained from individuals with only one axis were not considered. Daily distances were estimated using the R package amt (Signer et al. 2019). For each study site, we calculated the Human Footprint Index (**HFi**: McGowan 2016, Venter et al. 2016) by drawing a radius of 5km around the center (mean longitude, mean latitude) of each separate study and calculating the respective mean HFi value.

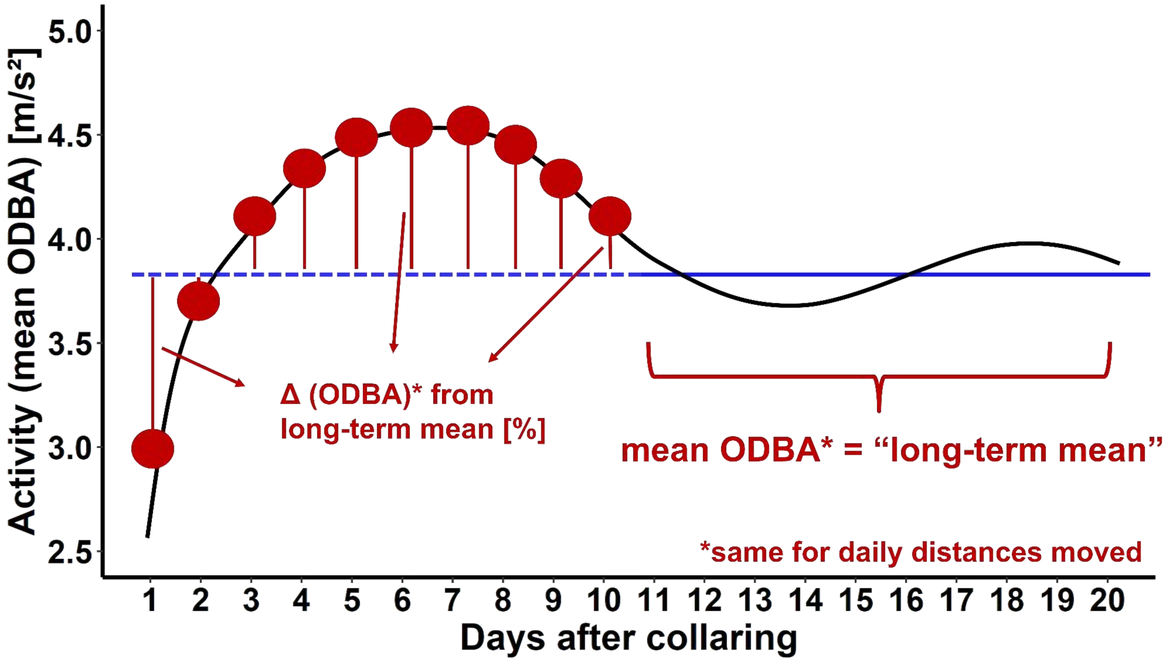

Fig. 5.2 Methods, calculating relative ODBA & distances: First, we calculated daily (days 1–10) activity (ODBA) & distances moved. Subsequently, we related daily values to the long-term mean (days 11–20). The analysis was conducted identically for activity and distances moved.

We divided the data into two parts, the first 10 days after the release of the individual and the days 11–20. We took days 11–20 as a "long-term" mean, implying that most of the reaction towards the collaring/handling process has leveled off after the initial 10 days. Subsequently, we related daily averaged values (daily distances, daily activity) to the respective mean during days 11–20 to obtain daily percentage deviation (Fig. 2).

Disturbance intensity

Consequently, we then applied a separate Generalized Additive Mixed Model with Gamma error distribution for the deviance in activity and distances using the R package mgcv (Wood et al. 2016) to estimate the effect of the study species in combination with time (i.e., days 1–10) on daily deviance. Since we did not expect a linear relationship, we specified the predictor variable time as a smooth term for each level of study species and a first-order auto-regressive correlation structure *corAR1* among the residuals of the model associated with each level of ID. Sex was included as an additional random effect.

The *disturbance intensity* model was specified as follows:

$$\begin{aligned} deviance_{id,t} &\sim Gamma(\eta_{id,t}, \alpha) \\ \eta_{id,t} &= \exp\left(f(t)_{species} + u_{id} + u_{sex} + \nu_{id,t}\right) \\ \nu_{id,t} &= \rho \nu_{id,t-1} + \epsilon_{id,t-1} \\ \epsilon_{id,t-1} &\sim \mathcal{N}\left(0, \sigma^2\right) \end{aligned} \tag{5.1}$$

Thus, the linear predictor $\eta_{id,t}$ includes an autoregressive process of order one (AR[1]). Here the parameter ρ accounts for the temporal autocorrelation, id represents the animal identifier, and t the corresponding time point. In addition, u indicates the use of random intercepts. Deviance was calculated and modeled separately for both activity and distances.

Recovery speed

For all individuals of significant species (Fig. 1, Tab. 1), we then calculated the slope at day 1 as a measure of recovery speed, i.e., how fast individuals adapt throughout the first days. The slope was calculated for each individual as the first derivative for $x = 1$ from the ID-specific fitted curve with $y \sim log(x)$. We applied a separate Linear Mixed Effect Model with Gaussian error distribution of the recovery speed of both, activity and distances, using the R package lme4 (Bates et al. 2015). Therefore, we took the absolute value of the respective measurements, |slope day 1|, as the dependent variable. As dependent variables, we implemented sex, dietary type (herbivore, omnivore, carnivore), body mass (Faurby et al. 2018, Tab. S1), and the Human Footprint Index (HFi) of the study area. The study species was implemented as a random effect. The response variables, as well as body mass and HFi, were log-transformed, and thus, the model was calculated with Gaussian distribution and the link function between the linear predictor and the response variable as a natural logarithm. Subsequently, we conducted model selection using the R package MuMIn (Bartoń 2022). By ranking model combinations via the Akaike Information Criterion AIC, we considered all independent variables that were in the best-fit models within 2 AIC units for the final model and report the respective summary. Models were calculated using all gap-less data available for the independent and dependent variables, resulting in minor variations in sample size and species analyzed for activity and distances.

The *recovery speed* model was specified as a linear mixed effect model:

$$\begin{aligned} \log(|slope\ day\ 1|)_{id,species,studysite} &\sim \mathcal{N}\left(\eta_{id,species,studysite}, \sigma^2\right) \\ \eta &= \beta_0 + \beta_1 \log(mass_{species}) + \beta_2 \log(HFi_{species,studysite}) \\ &+ \beta_{sex} sex_{id} + \beta_{diet} diet_{species} + u(species), \end{aligned} \tag{5.2}$$

where sex and $diet$ were specified as categorical variables; $slope\ day\ 1$ was calculated and modeled separately for both activity and distances.

5.3 Results

Disturbance intensity

Half of the mammal species analyzed were sensitive to collaring and significantly changed their activity and daily distances during the first 10 days after release. 26 out of 41 species changed their activity (Fig. 3 upper panel, Tab. 1), and 19 out of 39 species the daily movement distances (Fig. 3 lower panel, Tab. 1). For 12 species ($n_{GPS} = 9.36 \pm 3.59$, $n_{ACC} = 9.75 \pm 3.55$; $mean \pm SD$), no significant reactions in activity and daily distances were found during the first 10 days. Sample size per species varied largely between 3 and 672 individuals. Within-species variability was high ($p_{ID_{GPS}}$ & $p_{ID_{ACC}} < 0.001$), while sex did not significantly influence species-specific reaction behavior ($p_{sex_{GPS}}$ & $p_{sex_{ACC}} > 0.05$).

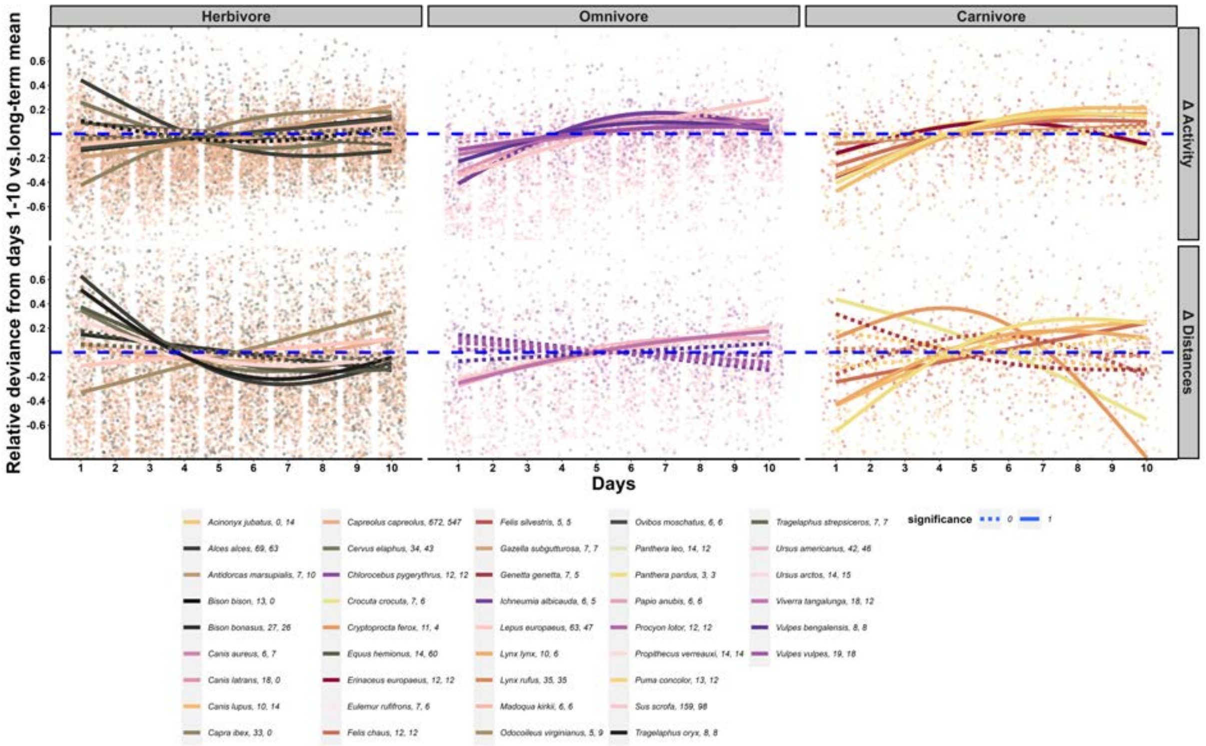

Fig. 5.3 Impacts of collaring on activity (upper) and daily distances (lower) during the initial days after release. Daily deviances from the long-term mean of distances moved and activity spent, species split by diet: herbivores (left), omnivores (middle), and carnivores (right). The first number after the species name refers to the number of individuals for activity and the second for daily distances. All species with $p \leq 0.05$ are shown as solid lines, and species with $p > 0.05$ as dotted lines. Activity: $R^2 = 0.374$, Dev. explained = 46.4%, distances: $R^2 = 0.25$, Dev. explained = 37.6%. Data of 42 mammal species.

The activity level of all species immediately after the release differed substantially from that of the following days, with a gradual stabilization during the initial days (Fig. S1), particularly evident in omnivores. While omnivores and carnivores were less active during the initial days than in the long-term mean, herbivore species show reactions in both directions. A similar pattern was revealed for distances moved; most species travel longer distances after collaring compared to the long-term mean. Activity: $R^2 = 0.374$, Dev. explained = 46.4%, distances: $R^2 = 0.25$, Dev. explained = 37.6. On day 1 after the release, moose (*Alces alces*) moved a 63% farther distance compared to the long-term mean, followed by the common eland *Tragelaphus oryx* (52%), and the spotted hyena *Crocuta crocuta* (44%). In contrast, daily movement distances of leopards *Panthera pardus* decreased by -65%, followed by wolves *Canis lupus* (-44%), and the Eurasian lynx *Lynx lynx* (-43%). Moose was also the relatively most active species on day one (44%), followed by red deer *Cervus elaphus* (26%), and the Mongolian khulan *Equus hemionus hemionus* (9%). Wolves were least active during day one (-48%), followed by the white-tailed mongoose *Ichneumia albicauda*, and leopards as well as golden jackals *Canis aureus* (both 41%). In general, herbivores were more active and traveled longer larger distances at day 1 compared to the long-term mean (days 11–20). In contrast, carnivores traveled shorter distances except for the spotted hyena ($Deviance\ day\ 1_{GPS} = 44\%$) and the fossa *Cryptoprocta ferox* ($Deviance\ day\ 1_{GPS} = 12\%$).

Table 5.1 Species model summary: Activity & Distances

	Activity				**Distances**			
species	*edf*	*ref.df*	*statistic*	*p-value*	*edf*	*ref.df*	*statistic*	*p-value*
Acinonyx jubatus					1.158	1.291	3.837	0.057
Alces alces	1.993	2.000	190.999	**<0.001**	1.994	2.000	76.537	**<0.001**
Antidorcas marsupialis	1.000	1.000	1.333	0.248	1.000	1.000	0.178	0.673
Bison bison	1.000	1.001	11.707	**0.001**				
Bison bonasus	1.859	1.98	6.7	**0.001**	1.000	1.001	6.918	**0.009**
Canis aureus	1.904	1.991	14.369	**<0.001**	1.000	1.000	0.444	0.505
Canis latrans	1.94	1.996	25.793	**<0.001**				
Canis lupus	1.894	1.989	37.055	**<0.001**	1.684	1.9	12.98	**<0.001**
Capra ibex	1.934	1.996	92.99	**<0.001**				
Capreolus capreolus	1.997	2.000	150.176	**<0.001**	1.996	2.000	30.117	**<0.001**
Cervus elaphus	1.942	1.997	28.795	**<0.001**	1.961	1.999	16.314	**<0.001**
Chlorocebus pygerythrus	1.000	1.000	0.302	0.583	1.000	1.000	0.083	0.774
Crocuta crocuta	1.875	1.984	4.426	**0.014**	1.387	1.624	9.789	**<0.001**
Cryptoprocta ferox	1.000	1.000	0.335	0.563	1.886	1.987	8.964	**<0.001**
Equus hemionus	1.000	1.000	5.466	**0.019**	1.925	1.994	30.444	**<0.001**
Erinaceus europaeus	1.891	1.988	5.815	**0.004**	1.000	1.000	0	0.984
Eulemur rufifrons	1.000	1.000	0.061	0.805	1.000	1.000	0.059	0.808
Felis chaus	1.812	1.965	14.059	**<0.001**	1.000	1.000	8.58	**0.003**
Felis silvestris	1.000	1.000	1.336	0.248	1.754	1.94	1.331	0.26
Gazella subgutturosa	1.279	1.481	9.763	**<0.001**	1.67	1.891	1.12	0.255
Genetta genetta	1.809	1.964	12.585	**<0.001**	1.448	1.695	2.98	0.128
Ichneumia albicauda	1.919	1.993	14.329	**<0.001**	1.000	1.000	1.284	0.257
Lepus europaeus	1.195	1.352	18.292	**<0.001**	1.000	1.000	6.666	**0.01**
Lynx lynx	1.811	1.964	20.902	**<0.001**	1.695	1.907	4.855	**0.025**
Lynx rufus	1.313	1.528	7.567	**0.006**	1.000	1.000	0.442	0.506
Madoqua kirkii	1.000	1.001	1.165	0.281	1.289	1.495	0.35	0.764
Odocoileus virginianus	1.000	1.000	0	0.993	1.000	1.000	18.598	**<0.001**
Ovibos moschatus	1.000	1.000	4.636	**0.031**	1.205	1.369	1.567	0.281
Panthera leo	1.000	1.000	1.889	0.169	1.008	1.016	0.028	0.883
Panthera pardus	1.758	1.941	8.782	**0.001**	1.685	1.901	5.727	**0.013**
Papio anubis	1.000	1.000	0.178	0.673	1.000	1.000	0.67	0.413
Procyon lotor	1.266	1.461	2.38	0.168	1.000	1.000	1.81	0.179
Propithecus verreauxi	1.000	1.000	0.099	0.753	1.718	1.921	4.144	**0.04**
Puma concolor	1.000	1.000	0.001	0.971	1.000	1.000	2.269	0.132
Sus scrofa	1.867	1.982	402.118	**<0.001**	1.000	1.000	53.596	**<0.001**
Tragelaphus oryx	1.76	1.943	1.99	0.166	1.861	1.981	7.562	**0.001**
Tragelaphus strepsiceros	1.096	1.183	0.438	0.483	1.000	1.000	0.376	0.54
Ursus americanus	1.928	1.995	76.156	**<0.001**	1.826	1.97	13.952	**<0.001**
Ursus arctos	1.552	1.799	2.92	0.121	1.529	1.778	3.185	0.102
Viverra tangalunga	1.563	1.809	12.38	**<0.001**	1.369	1.601	5.174	**0.026**
Vulpes bengalensis	1.811	1.964	6.689	**0.004**	1.000	1.000	0.505	0.477
Vulpes vulpes	1.65	1.878	6.532	**0.008**	1.000	1.000	1.372	0.242
s(ID)	1247.941	1450	6.588	**<0.001**	1041.878	1237	4.601	**<0.001**
s(sex)	0.08	1.000	0.406	0.317	0.529	1.000	13.637	0.278
R-sq. (adj)	0.374				0.25			
Deviance explained	46.4 %				37.6 %			
n	14510				12430			

Recovery speed

During the first 10 days of tracking, mean absolute deviance of distances moved compared to days 11−20 decreased from 33±17% to 21±20%, while absolute deviance in activity decreased from 24 ± 14% to 12 ± 6% ($deviance_{day\ 1}$ $vs.$ $deviance_{day\ 10}$ for all species with $p \leq 0.05$, Fig. 3, Tab. 1). Relating the days 11−20 with the long-term mean revealed regular mean daily deviance of 14% for activity, and 35% for distances moved (Fig. S1). For all individuals, we calculated the |slope day 1| as a measure of recovery speed. Hence, we classified the immediate reaction behavior after collaring/release and the adaption in terms of activity and daily distances. The steeper the slope (high values), the faster the individuals were adapting/settling down (Tab. S2). Separating species by their diet (color code) hints towards different response behaviors for herbivores, omnivores, and carnivores. Especially herbivores seem to react clearly differently. Recovery speed was found to be significantly influenced by body mass, sex, diet, and the human footprint of the focal area (Fig. 4, Tab. 2 & 3).

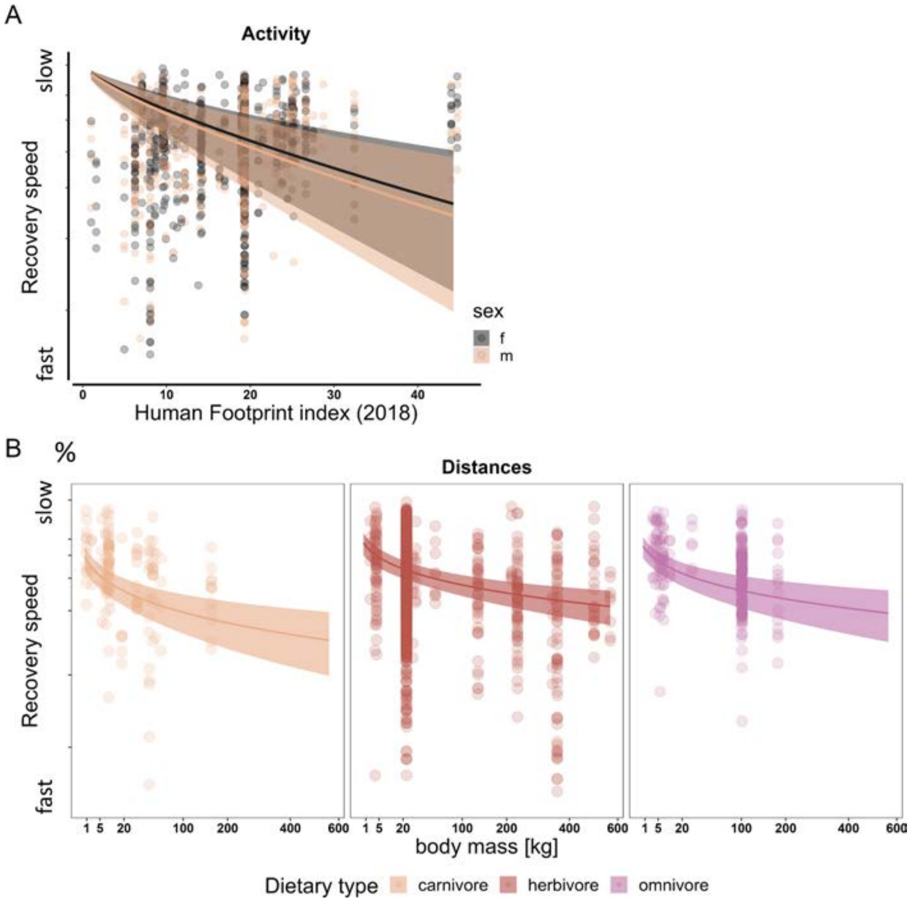

Fig. 5.4 Recovery speed (|slope day 1|) is best explained by the species' dietary type, the human footprint of the study region, the sex of the individual, and the body mass (Faurby et al. 2018, Tab. S1). A: Recovery speed (activity) described in relation to sex and the Human Footprint index. High values indicate a strong anthropogenic influence and low values indicate a high degree of remoteness. B: Recovery speed (distances) described in relation to diet and body mass. Note that the y-axis is sqrt-transformed in both plots (A & B).

While a quick recovery in activity is best explained by a high human footprint index of the respective study site and the individuals' sex [+male] (Fig. 4A), a slow recovery in distances is best explained by the species-specific diet [-omnivore] as well as its body mass, with heavy species recovering considerably quicker (Fig. 4B). Overall, dietary type, sex, and the Human footprint of the respective study area were highly relevant in determining the recovery speed (Fig. 4, Tab. 2 & 3).

Table 5.2 Recovery speed: Activity. The best-fit model to describe recovery speed in terms of activity spent included the species' body mass, sex, dietary type, and the study site's Human Footprint Index (HFI) as independent variables. Study species was implemented as a random effect (see methods, formula 2).

Recovery speed (activity)

Predictors	*Estimates*	*CI*	*p*
(Intercept)	-4.24	-7.27 – 1.20	**0.006**
mass	0.22	-0.05 – 0.49	0.116
sex [m]	0.17	0.01 – 0.32	**0.039**
diet [herbivore]	0.47	-0.69 – 1.63	0.431
diet [omnivore]	-0.05	-1.18 – 1.08	0.935
HFi	1.57	1.18 – 1.96	<**0.001**
Random Effects			
σ^2	1.95		
$\tau_{00\,study\,species}$	1.78		
ICC	0.48		
$N_{study\,species}$	40		
Observations	1428		
Marginal R^2 / Conditional R^2	0.111 / 0.536		

Table 5.3 Recovery speed: Distances. The best-fit model to describe recovery speed in terms of daily distances included dietary type and the species' body mass as independent variables. Study species was implemented as a random effect (see methods, formula 2).

Recovery speed (daily distances)

Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.35	-0.55 – 1.25	0.444
diet [herbivore]	-0.25	-0.63 – 0.12	0.183
diet [omnivore]	-0.61	-1.00 – -0.23	**0.002**
mass	0.26	0.17 – 0.35	<**0.001**
Random Effects			
σ^2	1.32		
$\tau_{00\,study\,species}$	0.11		
ICC	0.07		
$N_{study\,species}$	38		
Observations	1232		
Marginal R^2 / Conditional R^2	0.087 / 0.155		

5.4 Discussion

The impact of tracking devices on animal behavior has long been a subject of debate in the scientific community. While tracking devices have enabled researchers to collect invaluable data on animal movements and behavior (Cooke et al. 2004), concerns have been raised about the potential negative effects of these devices on the animals being studied (Godfrey and Bryant 2003, Mech and Barber 2002). Undoubtedly, studies involving telemetry have yielded considerable knowledge, yet proper evaluation and reduction of any adverse collaring impacts is still a difficult task that merits increased research attention (McIntyre 2015). Clearly, a structured approach to animal welfare and profound research is needed that addresses both the ethical implications and scientific objectives of the research (Minteer and Collins 2005, Wilson and McMahon 2006). In furtherance of this goal, we analyzed the activity and movement of mammals, particularly after being caught and collared, on a large scale. Essentially, we found that individuals are influenced by collaring events regarding activity spent, and distances traveled. However, with an immediate response after successful collar deployment, visible for the initial days of tracking, a gradual stabilization occurred within the first few days. As a consequence, the impact of the disruptive event shows up clearly in the data, but also the visible effect diminishes within the first few days.

All species deviated from their long-term activity levels during the first days of tracking. However, for most species, the deviation in terms of activity spent and distance traveled leveled out during the initial days. Reactions found in our dataset are consistent with the findings of case studies of the respective species: For moose, (*Alces alces*), the observed reaction is in accordance with the findings of Neumann et al. (2011), who identified larger spatial displacements for up to 4.5 days after capture (Neumann et al. 2011), presumably accompanied by higher activity levels. For wild boars (*Sus scrofa*), the first post-capture days were characterized by low activity, calculated from dual-axis accelerometers, and low mobility levels. Then, stable levels were restored gradually (Brogi et al. 2019). The opposite behavior in red deer, with increased movement rates immediately after release, was also found by Becciolini et al. (2019).

Males recovered more quickly compared to females from collaring-induced changes in activity, which aligns with findings in roe deer (Morellet et al. 2009), yet this effect was not visible across species in terms of daily distances. The fact that females may require a longer recovery time can be attributed to various biological and hence, related behavioral factors. In mammals, females are responsible for gestation, birth, and rearing of offspring (5–10% of mammalian species engage in paternal care; Woodroffe & Vincent, 1994), These reproductive responsibilities can make females more susceptible to stress and physical strain during capture and handling. Moreover, females may face additional challenges related to hormonal fluctuations, which are necessary to allocate energy and resources for successful reproduction. These factors may contribute to aggravating negative impacts associated with the attachment of tracking devices, potentially leading to increased stress levels, reduced foraging efficiency, or as a consequence, compromised reproductive success. We would expect this effect to be even more pronounced in pregnant or lactating females; however, due to the heterogeneous data set, where different species were captured over different time periods across continents, we did not account for an individual's ecological or behavioral seasons.

Omnivores and carnivores were generally less active after the release, whereas 65% of the herbivores increased their activity on the first day post-collar attachment. As carnivores and omnivores are often caught with bait, they may simply not have to move around as much to find food in the following days as they would under normal circumstances. In herbivores, the recovery speed of activity and daily distances after capturing, collaring, and releasing was slower than in omnivores and carnivores. From an evolutionary perspective, this is surprising since many wild herbivores are frequently chased by predators and thus may be better adapted and recover faster from such extreme events. Yet, the strong anesthesia used, particularly for heavy herbivores, could also be reflected in the data here. Especially for larger herbivores (i.e., *Alces alces, Tragelaphus strepsiceros, Cervus elaphus*), hiding or saving energy seemed not a legitimate reaction to being chased and immobilized, as their natural response for being chased by predators is escaping by moving. Another explanation for the strong response of the larger herbivores could be that they were given particularly strong sedatives due to their high body mass. For all species, we found a strong intraspecific variation in the response behavior, which may be context-specific or also linked to animal personalities (Roche et al. 2016), traditionally assessed along a bold-shy continuum (Wilson et al. 1994, Schirmer et al. 2019).

In places with significant anthropogenic influence, animals frequently display enhanced tolerance and adaption to human presence. Animals that adapt to human presence may experience reduced competition for resources compared to natural habitats (Santini et al. 2019). Furthermore, some species demonstrate behavioral flexibility and can adjust their activity patterns or habitat preferences (Alberti et al. 2017) and their movement behavior (Tucker et al. 2023) to avoid direct conflicts with humans. For example, some mammals, such as raccoons (*Procyon lotor*) and coyotes (*Canis latrans*), have been observed thriving in urban areas by utilizing human-associated food resources and adapting their behavior to coexist with humans (Gehrt et al. 2009; Prange et al. 2003), yet, the impact of anthropogenic influence is species-specific (Erb et al. 2012). Previous studies have shown that animal behavior can be strongly influenced by human interactions. For example, the coexistence of humans and wildlife in urban areas often selects for individuals with a bold personality (Tuomainen & Candolin 2011, Gaynor et al. 2021, Martínez-Abraín et al. 2022). On the other hand, animals inhabiting remote areas have less exposure to human presence and, consequently, encounters. Hence, when such animals encounter humans, they might show an exacerbated response behavior toward the disturbance and remain alert for a prolonged time. While this assertion is speculative, it is supported by the finding that individuals in remote areas recover slower from the collaring process than those in highly anthropogenically influenced areas. Nonetheless, we cannot conclude whether the disturbance intensity differs along an HFi gradient, similar to an individual's recovery speed.

There is a fine balance between obtaining valuable data and ensuring the well-being of the tracked animals. Researchers must consider these ethical dilemmas carefully and implement tracking methods that minimize harm and maximize animal welfare. Our study shows that animal-borne data might be biased during the initial days of animal tracking due to the invasive collaring procedure. Impacts, however, are fading within a relatively short time frame, and, therefore, initial data can be omitted to obtain more unbiased results. In contrast, it may be difficult to detect the effects of the collar during short-term deployments, as the data obtained is highly time-constrained. Here, the miniaturization of tracking devices, improved battery life, and more accurate positioning technologies can help overcome some of the technological limitations. Ethical considerations should guide the selection and implementation of tracking methods, ensuring that the benefits outweigh any potential animal harm.

Conclusion

While disturbances as a result of the collaring procedure are clearly visible in animal telemetry data, they sharply decrease during the initial days of tracking. This, however, may still be problematic if focal species are only tracked for a limited time. Considering this, researchers should still strive to develop methods that minimize collaring effects but also be aware of possibly biased data to benefit both animal welfare and the science bolstered by localization studies. Animal tracking is crucial for understanding wildlife dynamics, guiding conservation efforts, and influencing management choices. Researchers can maximize the advantages of GPS-collaring while limiting any adverse effects on the studied animals by understanding and actively addressing the limitations. Without a doubt, animal tracking will continue providing a substantial contribution to the knowledge of our environment, with ongoing technological developments, improved techniques, and consideration of ethical concerns inevitably being involved.

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5.6 Declarations

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Animal Tracking Permits

Acinonyx jubatus: All experimental procedures described were approved by the Internal Ethics Committee of the Leibniz Institute for Zoo and Wildlife Research (Leibniz-IZW, Berlin, Germany) (permit number: 1 April 2002) and the Ministry of Environment, Forestry and Tourism of Namibia (permit numbers: 1689/2012, 1813/2013, 1914/2014, 2067/2015, 2194/2016, 2208/2017, RCIV00082018/2018050101).

Alces alces: The capture and handling of GPS-marked moose in Norway was approved by the Norwegian Environment Agency (capture) and the Norwegian Food Safety Authority, which is the Norwegian animal research authority (permits no. 16/258650, 07/68902 and 2015/232016).

Antidorcas marsupialis: Approved by the Namibian Council on Research, Science and Technology, certificate: RCIV00032018.

Genetta genetta: Approved by The National Council of Science Technology and Innovation (permit number NACOSTI/P/14/357/2062), Kenya Wildlife Service (permit number KWS/BRM/5001) and through the Smithsonian Institution's National Museum of Natural History's Animal Care and Use Committee (Animal Study Proposal 2014-11).

Bison bison: Approved by the Nature Conservancy (Missouri) and Missouri Department of Natural Resources.

Bison bonasus: This study was carried out under research permits no. DLOPiK-op/ogiz-4200/IV.A-38-1/8310,10568/07/wo from the Polish Ministry of Environment and no. DOPozgiz-4200/IV.A-4/208/10/ls from the General Director for Environmental Protection in Poland, as well as ethics, permits no. 31/2006, and 2009/52 from the Local Ethical Commission in Białystok, Poland.

Canis aureus: All captures and handling were approved by the Maharashtra State Forest Department: permit no. SPP-147, dated 17.3.2015.

Canis latrans: Approved by Mississippi State University Institutional Animal Care and Use Committee, protocols 09-004, 12-012.

Canis lupus: Approved by Mississippi State University Institutional Animal Care and Use Committee, protocols 09-004, 12-012.

Capra ibex: The body in charge of the Alpine ibex capture was the Gran Paradiso National Park. Ibex capture and handling protocols were approved by the Italian Ministry of Environment (Protoc. no. 25114/04).

Capreolus capreolus: (IZW-Berlin) Approved by the "LUGV Brandenburg", permit: 23-2347-1-2009.

Capreolus capreolus: Game captures were conducted in accordance with European and French laws. The experiment was designed to minimize animal stress and handling time and to ensure animal welfare, as defined in guidelines for the ethical use of animals in research. A specific accreditation was also delivered to the OFB for capturing animals for scientific and wildlife management purposes. All methods were approved by the authorities (French Ministry of Environment). Roe deer captures and experimental procedures were in line with the French Environmental Code (Art.R421-15 to 421-31 and R422-92 to 422-94-1) and duly approved by legislation from the Prefecture of Paris (Prefectural Decree no. 2009-014).

Capreolus capreolus: All capture and marking procedures were done in accordance with French and European laws for animal welfare (prefectural order from the Toulouse Administrative Authority to capture and monitor wild roe deer and agreement no. A31113001 approved by the Departmental Authority of Population Protection).

Capreolus capreolus: Permit provided by the government of Upper Bavaria (ROB-55.2Vet-2532.Vet 02-17-190).

Capreolus capreolus: Resolution of the Provincial Government n. 602, under approval of the Wildlife Committee of 20/09/2011, and successive integration approved on the 23/04/2015.

Capreolus capreolus: The animal capture and handling protocols were authorized by the cantonal veterinary and animal welfare services with permit number BE75/11.

Cervus elaphus: Game captures were conducted in accordance with European and French laws. The experiment was designed to minimize animal stress and handling time and to ensure animal welfare, as defined in guidelines for the ethical use of animals in research. A specific accreditation was also delivered to the OFB for capturing animals for scientific and wildlife management purposes. Red deer captures, and experimental procedures were in line with the French Environmental Code (Art.R421-15 to 421-31 and R422-92 to 422-94-1) and duly approved by legislation from the Prefecture of Paris (Prefectural Decree no. 2009-014 and no. 2015-020).

Cervus elaphus: Permit provided by the Ministry of the Environment of the Czech Republic, number MZP/2019/630/361.

Cervus elaphus: Permit provided by the government of Upper Bavaria (Az. 55.2-1-54-2531-89-09).

Chlorocebus pygerythrus: The study was conducted with permission from the Kenya Government (NACOSTI permit no. P/15/5820/4650) and under IACUC protocol no. 17477 from the University of California, Davis.

Crocuta crocuta: Animal handling protocols were approved and conducted with the ethical clearance of the Animal Research Ethics Committee of the University of KwaZulu-Natal, South Africa (009/13/Animal), and the Institutional Animal Care and Use Committee of University of California at Berkeley (IACUC Protocol #R217-0512B) and Virginia Tech (IACUC Protocol #15-012). Scientific collecting permits were authorized from the Ministry of Environment and Tourism, Namibia (Research/Collecting Permits 1724/2012, 1834/2013, 1956/2014) and from the Department of Wildlife and National Parks, Botswana (Research Permit EWT 8/36/4 XXVIII [35]).

Cryptoprocta ferox: All research protocols were approved by the appropriate animal Use and care committees of Germany ("Bundesministerium für Naturschutz, BfN") and Madagascar ("Ministère de l'Environnement et des Eaux et Forêts, MINEEF").

Equus hemionus: Animal tracking permit provided by the Ministry of Environment and Tourism, Mongolia.

Erinaceus europaeus: (IZW-Berlin) Approved by ethical standards of the institution (IZW permit 2016-02-01), German law "Tierversuchsgenehmigung" permission numbers: Reg0115/15, and G0104/14, and the local nature conservation authority.

Eulemur rufifrons: All research protocols were approved by the appropriate Animal Use and Care Committees of Madagascar (Ministère de l'Environnement et des Eaux et Forêts, MINEEF: No 90/16/MEEMF/SG/DGF/DAPT
No 72/17/MEEMF/SG/DGF/DSAP/SCBT.RE.

Felis chaus: All captures and handling were approved by the Maharashtra State Forest Department: permit no. SPP-147, dated 17.3.2015.

Felis silvestris: Approved by the local nature conservation authority, permit number: ASTURIAS 2018/002528 LEON EP/CYL/666/2018.

Gazella subgutturosa: Animal tracking permit provided by the Ministry of Environment and Tourism, Mongolia.

Genetta genetta: Approved by The National Council of Science Technology and Innovation (permit number NACOSTI/P/14/357/2062), Kenya Wildlife Service (permit number KWS/BRM/5001) and through the Smithsonian Institution's National Museum of Natural History's Animal Care and Use Committee (Animal Study Proposal 2014-11).

Ichneumia albicauda: Approved by The National Council of Science Technology and Innovation (permit number NACOSTI/P/14/357/2062), Kenya Wildlife Service (permit number KWS/BRM/5001) and through the Smithsonian Institution's National Museum of Natural History's Animal Care and Use Committee (Animal Study Proposal 2014-11).

Lepus europaeus: Animal tracking was obtained in accordance with the Federal Nature Conservation Act (§ 45 Abs. 7 Nr. 3) and approved by the local nature conservation authority (reference numbers: 2347-6-2019, LUGV V3- 2347-22-2013, and 55.2-1-54-2532-229-13).

Lynx lynx: Approved by the PLA Moravian Karst Administration and the Czech Ministry of Environment, permit numbers: SR/0081/JM/2017; 34128/ENV/17-2146/630/17). Lynx live-trapping in Poland was approved by the National Ethics Committee for Animal Experiments (no. DB/KKE/PL—110/2001) and the Local Ethics Committee for Animal Experiments at the Medical University of Białystok, Poland (no. 52/2007).

Lynx lynx: Permit provided by the government of Upper Bavaria (Az. 55.2-1-54-2531-89-09).

Lynx rufus: All animal capture, handling, collaring, and sample collection was approved by the Institutional Animal Care and Use Committee (IACUC) of the University of California, Santa Cruz (Protocols "Seril 1701", and "Seril 1701 a1"). Scientific collecting permits were authorized by the California Department of Fish and Wildlife (Aromas, SCP-11968; Coyote Valley, SCP-13565).

Lynx rufus: Approved by Mississippi State University Institutional Animal Care and Use Committee, protocols 09-004, 12-012.

Madoqua kirkii: The research permit was approved by Mpala Research Center, Laikipia, Kenya.

Odocoileus virginianus: All activities were conducted according to guidelines established by the American Society of Mammalogists, and with authorization from the Oklahoma Department of Wildlife Conservation.

Ovibos moschatus: The study was approved by the Government of Greenland (permit no. 2019-88).

Panthera leo: Animal handling protocols were approved and conducted with the ethical clearance of the Animal Research Ethics Committee of the University of KwaZulu-Natal, South Africa (009/13/Animal), and the Institutional Animal Care and Use Committee of University of California at Berkeley

(IACUC Protocol #R217-0512B) and Virginia Tech (IACUC Protocol #15-012). Scientific collecting permits were authorized from the Ministry of Environment and Tourism, Namibia (Research/Collecting Permits 1724/2012, 1834/2013, 1956/2014) and from the Department of Wildlife and National Parks, Botswana (Research Permit EWT 8/36/4 XXVIII [35]).

Panthera pardus: The study was conducted with permission from the Kenya Government (NACOSTI permit no. P/15/5820/4650) and under IACUC protocol no. 17477 from the University of California, Davis.

Papio anubis: The study was conducted with permission from the Kenya Government (NACOSTI permit no. P/15/5820/4650) and under IACUC protocol no. 17477 from the University of California, Davis.

Propithecus verreauxi: All research protocols were approved by the appropriate Animal Use and Care Committees of Madagascar (Ministère de l'Environnement et des Eaux et Forêts, MINEEF: No 90/16/MEEMF/SG/DGF/ DAPT/SCBT.RE, No 72/17/MEEMF/SG/DGF/DSAP/SCBT.RE.

Procyon lotor: Approved by the "LUGV", permit number: 2347-7-2020.

Puma concolor: Research was approved by UCSC IACUC, proposal code Wilmc1312, and conducted under permit #11968.

Sus scrofa: All activities were conducted according to guidelines established by the American Society of Mammalogists; as defined by the Oklahoma Feral Swine Control Act (O.S § 6-601), only Judas pigs with tracking collars were released, all others were euthanized by law.

Sus scrofa: Approved by the ethics committee of the Ministry of the Environment Czech Republic number MZP/2019/630/361.

Sus scrofa: Approved by the Tuscany Regional Administration (permit number 103/5936/152 - 13/03/2002) and the Arezzo Province Administration (permit number 144160/42-41-2013 30/07/2013).

Sus scrofa: Approved by the Foreste Casentinesi National Park, permit numbers 626 - 10/12/2015 and 969 - 28/12/2018.

Sus scrofa: Approved by Regione Autonoma della Sardegna, permit number: 4753-74 del 07/03/2017.

Sus scrofa: Approved by regional council Tübingen, according to animal welfare law § 8.1 of the Federal State Baden-Württemberg, permit number: WFS1/12.

Tragelaphus oryx: Approved by the Namibian Council on Research, Science and Technology, certificate: RCIV00032018.

Tragelaphus strepsiceros: Approved by the Namibian Council on Research, Science and Technology, certificate: RCIV00032018.

Ursus americanus: Approved by Mississippi State University Institutional Animal Care and Use Committee, protocols 09-004, 12-012.

Ursus arctos: All captures and handling were approved by the Polish authorities (no. DOPOZ.6401.08.2.2013.ls, DOP-OZ. 6401.08.2.2013.ls.1, DZP-WG.6401.08.8.2014.JRO), Polish ethical committee (no. 21/2013 and 101/2014) and Decree of Polish Ministry of Environment (Dz.Urz.M.Ś. 2017 poz. 2) and/or Slovak Ministry of Environment (MZP SR c. 3555/2012-2.2).

Viverra tangalunga: Approved by the Sabah Biodiversity Centre and the Sabah Wildlife Department, license ref.no: JKM/MBS.10000-2/2 JLD.6[8].

Vulpes bengalensis: All captures and handling were approved by the Maharashtra State Forest Department: permit no. SPP-147, dated 17.3.2015.

Vulpes vulpes: Approved by the Himachal Pradesh Forest Department: WLM/Research study/1259, dated 10/05/2019.

Vulpes vulpes: Approved by the "Landesamt für Umwelt, Gesundheit und Verbraucherschutz Brandenburg" LUGV, permit number: 2347-25-2015 and V3-2347 13-2011.

Vulpes vulpes: Approved by the animal welfare licensing committee of Berlin ("Landesamt für Gesundheit und Soziales" LaGeSo), permit number: G0211/15.

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5.8 Supporting information

Mean daily deviance of activity and distances

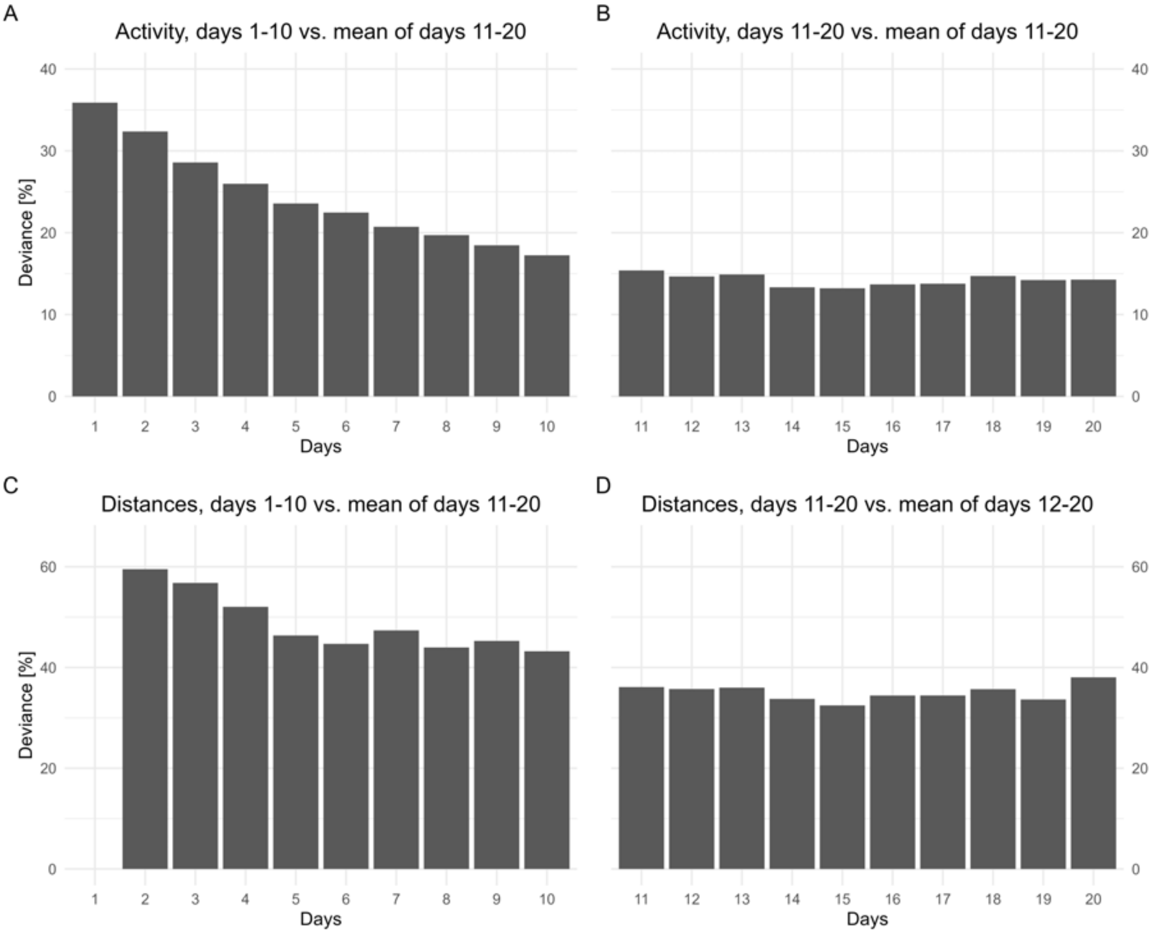


Fig. 5.5 S1: Absolute mean daily deviance of activity (ACC) and moved distances (GPS) of all individuals (n_{ACC} = 1243, n_{GPS} = 1451). A: Days 1 to 10 in relation to the mean of days 11-20 (ACC); B: Days 11 to 20 in relation to the mean of days 11-20 (ACC); Days 1 to 10 in relation to the mean of days 11-20 (GPS); Days 11 to 20 in relation to the mean of days 11-20 (GPS). Data of 42 mammal species.

Collar to body mass ratio

For species where we received true measurements of body mass and collar mass, we calculated the collar-body mass ratio (collar mass in percent of individuals body mass). From our data, it does not seem that individuals carrying a higher percentage load are more impaired than others (Fig. 7, S1). Yet, our maximum ratio is only 4.15%, with most of the animals carrying < 2%.

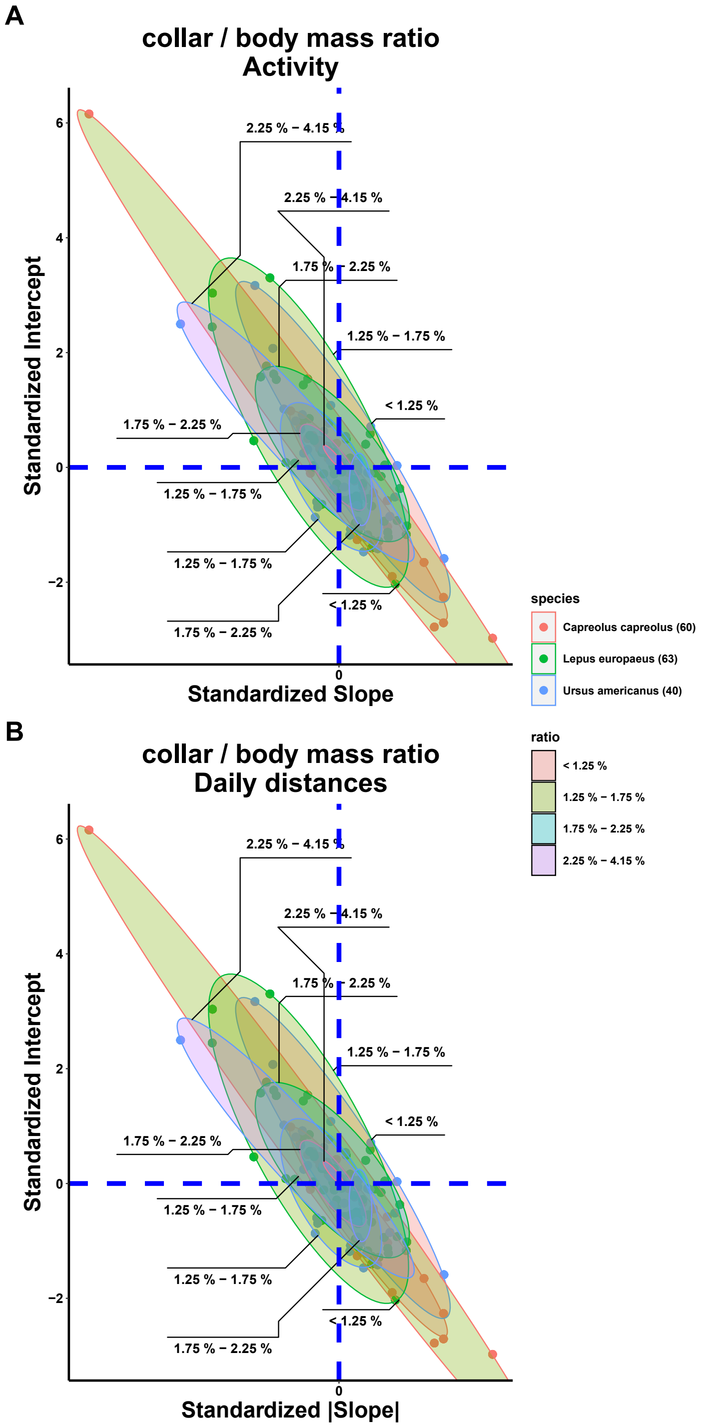


Fig. 5.6 S2: Classification of immediate reaction behavior (day 1) for activity (A) and distances (B) after collaring/release related to an individual's collar-body mass ratio.

Species table

Tab. S1: Overview of mammal species included in this study, the respective sample sizes, body mass, and dietary type.

Family	**Genus**	**Species**	$\mathbf{n_{ACC}}^{\alpha}$	$\mathbf{n_{GPS}}^{\alpha}$	**Mass [g]**$^{\beta}$	**Diet**
Felidae	*Acinonyx*	*jubatus*	0	14	46700	carnivore
Cervidae	*Alces*	*alces*	69	63	356998	herbivore
Bovidae	*Antidorcas*	*marsupialis*	7	10	31500	herbivore
Bovidae	*Bison*	*bison*	13	0	579255.3	herbivore
Bovidae	*Bison*	*bonasus*	27	26	500000	herbivore
Canidae	*Canis*	*aureus*	6	7	10345.2	omnivore
Canidae	*Canis*	*latrans*	18	0	13406.3	omnivore
Canidae	*Canis*	*lupus*	10	14	32183.3	carnivore
Bovidae	*Capra*	*ibex*	33	0	85166.5	herbivore
Cervidae	*Capreolus*	*capreolus*	672	547	22500	herbivore
Cervidae	*Cervus*	*elaphus*	34	43	131250	herbivore
Cercopithecidae	*Chlorocebus*	*pygerythrus*	12	12	3975	omnivore
Hyaenidae	*Crocuta*	*crocuta*	7	6	62999.9	carnivore
Eupleridae	*Cryptoprocta*	*ferox*	11	4	9500	carnivore
Equidae	*Equus*	*hemionus hemionus*	14	60	230000	herbivore
Erinaceidae	*Erinaceus*	*europaeus*	12	12	771	carnivore
Lemuridae	*Eulemur*	*rufifrons*	7	6	1820	herbivore
Felidae	*Felis*	*chaus*	12	12	7393	carnivore
Felidae	*Felis*	*silvestris*	5	5	5500	carnivore
Bovidae	*Gazella*	*subgutturosa*	7	7	28500	herbivore
Viverridae	*Genetta*	*genetta*	7	5	1800	carnivore
Herpestidae	*Ichneumia*	*albicauda*	6	5	3500	omnivore
Leporidae	*Lepus*	*europaeus*	63	47	3740	herbivore
Felidae	*Lynx*	*lynx*	10	6	17950	carnivore
Felidae	*Lynx*	*rufus*	35	35	8904.1	carnivore
Bovidae	*Madoqua*	*guentheri*	6	6	7500	herbivore
Cervidae	*Odocoileus*	*virginianus*	5	9	55508.6	herbivore
Bovidae	*Ovibos*	*moschatus*	6	6	340501.1	herbivore
Felidae	*Panthera*	*leo*	14	12	161499.1	carnivore
Felidae	*Panthera*	*pardus*	3	3	54999.7	carnivore
Cercopithecidae	*Papio*	*anubis*	6	6	28329.2	omnivore
Procyonidae	*Procyon*	*lotor*	12	12	6550	omnivore
Indriidae	*Propithecus*	*verreauxi*	14	14	3250	herbivore
Felidae	*Puma*	*concolor*	13	12	51600	carnivore
Suidae	*Sus*	*scrofa*	159	98	101052.1	omnivore
Bovidae	*Tragelaphus*	*oryx*	8	8	569993.6	herbivore
Bovidae	*Tragelaphus*	*strepsiceros*	7	7	213501	herbivore
Ursidae	*Ursus*	*americanus*	42	46	99949.4	omnivore
Ursidae	*Ursus*	*arctos*	14	15	180520.4	omnivore
Viverridae	*Viverra*	*tangalunga*	18	12	6885	omnivore
Canidae	*Vulpes*	*bengalensis*	8	8	2726	omnivore
Canidae	*Vulpes*	*vulpes*	18	18	5318.2	omnivore

$^{\alpha}$ only individuals with continuous data during the first 20 days of tracking were considered.

$^{\beta}$ data from trait database: Faurby et al. 2018, Phylacine 1.2: The Phylogenetic Atlas of Mammal Macroecology. *Ecology* 99:2626.

Recovery speed - species table

Tab. S2: Recovery speed, i.e., |slope day 1| for all species with significant disturbance effects (Fig. 1, Tab. 1), mean + sd values for both, distances (GPS) and activity (ACC). Higher values indicate a faster recovery.

study species	**mean (ACC)**	**sd (ACC)**	**mean (GPS)**	**sd (GPS)**
Alces alces	50.82	51.89	97.26	97.54
Bison bison	11.98	3.76	-	-
Bison bonasus	10.79	8.28	55.30	123.65
Canis aureus	21.15	9.71	-	-
Canis latrans	18.30	14.50	-	-
Canis lupus	24.69	7.43	22.54	13.53
Capra ibex	20.55	12.34	-	-
Capreolus capreolus	10.65	8.69	31.79	44.08
Cervus elaphus	31.78	29.56	35.69	32.49
Crocuta crocuta	16.44	14.26	286.43	419.38
Cryptoprocta ferox	-	-	22.50	15.75
Equus hemionus	11.39	10.75	46.13	55.07
Erinaceus europaeus	16.92	21.34	-	-
Felis chaus	17.53	9.48	20.26	15.23
Gazella subgutturosa	20.36	10.66	-	-
Genetta genetta	23.71	17.30	-	-
Ichneumia albicauda	17.92	15.76	-	-
Lepus europaeus	11.43	7.46	19.70	17.56
Lynx lynx	20.77	15.13	58.06	28.57
Lynx rufus	8.92	8.85	-	-
Odocoileus virginianus	-	-	19.07	11.65
Ovibos moschatus	16.05	12.39	-	-
Panthera pardus	22.67	14.08	34.96	26.46
Propithecus verreauxi	-	-	31.17	65.78
Sus scrofa	18.97	12.17	24.17	21.80
Tragelaphus oryx	-	-	37.45	18.26
Ursus americanus	-	-	20.25	13.72
Viverra tangalunga	15.44	6.71	17.47	14.16
Vulpes bengalensis	13.16	6.91	-	-
Vulpes vulpes	15.91	8.56	-	-

General Discussion

6.1 Movement ecology across scales

Movement ecology is a still-growing field of research seeking to understand the underlying factors that influence an animal's movement processes. Since as early as 1960, when the first animal, a ruffed grouse (*Bonasa umbellus*), was equipped with a radio tag to inform ecologists of its whereabouts (Benson 2010), researchers have constantly been striving to utilize and further advance technological capabilities (Bridge et al. 2011). Consequently, the use of tracking technologies has led to major discoveries in animal ecology and has profoundly advanced behavioral science and nature conservation strategies. For example, satellite tagging has enabled the tracking of blue whale (*Balaenoptera musculus*) movements across vast distances ($108 \pm 33.3 \frac{km}{day}$). Unraveling the migratory patterns of these endangered animals helped to guide conservation efforts (Mate et al. 1999). Lohmann (2007) discovered that sea turtles use magnetic cues to navigate long distances and return to the same nesting sites year after year, and Egevang et al. (2010) used geolocator-tracking to reveal that the Arctic tern (*Sterna paradisaea*) embarks on the longest animal migration, traveling from the Arctic to the Antarctic and back each year, with individuals recently shown to have covered distances of more than 96,000 km annually (Redfern and Bevan 2020).

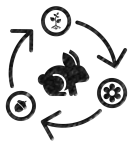
In large terrestrial herbivores, long-distance migrations may have evolved in order to obtain access to high-quality food and/or to reduce predation risk (Fryxell and Sinclair 1988). As a consequence, many populations of large herbivores migrate seasonally between discrete home ranges (Berger 2004, Gnanadesikan et al. 2017). Yet, anthropogenic landscape modifications, especially fences, hamper (Hering et al. 2022a, 2022b) or even prevent (e.g., Bartlam-Brooks et al. 2011) such migrations. Since many wildlife fences are prominent structures traversing large distances, their presence impedes animal movements and thus has far-reaching consequences on ecosystems (Vanak et al. 2010, Pirie et al. 2017). Fragmentation, in general, is an ever-increasing challenge for animals (Sala et al. 2000, Lino et al. 2019) and plant populations (Young et al. 1996, Wilson et al. 2016) worldwide. In Europe, agricultural landscapes currently account for 45% of land use (Ramankutty et al. 2008). With the resulting disappearance of semi-natural habitats (Benton et al. 2003), disproportionately growing field sizes led to depleted landscapes, with low diversity of crop types, fewer field edges, less non-crop habitats (Baguette and Van Dyck 2007), and overall comparatively little biodiversity (Stoate et al. 2009).

Hares play a crucial role as an umbrella species in agricultural landscapes (Schai-Braun et al. 2020). They contribute to seed dispersal (genetic link), further influence vegetation dynamics interactions through grazing (process link), and nutrient transfer across trophic levels via defecation (resource link) by feeding on a variety of herbs, grasses, and field crops (Tapper and Barnes, 1986; Schai-Braun et al. 2013). Yet, the efficiency of such mobile links is highly determined by the unpredictability of agricultural measures in such fragmented landscapes.

Farming practices can not only affect the ecological functions provided by hares (e.g., trough mowing or plowing) but also disrupt an individual's movement patterns, further influencing the overall dynamics of these functions.

In the preceding chapters, I investigated a hare's seed germination success after digestion in a controlled feeding experiment to determine its potential as a seed disperser. I explored the effect of seed characteristics on germination while controlling for phylogenetic relatedness. In addition, I used GPS data from hares to assess landscape connectivity in two contrasting landscapes (Chapter I). To reveal differences in space use that may reflect different exploration styles along the shy-bold continuum (Chapter II), I conducted standardized box emergence tests on captive and wild European hares to assess behavioral differences. I determined individual boldness levels in a wild hare population by measuring behavioral response latencies and, further related those to general activity and space use. In Chapter III, I studied the impact of extreme weather conditions on hare activity during their peak reproduction period. By examining their sensitivity to rising temperatures, wind speed, and humidity, I investigated the potential effects on hares as they invest energy in mating, competing, and lactating. Given the ongoing climate change, extreme weather events will directly affect the fitness and population dynamics of hares and other wildlife species. Using GPS tracking and acceleration data from 1451 terrestrial mammals out of 42 species, in Chapter IV, I quantified the effects of trapping and handling. By considering life history traits and analyzing activity and movement patterns, I assessed disturbance intensity and the recovery speed of different species from the collaring procedure. Based on these findings, I provided recommendations for data analysis during the initial tracking period.

6.2 Lessons from a mobile linker



We used GPS devices in combination with tri-axial accelerometers deployed on European hares (*L. europaeus*) to shed light on its role as a mobile linker. While disentangling the effects of seed morphological traits on germination success and controlling for phylogenetic relatedness, we further measured the landscape connectivity via hares in two contrasting agricultural landscapes in Brandenburg (homogeneous, large field sizes) and Bavaria (heterogeneous, small field sizes) using GPS- based movement data. Anthropogenic disturbances can have direct (e.g., fragmentation) and indirect effects (e.g., changing plant communities) on habitat connectivity (Wenner et al. 2022). Plant species with restricted dispersal ability, as well as those unable to inhabit the urban matrix, show greater levels of genetic divergence in response to human influences (Epps and Keyghobadi 2015), indicating a limited dispersal capability. In disturbed landscapes, such as agricultural fields, mobile linkers like hares can act as mediators of recolonization by importing seeds from off-site areas, such as grasslands or field margins, to areas where the resources for natural succession are depleted (Duncan and Chapman 1999, Lundberg and Moberg 2003). By analyzing habitat connectivity through hares and considering seeds' germination success, they clearly can act as effective mobile linkers contributing to ecosystem stability in times of agricultural intensification, not only in heterogeneous but also in homogeneous landscapes. The direction of ecosystem development following a disturbance is often determined by the presence of mobile linkers, which are generally crucial for ecosystem resilience (Cox and Elmqvist 2000, Nyström and Folke 2001), but also by the seed availability. Tsoar et al. (2011) applied the movement ecology framework to the movement of passively transported organisms, such as diaspores (Damschen et al. 2008, Wright et al. 2008). Thereby, they demonstrated a twofold nested design of the movement ecology framework by considering both (the seed and the animal) as a *focal individual* (Fig. 6.1). In the case of hares, individuals connected more fields, but fewer isolated grassland patches in heterogeneous compared to homogeneous landscapes, within their species-specific retention time. Despite animal movement being the key factor affecting the seed's fate, it might also be relevant to consider additional factors essential for epi- or endozoochoric seed dispersal. The seed traits identified in Chapter 1, crucial for successful endozoochorous seed dispersal in hares, are those that reduce the seed's exposure to the stomach or gut and their associated digestive fluids. These traits are characterized by denser seeds with less surface area. In addition, supported by the inclusion of phylogeny and that seeds with similar traits show different germination rates, we argue that specific compositions of the seed coat are better adapted to survive digestion than others. Further, despite the overall fairly low germination rates following hare digestion (mean standardized germination success: 6%), we underscore that long-distance dispersion by endozoochory (Nathan et al. 2008, Schurr et al. 2009) may have disproportionately huge effects on plant community composition and species survival in dynamic agricultural landscapes.

Our findings further suggest that management plans for agricultural landscapes must consider the functional role of mobile linkers like hares in maintaining ecosystems and contributing to ecosystem resilience. Rare and non-neophytic species showed higher germination rates in our study, highlighting the importance of maintaining high plant diversity at field margins. This can be achieved by establishing flowering strips or temporary set-aside fields (Wietzke et al. 2020, Eccard 2022). Overall, we highlight the importance of mobile linkers such as hares in promoting ecosystem resilience and emphasize the need for targeted conservation efforts to preserve their natural habitats and, thus, protect their populations and their functions.

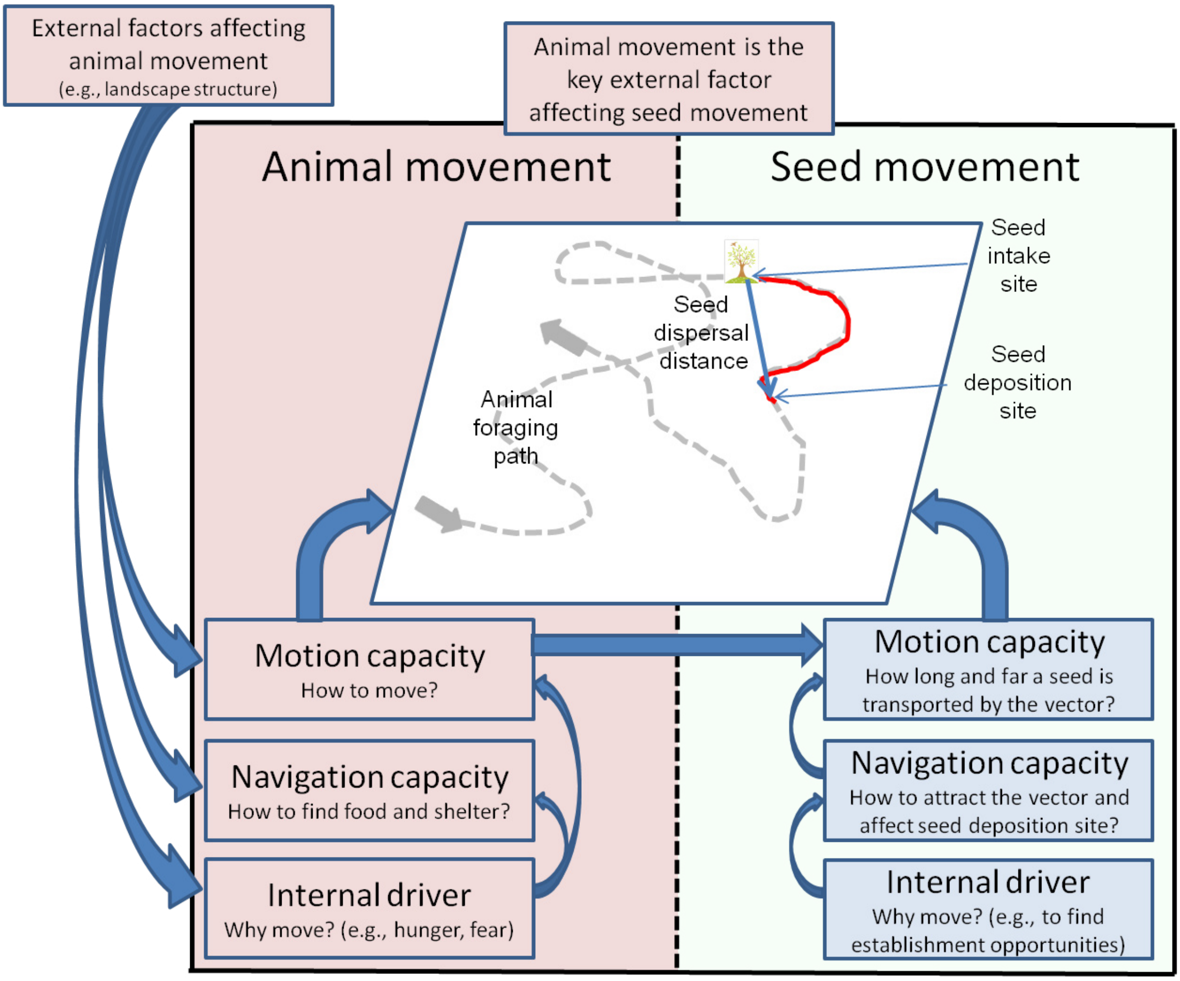


Fig. 6.1 From Tsoar et al. (2011). A general conceptual framework for endozoochoric seed dispersal. The framework has a twofold nested design: In the inner loop, the dispersed seed is the focal individual and the animal (the dispersal vector) is the major external factor affecting its movement. In the outer loop, the dispersal vector is the focal individual.

6.3 Animal personality - individual behavior and ecological consequences

The phenomenon of individual differences in behavior has become known as ‘animal personality’ and has many synonyms in the literature, such as temperament, coping style, and behavioral type (Sih et al. 2004, Réale et al. 2007). Traits like boldness (Ward et al. 2004), activity level (Eccard and Herde 2013), and exploration tendency (Réale et al. 2007) can impact an animal’s ability to navigate complex environments (Conrad et al. 2011), respond to potential threats (Krause and Ruxton 2002, Leclerc et al. 2017), and effectively exploit resources (Patrick et al. 2017, Gharnit et al. 2020). For hares, we found behavioral responses to be consistent over time and further show a positive correlation between general activity and boldness in both captive and wild hares. In wild hares, space use also varied with boldness, with shy individuals having smaller core areas with larger home ranges compared to bolder conspecifics. We assume this pattern arises due to shy individuals avoiding high-risk, energy-consuming competition for valuable resources. In fragmented landscapes where valuable food resources are scarce and highly scattered, additional research is needed to understand the influence of behavioral traits on the scale of mobile link functions. Specifically for seed dispersal, it might be intriguing to investigate whether nutritious seeds show different patterns of endozoochoric dispersal compared to less nutritious seeds, as such might be dominantly foraged by bold individuals. Information on individual behavioral types can help to explain variation in state-dependent behavior (e.g., risk-taking) or an individual's space use and further facilitate mechanistic understanding of processes that drive spatial, ecological, and evolutionary dynamics. Several personality traits linked to movement have been found to be heritable (Réale et al. 2007). For example, in three different populations of great tits *Parus major* (Drent et al. 2003, Quinn et al. 2009, Nicolaus et al. 2012), variation in exploration behavior was found to have a significant heritable component, making the trait liable for evolutionary change (van Oers et al. 2004a). Moreover, Dingemanse et al. (2003) found offspring from fast-exploring great tits to disperse further distances compared to slow-exploring parents, while fast explorers also took larger risks. Van Oers et al. (2004b) found risk-taking behavior heritable and to diverge significantly after two generations. In conclusion, animal personality can significantly impact movement characteristics and, in turn, have important ecological and evolutionary consequences. Evidence is accumulating that variation in animal personality is extremely widespread and significantly affects ecological and evolutionary processes (Sih et al. 2012, Wolf and Weissing 2012). Activity measurements, particularly ODBA, derived from tri-axial accelerometers, can be a beneficial tool for remotely analyzing behavioral types based on thorough validation under defined conditions. Since accelerometers are readily obtainable in GPS devices, we suggest utilizing these sensors, especially during the very first days of animal tracking, to assess individual variations in activity patterns. This technique will help us understand the underlying mechanisms influencing ecological and spatial changes in various habitats. Considering animal personalities in space use studies might be crucial, as there is increasing evidence that sampling bias may inevitably influence the composition of animal personalities within a drawn sample and, therefore, the results of the respective study (Réale et al. 2007, Morton et al. 2013). Behavioral and ecological studies of various species may be affected, as the test subjects may not represent larger populations whose ecological patterns the researchers seek to understand.

6.4 Climate change - Another challenge for wildlife

Changing weather conditions due to climate change can significantly affect the activity, movement behavior, and energy expenditure of wildlife, which are crucial for individual fitness (Brown et al. 2004). For hares, in the peak breeding season during summer, we found a non-linear relationship between temperature and activity with contrasting changes in activity between day and night: Activity increased at higher temperatures during the inactive period (day) and decreased during the active period (night) - with the strongest decrease during hot tropical nights. Our findings highlight the importance of understanding the complex relationships between extreme weather conditions and mammal behavior, which is critical for conservation and management. In three African antelope species (*Antidorcas marsupialis*, *Tragelaphus strepsiceros*, and *T. oryx*), individuals were shown to reduce their activity with rising temperatures, with the effect size decreasing with increasing species' body mass (Berry et al. 2023); concluding that body size may further affect activity responses under heat load, possibly being further associated with predation pressure (Owen-Smith and Mills 2008, Berry et al. 2023). With ongoing climate change, extreme weather periods, such as heat waves, extreme precipitation events, or prolonged droughts witnessed during the recent summers in Europe, are predicted to occur more often and to last longer (IPCC 2023; Kahlenborn et al. 2021). Our study area lies in the middle of the temperature range of the hare distribution in Europe, where there has been a significant increase in temperature over the last decade (2010−2020) compared to 1970−2010. While precipitation is generally considered more important than the temperature for short-term hare population fluctuations (Rödel and Dekker 2012), we found strong evidence that hares exhibit immediate changes in activity when faced with high-temperature extremes. Specifically, hares showed decreased activity during hot tropical nights and increased their activity during the resting period at daytime. The substantial decrease in nighttime activity means lost time for essential activities such as foraging and mating.

Climate change is known to affect survival and reproduction negatively and, consequently, population dynamics of several species (Román-Palacios and Wiens 2020), with the leading cause attributed to increasing temperature extremes (Sinervo et al. 2010, Fuller et al. 2010). With habitat loss and climate change being the two greatest threats to global biodiversity (Barlow et al. 2018; Ducatez and Shine 2017), animals living in large agricultural matrices, such as deer, rodents, or small carnivores, are particularly prone to suffer from its consequences. In the case of hares, however, it remains unclear whether their populations will eventually relocate to more northern regions or if they can withstand climate extremes by adjusting their behavior accordingly.

6.5 The dilemma with animal-borne sensors

GPS- collaring has become an important tool for studying the ecology and behavior of animals across the globe. However, this strategy presents a quandary as the collaring process (Murray and Fuller 2000) or even the collar *per se* may affect animal behavior (Powell and Proulx 2003), possibly resulting in biased data. To gain insights on the effects of the process of being trapped, handled, and equipped with a GPS collar, we conducted a global outreach to researchers involved in animal tracking, collecting GPS and accelerometer (ACC) data of the initial days of tracking from 1451 individuals out of 42 mammal species. By looking at the activity (ACC) and movement (GPS) patterns of multiple mammal species across different ecosystems, we explored how long handling impacts affect movement behavior. We discovered that collaring events affected individuals in terms of both activity and distance traveled. While an immediate change in behavior after successful collaring was clearly evident in the data during the initial days of tracking, a gradual stabilization occurred in subsequent days. We observed substantial intraspecific variation in activity and movement patterns, with individuals being either more or less active or traveling shorter/larger daily distances after release. Animal personalities may explain a fraction of this intraspecific variation. However, most tracking studies included in this global meta-analysis were focussing on other research questions. Females are mainly responsible for gestation, delivery, and child-rearing in mammals (5-10% of mammalian species engage in paternal care [Woodroffe & Vincent, 1994]). Females may be more vulnerable to stress and physical strain during capture and handling due to their reproductive obligations, which may explain why females recover more slowly than males. The recovery speed of activity and daily distances after capturing, collaring, and releasing was slower in herbivores than in omnivores and carnivores. This is intriguing from an evolutionary perspective since predators frequently hunt many wild herbivores, and hence, these would be expected to be better adapted and recover faster from such stressful events. However, the severe anesthetic utilized, especially for large herbivores, may also be reflected in this data. To avoid direct interactions with humans, several species display behavioral flexibility and can change their activity patterns, habitat choices, and movement behavior accordingly (Tucker et al. 2018, Tucker et al. 2023). On the other hand, animals living in rather remote areas are less likely to encounter humans and are, therefore, less exposed to anthropogenic disturbances. As a result, when these animals eventually get caught & collared, they might show an exacerbated response behavior toward the disturbance and remain alert for a prolonged time, as strongly indicated by our analysis. Most importantly, our results enable further development of methods to minimize collaring effects and identify potentially biased data, to improve both animal welfare and the science bolstered by localization studies. Ethics committees can use these results to make decisions about whether to allow studies involving animal biotelemetry. Animal tracking is essential for gaining insight into the behavior of wildlife, directing conservation efforts, and influencing management decisions. By being aware of and actively addressing the constraints, researchers can maximize the benefits of GPS-collaring while minimizing any negative consequences on the animals being examined.

6.6 Synthesis

Mobile linkers such as the hare play an important role in seed dispersal across agricultural matrices with fragmented habitats. They operate as recolonization mediators by bringing seeds from distant locations to regions with limited opportunities for natural succession. While hares will eventually disperse a great variety of plant species in such landscapes through epi- or endozoochory, certain seed traits allow diaspores to attain higher germination rates after complete digestion than others (i.e., dense seeds with comparatively small surface areas and flat, elongated shape). As a result, the occurrence of hares will have a considerable impact on the direction of ecosystem development, particularly following disturbances, by influencing local plant communities. Thereby, individual movement decisions and prevailing weather conditions will ultimately determine the fate of the diaspores. When interpreting such movement patterns, it is hence critical to further include differences in space use among individuals, as those might reflect different exploration strategies that are consistent over time. These consistent strategies, i.e., animal personalities, provide vital insights into state-dependent behaviors and help to comprehend spatial and ecological dynamics in heterogeneous environments. Undoubtedly climate change, especially heat extremes, will and already does challenge hares' activity patterns and their use of space. Similar responses have been documented, e.g., for red deer (Rivrud et al. 2010), Arabian oryx (Hetem et al. 2012), or tropical bats (Appel et al. 2019). This may even lead to changes in the community composition of mammals and other taxa, as suggested by Berry et al. (2023) in African antelopes. According to climate change forecasts, the frequency and duration of extreme weather events, particularly heat waves, will increase. Hares can adjust their activity patterns in response to high-temperature extremes, such as decreasing activity during hot nights and increasing activity during resting times throughout the day. Heat waves further reduce food availability and thus may negatively impact hare populations, thereby limiting mobile links. In general, when working with GPS-based data, it is also important to consider and, if possible, account for the resulting impacts of the collaring procedure and the collar *per se* on the focal animal. Collaring mammals can substantially influence movement characteristics and activity patterns, thereby potentially leading to biased data, especially throughout the initial days of tracking. While tracking animals is important for studying wildlife dynamics, conservation efforts, and guiding management decisions, researchers can maximize the benefits of GPS collaring while maintaining animal welfare by limiting collaring impacts and resolving potential biases.

While understanding the far-reaching anthropogenic influence on animal movements is paramount to effective land use planning and conservation strategies, animal tracking will undoubtedly continue to significantly contribute to our understanding of the environment, with continual technical advancements, improved methods, and consideration of ethical concerns inevitably being involved.

6.7 References

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Declaration

Herewith I declare to have prepared this dissertation independently and with the help of my supervisors. I marked all parts, which originate from publications. This thesis has not been submitted to any other university or institution before.

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Place, Date

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Jonas Stiegler