TURUN
YLIOPISTO
UNIVERSITY
OF TURKU

INVESTIGATING THE HUMAN-ANIMAL RELATIONSHIP IN WORKING ANIMALS

Océane Liehrmann

TURUN YLIOPISTON JULKAISUJA – ANNALES UNIVERSITATIS TURKUENSIS
SARJA – SER. AII OSA – TOM. 403 | BIOLOGICA – GEOGRAPHICA – GEOLOGICA | TURKU 2023

TURUN
YLIOPISTO
UNIVERSITY
OF TURKU

INVESTIGATING THE HUMAN-ANIMAL RELATIONSHIP IN WORKING ANIMALS

Océane Liehrmann

TURUN YLIOPISTON JULKAISUJA – ANNALES UNIVERSITATIS TURKUENSIS
SARJA – SER. AII OSA – TOM. 403 | BIOLOGIA – GEOGRAPHICA –GEOLOGICA | TURKU 2023

University of Turku

Faculty of Science
Department of Biology
Section of Ecology
Doctoral programme in Biology, Geography and Geology (BGG)

Supervised by

Professor, Virpi Lummaa
Department of Biology
University of Turku, Finland

Docent, Mirkka Lahdenperä
Department of Biology
University of Turku, Finland

PhD, Léa Lansade
UMR Physiologie de la Reproduction &
des Comportements
INRAE Centre Val-de-Loire, France

Reviewed by

Associate Professor, Katrina Merkies
Department of Animal Biosciences
University of Guelph, Canada

PhD, Christian Nawroth
Research Institute for Farm Animal
Biology (FBN)
Institute of Behavioural Physiology,
Germany

Opponent

Associate Professor, Maria Vilain Rørvang
Department of Biosystems and Technology
Swedish University of Agricultural Sciences, Sweden

The originality of this publication has been checked in accordance with the University of Turku quality assurance system using the Turnitin Originality Check service.

Cover Image: Océane Liehrmann

ISBN 978-951-29-9428-1 (Print)
ISBN 978-951-29-9429-8 (PDF)
ISSN 0082-6979 (Print)
ISSN 2343-3183 (Online)
Painosalama, Turku, Finland 2023

À ma Mamie Claude (1928-2022)

UNIVERSITY OF TURKU
Faculty of Science
Department of Biology
Biology
OCEANE LIEHRMANN: Investigating the Human-Animal Relationship in Working Animals
Doctoral Dissertation, 138 pp.
Doctoral Programme in Biology, Geography and Geology (BGG)
August 2023

ABSTRACT

Throughout history, humans have coexisted with animals, fulfilling various roles in human life including providing food, clothing, and assistance in research and labor. The study of human-animal relationships has been a subject of interest for centuries; however, studies have predominantly focused on pets, livestock, and zoo animals, leaving a lack of attention to the relationships between humans and working animals despite their significant time spent in proximity to humans.

With this thesis I aimed to address this gap by exploring overlooked factors that influence the relationship between working animals and their handlers. Specifically, I delved into the impact of familiarity, relationship duration, the number of handlers and past owners, handler experience, and animals' own experiences as well as the effects of different living environments on the human-animal relationship.

To achieve these research goals, I conducted experiments with three species of large ungulates used for transportation purposes: timber working Asian elephants, leisure horses, and sledge reindeer. Ungulates are the biggest representative of the working animals and a focus on these three populations, having different history with humans and living in different contexts, allowed the investigation of various aspects of the human-working animal relationship. The experiments focused on exposure to novelty in the presence of human handlers and communication tasks between animal and handler. The goal was to reproduce situations that are commonly encountered and crucial in a human-animal working context.

The findings revealed that longer and more familiar relationships between handlers and animals led to reduced reluctance towards novelty in Asian elephants and horses. However, reindeer appeared to be less sensitive to handler familiarity. These differences could be attributed to the amount of time the different species in our populations spend with their familiar caretakers. These results suggest that the development of a positive human-animal relationship may require a significant amount of time, influenced by multiple factors, including the animal’s previous interactions and experiences with humans, as well as the cumulative impact of repeated interactions shaping the animal's daily life. Age and training experience played important roles in all three species, with younger individuals showing more exploratory behaviours and older individuals demonstrating increased success in communication. This finding suggests that as animals mature and receive more training, they become more adept at understanding and responding to human

communicative cues. The social and physical environment strongly influenced horses' success at following human cues, with larger groups and larger fields leading to higher success rates. An appropriate living environment can enhance animals' cognitive development and performance in communicative tasks with humans.

Altogether, the five chapters of this thesis offer a fresh and comprehensive perspective on the study of the human- working animal relationship, specifically from the vantage point of working animals. These findings hold valuable implications for practices and training techniques concerning draft working animals, empowering handlers to customise their approaches based on the distinct characteristics and sensitivities of each species. It is imperative to acknowledge and address the specific needs of working animals and to establish suitable living conditions that cater to their physical, social, and cognitive requirements. The creation of environments that foster cognitive growth, cultivate positive relationships between animals and handlers, and provide opportunities for learning and exploration can significantly enhance the well-being and effectiveness of working animals.

KEYWORDS: Human-animal interaction; Asian elephant; Horse; Reindeer; Draft animals; ungulate behaviour; Novel object test; referential communication; human familiarity; social environment

TURUN YLIOPISTO
Matemaattis-luonnontieteellinen Tiedekunta
Biologian Laitos
Biologia
OCEANE LIEHRMANN: Tutkitaan ihmisen ja eläimen suhde työeläimissä
Väitöskirja, 138 s.
Biologian, maantieteen ja geologian tohtoriohjelma (BGG)
Elokuu 2023

TIIVISTELMÄ

Kautta aikojen ihmiset ovat eläneet yhdessä eläinten kanssa ja hyödyntäneet niitä eri tavoin, kuten ruoan ja vaatetuksen hankkimiseen ja käyttämällä eläimiä apuna tutkimuksessa ja työssä. Ihmisten ja eläinten suhteiden tutkimus on ollut kiinnostuksen kohteena vuosisatojen ajan, mutta nämä tutkimukset ovat pääosin keskittyneet lemmikkeihin, karjaan ja eläintarhaeläimiin, jättäen huomiotta ihmisten ja työeläinten väliset suhteet, vaikka nämä eläimet viettävät huomattavan paljon aikaa ihmisten läheisyydessä.

Tämän väitöskirjan tavoitteena oli paikata tämä aukko tutkimalla huomiotta jääneitä tekijöitä, jotka vaikuttavat työeläinten ja niiden hoitajien väliseen suhteeseen. Keskityin erityisesti tutkimaan tuttavuuden, suhteen keston, hoitajien ja entisten omistajien määrän, hoitajien kokemuksen ja eläinten omien kokemusten sekä erilaisten elinympäristöjen vaikutusta ihmisen ja eläimen väliseen suhteeseen.

Saavuttaakseni nämä tutkimustavoitteet suoritin kokeita kolmen suurikokoisen, kuljetustarkoituksiin hyödynnetyn eläinlajin kanssa: metsätyössä käytettävien aasiannorsujen, vapaa-ajan hevosten sekä rekiporojen. Sorkka- ja kavioeläimet edustavat suurinta osaa työeläimistä ja näiden kolmen eläinpopulaation suuret erot historian ja elinympäristön suhteen mahdollistivat laajan näkökulman ihmisen ja työeläimen väliseen suhteeseen. Kokeissa keskityttiin uutuudelle altistamiseen ihmishoitajien läsnä ollessa sekä eläimen ja hoitajan välisiin kommunikaatiotehtäviin. Tavoitteena oli toisintaa tilanteita, jotka ovat yleisiä ja ratkaisevan tärkeitä ihmis-eläin -työkontekstissa.

Tulokset osoittivat, että pidemmät ja tutummat suhteet hoitajien ja eläinten välillä johtivat vähentyneeseen vastahakoisuuteen uutuutta kohtaan aasiannorsujen ja hevosten kohdalla. Porot vaikuttivat sen sijaan vähemmän herkiltä hoitajien tuttuudelle. Nämä erot voitiin liittää siihen, kuinka paljon aikaa eri lajien yksilöt viettävät tuttujen hoitajiensa kanssa. Tulokset viittaavat siihen, että myönteisen ihmisen ja eläimen välisen suhteen kehittäminen voi vaatia merkittävän määrän aikaa ja että prosessiin vaikuttavat monenlaiset tekijät, mukaan lukien eläimen aiemmat vuorovaikutukset ja kokemukset ihmisten kanssa sekä toistuvien vuorovaikutusten kumulatiivinen vaikutus eläimen päivittäiseen elämään. Ikä ja koulutuskokemus olivat tärkeitä kaikkien kolmen lajin kohdalla: nuoremmat yksilöt osoittivat enemmän tutkivia käyttäytymismuotoja, kun taas vanhemmat yksilöt onnistuivat paremmin kommunikaatiossa. Tämä löydös viittaa siihen, että eläinten kypsyessä ja saadessa enemmän koulutusta ne kehittyvät taitavammiksi ihmisten

viestintämerkkien ymmärtämisessä ja niihin reagoimisessa. Sosiaalinen ja fyysinen ympäristö vaikutti voimakkaasti hevosten onnistumiseen ihmisen vihjeiden seuraamisessa: suuremmat ryhmät ja laajemmat alueet johtivat korkeampiin onnistumisasteisiin. Sopiva elinympäristö voi edistää eläinten kognitiivista kehitystä ja suorituskykyä kommunikaatiotehtävissä ihmisten kanssa.

Kaiken kaikkiaan tämän väitöskirjan viisi osaa tarjoavat tuoreen ja kattavan näkökulman ihmisen ja työeläimen suhteen tutkimukseen, erityisesti työeläinten näkökulmasta. Tutkimuslöydökset ovat erityisen arvokkaita tarkasteltaessa työeläimiä koskevia käytäntöjä ja koulutustekniikoita. Hoitajilla on mahdollisuus muokata lähestymistapojaan kunkin lajin erityispiirteiden ja herkkyyksien perusteella. Työeläinten erityistarpeet on tärkeää tunnustaa ja niihin tulee vastata sekä luoda sopivia elinolosuhteita, jotka vastaavat eläinten fyysisiä, sosiaalisia ja kognitiivisia tarpeita. Kognitiivista kasvua tukevien, kokeilemista ja oppimista mahdollistavien sekä eläinten ja hoitajien välisten myönteisten suhteiden kehittymiseen kannustavien ympäristöjen luominen voi merkittävästi parantaa työeläinten hyvinvointia ja tehokkuutta.

ASIASANAT: Ihmisen ja eläimen vuorovaikutus; aasialainen elefantti; hevonen; poro; työeläimet; sorkka- ja kavioeläinten käyttäytyminen; novel object -testi; referentiaalinen kommunikaatio; ihmisen tuttuus; sosiaalinen ympäristö

Table of Contents

Abbreviations

HAR	Human-Animal Relationship
FAO	Food and Agriculture Organisation
MTE	Myanma Timber Enterprise
SPANA	Society for the Protection of Animals and Nature

List of Original Publications

This dissertation is based on the following original publications, which are referred to in the text as "Chapters" followed by their Roman numerals:

I Crawley, J.; Liehrmann, O.; Franco dos Santos, D.; Nyein, K.; Aung, H. H.; Htut, W.; Oo, Z. M.; Seltmann, M.; Webb, J.; Lahdenperä, M.; Lummaa, V. Influence of handler relationships and experience on the health, stress and behaviour of semi-captive Asian elephants. *Conservation Physiology*, 2021; 00(00): coaa116.

II Liehrmann, O.; Crawley, J.; Seltmann, M.; Feillet, S.; Nyein, K.; Aung, H. H.; Htut, W.; Oo, Z. M.; Lahdenperä, M.; Lansade, L.; Lummaa, V. Handler familiarity helps to improve working performance during novel situations in semi-captive Asian elephants. *Scientific Reports*, 2021; 11, 15480.

III Liehrmann, O.; Viitanen, A.; Riihonen, V.; Alander, E.; Koski, E.S.; Lummaa, V.; Lansade, L. Multiple handlers, numerous owner changes and short relationship length affect horses' responses to novel object tests. *Applied Animal Behaviour Science*, 2022; 11, 15480.

IV Liehrmann, O.; Cosnard, C.; Jardat, P.; Viitanen, A.; Riihonen, V.; Alander, E.; Koski, E.S.; Lummaa, V.; Lansade, L. What drives horse success at following human-given cues? An investigation of handler familiarity and living conditions. *Animal Cognition*, 2023; 1-12

V Liehrmann, O.; Ollila, A.; Lummaa, V.; Lansade, L; Seltmann, M. First observation of reindeer responding to human given cues. *Journal of Comparative Psychology*, 2023; Advance online publication

Author contributions to the original publications/manuscripts:

CHAPTERS	I	II	III	IV	V
ORIGINAL IDEA	JAHC, ML, VL	JAHC, MS, ML, VL	OL, LL, VL	OL, LL, VL	OL, MS
DATA COLLECTION	DJFDS, HHA, UKN, OL, JLW, JAHC, MS	JAHC, MS, OL, SF, UKN, HHA	OL, AV, VR, EA	OL, AV, VR, EA, CC	OL, MS, AO
LAB ANALYSES	JB, DJFDS,	-	-	-	-
STATISTICAL ANALYSES	JAHC, OL	OL, SF	OL, AV	OL, CC	OL
PROJECT ADMINISTRATION	WH, ZMO, VL	WH, ZMO, VL	OL	OL	OL, MS
WRITING: ORIGINAL DRAFT	JAHC	OL	OL	OL	OL
WRITING: REVIEW AND EDITING	JAHC, VL, ML, OL, JLB	OL, JAHC, MS, VL, ML, LL	OL, SK, VL, LL	OL, CC, PJ, SK, VL, LL	OL, MS, VL, LL, AO

1 Introduction

1.1 The human-animal relationship

Humans have always shared their environment with other animals, which play diverse roles in human life. They provide food and clothing, serve in medical and cosmetic research, and are used for mechanical force, entertainment, leisure, and companionship. The earliest signs of domestication can be traced back around 30,000 years with wolves (Thalmann et al. 2013), while the domestication of ungulates began approximately 12,000 years ago and expanded with human sedentism. Zeder (2012) describes three common pathways of domestication: The commensal pathway with naturally anthropophilic commensal species adapting to human environments (e.g. wolves foraging on human food waste); the prey pathway, such as the transition from traditionally hunted prey species to managed stocks (e.g. goats, sheep, pigs, reindeer); and the directed pathway leading to the use of species for a particular purpose (e.g. horses, donkeys, elephants and camels used for transportation). The study of human-animal relationships and interactions has been a subject of interest for centuries (Serpell 1996, Beierl 2008), with experimental research in this field growing since the 1980s. Previous studies have focused on companion and agricultural animals, but there is an increasing body of literature on laboratory, zoo, and wild animals (Hosey and Melfi 2014).

Key terms that are central to the scientific literature on human-animal relationships include human-animal interactions, human-animal relationship, and human-animal bond. These terms often lack precise definitions and can be a source of debate and confusion. However, in this thesis, they are discussed within the following context:

- **Human-animal interactions**: "A sequence in which individual A shows behaviour X to individual B, or A shows X to B and B responds with Y" (Hinde 1976). An interaction is a single event, and its nature can be positive, neutral, or negative but must result in the behavioural reaction of one individual in response to a behaviour performed by another.

- **Human-animal relationship**: "a series of interactions over time between two individuals known to each other" (Hinde 1987). The relationship is

developing on the basis that animals can memorise and predict future interactions with humans. The quality of the relationship relies upon the quality of the interactions on which it is based (Rault et al. 2020).

- **Human-animal bond**: "mutually beneficial and dynamic relationship between people and animals that is influenced by behaviours that are essential to the health and well-being of both. This includes, but is not limited to, emotional, psychological, and physical interactions of people, animals, and the environment." American Veterinary Medical Association (AVMA, 1998). The human-animal bond, through its mutual beneficial dynamic can be considered as the by-product of a human-animal relationship based on net positive interactions (Hosey and Melfi 2014).

1.1.1 The human-animal relationship and welfare

The human-animal relationship is a crucial factor in determining animal welfare, and it can have either detrimental or positive effects on the overall well-being of animals (Rault et al. 2020) (Table 1). Numerous studies have observed the detrimental impacts of human-animal relationships on animal health, stress, and productivity. Inappropriate behaviours from handlers or caretakers, such as shouting, slapping, hitting, and kicking, can result in high levels of fear and avoidance of humans in farm animals, leading to increased production of stress hormones like corticoids during handling. Over time, regular exposure to negative interactions can adversely affect the health and welfare of the animals (reviews: Mota-Rojas et al. 2020; Acharya et al. 2022). Conversely, positive human-animal relationships and the human-animal bond formed through positive interactions, such as grooming and feeding, appear to benefit animals (Rault et al. 2020). Domestic animals and even captive zoo animals may actively seek proximity to humans beyond interactions involving food rewards (Tallet et al. 2005; Lazzaroni et al. 2020), suggesting that they find advantages in human company and interactions.

Table I: Detrimental and beneficial outcomes of negative and positive human-animal relationships (HAR) on animal well-being based on information collected from reviews: Rault et al. 2020; Mota-Rojas et al. 2020; Escobar-Ibarra et al. 2021; Acharya et al. 2022.

Costs of a negative HAR	Benefits of positive HAR
Avoidance of humans	Proximity seeking from the animal to humans
Aggressive and defensive behaviour towards humans	Affiliated interactions with humans
Erratic/unpredictable behaviours during handling	Behavioural synchrony and matching cooperation
Refusal of human constrains (e.g., Animal acting wayward when asked to fulfil an action that can be perceived as negative such as vet exam or climbing into a truck for transportation)	Acceptance of human constrains (e.g., Animal do not show reluctant behaviour when asked to fulfil actions of potentially negative value such as vet exam or climbing into a truck for transportation)
Increased fear/aggressive reactions during conflicts and stressful situations	Increased tolerance in conflicted situation, human act as a secure base and provide reassurance in stressful situation
Increased risk of injury and accidents during interactions with humans due to inappropriate behaviour and response	Lower risk of injury during interactions
Generalisation of the fear of human to any human	Generalisation of the appreciation of human to any human
Humans act as a stressor through their negative interactions.	Humans act as an environmental enrichment through their positive interactions.
Increase in corticoids production and stress behaviours	Increased stress resilience, enhanced health
Impaired welfare and health	Relaxation, reassurance provided by human interactions.

1.2 The forgotten working animals

To date, studies on human-animal relationships have primarily focused on pets, livestock, and zoo animals. However, there has been a lack of attention given to the relationships between humans and working animals, despite the significant amount of time these animals spend in proximity to humans. Working animals require specialized handling expertise to successfully perform their tasks, which entails spending a considerable amount of time interacting with humans daily, often with a specific person who is also their caretaker. These interactions encompass a wide range of activities, including daily caregiving (such as feeding and veterinary care) and work-related interactions (such as working commands and riding). The complexity of these interactions can contribute to the development of a unique relationship between a working animal and its handler. While the review by Hosey

and Melfi (2014) grouped working animals with studies on human-livestock relationships, I believe that the nature of interactions between a handler and a working animal is substantially different from those between a caretaker and livestock animals. As a result, it is necessary to investigate the human-working animal relationship separately and establish a proper definition of what constitutes a working animal. In this context, I decided to take the perspective of the animal into account, and I define "working animals" as **animals that are regularly trained and used to perform specific tasks at the request of a human handler**. This includes animals involved in agricultural draught work, military tasks, tourism, search and rescue, law enforcement assistance/service, herding, but also animals used for sport and leisure activities even though they are not associated with material or financial benefits to their owners. Because they are the most represented working animals, in this thesis, I focused specifically on large working force ungulates used in draught agricultural work, tourism, and leisure.

The Society for the Protection of Animals and Nature (SPANA) estimates that there are approximately 200 million working force animals worldwide (SPANA: annual report 2021). These animals are primarily used for transportation, agricultural tasks, and tourist safaris. Various species of large ungulates are involved in these roles, with the most common being equids (horses, donkeys, and mules), oxen, and buffaloes. Additionally, other animals such as cows, camels, llamas, yaks, reindeer, and elephants are also employed. In the past, working force animals could be found in abundance throughout the world. However, due to the Green Revolution (1960 - 1990) and the technological advancements in agriculture, most labour animals have all but disappeared in the Western world. Nevertheless, in developing countries, billions of people still rely on animal power as their primary source of energy. Draught animals contribute over 50% of the world's agricultural energy for traction, covering more than 50% of the planet's cultivated areas (FAO 2014, Wilson 2003).

In contrast to trends in draught animal use, animal-based tourism has experienced significant growth worldwide and is expected to further intensify due to the increasing demand for animal interactions and experiences driven by urbanization (Carr and Broom 2018). Animals used in tourism encompass a portion of working animals employed for transportation to visit points of interest, access remote landscapes, assist on treks and expeditions, and provide entertainment through rides. While equids are predominantly involved, other animals such as elephants, camels, reindeer, and even ostriches are also utilised. These recreational activities contribute to sustainable livelihoods for local communities (FAO 2014). One notable aspect of tourism is that working animals not only interact with their familiar handlers but also engage daily with numerous strangers. Interactions with inexperienced tourists can result in a higher occurrence of inappropriate behaviours towards working animals, leading to an accumulation of negative interactions (Carr

and Broom 2018). In zoos, various studies have demonstrated the negative effects of visitor presence on animals, including increased hiding and avoidance of humans, as well as reduced occurrence of behaviours associated with good welfare, such as grooming, play, foraging, and active time. Additionally, many zoo animals, an increase in visitor numbers has been linked to elevated concentrations of faecal glucocorticoids which are markers of stress response (Sherwen and Hemsworth 2019). Similarly, farm animals in petting zoos have been observed to avoid contact with visitors (Anderson et al. 2002). However, working animals in the tourism industry can indirectly benefit from tourists through media exposure, which increases awareness among tourists who now consider animal welfare a key factor in their overall experience (Notzke 2019). Sheppard and Fennell (2019), in their content analysis of tourism policies across 73 countries, revealed substantial progress regarding the consideration of animal welfare.

In less economically developed countries, working animals play a fundamental role in various sectors. They often serve as the primary or a key source of income for families and contribute to the community through their transport services, draught power, and involvement in small-scale commercial activities such as taxi services. Additionally, they provide manure for fertilising soil and, in some cases, milk or meat. However, working animals are largely overlooked in national and international policies and legislation worldwide, particularly in less economically developed countries. As a result, critical services, and resources for working animals are lacking, and there is a lack of adequate protection frameworks to enhance their welfare in these industries. This situation is exacerbated by the absence of specific data, incomplete statistics, and a gap in research and technical information (FAO 2014). The literature on working animal welfare, as well as relationships and interactions with humans, is scarce and primarily relies on interviews with animal handlers rather than experimental designs. The case of horses is particularly complex as they can serve as both draught animals and be involved in sports competition, leisure activities, and companionship, including their use as therapy animals. As a result, the scientific literature on the human-horse relationship is more extensive than that of any other working animal, although these studies primarily focus on leisure and sport horses (reviews: Hausberger et al. 2008; Argent and Vaught 2022). In 2005, Pritchard et al. published a protocol for assessing the welfare of working horses, mules, and donkeys in urban and peri-urban areas, which involves direct observation of health and behaviour parameters. However, it is worth noting that in the World Organization for Animal Health (OIE) and the most recent Terrestrial Animal Health Code, the one chapter dedicated to working animals only refers to working equids, and the mention of human-animal interactions is limited to “Owners and users of working equids should be discouraged from using whips and harmful goads such as sticks. Instead, humane training practices for equids should be

promoted which focus on developing good driving practices." and "Human-animal interaction should be positive in order not to compromise the welfare of the working equid." (OIE 2022).

1.3 Three working ungulates, three stories

In this thesis, my aim is to investigate and identify overlooked factors that may influence human-animal interactions during working tasks, thereby impacting the welfare and safety of both handlers and animals. To achieve this goal, I have focused on large working ungulates because they represent the most commonly used working animals. My experiments were then conducted with three long-lived working ungulates used for transportation purposes: Asian elephants employed in timber work, reindeer involved in safari sledging, and privately owned horses used for leisure activities such as outdoor riding or amateur jumping and dressage competitions.

Examining the human-animal relationship within these three working animal systems is significant because, while they share some similarities in terms of their usage, they differ in their historical association with humans, level of domestication, and population management (Table 2). This offers an opportunity to explore various aspects of the human-animal relationship and determine whether, despite these inherent differences, common elements in their interactions with humans may affect them in similar ways.

1.3.1 The Asian elephants

Historical records indicate that Asian elephants (*Elephas maximus*) have been closely associated with humans for thousands of years (Sukumar 2003). However, these elephants are not classified as fully domesticated since they have not undergone selective breeding by humans to develop specific traits, and captive elephants do not exhibit the morphological, physiological, and behavioural characteristics associated with the domestication syndrome (Wilkins et al. 2014).

Asian elephants have a lengthy lifespan, reaching up to 80 years, and they reach reproductive maturity relatively late, at an average age of 19.8+5.7 years (Hayward et al. 2014, Lahdenperä et al. 2014). Their social structure is matriarchal, with the presence of a female leader, which significantly impacts their survival and renders them sensitive to anthropogenic disturbances (Lahdenperä et al. 2016, Lynch et al. 2019). These characteristics make human reproductive management challenging (Sukumar 2006, Driscoll et al. 2009). Furthermore, Asian elephants are renowned for their advanced cognitive abilities, including self-awareness (Plotnik et al. 2010) and relative quantity judgment (Irie et al. 2019, Plotnik et al. 2019).

The World Animal Protection has estimated that approximately 16,000 Asian elephants are held in captivity, which accounts for approximately one-third of the remaining population. Most captive elephants are located in their range countries (Jackson et al. 2019) and are used as working animals in various industries such as logging, transportation, patrolling, and tourism (Riddle and Stremme 2011). Additionally, elephants hold cultural significance in local traditions and religions, further contributing to their use in cultural activities (Hart and Locke, 2007; Mar, 2007). While the large-scale capture of elephants from the wild for captivity has declined in recent years (Riddle and Stremme 2011), all 13 range countries of Asian elephants maintain a captive population. However, the numbers, purposes, and management of captive elephants vary across countries, as they are overseen by government agencies, commercial organizations (such as tourist resorts and circuses), religious institutions, or private individuals (Riddle and Stremme 2011, AsERSM 2022).

The management of working elephants heavily relies on the extensive knowledge passed down through generations of elephant handlers. These individuals, known by their Hindi name as mahouts (Crawley 2021), are responsible for the training, care, and well-being of the elephants they work with. Traditionally, mahouts and elephants develop long-lasting relationships, often lasting a lifetime in many countries. Mumby's (2019) interviews with mahouts further revealed a genuine attachment and affection towards their elephants.

In a study conducted by Hart (1994), the perception of mahouts regarding their elephant's behaviour and their interactions in Nepalese tourist camps was investigated. The findings indicated a mutual attachment between the mahouts and their elephants. However, the prestige associated with being a mahout has declined in countries such as India, Nepal, Laos, Thailand, and Myanmar (Phuangkum et al., 2005; Hart and Locke, 2007; Vanitha et al. 2009; Suter et al. 2013; Crawley et al. 2019). The profession of mahouts nowadays suffers from lower incomes, and it remains a dangerous job with numerous fatal accidents (Vanitha et al. 2009, Crawley et al. 2019). The rapid urbanization of recent decades has likely affected the traditional mahout lifestyle and influenced the availability of more attractive alternative professions. Consequently, there has been a decline in the number of experienced mahouts in the elephant industry. Crawley et al. (2019) observed a decrease in mahout experience and long-term relationships between elephants and mahouts in Myanmar, which was previously considered a reservoir of traditional mahout knowledge and expertise (Lair, 1997; Sukumar, 2003). These changes in the mahout profession have resulted in elephants frequently experiencing changes in their mahouts, often being paired with younger and less experienced handlers (Crawley et al. 2019).

The objective of this thesis is to enhance our understanding of the mechanisms underlying the mahout-elephant relationship and to investigate how frequent mahout changes impact the interactions between elephants and their handlers during work. The study focused on a population of semi-captive Asian elephants employed in timber work in Myanmar (Table 2).

1.3.2 The reindeer

Reindeer (*Rangifer tarandus tarandus*) are the only deer species to have been domesticated. Like most ungulates, their initial interactions with humans were related to hunting. Several rock paintings in Europe, dating back to the end of the Palaeolithic era, depict reindeer as game meat, such as those found in the Font de Gaume cave in Dordogne, France. A mention of a herd of tamed reindeer used as decoys to hunt wild individuals in Lapland can be found in "*Historiarum libri VII adversus paganos"* written by Paulus Orosius in AD 893. The exact time when reindeer began to be commonly used for sledging and riding is difficult to determine. Harness parts discovered in Siberia were dated back to 2000 years ago (Losey et al. 2021). It is likely that the use of working reindeer spread as large-scale reindeer herding expanded among the Sámi people in northern Fennoscandia during the 14th century (Bergman et al. 2013, Salmi et al. 2021).

Olaus Magnus (1490-1557), a Swedish writer and cartographer, was the first to provide a description of the reindeer herding and husbandry system in the Nordic countries in his work "*Historia de Gentibus Septentrionalibus*," published in 1555. Reindeer were primarily valued for their meat, but their fur and antlers were also highly valuable for clothing and tool crafting. Working reindeer were used for draught tasks and transportation of people well into the 20th century (Salmi et al. 2022). Their use declined with the introduction of new technologies such as snowmobiles, but in recent decades, sledding reindeer have made a comeback for tourist safaris. Today, Nordic countries incorporate animal tourism into their marketing strategies and offer reindeer and husky sledging tours as one of their main attractions. In 2018, the estimated number of reindeer used for tourism in Finnish Lapland was 750 individuals spread across 34 reindeer farms. These reindeer contribute to over 23% of the annual revenue generated by animal-based services in tourism, amounting to approximately 15 million euros per year (García-Rosell and Tallberg 2018). Consequently, their numbers are expected to continue growing.

Reindeer, along with moose, are the only species of Cervidae that inhabit the Arctic circle. They can be found in the tundra, mountains, and woodlands of the Arctic and sub-Arctic regions in the northern hemisphere. Despite their remarkable adaptation strategies to cope with seasonal changes, reindeer cognition has not yet been extensively studied. One interesting characteristic of reindeer is their extended

visual range, including the ultraviolet spectrum (Hogg et al. 2011), which may enhance their ability to distinguish contrasts in snowy environments (Tyler et al. 2014). Additionally, they are the only known mammals to undergo structural adjustments in their eyes to adapt to the blue hue of the extended twilight during the Arctic winter (Fosbury and Jeffery 2022). Reindeer have a lifespan of up to 18 to 20 years and can begin reproducing at around 2 to 3 years of age. They exhibit gregarious behaviour and follow a fission-fusion group dynamic throughout the year (Body et al. 2015*a*, *b*). Reindeer herds can range in size from a few individuals to many hundreds, and they are known to migrate up to a thousand kilometres between their summer and winter ranges.

The husbandry system for domestic reindeer is primarily based on free ranging, allowing the reindeer to roam and forage in the forest. In winter, they may be supplemented with food. However, sledging reindeer have a semi-captive status. During the winter season, they are kept in enclosures for training and to work in safari tours for tourists. As a result, their direct contact with humans is limited to several months each year. Although reindeer exhibit complex social structures within large herds composed of hundreds of individuals (Body et al. 2015*a*, *b*), they rarely engage in affiliative behaviours that involve direct physical contact, such as allogrooming. Reindeer are highly sensitive to touch and naturally avoid physical contact with both other reindeer and humans (based on personal observations and information collected from herders).

Previous studies on the human-reindeer relationship have primarily relied on interviews with herders (Brown-Leonardi 2016, García-Rosell and Tallberg 2021), rather than experimental or observational research from the reindeer's perspective. Therefore, there is a need to investigate how reindeer are affected by interactions with humans and how they adjust to different individuals when compelled to interact with them. In this thesis, I focused on studying the reindeer used for sledge safaris in the Finnish Lapland (Table 2).

1.3.3 The horses

The domestication of modern horses (*Equus caballus*) and the growth of equestrian culture have recently been re-dated to around 2000 B.C. and are believed to have originated from the Western Eurasian steppes (Librado et al. 2021). The rise of horseback riding and the use of horses as a means of transportation is considered one of the most significant events in the history of human societies. It allowed people to explore and conquer new territories, expand trade in goods, and greatly improve farming efficiency, thereby transforming the agricultural landscape (Skinner et al. 2022). Consequently, horses have been highly valued in various cultures, and their human uses have expanded beyond working animals to include athletes and beloved

companions in leisure riding. These changes in the status and use of horses have also had a significant impact on human perception and interaction with them (Hausberger et al. 2008, Freeman 2019). According to the Food and Agriculture Organization of the United Nations, the global population of domestic horses is estimated to be approximately 59 million (UNDATA - FAO 2020).

Domestic horses often spend several hours each day in close contact with humans, which can have an impact on their welfare, physiology, and behaviour (Kelly et al. 2021). Supposedly, due to their long history of co-evolution with humans, horses have developed various socio-cognitive skills in their interactions with humans. They can recognize human emotions, follow human attentional cues, and engage in referential communication with them (Jardat and Lansade 2021).

Privately owned horses, used for leisure activities or competitions, may form relationships with one or a few individuals. However, they often must cope with changes in ownership, sometimes experiencing multiple changes throughout their lives. This means that they have to establish new relationships with different humans on multiple occasions. Therefore, it is crucial to investigate how familiarity the relationship length with a handler affect a horse's ability to understand and interact effectively with the handler, as communication plays a vital role in the development of their relationship. Despite an increasing number of studies focusing on the human-horse relationship, recent literature reviews have highlighted significant gaps in our understanding of horses' emotional states during human interactions (Kelly et al. 2021) and the factors related to both the horse and the owner that influence their relationship (Freeman 2019).

Horses are long-lived mammals, with an average life expectancy of about 25 to 30 years, although this can vary depending on the breed. They typically reach reproductive maturity around the age of 3 years. In the wild, horses live in complex social and familial groups (Klingel 1982, Ransom and Kaczensky 2016) and allocate a significant portion of their time to foraging, which can account for up to 75% of their daily activities (Salter and Hudson 1979). To meet their dietary needs, free-ranging feral horses have the freedom to move and cover substantial distances. On average, they can travel between 9 to 16 km per day and occupy areas of up to 40 km2 during the summer (Hampson et al. 2010; Henning, Beck, and Scasta, 2018). In contrast, captive domestic horses do not have the same freedom of movement or the ability to choose their social groups as feral horses do. The housing conditions for domestic horses can vary widely, ranging from enclosures of different sizes with varying numbers of conspecifics, to individual stalls or paddocks. The specific horse housing system significantly impacts their time-activity budget, including factors such as sleeping, feeding, and exercising patterns.

In larger pastures, horses are more active compared to when confined in small paddocks (Maisonpierre et al. 2019). They have the freedom to move according to

their needs, such as seeking shade or finding shelter from wind and rain, and they have ample space to exercise as they please. Horses that have access to pastures with conspecifics have been shown to exhibit better learning performance (Lansade et al. 2014) and develop better relationships with humans, displaying fewer instances of aggression (Søndergaard and Ladewig 2004, Ruet et al. 2020) compared to horses kept individually in stables. Hockenhull and Creighton (2014) reported that the main source of behavioural problems and aggression towards humans in leisure horses is related to their husbandry practices. Consequently, understanding how different housing conditions impact horses' behaviour and their interactions with humans has become a matter of concern in the equestrian community. To explore these various aspects of horses' lives, I recruited volunteers from Southwest Finland to participate in a series of experiments involving their leisure horses (Table 2).

Table 2: Description of the three study species and populations used in this thesis.

	Asian Elephant *Elephas maximus*	**Reindeer** *Rangifer tarandus*	**Horse** *Equus caballus*
	 © J. Webb	 © V. Lummaa	 © B.Pantet
General details about the species			
Life expectancy	~ 70 - 80 years	~ 18 - 20 years	~ 25 - 30 years
Age at first reproduction	~ 15 - 19 years	~ 2 - 3 years	~ 2 - 4 years
Domestication status	Not fully domesticated	Recent domestication (1600 AD)	Ancient domestication (2000 BC)
Active human selection	None	Low (Morph is different from the wild sub-species)	Strong (over 400 breeds)
Working usages	Draft, tourism, religious processions	Tourism, sport (races)	Draft, sports, leisure, tourism
World captive population	~ 16 000	World estimation unknown Finland: ~ 750	~ 58 million
Details of the Population used in the thesis			
Captive status	Semi-captive: Free ranging at night	Semi-captive: Free ranging from April to November	captive
Ownership	State owned by the Myanma Timber Enterprise	Privately owned by the Reindeer Journey herders	Privately owned by 57 volunteer participants
Working usages	Draft, timber work	Tourism	Leisure and sport

1.4 Factors involved in the human-animal relationship

1.4.1 Handlers' characteristics

1.4.1.1 Familiarity and relationship length

Working animals that are used for recreational purposes, such as in tourist safari tours or in riding schools, experience numerous daily interactions with strangers. Interacting with unfamiliar humans is a fundamental aspect of their lives. On one hand, they must navigate the requests of various individuals with different levels of experience in handling animals and different ways of expressing their intentions. On the other hand, these animals may also develop long-term relationships with their familiar handlers and caregivers who interact with them daily. Asian elephants can discriminate between familiar and unfamiliar humans, relying on visual and olfactory cues (Polla et al. 2018), and horses have demonstrated proficiency in discriminating and recognizing humans from pictures (Jardat and Lansade 2021). This suggests that the identity and familiarity of the handler can be highly significant during interactions with these species. While there have been no specific studies conducted on the ability of reindeer to discriminate between humans, research on other artiodactyl species such as cattle, pigs, goats, and sheep has shown their capability in this regard (Jardat and Lansade 2021), implying that reindeer may possess similar recognition and discrimination abilities.

The effect of handler familiarity on horses' behaviour remains unclear. Previous studies have observed similar responses from horses when they were separated from and subsequently reunited with a familiar or unfamiliar person (Lundberg et al. 2020). Similarly, in a study by Hartmann et al. (2021), horses did not exhibit different reactions to novelty based on whether the handler was familiar or unfamiliar. However, in that study, the familiar handler was not the owner or caretaker of the horse but an experimenter who trained the horse for 10 sessions of 15 minutes each. Therefore, their relationship with the horse may not have been well-established. Horn et al. (2013) present evidence suggesting that social familiarity alone is not sufficient to explain dogs' heightened attention towards their owners. Dogs not only paid less attention to unfamiliar individuals but also to people they were familiar with but did not share a close relationship with, such as family friends.

Familiarity is a broad term that encompasses various types of human-animal relationships, ranging from occasional interactions to long-term bonds (Hausberger et al. 2008). One way to be more specific is to consider the length of the relationship between the familiar person and the animal, as well as the regularity of their interactions. The relationship length between the handler and the animal may

significantly influence the outcomes of their interactions during work. It takes time for handlers to comprehend and establish a bond with their animal partners. For example, dog-sleigh drivers emphasize the importance of trust in their relationships with their dogs (Kuhl 2011). Mahouts, who work with elephants, suggest that it takes approximately three years to understand an elephant's behaviour and eight years to develop trust and form a strong bond (Srinivasaiah et al., 2014). Currently, there is limited knowledge about how the familiarity of the handler impacts human-animal interactions in a working context. Furthermore, to the best of our knowledge, studies have primarily focused on comparing familiar and unfamiliar handlers, rather than exploring the gradient of familiarity, such as their relationship length.

1.4.1.2 Handlers' experience

To effectively work with animals and train them for specific tasks such as draft work, riding, and responding to commands, handlers must possess the necessary knowledge and experience. This is particularly crucial for draft animals, as they are typically less docile and anthropophilic compared to other domesticated animals, and their large size necessitates specialized handling techniques (Zeder 2012). In the case of horses, riders/trainers should be capable of designing appropriate training routines that condition the horse for the specific demands of the working task, thereby enhancing its neural and motor skills (Williams and Tabor 2017). According to Merkies et al. (2018), therapy horses demonstrate higher attentiveness towards humans with experience in handling horses compared to inexperienced individuals. This increased attentiveness is likely attributed to the distinct way in which inexperienced humans approach the horse and carry themselves, in contrast to experienced individuals who display more confidence and directness in their approach and body language. The same horses were also calmer with inexperienced patients. Although this behaviour could be the result of selecting individuals with a better-suited temperament to work as therapy horses. Studies conducted on dogs have indicated that dogs owned by individuals with less experience have a higher risk of exhibiting aggressive and fearful behaviour (Jagoe and Serpell 1996, Pérez-Guisado and Muñoz-Serrano 2009). Conversely, research focusing on zoo animals in the USA (Carlstead 2009) and semi-captive elephants in India (Srinivasaiah et al., 2014) suggests that caretakers with extensive experience may become complacent over time, potentially leading to neglect of the animals under their care. Therefore, it is necessary to investigate how handler experience can impact the human-animal relationship.

1.4.1.3 Number of past and current handlers

Working animals frequently develop a close and exclusive relationship with a specific handler, although, as mentioned with working Asian elephants, this specific handler may change over the animal's lifetime. This is also quite common in horses, as they are often sold to different individuals throughout their lives, resulting in multiple one-on-one relationships with different handlers. The number of times animals have changed owners may also impact the quality of the relationship with the current caretaker. In the case of dogs, changing owners can affect their behaviour towards humans, as foster and shelter dogs exhibit signs of disinhibited attachment (Thielke and Udell 2019). Interestingly, despite horses often experiencing changes in ownership, very little is known about how this affects them. Undergoing multiple owner changes throughout life could potentially have a negative impact on the animal's behaviour towards humans in a new relationship, and further research is needed to understand this aspect of their lives.

If working animals often develop a more exclusive relationship with one handler or caregiver, they may also be handled and trained by a variety of different individuals on a regular basis. This is particularly common in the case of leisure and sport horses. Elite sport horses, for example, are ridden by the competitor but are also cared for and often trained or warmed up by another person known as a groom. In the case of leisure horses, it is very common for the horse to be leased or rented to other riders to share the expenses associated with the horse. As a result, these horses interact with multiple individuals on a regular basis, and these handlers may differ in their level of experience, attitude, or the nature and duration of their interactions with the horse. Consequently, the quality of the relationship between the horse and each of these handlers may vary. Considering that horses are sensitive to human emotions (Trösch et al. 2019, Merkies and Franzin 2021, Jardat et al. 2023), having multiple relationships with humans that can differ in quality and intensity may influence how a horse behaves towards humans in general. These aspects of the human-animal relationship warrant further investigation, and leisure horses serve as an excellent model for exploring the effects of having multiple regular handlers on the human-animal relationship.

1.4.2 Animals' age and experience

When studying the human-animal relationship, it is important to consider the life history and experience of the animal, particularly in the case of working animals that undergo specific training to perform their tasks. Training is crucial to ensure that the animals can carry out their jobs effectively and enhance the desired interactions. However, one challenge lies in disentangling the effects of training from the animal's

age, particularly in populations where animals are bred, raised, and trained under the same conditions and environment.

For instance, in many working Asian elephant populations, the taming of young elephants occurs at a predetermined age, followed by a ritualized training process spanning several years (Crawley, 2021). Similarly, if a breeder also functions as an animal trainer, it is likely that they will employ the same taming and training procedures for all their animals. Consequently, animals of similar ages are likely to have undergone similar levels of training and experienced similar degrees of human interaction. Determining whether age or training level holds greater significance needs to be assessed on a case-by-case basis.

Similarly, age can also influence an animal's temperament. In their cross-species review, Cabrera et al. (2021) observed that while personality traits tend to remain stable within life stages, they often vary across critical developmental events. For instance, in many species, juveniles exhibit more exploratory behaviours as they learn what to avoid over time, resulting in greater neophobic tendencies at older ages (Mata et al. 2013; Sherratt and Morand-Ferron 2018). Hence, it is crucial to account for the effect of age, as different life stages may be associated with distinct attitudes of animals towards humans.

1.4.3 Living environment

The keeping system may significantly influence animals' ability or willingness to interact with humans. Several studies have emphasized the positive effects of environmental enrichment and voluntary physical exercise on neurogenesis, learning, and memory in animals (van Praag et al. 2000; Bekinschtein et al. 2011). Therefore, when exploring the socio-cognitive skills of social species, it is important to consider the social and physical environment in which they evolve. Numerous studies have observed the positive impacts of sociality and environmental complexity on the cognitive performance of social species (Ashton et al. 2018; Ashton et al. 2020; Lambert and Guillette 2021), although they have rarely been investigated in long-lived mammals. Furthermore, to the best of my knowledge, the effect of animals' social and physical environments on the human-animal relationship and their ability to interact with humans has not been investigated.

1.5 Experimental assessment of human-animal relationship

While the literature on the human-horse relationship is expanding (Argent and Vaught 2022), research on the relationships and interactions between humans and other working animals is limited, often relying heavily on interviews with animal

handlers rather than experimental designs (eg: donkey: Swann 2006, elephants: Münster 2016, Crawley et al. 2019, Mumby 2019, reindeer: Stépanoff 2012). Consequently, responses regarding animal welfare and emotional state may be influenced by human biases and may lack a comprehensive understanding from the animal's perspective. In light of this, I have chosen to adopt an experimental approach in my thesis to identify and assess the influence of specific factors on the interactions between humans and animals within a working context.

I chose to focus on creating situations that involve interactions inherent to the working context. Working animals often follow a routine of performing repetitive or similar tasks over an extended period. However, in the event of unexpected disruptions occurring in this routine, it becomes crucial for the handler to anticipate the animal's reactions. Therefore, I firstly, examined the impact of novelty exposure, which can induce stress in animals and elicit strong and spontaneous behavioural responses that may be modulated or amplified depending on the relationship between the animal and the handler. Secondly, in a working context, effective communication and mutual understanding between animals and humans are essential for establishing a productive working relationship and ensuring the safety of both the handler and the animal (Kalof 2017). I assessed the animals' willingness to respond to communicative gestural and/or verbal cues from handlers according to the human-animal relationship factors I am investigating in this thesis.

By using these experimental methods, I aim to provide valuable insights into the human-animal dyad interactions in a working context, allowing for a more objective assessment of the factors that influence these interactions.

1.5.1 Animal reaction to unusual situation

By understanding the animal's behaviour and by developing a strong relationship, the handler can effectively respond to various situations, such as encounters with novelty or frightening events. One approach to investigating the factors influencing the human-animal relationship is to expose working dyads to unusual situations and observe the animal's reactions. Introducing novelty is an interesting method to create such unusual situations. Novelty is known to elicit stress responses and is commonly used as a fearful stimulus in studies involving species with neophobic behaviours (King et al. 2003; Dalmau et al. 2009; Dai et al. 2015). In my thesis, I explore how working animals react to novel situations based on the characteristics of their handlers.

1.5.2 Communication in working-dyads

Since the animals are working to benefit humans, a significant portion of the communication within this context relies on the animals' ability to comprehend and respond to human-given cues and commands. To evaluate the communication dynamics within the working dyads and to assess the animals' ability to understand human cues, I have implemented a referential communication task. This task allows me to examine how well the animals respond to gestural cues provided by humans, according to the factors under investigation in this thesis. Additionally, I have conducted a calling test to assess the animals' responses to the handler's vocal commands, further exploring their ability to interpret and act upon verbal instructions.

1.5.2.1 The use of referential communication

Humans widely use the manual pointing gesture as a form of referential communication to convey their intentions (Leavens and Hopkins 1999). This gesture is often accompanied by gazing at the target and moving closer to it. Due to its significance in human communication, gestural cues have been extensively used in cognitive experiments involving animals to explore their understanding and interpretation of human cues (e.g., goats (Nawroth et al. 2020); horses (Maros et al. 2008); African elephants (Smet and Byrne 2013), pigs (Nawroth et al. 2014); see Krause et al. (2018) for a review). In these tests, individuals are presented with multiple identical objects, and a person uses the pointing gesture, along with/or only use gaze direction and/or proximity to the target, to indicate which object to approach in order to obtain a food reward. Most studies focus on assessing the animals' ability to utilize these human-given cues, but few explore the potential influence of external factors on the animals' response.

For example, in the case of horses, individuals trained using the Parelli natural horsemanship method (which is based on understanding the horse's ethology and primarily employs positive and negative reinforcement) demonstrated faster learning of following momentary distal points compared to those trained using traditional methods (which often rely on negative reinforcement and/or positive punishment) (Dorey et al. 2014). Cook et al. (2014) investigated whether human familiarity plays a role in how dogs respond to human signals and found that dogs tend to prioritize social signals from familiar humans when making decisions. In this thesis, my objective is to examine whether the characteristics of human experimenters or the animals' living environment can influence the willingness of working animals to follow human-given cues.

1.5.2.2 Animal response to vocal commands

With working animals, it is common for the handler to use vocal commands to request a specific action from their animal. This is the case in the mahout-elephant system where mahouts constantly talk to their elephants. Therefore, I wanted to explore whether human experimenters' characteristics, such as familiarity, relationship length, or handler experience, could affect the willingness and reaction time of elephants to respond to the call of mahouts. For example, Scandurra et al. (2017) observed that dogs took longer to respond to verbal stimuli from a stranger asking to join them compared to when they were called by their owner.

1.6 Aims of the Thesis

This thesis aims to contribute to our understanding of the dynamics of the human-animal relationship in working draft animals and identify the factors that influence the quality of interactions between these animals and their handlers. To achieve this, behavioural experiments were conducted on three distinct species of working animals: semi-captive Asian elephants used for draft timber work in Myanmar, semi-captive sledge reindeer employed for tourist safaris in Lapland, and privately owned leisure horses in Southwest Finland. By examining these study populations living in diverse contexts and environments, this research enables a multifaceted exploration of the human-working animal relationship from various angles and perspectives.

1) I first investigated how the handler's familiarity and the relationship length between the handler and the animal affected the animal's behaviour in everyday tasks (**Chapter I**), unusual contexts (**Chapter II** and **III**), as well as during communication events (**Chapter IV**). This is particularly relevant in the case of Asian elephants and horses, as they interact daily throughout the year with their main caretakers. I expect these animals to show better responsiveness and to follow cues more effectively when interacting with their familiar caretakers compared to unfamiliar individuals. However, in the case of reindeer, which only interact with humans daily during the winter tourist season (approximately 4 months), I anticipate that their behaviour would be less influenced by the handler's familiarity compared to the other two species.
2) Through the mahout-elephant system, my aim was to study how the handler's own experience may influence the communication within the working dyad (**Chapter I**) and the animal's response to novelty (**Chapter II**). I expect that elephants under the command of more experienced mahouts would demonstrate a stronger comprehension of the commands and be more

inclined to interact with novelty when asked to. Conversely, elephants under less experienced mahouts might display reduced assertiveness, resulting in lower success rates in working tasks.

3) My aim was to explore how the way in which an animal experiences a relationship with humans, whether through exclusive or multiple relationships at a given time, as well as past experiences, may impact its behaviour during interactions with humans. In **Chapter III**, I specifically examined the effect of the number of current and past handlers on the animal's response to novel situations, both with familiar and unfamiliar handlers, in leisure horses. I expected that individuals with multiple relationships with humans, who have lived with different owners, would exhibit reduced sensitivity to novelty and experience less stress when interacting with unfamiliar handlers, owing to their habituation from being handled by various persons.

4) I intended to explore how the physical and social environment in which animals live and evolve may affect their interactions with humans. In **Chapter IV**, I compared the success of leisure horses at following human-given cues based on the characteristics of their living environment. Considering that horses are social ungulates, I anticipate that individuals living in suitable conditions (in groups and on larger surfaces) would perform better in tasks involving human-given cues compared to those living alone in smaller spaces. Additionally, because the sledging reindeer live in complete freedom for more than half of the year with limited contact with humans, I explored whether working animals living in their natural environment with lower human contact than other domestic species can also make use of human-given cues (**Chapter V**).

5) I also wanted to test the effect of the animal's own experience on the human-animal interactions, particularly through age (**Chapter I, II, III, IV, and V**) and training level (**Chapter I, II, and V**). It is anticipated that as animals accumulate experience with humans, their response to human commands and during interactions should improve.

All together, these chapters bring new insights to the study of the human-animal relationship and gather information on overlooked factors that should be taken into consideration to improve human and animal welfare in a working context (Table 3).

Table 3: Summary of the aims and chapters of this thesis.

Aims	Factors	Experimental tasks	species	Chapters
1	Familiarity and relationship length with handler	Communication task	Asian elephant	Chapter I
			Horse	Chapter IV
		Exposition to novelty	Asian elephant	Chapter II
			Horse	Chapter III
			Reindeer	Extra experiments
2	Handler experience	Communication task	Asian elephant	Chapter I
		Exposition to novelty	Asian elephant	Chapter II
3	Number of current and past handlers	Exposition to novelty	Horse	Chapter III
4	Physical and social environment	Communication task	Horse	Chapter IV
			Reindeer	Chapter V
5	Animal age and training level	Exposition to novelty	Asian elephant	Chapter II
			Horse	Chapter III
			Reindeer	Extra experiments
		Communication task	Asian elephant	Chapter I
			Horse	Chapter IV
			Reindeer	Chapter V

2 Materials and Methods

2.1 Study populations and handler information

2.1.1 Asian Elephant

2.1.1.1 The Myanma Timber Enterprise elephants

The largest captive Asian elephant population in the world is comprised of approximately 6,000 semi-captive elephants in Myanmar. Among these, around 3,000 elephants are employed by the Myanma Timber Enterprise (MTE), as reported by Hedges et al. (2018). The MTE is a governmental institution in Myanmar, and the captive status of these elephants is authorized by the Myanmar Ministry of Natural Resources and Environmental Conservation. To ensure the safety and welfare of the elephants, the MTE conducts monthly health inspections carried out by trained veterinarians.

Most of the elephants in this population are captive-born and are primarily used for hauling felled logs in the forest. They work in groups consisting of approximately six elephants, guided by an assigned mahout who oversees their daily care. The group's operations are managed by an experienced head mahout, also known as "sin-gaung." Beyond their working hours, the elephants are released into the forest, where they can freely engage in foraging, socializing, and mating with other elephants, including those in the wild, without human supervision. The reproduction of these elephants is not controlled, hence the term "semi-captive" to describe their status. This arrangement allows them to exhibit their natural behaviours and avoid the stress associated with captivity and confinement, which are known to have negative impacts on elephant welfare (Clubb et al. 2008, Doyle 2018). Their diet is minimally supplemented with occasional fruit, salt, and rice when traveling. Each elephant is assigned an individual ID number, and their information is recorded in a corresponding logbook maintained by the MTE. These logbooks contain details such as birth date, offspring information, sex, origin (whether captive-born or wild-caught), as well as health reports from regular veterinary inspections assessing their working ability and medical condition.

The elephants used in **Chapter I** and **Chapter II** consisted of 81 (41 females and 40 males) and 52 individuals (26 females and 26 males) respectively owned by the MTE that ranged in age from 5 to 71 years.

2.1.1.2 MTE elephants' training and workload

Calves are separated from their mothers and undergo taming when they reach 4-5 years of age. The taming process always takes place during the cold season, specifically in November to December. It typically lasts for about four weeks and follows strict rules and religious rituals. The elephant taming is generally considered aversive, a veterinarian is always present at the taming camp to ensure that the elephants stay healthy. The detailed procedure of MTE elephant taming can be found in Crawley's work (2021). During the taming period, each elephant is assigned a mahout who will initiate the process of human habituation and train the elephant to be ridden. The training continues in the subsequent years as the elephants are further trained and utilized for light work duties until they reach the age of 18, at which point they begin working full-time. The elephants are retired at the age of 55 and continue to receive the same level of daily care until their passing. To ensure the health and welfare of the elephants, various regulations are in place. Their working hours are limited to approximately 4-8 hours per day, 5 days per week. The amount of tonnage they are required to drag and the workload they handle are adjusted based on factors such as the season, the elephant's size and condition, and their age. Additionally, elephants are given a rest period during the hot season, typically from March to May (Mar, 2007). Female elephants are relieved of their working duties from mid-pregnancy until their calves reach approximately 18 months of age. During this time, the calves freely accompany their mothers but have limited contact with humans until the taming process begins.

2.1.1.3 Mahouts' information

From the moment of taming, each MTE elephant is associated with a mahout who assumes responsibility for the elephant. The assigned mahout oversees the elephant's training and daily care. They retrieve the elephant from the forest daily, ensure proper feeding, and monitor for any injuries or abnormal behaviour (Crawley et al. 2019). Data regarding the mahouts' identities and the dates they were paired with their respective elephants were collected through direct interviews with the mahouts and head mahouts, as well as by consulting the elephants' logbooks. With this information, the duration of each mahout's partnership with their elephant at each measurement date was determined, along with the mahouts' ages and total time spent working with elephants at the time of measurement.

2.1.2 Reindeer

2.1.2.1 Reindeer Journey farm sledging reindeer

In Finland, the reindeer husbandry area covers roughly the northern half of the country, corresponding to 36% of Finland's total area, and is home to an estimated 200,000 to 300,000 reindeer. This area is legally designated, allowing herders to let their reindeer roam freely regardless of landownership (Reindeer Herders' Association 2020) The reindeer husbandry area is divided into 56 cooperatives, each responsible for maintaining the livestock quota allocated to them. The rhythm of reindeer herding follows the seasons. In June and July, herders earmark their newborn calves by making cuts in the tip and sides of their ears using a sharp knife. This marks the first interaction between reindeer and humans. During the summer, the reindeer are free to wander in the Finnish Lapland until the autumn roundup. During the roundup, all the reindeer are gathered in small batches and driven into wooden fenced holding pens. This allows for the separation of reindeer selected for slaughter from the rest. All reindeer are registered and treated for parasites at this time. After the roundup, the reindeer are released again to roam freely for the winter, except for male calves, young males in training, and working sledge reindeer. These reindeer are kept in enclosures near the farm, where they can be supplemented with food and easily accessed for training and work.

For this thesis, I worked with 16 sledge reindeer from the Reindeer Journey farm near Rovaniemi. These reindeer ranged in age from 2 to 12 years old and were classified into two groups: reindeer in training and active working reindeer. All 16 reindeer were castrated males used for experiments involving novel objects (see section Material and Methods), and eight of them were used to investigate human-reindeer communication in **Chapter V**. These reindeer were part of a larger herd consisting of several hundred animals and were either already used or being trained to be used as sledging reindeer for tourist safaris in Rovaniemi and Levi.

2.1.2.2 Sledging reindeer's training

The training process described in this section specifically refers to the methods used by the herders at the Reindeer Journey farm, based on the principles of positive reinforcement. It is important to note that methods may vary in other farms. Traditionally, only male reindeer are used to pull the sledge, and their training begins in their first winter. In December, male calves are separated from their mothers and the rest of the herd when they are around 7-8 months old. They are placed in a roaming enclosure spanning several hectares, which is connected to a smaller feeding pen. No humans are allowed in the roaming enclosure, as it serves as a safe

space for the reindeer to retreat to if they prefer not to interact with humans. In the feeding pen, they are provided with hay and pellets daily, and the herders, as well as occasional tourists, hand-feed them their favourite food: lichen. This initial step aims to habituate the reindeer to human presence. During their time at the farm, which lasts until the snow melts (around April), each calf undergoes a few days (5 to 7 days) of proper handling. The herders put a halter on the reindeer's head to familiarise them with it and the attached rope. The reindeer also begin learning how to walk on a leash without panicking, stay still, and wait. On their second winter, the individuals that have survived the summer in the wild are captured again. During this season, each reindeer spends 10 to 15 days reviewing what they learned previously and becomes accustomed to wearing a harness. They gradually progress from pulling a light tire to a light sleigh, and those deemed strong enough and ready can start pulling an empty sleigh. At this stage, the herders assess which reindeer show potential for sledge pulling and continue their training each subsequent winter until they are deemed ready to work with tourists, typically around 3 to 4 years old. Once the reindeer are considered ready for work, they are castrated before joining the working reindeer at a tourist station in the following winter for their first season of work. Initially, they only pull the sledge once or twice per week. Reindeer tourist safaris involve a line of reindeer walking in a formation called a "raito," with sledges tied to each other and carrying a maximum of 3 to 4 persons. Only the first reindeer is led on a leash by a herder. Safaris can range in duration from 30 minutes to 3 hours, and the reindeer typically pull sledges for a maximum of 3 hours per day.

2.1.2.3 Herders' information

The Reindeer Journey is a small-scale family farm located in Rovaniemi, Lapland, Finland. We gathered information about their working experience through direct discussions during our visit to the farm. Their reindeer herding tradition and knowledge are the result of the Sami heritage passed down from generation to generation on the husband's side of the family. I have been collaborating directly with a member of the family who has been working at the farm for over 25 years. They are also a professional animal trainer, specialising in reindeer, dogs, and horses. Additionally, another herder from the farm, who is responsible for safari tours in Levi, has been assisting in the experiments. Both individuals have known their sledging reindeer since the animals' first year of training.

2.1.3 Horse

2.1.3.1 Leisure horses from the Southwest Finland

The number of horses in the Europe is estimated to be more than 5 million individuals, used for competition, draft, and leisure (UNDATA - FAO, 2020). In Finland, the number is estimated at 75,000, with half of them being used for trotting races. There are 35,000 horse owners distributed among 16,000 stables (FEI 2023). The horses used in this thesis were recruited through advertisements on social media targeting horse owners from the southwest of Finland. The requirement for a horse to be eligible to participate in the experiments was that it had received sufficient training to walk safely on a leash in a familiar environment. A total of 76 horses participated in the study, consisting of 38 mares and 41 gelded males ranging in age from 2 to 26 years, originating from 26 different locations (private homes or private stables). Each horse owner was asked to complete a questionnaire to provide information about the size of their herd, the type of housing provided to their horse(s), the number of riders, the number of previous owners, basic training information, and the breed. Housing styles varied from individual stalls to pastures in a herd. All horses were fed with hay and water, and their diet could be supplemented with pellets depending on their nutritional requirements. The subjects represented a range of breeds, including Finnish cold and warm bloods, Estonian breeds, Fjords, Haflingers, Tinkers, Spanish purebreds, Icelandic horses, Shetlands, Welsh, and Gotland ponies.

2.1.3.2 Horses' training

Horses are typically trained for riding between the ages of 3 and 5 years old (commonly said as breaking a horse under the saddle), although for racehorses, training may begin as early as 2 years old. The methods employed to initiate this training can vary widely, ranging from traditional and classical approaches to more modern horsemanship training methods originating from the US. In this study, the participants were volunteers who had varying riding and training methods, and their horses were used for different activities such as outdoor trekking, jumping, and dressage. Additionally, it is common for horse owners to purchase adult horses that have already undergone training by previous owners, which may result in them being unaware of the methods used during the initial training process. The potential biases arising from such variations among the subjects are discussed in **Chapters III** and **IV**. However, these variations are likely unavoidable and reflect the diverse environments in which horses can thrive. Therefore, the sample used in this study

can be considered a good representation of privately owned leisure horses in Finland and Western countries.

2.1.3.3 Horse owners' information

The 55 volunteers that participated in the study were the owner and/or main caretaker/rider of the horse. They were requested to provide information on their age, their equestrian experience, and the relationship length with their horse.

2.2 Data collection

2.2.1 Physiological data

For **Chapter I**, the veterinary management and comprehensive documentation of elephant-mahout relationships in semi-captive Asian elephants allowed the assessment of multiple welfare indicators that could be investigated in relation to specific mahout–elephant relationship lengths and mahout experience. Faecal samples from 151 elephants were collected between February 2012 and April 2018 approximately once a month throughout the year to further extract the FGM and analyse their concentration. Blood samples were also collected from a total of 148 elephants between 2015 and 2018 during the hot season in March-April, at the monsoon in July and during the cold season in November. These samples were used to perform measures of physiological stress (the faecal glucocorticoid metabolite, heterophil:lymphocyte ratio), muscle damage (creatine kinase) and immunological health (total white blood cell count). **Chapter I** is a collaboration with Dr. Crawley, for which I was responsible for the behavioural analyses, therefore the methodology on the physiological analyses will not be fully detailed in this thesis but can be found in the material and methods section of **Chapter I**.

2.2.2 The exposition to novelty

To observe if working animals are more willing to participate in unusual exercises with a familiar handler compared to an unfamiliar handler, we chose to expose the animals to novelty in order to elicit stress reactions (King et al. 2003, Sneddon et al. 2003, Lansade et al. 2008, Dalmau et al. 2009, Lee et al. 2021). The animals in the study were exposed to various novel stimuli, such as walking on a novel surface, approaching a novel object, or being touched with a novel object, while being handled by either an unfamiliar or familiar handler. The objective here was to investigate how factors related to the human-animal relationship could influence the animals' behaviour in unusual situations.

2.2.2.1 The novel object

In a second experiment, either the familiar handler or an unfamiliar experimenter presented a novel object to the horse or reindeer. The animal was given one minute to approach and interact with the experimenter and the object. After that, the experimenter attempted to approach the animal and touch it on the shoulder with the object (Fig. 1a,b). I measured the reluctance of the animal to be touched with the novel object and recorded the latency, or the time it took for the animal to approach and touch the novel object.

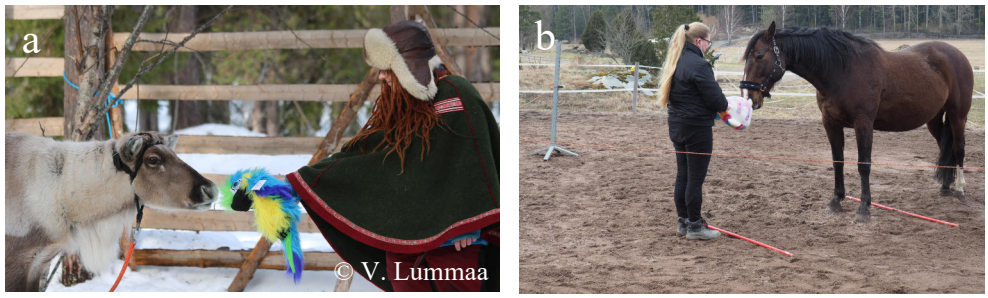

Fig. 1: **a)** reindeer being presented with a novel object. **b)** Horse being presented with a novel object.

2.2.2.2 The novel surfaces

The behavioural tests described in **Chapter II** were conducted and designed by Jennifer Crawley and Martin W. Seltmann in 2018 with the MTE elephants. In these tests, mahouts asked the elephants to cross a white plastic tarpaulin towards them by calling the elephant from the other side of the novel surface. The elephants were given the freedom to choose whether to join the mahout by walking on the tarpaulin or to go around it (Fig. 2a). The measure of success in this test was based on whether the elephants walked with all four feet on the surface. Since the elephants were not directly led by the mahout with a lead rope onto the novel surface and had complete freedom during the task, we used the results of the calling test without a surface to cross as a control to determine if the elephants were responding to the mahouts' call even in a familiar context without any interfering novel elements.

I conducted and designed the behavioural tests on horses (**Chapter III**) and reindeer in 2021 and 2022. In the first test, the animals were asked to cross two different novel surfaces: white tarpaulin and blue fluffy blanket for horses, and blue tarpaulin and yellow plastic tablecloth for reindeer (Fig. 2b, 2c). Each animal was led on one surface by their familiar handler and on the other surface by an unfamiliar experimenter. I assessed the animals' reluctance to the novel surface and their success in stepping on the surface.

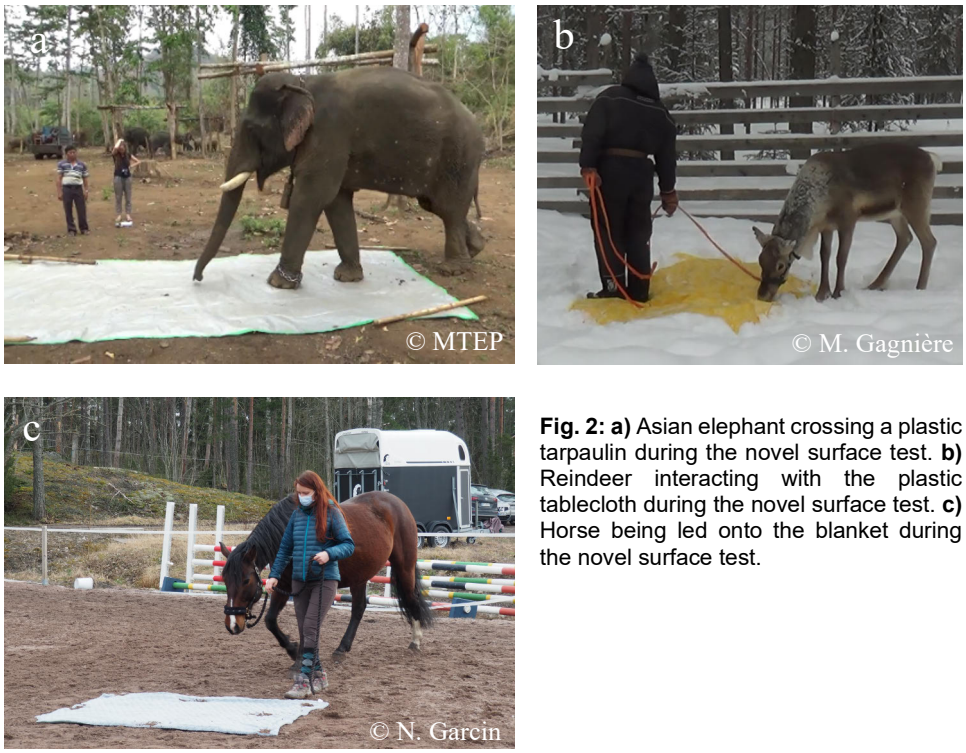

Fig. 2: a) Asian elephant crossing a plastic tarpaulin during the novel surface test. **b)** Reindeer interacting with the plastic tablecloth during the novel surface test. **c)** Horse being led onto the blanket during the novel surface test.

2.2.2.3 The arches

During the preliminary tests conducted with captive reindeer from the Nuuksio reindeer park, I realized that the novel surface may not elicit as strong reactions in reindeer as it does in horses or elephants. To further challenge them, I added another test involving a novel object. This test was conducted in the same manner as the previous novel surface test, except that instead of walking on the surfaces, the animals had to walk under two arches made of different materials. One arch had

Fig. 3: a,b) Reindeer being led under the CDs arch. **c,d)** Reindeer going under the yellow jacket arch.

compact discs hanging on a string (Fig. 3a,b), and the other had yellow jackets hanging on a string (Fig. 3c,d).

For all three species, it was ensured that the novel surfaces, objects, and arches were constructed with elements that contrasted from the ground and surrounding environment through their texture and colours – the shades of red were avoided as there are not part of the chromatic visual spectrum of elephants (Yokoyama et al. 2005), horses (Carroll et al. 2001) and reindeer (Hogg et al 2011).

2.2.3 The communication tasks

2.2.3.1 The calling test

In **Chapter I**, the behavioural tests were conducted and designed by Jennifer Crawley and Martin W. Seltmann in 2017 and 2018 using the MTE elephants. The objective of the test was to evaluate the willingness of elephants to respond to vocal commands from their familiar mahout compared to the same commands from an unknown mahout. An arena marked with wooden planks, measuring 7.75 m x 3.2 m (Fig. 4), was used. The calling mahout stood at the far end of the arena and issued verbal commands to the elephant to cross towards them. The test was repeated with both the elephant's own mahout and the mahout of another elephant, with the sequence randomized. Three measures were recorded: (i) task success (whether the elephant successfully crossed the arena), (ii) response time (the time taken from the initial command to the elephant's first step into the arena), and (iii) command rate (the number of commands given per second during the test period).

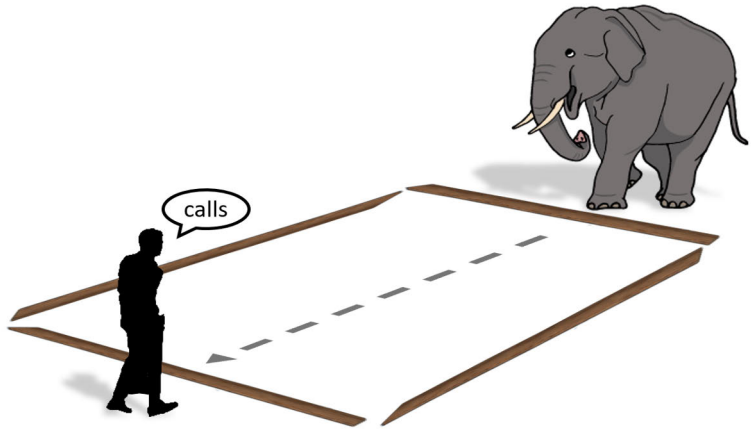

Fig. 4: Schematic representation of the calling test.

2.2.3.2 The pointing task

In **Chapters IV** and **V**, I investigated the factors influencing human-animal communication. I designed a two-way choice task in which an experimenter used a complete set of cues (pointing gesture, gaze, and standing next to the target) to indicate to the animal where to find a food reward. The experimenter stood between two buckets, each closed with a lid, and faced the tested animal, which was held by an assistant 2 meters away. The experimenter took one step towards one of the buckets, gazed and pointed at it (Fig. 5). The animal was then released and free to choose one of the buckets by touching it with its nose. If the animal chose the pointed bucket, the experimenter opened the lid and allowed the animal to eat the hidden reward. If the wrong bucket was chosen, the animal was returned to its initial position without receiving a reward. The test was repeated 10 times, and prior training was conducted to assess the animals' motivation to participate and train them to approach and touch the bucket for the reward.

In **Chapter IV**, 57 horses were tested with either a familiar or unfamiliar experimenter, and the success rate in following the human-given cues by selecting the pointed bucket was examined. In **Chapter V**, due to the limited number of reindeer available for testing (n=8), only unfamiliar experimenters conducted the test. Since there were no existing preliminary studies on the sociocognitive skills of reindeer, this experiment was considered a pilot and the first attempt to assess reindeer responsiveness to human-given cues. Unfortunately, I was unable to perform these experiments with the working Asian elephants as initially planned due to the Covid-19 pandemic followed by the political coup in Myanmar.

All the experiments happened in places familiar to the tested individuals and were video recorded for later analyses of the behaviours and latencies with the Behavioural Observation Research Interactive Software (BORIS: Friard and Gamba 2016).

Fig. 5: **a)** Horse owner pointing at the left bucket. **b)** Unfamiliar experimenter pointing at the right bucket to a reindeer.

2.3 Statistical analyses

2.3.1 Response and explanatory variables

In the calling test for the **Chapter I**, I used as response variables: the task success (whether the elephant successfully crossed the arena) as a binomial response (1: success/0: fail), and the response time (the time taken from the initial command to the elephant's first step into the arena) in seconds. I investigated these measures according to the familiarity of the mahout calling (familiar/unfamiliar), the relationship length between the elephant and calling mahout (unfamiliar mahout = 0, familiar mahout: mean ± SD = 1.82 ± 1.41 years; min= 10 days; max = 11 years) , the working experience of the mahout categorized into quartiles (1: <24 months, 2: 24–38 months, 3: 39–119 months, 4: >120 months) and the age (mean ± SD = 22.5±17.8 years ; min =5 ; max =71) and the sex of the elephants.

In **Chapter II**, I tested the success of the elephants to walk on the novel surface (4 feet on the surface) and cross the test arena as binomial responses (1: success/0: fail). I investigated these measures according to the relationship length between the elephant and calling mahout divided in three categories (1: unfamiliar mahout, 2: mahout known for less than a year, 3: mahout known for more than a year), the working experience of the mahout divided in three categories (less experienced: 1 month–1 year, experienced: 1–4 years, and more experienced: >4 years), the age (mean ± SD = 15 ± 16.8 years; min = 5; max = 58) and the sex of the elephants.

For **Chapter III**, in the novel surfaces' tests, I recorded the reluctance of the horse towards each surface coded as three ordinal levels (1: no reluctance, 2: mild reluctance, 3: strong reluctance) and the success at stepping on the surface with at least one front leg was recorded as a binomial response (1: success/0: fail). With the novel object test I recorded the time from when the horse was released until they freely came to interact with the object and I assessed the reluctance of the horse towards the novel object when the handler tried to touch the horse with it (1: no reluctance, 2: mild reluctance, 3: refused to be touched). These response variables were investigated regarding the handler familiarity (familiar/unfamiliar), the relationship length between the owner and the horse (mean ± SD = 5.25 ± 3.96 years; min = 0.5; max = 15), the number of owner changes the horses had faced (1: horses still owned by their breeder or bought directly from the breeder, 2: horses sold more than once), the number of regular handlers (1: horses handled exclusively by the familiar person, 2: horses also trained or ridden by other people at least once a week (e.g. horse rental, or shared with family members). I also tested the effect of the horses age (mean ± SD = 12.73 ± 5.6; min = 2; max =26) and sex.

From the novel surfaces and novel objects experiments performed with reindeer the success at stepping on the surface with at least one front leg and the success at

passing under the arches with at least one front leg were both recorded as binomial responses (1: success/0: fail). With the novel object test I recorded the time from when the reindeer was released until they freely came to interact with the object. Because the reindeer reactions to novelty were very mild, I could not classify their level of reluctance towardsnovelty. All response variables were analysed according to the handler familiarity (familiar/unfamiliar) and the reindeer training level (still in training, number of seasons of work).

In **Chapter IV**, I examined the horses' success at following the human-given cues by picking the pointed bucket according to the familiarity of the experimenter (familiar/unfamiliar), the relationship length between the owner and the horse (mean ± SD = 4.56 ± 3.36 years; min = 0.5; max = 14), the physical environment (1. small paddock/stall, 2: pasture, 3: alternating between paddock and pasture), the social environment (horses living 1: alone, 2: in dyad, 3: in groups). I also investigated the effect of the horses age (mean ± SD = 12.21 ± 5.56; min = 2; max = 26) and sex.

In **Chapter V**, I analysed the reindeer's success at fulfilling the training requirement to be selected to the test phase (1: success/0: failed the training) and for the individuals which pass the test (n = 4) I measured their percentage of success at following the human-given cues by picking the pointed bucket. I compared these measures according to the reindeer working experience with tourists (still in training, number of seasons of work).

I checked for potential collinearity between the explanatory variables (e.g.: relationship length, social environment, physical environment, age and sex) using Spearman and χ^2 correlation tests. Variables could be kept in the same model if the rs was < 0.7 (Zuur et al. 2010).

2.3.2 Modelling

The statistical analyses performed in this thesis were all carried out in the statistical software R, version 3.6.3 (R Core Team 2023) and figures were created using the '*ggplot2*' package (Wickham 2016), I made use of Generalised Linear Mixed Models using both: Bayesian Framework (**Chapter I and II**), and Maximum Likelihood (**Chapters I, III, IV** and Novel objects experiments with reindeer – see results in supplementary materials), survival analyses (**Chapter III**) and Cumulative Linked Mixed Models (**Chapter III**). Due to the limited sample size, non-parametric Wilcoxon test and binomial test with greater alternative were used in **Chapter V**. Details of the statistical methods can be found in material and methods sections of each chapter. Statistical significance was evaluated at 95% in Maximum Likelihood models ($P < 0.05$, with tendencies recognised at $P < 0.10$). When using the Bayesian Framework, the importance of the effect sizes of regression coefficients was evaluated based on the credible intervals. Significance was considered when the

credible intervals did not encompass zero, and trends were considered when the credible intervals encompassed zero and one of the intervals was between -1 and 1.When working with Maximum Likelihood models, the likelihood family used for each model was selected according to the type and the distribution of the response variable modelled (Zuur et al. 2009). Then I controlled for their appropriateness through residual diagnostic using the '*DHARMa*' package (Hartig, 2021). I selected the most appropriate version of the model using model comparisons with two tailed ANOVA (Rouder et al. 2016) comparing the null model against the original model and simpler models using backward stepwise selection. When necessary, post-hoc analyses based on the Tukey method were performed with the function emmeans() using the 'emmeans' package (Lenth, 2021) or by changing the composition the models' intercept. When using Bayesian Framework, the model selection was performed according to leave-one-out cross-validation (Vehtari et al. 2017) using the LOO function from the "brms" package (Bürkner 2018). When there were repeated measures per individual, the individual ID was included as a random factor to account for the effect of replication.

3 Results and Discussion

3.1 Handler familiarity and relationship length with their animal

3.1.1 Communication tasks

Within a working context, the effectiveness of communication depends on the animals' ability to understand and respond to cues and commands provided by humans. To investigate how the familiarity of the handler and the relationship length of the working dyad influenced the animal response to communication cues, I conducted the calling test (**Chapter I**) and the referential communication test (pointing task) (**Chapter IV**). I expected animals to respond better and faster to familiar handlers, as opposed to unfamiliar handlers, and that their performance would improve with the length of their relationship.

In the calling test conducted with Asian elephants (**Chapter I**), I evaluated their response to a basic command (equivalent to "come here") depending on whether the command was given by their assigned mahout or an unknown mahout. It revealed that more than one-third of the elephants only responded to the call of their assigned mahout and disregarded the calls from unknown mahouts. Furthermore, I found that elephants were quicker in responding to the call of mahouts with whom they had a longer history of working together. This suggests that elephants may have a better understanding of commands when they come from individuals they are accustomed to working with on a daily basis, especially those with whom they have had a longer relationship. It is possible that elephants may have been confused or less responsive when called by someone else. Similar findings have been observed in dogs during training scenarios, where dogs display a significantly higher obedience rate to commands given by their handlers compared to commands given by strangers (Coutellier 2006, Kerepesi et al. 2015).

Interestingly, in **Chapter IV**, when examining human-horse communication, I observed that neither the familiarity of the informant nor the relationship length between the horse and the familiar person had an impact on the horse's performance during the pointing task. Horses tested with their familiar caretaker did not demonstrate better performance compared to horses tested with an unfamiliar

individual. This finding aligns with the results of Krueger et al. (2011), who, in a three-choice task, discovered that while horses directed more attention towards familiar informants, their performance did not improve with familiar informants.

It appears that Asian elephants are more sensitive to the familiarity of the handler compared to horses when it comes to responding and following human cues, although the two tests were different in nature. This species difference can likely be attributed to the extensive amount of time MTE elephants spend with their mahouts. First, they go under a very long training (from the age of 5 to 18 years) but Elephants from the MTE engage in a daily routine with their assigned mahout, which includes activities like bathing in the river and engaging in close physical interactions that can span several hours, depending on the workload. Consequently, the substantial duration of time spent with their assigned mahout may significantly heighten the elephants' sensitivity towards the individual's identity with whom they are interacting. In the horse population used in this thesis, the amount of time spent with their caretaker and their daily routines could vary from one individual to another, potentially explaining why there was no effect of familiarity in the communication task. It is also possible that working animals show a greater sensitivity to handler familiarity when it involves verbal cues rather than gestural cues. In a study by Scandurra et al. (2017), it was demonstrated that dogs' response to gestural stimuli was independent of informant familiarity, similar to what I observed in horses. However, dogs were less likely to perform requested behaviours when verbal signals were given by a stranger and took more time to respond to commands such as "Come" and "Sit" when given by a stranger compared to verbal stimuli given by the owner, similar to what I observed with the elephants. Another hypothesis is that in the referential communication task involving pointing gestures with food rewards, the horses' motivation for food may have overridden any hesitation in responding to cues given by an unfamiliar person.

In summary, Asian elephants were more responsive to commands given by their assigned mahouts compared to unknown mahouts. Elephants also responded more quickly to mahouts they had a longer history of working with. On the other hand, familiarity and relationship length did not significantly affect the performance of horses during a pointing task. This suggests that elephants may be more sensitive to handler familiarity than horses when it comes to responding to human cues. The difference may be due to the extensive time elephants spend with their mahouts and the daily routines they engage in together. The results suggest that working animals may show a greater sensitivity to handler familiarity with verbal cues rather than gestural cues.

3.1.2 Exposition to novelty

Exposition to novelty can induce fear (King et al. 2003, Sneddon et al. 2003, Lansade et al. 2008, Dalmau et al. 2009, Lee et al. 2021) and generate unwelcomed flight reactions that can be dangerous for both human in animals in a working context. To explored whether the familiarity of the handler and the relationship length between the main caretaker and the animal could affect the animals' reactions in unusual situations. I ran experiments where handlers invited the animals to interact with novel objects (**Chapter II, III** and novel objects experiments with reindeer). I expected that a familiar handler would act as a secure base and decrease the animals' reluctance towardsnovelty. During threatening situations, dogs' heart rate increase was significantly less pronounced when they were in the presence of their owner (Gácsi et al. 2013). In 2019, Scopa et al. observed that horses showed more signs of relaxation when groomed by someone familiar compared to being groomed by a stranger.

In **Chapter II**, elephants showed a higher willingness to step on a novel surface when commanded by a mahout they knew for at least a year, indicating their attentiveness and engagement with familiar handlers. Disrupted relationships could negatively impact their work efficiency. Mahouts have reported that elephants may behave slowly or dangerously with other mahouts, and it may take several years to establish understanding and trust (Hart 1994; Mumby 2019; Srinivasaiah et al. 2014). Given the regular changes of mahouts within the MTE system, with an average relationship lasting less than 2 years, maintaining longer bonds between mahouts and elephants poses a significant challenge. To foster trust and better understanding between humans and elephants, it could be beneficial to encourage prolonged working relationships between them. One potential approach is to pair elephants with multiple mahouts, enabling them to develop strong connections with each one. This way, if a particular mahout is unavailable to work, other assigned mahouts can step in safely.

Horses and reindeer were tested on two different novel surfaces with both familiar and unfamiliar handlers. In the case of Asian elephants, they were tested once with either a familiar or an unfamiliar mahout. Additionally, horses and reindeer were introduced to a novel object by either their familiar handler or an unfamiliar handler.

In **Chapter III**, when comparing responses of horses handled by familiar versus unfamiliar handlers, there were no significant differences in their reluctance towardsthe novel object or surfaces. These findings align with previous studies by Ijichi et al. (2018) and Hartmann et al. (2021), that also found no effect of handler familiarity in novel object and novel surface tests. However, when considering the interaction between handler familiarity and horse age, older horses (18 years and older) showed a higher refusal to step on novel surfaces when led by unfamiliar

handlers compared to familiar ones. Geriatric horses who may suffer from corneal degeneration and loss of eyesight (Berryhill et al. 2017), exhibit more anxiety towards novelty than younger horses (Lee et al. 2021). Familiar handlers may serve as a secure base for them, making older horses feel safer to step on unknown materials. However, I found that horses with longer relationships with familiar handlers showed less reluctance towards novel objects and surfaces. Horses with relationship length of at least four to six years with their familiar handler displayed no reluctance when interacting with the novel object or approaching the novel surfaces which is similar to the average relationship length of the study sample. This supports the assumption that the development of a bond between a horse and its caretaker may take time. Interestingly, this result was not affected by the familiarity of the handler during the tests. Horses with longer relationships with the familiar handler (also main caretaker), were also less reluctant towards novelty when handled by a stranger. This finding supports the theory that horses form distinct recollections of humans based on prior interactions, which leads them to generalize their trust or appreciation of humans depending on the positive or negative nature of those memories (Fureix et al. 2009, Sankey et al. 2010a, c). Similarly, beef calves that had minimal contact with humans during rearing were more willing to be approached by a familiar caretaker than a stranger, whereas the identity of the human did not affect the calves that were reared with extensive contact with a caretaker (Boivin et al. 1998).

The reindeer's success at crossing the novel surfaces or arches was not related to handler familiarity. Interestingly, if some reindeer chose to avoid the surfaces (41%) or the arches (25%), they remained calm and showed no obvious signs of stress unlike what was observed with the elephants and horses. Since the familiar handlers for the reindeer were two of the herders who breed them, the relationship length aspect was not investigated. When introduced to the novel object and given the freedom to interact with it, only 2 out of the 16 reindeer approached and quickly smelled the object before turning around. All reindeer refused to be touched with the novel object.

Sledging reindeer live freely in the forest for more than seven months per year and have significantly less interaction with humans compared to working elephants and leisure horses. They are less tamed and generally do not seek physical contact with humans. To minimize their stress, their handling is usually limited to calmly walking on a lead rope while pulling a sledge. As food reward is often associated to a positive human animal interaction (Sankey et al. 2010*a*,*b*) the main way of maintaining a positive relationship with reindeer is to daily feed them lichen by hand. Since lichen is their favourite food, this ensures a positive association with human interactions. However, they do not experience a wide range of positive interactions with humans that could result in a strong bond or valued relationship. In contrast,

mahouts often bathe their elephants daily, provide them with scratches, and spend a significant amount of time in close contact with them (Crawley 2021). Similarly, horse owners engage in activities such as grooming, scratching, and playing with their animals, creating numerous opportunities for positive interactions. Therefore, I believe the nature of the relationship between herders and sledge reindeer differs from that of mahouts and elephants, as well as horse owners and horses. Given the choice, when there are no food rewards involved, reindeer generally prefer not to engage in physical interaction with humans. During our fieldwork observations, we noticed that while they can be curious about humans, some individuals would approach and investigate the materials we had but always maintained a distance, ensuring they remained out of our reach. Interestingly, reindeer herders often describe their sledge reindeer as their co-workers and emphasize the notion of negotiation rather than forcing the reindeer to work. They believe in exchanging a "salary" in the form of lichen or salt in return for the reindeer's cooperation (Stépanoff 2012; personal discussions).

In both Asian elephants and horses, longer relationships were associated with less reluctance towards novel surfaces, although for horses, this was generalised to unfamiliar handler as well. Unfortunately, this could not be directly tested with elephants, and it cannot determine if an elephant with a long-standing relationship with its mahout would agree to cross a novel surface with an unfamiliar mahout. However, considering their higher responsiveness to their own mahout in the calling test (**Chapter I**), it is likely that they would refuse to cross a novel surface when commanded by someone unfamiliar. Unlike horses, Asian elephants may consider each human relationship independently rather than generalizing their behaviour based on overall interactions. This complexity may stem from the elephants' intricate social structure and the diversity of interactions within their conspecific groups (Vidya and Sukumar 2005). African female elephants, in particular, have a fluid social system and can recognize calls from different categories of female group members, including those from more distantly related family units. McComb et al. (2000) estimate that they can discriminate between about 100 different individuals.

In contrast, reindeer did not rely on handler familiarity when crossing novel surfaces or arches. While the relationship length could not be directly tested, all reindeer in our study had known the familiar experimenter since they were six months old, indicating a minimum acquaintance of three years with their herder. It is possible that, alike horses, reindeer perceive their well-known herders as a secure base and generalize this behaviour to unknown humans, explaining their lack of reluctance towards the novel surfaces and arches regardless of handler familiarity. Considering that the novel surfaces and arches did not elicit fearful behaviour, this type of novelty test may not be suitable for reindeer. Since they live freely in the forest for most of the year and can be exposed to predators such as bears, lynx,

eagles, and wolverines, it is worth considering tests involving simulated predators or dogs, which could potentially induce more reluctance and allow us to observe whether reindeer perceive humans as a secure base or not. Despite the absence of outward behavioural signs of stress in the reindeer, it remains possible that they may have internalized stress. In horses, it was shown that the behavioural stress response to novelty was not always representative of the physiological stress (Squibb et al., 2018). It would be interesting to associate these behavioural tests with the sampling of physiological stress markers, such as blood and saliva corticoids as well has the internal temperature and the heart rate variation.

To summarise, I found that Asian elephants were more willing to step on a novel surface when commanded by a familiar mahout while horses did not show significant differences in their response to novel objects or surfaces based on handler familiarity, except for older horses who did not step on the novel surface with unfamiliar handlers. However, horses with longer relationships with their caretaker showed less reluctance towards novelty regardless of the handler during the test, suggesting the generalisation of their behaviour with humans according to the overall experience with humans. Reindeer, on the other hand, did not rely on handler familiarity when crossing novel surfaces or arches although the tests designs did not promote fear reactions and may have not been suitable for reindeers.

3.1.3 The familiarity, a matter of context?

Interestingly, familiarity did not play the same role in the different experimental setups. Relationship length affected the horses' behaviour during the novelty tests (**Chapter III**) but not during the referential communication task (**Chapter IV**). Elephants were sensitive to the handler's familiarity during both the novelty tests and the communication task (calling test). In the referential communication setup, the experiment involved free participation from the horses and included a food reward, so the informant was probably quickly associated with something positive regardless of who they were. The novel object tests from **Chapter II** and **III** are more stressful situations, and the calling test in **Chapter I** does not involve a food reward. I hypothesize that the context may play a role when investigating the effect of human familiarity in human-animal interactions. In a more stressful environment, animals may rely more on a familiar human as they act as a secure base, while in a positive context where animals already feel safe, the identity of the interacting human may matter less. This theory is supported by the findings of Kerepesi et al. (2015) in dogs. In their study, they observed that dogs did not show a difference in responding to different partners in obedience tasks but relied more on their owner than on a familiar

or unfamiliar person in situations provoking anxiety. They concluded that the discrimination between the owner and a less familiar person is context specific.

Likewise, the elephants' increased willingness to cross the tarp when prompted by their familiar mahouts might be attributed to their freedom during the test, as opposed to being led with a rope by the handler. While all animals had the freedom to decide whether to walk on the surfaces or not, the decision of the horses and reindeer to cross the surfaces could have been influenced more by being led than by the identity of the handler. Furthermore, since fearfulness, boldness, and exploratory behaviours are frequently employed as personality items (Carere and Maestripieri, 2013), we cannot rule out the possibility that the stress induced by novelty might have overshadowed the stress response from being handled by a stranger. Consequently, in these animals, their apprehension towards unfamiliar humans could have become indistinguishable due to the combined stressors. Further studies should investigate the role of familiarity with the caretaker in various contexts. More generally, the experimenter's familiarity should be given more consideration in studies experimentally investigating animals' socio-cognitive skills and human-animal interactions.

These findings suggest that the context of the interaction may play a significant role in investigating the effects of human familiarity in human-animal interactions. Therefore, it would be valuable for future studies to explore the role of familiarity with the caretaker across various contexts.

3.2 The handlers' experience and command styles

One aspect that has not been sufficiently studied to date is the level of working experience of the handlers, although it may influence the handler's behaviour towardsan animal and, therefore, the animal's behaviour. A study observed that older and more experienced beef producers showed more positive attitudes towards cattle and were more sensitive to cattle pain than younger producers (Wikman et al. 2016). The elephant-mahout system from the MTE is a great model to study this aspect as all mahouts follow the same training and are requested to perform the same tasks with their elephants. Therefore, the time since they started working as mahout can reflect their level of professional experience. In **Chapter II**, I expected mahouts with more experience to have better success in commanding their elephants to walk on the novel surface. Intriguingly, the mahout's experience had less impact on the elephant's response than their specific relationship lengths with the focal elephants, which corroborates findings by Srinivasaiah (2014): unfamiliar mahouts who knew all the commands could not be assured of an elephant's compliance to a command.

Along those lines, the way mahouts gave the commands influenced the elephant's response in **Chapter I**. Although the command to call an elephant is similar for all MTE mahouts, they varied in their way of expressing it. The command is one syllable, "Lah," and some mahouts repeated the word every few seconds, while others would repeat it almost constantly until the elephant joined them. While the command rate did not affect the success of the elephant in joining the mahout, I observed that the elephants responded faster to mahouts calling more frequently. This result suggests that repeated calls may be more efficient in catching elephants' attention. Although outside the scope of this study, future behavioural experiments could benefit from measuring other variables related to command style, such as verbal pitch and intensity, which have been found to be important in human-horse communication (Lansade et al. 2021). Thus, although the handler's experience may not have a direct impact, it is crucial to consider the nuanced communication dynamics between handlers and their animals, including variations in vocalizations and individual handling styles, which can influence the working animals' responses in different situations.

In conclusion, the specific relationship length between elephants and mahouts had a greater influence on the elephants' response compared to the mahout's experience. This finding supports previous research showing that unfamiliar mahouts cannot guarantee compliance from elephants, even if they know all the commands. Additionally, the way mahouts gave commands affected the elephants' response, with more frequent calls resulting in faster reactions. While this study did not explore other variables related to command style, future experiments should consider factors such as verbal pitch and intensity.

3.3 The number of current and past handlers

Leisure horses can not only be considered as pets but also part of the family, being cared for and ridden by several family members. Furthermore, owning and maintaining a horse can be costly, leading owners to share their horses with other riders to reduce expenses. In **Chapter III**, I explored the behaviour of horses with multiple relationships and their exposure to different handlers. Surprisingly, my findings revealed that horses with multiple handlers exhibited more reluctant behaviours towards novel surfaces and objects, regardless of the handler's familiarity.

In contrast, horses with a single handler demonstrated less reluctance towards the object. This suggests that horses with only one handler may have had more opportunities to establish a strong bond with a particular individual, enabling them to generalize their behaviour and to exhibit trust towards other humans based on the

secure emotional foundation in their relationship with their main caretaker. This finding aligns with our previous discovery that horses with longer relationships with their familiar caretakers also display less reluctance towards novel objects. Previous research has demonstrated that horses can have negative emotional experiences due to improperly implemented training and handling techniques (McLean and McGreevy 2010, McGreevy et al. 2011), leading to musculoskeletal injuries such as back or teeth pain caused by poorly fitted gear during riding sessions gear (Bondi et al. 2020, Dyson et al. 2020). Consequently, having multiple handlers with varying abilities to respond to horse behaviour, especially when some handlers are only involved in riding or training sessions and not daily care, increases the likelihood of negative emotional experiences for horses. Horses that have multiple relationships with different handlers may be more susceptible to developing anxious behaviours in unfamiliar situations.

Similarly, horses that have gone through multiple ownership changes exhibited more reluctant behaviours when confronted with a novel object. While it is true that horses have varying temperaments (Lansade et al. 2017, Rankins and Wickens 2020), and this finding could be attributed to the possibility of fearful and challenging horses being sold more frequently than easy-to-handle ones, it is also worth considering that changes in ownership often come with a shift in the physical and social environment, which can be a stressful experience for horses. Consequently, it may take a considerable amount of time for the horse and the new owner to establish their bond and for the horse to feel at ease in human company once again. These findings align with our previous results, as horses with longer relationships with their familiar caretakers demonstrated less reluctance towards novel objects. This supports the general assumption that developing a bond between a horse and its caretaker is a gradual process that requires time.

In conclusion, horses with multiple handlers and who experienced multiple ownership exhibited more reluctance towards novel surfaces and objects. Horses may benefit from establishing a strong bond with a particular handler, allowing them to generalize their trust towards other humans. Multiple ownership changes and exposure to different handlers may increase the likelihood of negative emotional experiences and anxious behaviours in horses. This suggests that the development of a positive horse-human relationship may require a significant amount of time. It is shaped by multiple factors, including the horse's previous interactions and experiences with humans, as well as the cumulative impact of repeated interactions that shape the horse's daily life.

3.4 The environment's impact on the interactions with humans

Studies have shown that social species can suffer from social deprivation and poor environmental conditions, which not only affect their welfare but also their performance in cognitive tasks (Lambert and Guillette 2021). However, these aspects have primarily been studied in laboratory settings and rarely with long-lived mammals, or within the context of human-animal interactions. In **Chapter IV**, I investigated whether, for working animals, living in appropriate conditions that respect their natural ecology would have an impact on their responses to humans during communicative tasks.

Feral horses have greater freedom of movement and more autonomy in choosing their social groups compared to domestic horses. Domestic horses may be confined to individual stalls for most of the day with limited outdoor access or live in groups within fenced pastures of varying sizes. In our study, both the social and physical environment were strongly associated with the horses' success in following human-given cues. During the pointing task, horses that lived in groups had a significantly higher success rate (82%) compared to those living in dyads (57%) or alone (63%). Similarly, horses living in larger fields throughout the year had a higher success rate of 79% compared to those living in stalls or small paddocks (62%). These housing factors are strongly correlated, making it difficult to determine whether social deprivation or the lack of space and enrichment has a greater impact on the results.

In (2014) Lansade et al. demonstrated that an enriched environment, such as access to pasture with conspecifics, can enhance the performance of horses in learning tasks involving understanding informative cues. Horses living in larger groups may benefit from increased cognitive stimulation as they can interact with various conspecifics, leading to more complex social situations. This can contribute to horses learning and improving their socio-cognitive skills, which may explain the higher success rate in the pointing task among horses living in larger groups. Temporary social changes can directly impact animals' brain structure, even beyond critical developmental stages. For example, rhesus macaques (*Macaca mulatta*) housed in larger groups for four months showed an increased amount of brain grey matter compared to those housed in smaller groups (Sallet et al. 2011). Several studies comparing animals reared in isolation versus in groups or different-sized groups have found positive effects of sociality on cognitive skills (Ashton et al. 2018*b*, *a*).

Regarding the reindeer (**Chapter V**), since they all lived in the same semi-captive conditions, the effects of group size could not e tested, social deprivation, or enclosure size on their ability to follow human-given cues. However, it is interesting to note that the tested reindeer are free ranging in the forest, their natural environment, for most of the year where they must find their own food and shelters.

Despite spending most of the year without contact with humans, two out of the four tested reindeer demonstrated surprisingly high scores in the pointing task (9 successes out of 10 trials). This aligns with the idea that for social species, living in an appropriate physically and socially enriched environment may contribute to promoting their cognitive development and, consequently, their socio-cognitive abilities towards humans.

In conclusion, our study found that the social and physical environment strongly influenced horses' success at following human cues. Horses in larger groups and larger fields had higher success rates, suggesting the benefits of social interaction and cognitive stimulation. Determining the greater impact between social deprivation and limited space remains challenging. These findings align with the observations made with semi-captive reindeer living freely in their natural habitat for most of the year. They showcased impressive performance in the pointing task, despite having less frequent contact with humans. These results suggest that an appropriate living environment that respects the fundamental needs of the animals can stimulate their cognitive development and enhance their performance in communicative tasks with humans.

3.5 The animal own experience

3.5.1 Exposition to novelty

I observed an effect of age and/or training experience on the response to novelty in Asian elephants and horses, but not in reindeer. In **Chapter II**, older elephants were more likely to refuse to walk on the novel surface compared to younger individuals. This finding aligns with the results from **Chapter III**, where older horses also showed a higher reluctance to walk on the novel surface, although this response was influenced by the familiarity of the handler, as mentioned earlier. When horses were given the freedom to approach the novel object, younger horses (2–6 years old) were the fastest to approach it. These results corroborate the findings of Baragli et al. (2014) who observed that younger horses (4–6 years old) exhibited more frequent and prolonged exploratory behaviour when confronted with an unfamiliar stimulus compared to older horses. A recent study by Christensen et al. (2021) further suggested that exploratory behaviour in horses reflects their curiosity and intrinsic motivation towards novelty, which may enhance learning performance in younger individuals.

The refusal of older individuals to walk on the novel surface could be attributed to neophobia, as many species in the wild tend to avoid interacting with unfamiliar elements as a survival strategy (Greggor et al. 2015). Juveniles often display more

explorative behaviours as they learn what to avoid over time, leading to greater neophobic tendencies among older individuals (Brown et al. 2013, Mata et al. 2013, Sherratt and Morand-Ferron 2018). Interestingly, there was no effect of age or training level observed in reindeer during the novelty tests. In the novel surface and arch tests, the reindeer appeared indifferent to the setups. If they were not afraid of the objects, they also rarely stopped to interact with the surface or the arch. They also showed no interest in freely approaching and interacting with the novel object when it was held by the experimenter. Furthermore, they consistently refused to be touched with the objects, regardless of the handler familiarity. To explore their response further, additional exploratory trials were conducted by leaving the novel objects on the ground in their main enclosure. When no human was holding the objects, the reindeer showed more interest and approached to smell them, particularly the younger individuals. However, their interest seemed to diminish quickly as they realized the objects were not food.

3.5.2 Communication tasks

Age and training level were also relevant when performing the communication tasks. In the **Chapter I**, fully trained elephants (over 18 years old) all responded to the call of their mahout, whereas the probability of younger elephants responding to the call of their mahout increased from about 30% at age 5 to 99% at age 18. This is not surprising as young elephants, still under training, may be less accustomed to responding to commands. The probability of elephants responding to an unknown mahout also increased with age, but not as drastically. It started with 30% of 5-year-old elephants responding to the calls and increased to about 75% at age 70. As elephants age, they may go through more mahout changes, making it easier for them to adjust to the commands of an unknown mahout.

In reindeer, when the task differs from their habits, younger individuals became more difficult to handle and quickly showed signs of stress when interacting with strangers., in the pointing task in **Chapter V** when they had to interact a bit more closely with humans, it seems that their level of experience with humans affected their performance in some degree. Compared to the working reindeer, the ones still in training are rarely exposed to tourists and unknown humans. Out of the eight reindeer used for the experiment, the four youngest were likely too stressed to pass the training phase and did not understand what was asked of them, despite the food rewards. Therefore, they did not participate in the pointing task. The four individuals that performed the task were active working reindeer, already well habituated to being hand-fed by tourists. Two of them followed the human indication significantly more than chance (9/10), another one achieved a result of 6/10 successes, and the oldest reindeer (13 years old) was the only individual who chose the wrong bucket

10 times out of 10 trials. It genuinely avoided the human-given indications. Of course, the sample size is too low to draw any conclusions regarding age, and the herder also described this individual as less affectionate towards strangers and less curious than the other reindeer participating in the study. This behaviour could be related to the reindeer's personality and its own perception of strangers.

In **Chapter IV**, the success rate of horses at the pointing task did increase with age. Over time, as leisure horses engage in a growing number of interactions with various humans, they might improve their ability to make use of human communicative cues. This acquired knowledge could explain why horses, with age, get better at following human-given indications, regardless of who the human informant is and how long they have known each other. Even though I did not use ostensive communicative cues, our data suggests that the best performers in using human-given cues are the older horses (> 19 years old), all of which scored with at least an 80% success rate. Previous studies that investigated the effect of age on the ability to follow human cues focused on comparing very young individuals (few months old) against mature individuals (dogs: Agnetta et al. 2000; goats: Kaminski et al. 2005). To my knowledge, no study has included samples covering animals of old age. There is a need for studies covering a wider age range when investigating human-animal interactions, as the experience of older individuals may be underestimated.

All three species showed improved performance with age when communicating with humans, highlighting the importance of the animals' experience with humans. Acquiring the skills to communicate and comprehend another species, which employs different cues than one's own, undoubtedly requires a certain amount of time. In the case of human-animal communication, this may be even more true for species which are less domesticated or do not live directly in human household. In the study conducted by Gácsi et al. (2009) on canids, it was demonstrated that dog puppies, when raised under similar conditions, outperformed wolf puppies in following distal pointing gestures by humans. However, in adulthood, dogs and wolves performed similarly, although wolves took more time to make their decisions. This difference was attributed to dogs' enhanced readiness to interpret human cues. Asian elephants, horses, and reindeer, despite having different degrees of domestication, do not live as closely to humans as dogs do. Therefore, they may require more time than dogs to adjust to human-given cues and develop effective communication skills.

The findings highlight the developmental changes, such as age, and training experience that influence animals' responses to novelty and their ability to comprehend and engage with human communicative cues. When exposed to novelty, younger individuals exhibited more exploratory behaviours, while older individuals

displayed a higher degree of reluctance. This can be attributed to the natural decline of curiosity and exploratory tendencies with age, a phenomenon observed in numerous species. Conversely, in communicative tasks, animal success rates improved with age and training level. This finding suggests that as animals mature and receive more training, they become more adept at understanding and responding to human communicative cues. Taken together, these results underscore the importance of considering animals' individual experiences and stages of development when designing training programs and promoting positive human-animal interactions, particularly for species with less domestication and limited exposure to humans.

3.6 Strengths and limits of the project

In my study, incorporating a diverse range of species and considering multiple dimensions of the human-animal relationship provides a holistic understanding of the topic. This sheds light on the intricate interplay between various elements influencing interactions between humans and working animals, allowing for a richer exploration of the inherent complexities and nuances in this dynamic relationship.

Working with volunteer participants for the horse experiments allowed for the investigation of new factors, such as relationship length, past ownership experiences, and the number of regular handlers, which have been rarely considered in previous studies. However, it also introduced uncontrolled sources of variation within the participant group. Participants had varying levels of experience and knowledge with horses, potentially influencing their attitudes and behaviours towards their horses (Hemsworth et al. 2015) and the horses' training. Additionally, the inclusion of horses from different breeds, known to impact emotional levels and personality traits (Hausberger et al. 2004, Lesimple et al. 2011, Vidament et al. 2021), added complexity. Despite potential confounding factors, the study's horse population is a representative sample of common leisure horses in western countries. This emphasizes the importance of considering often-overlooked factors in the human-animal relationship. Future research should focus on investigating these factors in more controlled environments.

Additionally, the categorization of animals as working or non-working is not straightforward and depends on the specific context and individual association between humans and animals. Considering leisure and sport horses as working animals can be discussed, as they do not bring any clear material and financial benefits to their owners; thus, they may be regarded and cared for differently by the owners. In that regard, results were always analysed with caution and taking the context into account.

The sample sizes, particularly for Asian elephants and horses, was substantial compared to typical studies on animal behaviour. This allowed us to examine aspects such as age and training level in a more nuanced and continuous manner. With larger sample sizes, we could employ statistical models that incorporated interactions between factors, enabling a comprehensive exploration of the intricate relationships among variables in the study.

Furthermore, studying an overlooked species like reindeer means venturing into uncharted territory without previous studies to provide guidance. The initial fieldwork session primarily served as a pilot study (**Chapter V** and novel object tests with reindeer), allowing us to assess what approaches are effective and what are not when working with reindeer. In that regard, it was a successful endeavour. Additionally, it highlights the potential of reindeer as an intriguing model for studying cognition in cervids.

Overall, while there are limitations to consider, this research offers valuable insights into the complex dynamics of the human-animal relationship. It lays the foundation for further exploration and encourages future studies to address the identified limitations to enhance our understanding of this fascinating subject.

4 Conclusions and future directions

4.1 Conclusions

All together, these five chapters offer a fresh and comprehensive perspective on the study of the human-animal relationship, specifically from the vantage point of working animals. By examining three distinct species, I was able to explore a wide array of factors that are integral to understanding the human-animal relationship. These factors encompass the level of familiarity between handlers and animals, the past and current human context within which the animals operate, the characteristics of the handlers themselves, as well as the animals' own experiences and their surrounding living environments.

Longer relationships and greater familiarity between handlers and animals were associated with reduced reluctance towards novelty in Asian elephants and horses. Furthermore, horses living in larger social groups and expansive fields exhibited higher success rates in communicative tasks. Age and training experience also played crucial roles, with younger individuals displaying more exploratory behaviours while older individuals exhibited increased success in communicative tasks.

This research suggests that the degree of domestication and proximity to humans may impact animals' ability to understand and respond to human cues. For example, dogs, which have been selectively bred for thousands of years to live closely with humans, exhibit enhanced readiness towards human cues. On the other hand, species like Asian elephants, horses, and reindeer may require more time and exposure to develop similar abilities. This highlights the significance of ongoing training and support for both animals and handlers. Continued training can help animals adjust to novel situations and strengthen their ability to understand and respond to human cues, ultimately improving their performance and reducing stress. Although horses have been domesticated for the longest period (4000 years) among the three species studied in this thesis, Asian elephants, which are not considered domesticated, displayed the highest sensitivity to handler familiarity, while reindeer exhibited the least reaction to handler familiarity. This becomes even more intriguing when considering that Asian elephants had, on average, shorter relationships with their main caretakers compared to horses. Despite not being classified as domesticated,

Asian elephants have a long-standing history of interaction with humans, serving as working animals for at least 4000 years. This sensitivity to human familiarity in Asian elephants could be attributed to both their historical relationship with humans and the specific context in which the tested elephants reside, MTE elephants spend extensive amounts of time with their mahouts. Additionally, Asian elephants possess a complex social structure that involves interactions and recognition of numerous individuals. In contrast, reindeer have limited contact with humans, and their interactions occur only for part of the year. Additionally, if they live in complex social structures, they engage in minimal physical contact with their conspecifics. As a result, human contact may often not be associated with something positive for reindeer, leading to lesser interest in the humans they interact with.

The insights gained from this study can inform practices and training methods for working animals, enabling handlers and caretakers to tailor their approaches based on the species-specific characteristics and sensitivities to handler familiarity. By understanding and addressing the unique needs and sensitivities of each species and individuals, we can enhance the welfare and effectiveness of working animals. This poses a significant challenge for working animals, as they may change hands multiple times throughout their lives. Consequently, they may find themselves in new environments, unfamiliar social conditions, and under the care of new handlers who may lack information about the animal's previous living conditions. These changes can be highly stressful for the animals, and they require ample time to adjust to their new circumstances. Handlers must display patience and allow the animals the necessary time to settle into their new life, even though there may be pressure to put them to work and generate financial benefits. By prioritizing long-term relationships between working animals and their handlers and encouraging regular positive interactions, we can foster positive human-animal relationships and the formation of strong bonds within the working dyad. This, in turn, leads to increased safety, calmer attitude, and greater compliance among the animals, during work and stressful situations that can pose risks to both the handlers and the animals themselves (Table 1).

These findings also emphasize the importance of providing working animals with appropriate living conditions that meet their physical, social, and cognitive needs. By creating environments that stimulate cognitive development, encourage positive relationships between animals and handlers, and provide opportunities for learning and exploration, we can enhance the well-being and performance of working animals.

4.2 Future directions

Overall, the familiarity revealed itself as an important factor that can truly affect the response of working animals during interactions with humans. Exploring and comparing how familiarity with handlers, along with prior experiences with humans, impacts other animals in human care, such as house pets, zoo animals, and livestock, presents a fascinating avenue for research. Undertaking such comparative studies could significantly enhance our understanding of the human-animal relationship and its implication for animal welfare.

To deepen our understanding of human-animal interaction on a cognitive level, investigating emotional changes experienced by animals during interactions at a physiological level is compelling. Stress and temperament have been shown to affect working memory and learning performances in horses (Valenchon et al. 2013b, a, 2017, Fortin et al. 2018). To address this, I plan to conduct behavioural experiments involving interactions with positive and negative valences for the animals. I'll monitor heart rate variations and assess thermal changes in the eye caruncle, linked to facial expression and behaviour. Preliminary findings show that petting reindeer by strangers results in a drop in eye caruncle skin temperature, suggesting that human touch may elicit stress responses in these animals (Liehrmann et al., in prep).

In this thesis I highlighted the remarkable ability of reindeer to effectively follow human cues to get hidden food, even with minimal training when appropriately tamed. This ground-breaking discovery represents the first demonstration of such cognitive abilities in cervids, propelling reindeer as a promising model system for further investigations into cervid cognition. These findings not only shed light on the impressive adaptability of reindeer but also emphasize the need for continued research to unravel their cognitive potential and deepen our understanding of cervid behaviour.

The thesis emphasizes the significance of considering environmental factors and past experiences when examining animal behaviour, especially in the context of work tasks. It is crucial to ensure that animals are situated in an appropriate environment that fosters their well-being and growth. These aspects warrant additional investigation, and one intriguing approach involves studying what motivates animal owners when selecting the living conditions for their animals. To explore this, I launched an online survey that delve into how the personality traits of working animal owners influence their attachment to their animals and, consequently, the living environment they choose for them. This research will shed light on how the owner's choices in the living environment are reflected in the behaviour of their animals.

5 Personal perspectives and background of the project

I embarked on this doctoral research project in January 2020 with the intention of beginning fieldwork with Asian elephants in Myanmar in March 2020. Unfortunately, like millions of others, my plans were disrupted by the global Covid-19 pandemic. Additionally, the political coup in Myanmar in February 2021 further compounded the challenges. Consequently, I had to accept that the planned behavioural experiments involving Asian elephants and their mahouts would not take place during my PhD.

Initially, my PhD plan solely focused on Asian elephants. Fortunately, I was able to utilize the data previously collected by my colleagues in 2017 and 2018 (**Chapter I** and **II**). However, without funding for experiments and fieldwork with other species, I had to develop a new plan. Working with horses naturally presented itself as an alternative, and I am grateful for the tremendous support I received from the Finnish horse rider community. Many volunteers responded to my call, and as a result, **Chapter III** and **IV** were produced through this collaboration.

During this time, I also obtained research grants to explore the reindeer behaviour, an emblematic animal that has intriguingly received little attention so far. Working with reindeer posed significant challenges, which made them even more fascinating. The Reindeer Journey farm provided us with optimal working conditions and led to the development of **Chapter V**, the novel objects experiments, and several upcoming papers. I sincerely hope to have the opportunity to continue my investigations and further expand our understanding of these remarkable animals.

Despite the frustration of not being able to pursue my initial plan in Myanmar and facing limitations in materials and funding, I must admit that this situation forced me to be resourceful and creative in navigating the obstacles along this journey. I learned far more than I expected and now feel prepared for the next academic challenges!

Acknowledgements

I have a feeling I could write another 50 pages just for acknowledgments, but don't worry I'll keep it light.

Wow, what a wild ride these past five years have been, packed with professional and personal challenges, a crazy world pandemic, and many downright scary political events. But guess what? So far, I made it through all of it, and here we are ready to celebrate!

First and foremost, I want to express my deepest gratitude to my three extraordinary supervisors. Virpi, you're a rockstar for believing in my wildest ideas and supporting me every step of the way. Who would have thought that when I signed up to study elephant personality in Myanmar, it would lead us to snowy Lapland, presenting fluffy unicorns to Santa Claus's reindeer? Your support and confidence-boosting magic always brought me back on track. Thank you, Léa, for your enthusiasm from the very first day I contacted you. Despite the physical distance, you have been a constant source of support, always making time for our meetings and offering guidance when I needed it most. Your unwavering dedication and belief in my potential have played a key role in my growth as a researcher. Thank you, Mirkka, for your wisdom. Your manuscript advice has been spot-on every time, and I'm truly grateful for your expertise and kindness. To my fantastic supervisors, thank you for being inspiring women and for making this journey so incredible. Your belief, support, and wisdom have made a world of difference. I couldn't have asked for better mentors.

I'm incredibly grateful to my pre-examiners, Professor Katrina Merkies and Dr. Christian Nawroth, for their invaluable insights and comments that greatly contributed to improving my final thesis. Thank you! I would like to express my sincere gratitude to Associate professor Maria Vilain Rørvang for accepting the role of my opponent. I have been an admirer of your work for some time, and I am confident that the defense will spark a captivating and thought-provoking discussion.

I also want to extend my thanks to Jon Brommer, my PhD director and custos. Your offer to join the BGG board as a student representative was a fantastic opportunity, and I am grateful for the knowledge I gained and the enjoyable experience of participating in the board meetings. Your wisdom and quiet mentoring

have been invaluable. I am also grateful to the BGG doctoral program for awarding me a fully funded 4-year position which allowed me to focus on my project without interruptions. I'd like to acknowledge two behind-the-scenes heroes, Anne Hemmi and Sari Järvi. You both have been my saviors in countless administrative nightmares. Anne, your assistance with translation issues has saved me on numerous occasions. And Sari, I couldn't be happier that you shared my enthusiasm for organizing BGG activities. Thank you both for your unwavering support.

Many thanks to my co-authors for their valuable contributions to the publications. Special shout-out to Sonja Koski for your countless advice and for adopting me in your horse team group! To Jonathan, as it was great to have you around and support each other during our Masters. And thank you Plotine for hosting and welcoming me during my stay at the INRAE.

I which to thank the amazing team of research assistants and interns that helped me on the horse and reindeer fieldwork. Veera, Alisa and Emmi, thank you for sacrificing your weekend mornings so I could drag you to all the surrounding stables (Today, we see a moose!). Thank you, Camille and Mélissa, for being the best first Master students I supervised! You guys are all absolute rock stars, and I know you'll all do great things!

I wish to extend my heartfelt gratitude to all the volunteers who wholeheartedly participated in the experiments with their horses, the mahouts and their elephants, the dedicated vets, and research assistants from the MTE, as well as the Ollila family from the Reindeer Journey. None of this would have been possible without you so from the bottom of my heart, thank you for making these projects come to life and for being instrumental in advancing our understanding and knowledge. Your involvement has made a significant difference, and I am deeply grateful for your participation and collaboration.

Now to my wonderful academic adventurers' guild! Martin, it's been so much fun to go on many crazy epic quests with you, from fighting basilisks and demon puppets in the meeting rooms to writing grants together and taming reindeer in Lapland. Hopefully, we'll team up for many more adventures together! Jennie, you're the sunshine that never fails to brighten our spirits! Whether it's bouldering up walls, going to pottery class, hitting the dance floor, or diving headfirst into any thrilling escapades that come our way, you're always up for it. Carly, you're forever ready for crazy embassy parties and fun holiday trips around Finland. Girls, your energy is infectious, and this journey would not have been the same without you both! Thank you, Simon, for all the awesome board game and RPG sessions, the constant dark humor, and the great "shit movie nights" we've had! I'm so grateful to all of you for the fast integration into our group. The teasing, sarcasm, and camaraderie in the "kids office" made me feel at home. You're not just comrades; you're my academic big sis and bros!

To the BGGossip crew and the 21st-century Peggy group: Heloise, Aditya, Farshad, Luigi, Leonie, Charlotte, Giorgio, Aino, Amelie, Aida, Aurelien, Aymeric, Carina, Prakhar, Miguel, Laura, Sophie, Antoine, Diogo, Michael, Verane, Giulia, Jasper, Pablo, Natacha, Nina, Marlene, Hoedrick, Venni, Luca, Rob and Emilly ... To all of you who have been part of this incredible journey, whether you were there from the very beginning or joined in later, and even those who accompanied me for just a few chapters... I am immensely grateful to have met so many wonderful souls. The moments we shared together, whether hiking, enjoying saunas, playing board games, doing sports, practicing disc golf, or simply going for drinks, have always been a pleasure. Never underestimate the transformative power of a good pint of beer (or GnT) shared with the right person to spontaneously resolve your R and stats head-scratchers! Your presence and friendship have enriched my experience, and I appreciate the memories we've created together. Here's to many more memorable moments and lasting connections! Of course, I can't skip mentioning my rock-solid emotional support: Ludo, the fries' tester, and the fish master! I have no idea where I'd be without you showing up just when I needed a pal like you! I'm beyond thrilled to have you as my friend and for the irreplaceable support you provide! Thanks a million, Ludo! Let's continue this journey together in Scotland as you're the fish to my chips!

To my dear friend, Yoan, I'm certain my PhD wouldn't have been completed without you and the magic chat! I've lost count of how many beers I owe you for saving me with the stats and being an amazing teacher with wise advice "The problem is always between the chair and the keyboard". Thank you so much for always being there, not only for stats but also as a fantastic listener as you've always allowed me to vent anytime and share my weirdest dramas. To my French crew, "Qui sont morts pour que vive la France" – Bastien, Mylene, Vincent, Laureline, and Arnaud – thank you for all the good moments of crazy laughter and collective games online. I am so glad that despite the distance, our friendship is still rock solid! Laureline and Nono, I owe you a very special thank you for welcoming me, hosting me, and guiding me through New Zealand. I'll always cherish the magical trip that lifted me out of a dark place! I love you guys and I'll come back soon! To the Pori/Tampere crew, thank you, Piotr, Mathieu, and Elina, for your friendship, which has been a tremendous support throughout this journey. It has always been wonderful to have the opportunity to escape from the academic world and Turku every now and then. I'm grateful for the memorable Christmas and New Year's eves, the exciting escape games, the delightful dinners, and here's to many more to come! (that's what they say!). I wish to thank my friends from *Ad naturam*. Despite my limited activity lately, this association has enriched my scientific writing and thinking, and I truly enjoy popularizing science with such a vibrant and fun group! I want to extend a

special thank you to Hugo, Marine, Laura, Orlane, and all the newest members who have joined, as well as those who have ventured towards other horizons.

To my incredible adopting family, Essi and Patrick, you two are like the superhero duo of hospitality, and I can't thank you enough for opening your home to me. Marion, my awesome housemate sister who is a great mushroom hunter and knitting partner and makes the best tiramisu! And Elie, the partner in crime when it comes to throwing epic parties, brunches and spying on the neighbours! Everyone knows our house is the best party place. We know how to bring the fun! Let's not forget our cozy TV night sessions and therapy gardening! Our backyard is like a mini oasis of calm (and chaos) that has appeased my mind countless times. Being with you all feels like being wrapped in a warm, cozy blanket. I've rarely felt more at home than I do with you guys.

I am profoundly grateful to my mother for instilling in me her passion for wildlife and animals. She has provided me with the most nurturing environment to grow as a child surrounded by nature and animals (Not every kid gets to nurse ducklings and rescued mice in their rooms …). She has always been pushing me forward and encouraging me to pursue my goals. Even during times when I doubted myself, she never wavered in her belief in my abilities. Thank you, Mum, for shaping me into the person I am today. I love you.

As I conclude this PhD journey, I find myself reflecting on the profound influence that animals have had on my thirst for knowledge and my commitment to work for a better world for them. Among them, Lustane, Star, MyFirst, Igor, Alex, Kaid, Pepette and all the horses and donkeys from the herds I grew up with, which probably taught me most of what I know about equine ethology and ecology today. To all the animals who have been instrumental in shaping my path, I dedicate my achievements and aspirations. It is with a heart full of compassion and a mind eager to make a difference that I step forward into the next chapter of my academic journey.

Turku, July 2023
Océane Liehrmann

List of References

Acharya, R.Y.; Hemsworth, P.H.; Coleman, G.J.; Kinder, J.E. 2022. The Animal-Human Interface in Farm Animal Production: Animal Fear, Stress, Reproduction and Welfare. *Animals* 12: 487.

Argent, G.; Vaught, J. 2022. Introduction: Humans and Horses in the Relational Arena. In: p.1–18.

Ashton, B.J.; Thornton, A.; Ridley, A.R. 2018a. An intraspecific appraisal of the social intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373: 20170288.

Ashton, B.J.; Kennedy, P.; Radford, A.N. 2020. Interactions with conspecific outsiders as drivers of cognitive evolution. *Nature Communications* 11: 4937.

Ashton, B.J.; Ridley, A.R.; Edwards, E.K.; Thornton, A. 2018b. Cognitive performance is linked to group size and affects fitness in Australian magpies. *Nature* 554: 364–367.

AsERSM. 2022. THIRD ASIAN ELEPHANT RANGE STATES MEETING. Report, Kathmandu Nepal.

AVMA. 1998. Statement from the Committee on the Human-Animal Bond. Journal of the American Veterinary Medical Association, 212, 1675.

Carere, C. and Maestripieri, D. eds., 2013. Animal personalities: behaviour, physiology, and evolution. University of Chicago Press.

Baragli, P.; Vitale, V.; Banti, L.; Sighieri, C. 2014. Effect of aging on behavioural and physiological responses to a stressful stimulus in horses (Equus caballus). *Behaviour* 151: 1513–1533.

Beierl, B.H. 2008. The Sympathetic Imagination and the Human—Animal Bond: Fostering Empathy Through Reading Imaginative Literature. *Anthrozoös* 21: 213–220.

Bekinschtein, P.; Oomen, C.A.; Saksida, L.M.; Bussey, T.J. 2011. Effects of environmental enrichment and voluntary exercise on neurogenesis, learning and memory, and pattern separation: BDNF as a critical variable? *Seminars in Cell & Developmental Biology* 22: 536–542.

Bergman, I.; Zackrisson, O.; Liedgren, L. 2013. From Hunting to Herding: Land Use, Ecosystem Processes, and Social Transformation among Sami AD 800–1500. *Arctic Anthropology* 50: 25–39.

Berryhill, E.H.; Thomasy, S.M.; Kass, P.H.; Reilly, C.M.; Good, K.L.; Hollingsworth, S.R.; et al. 2017. Comparison of corneal degeneration and calcific band keratopathy from 2000 to 2013 in 69 horses. *Veterinary Ophthalmology* 20: 16–26.

Body, G.; Weladji, R.B.; Holand, Ø.; Nieminen, M. 2015a. Fission-fusion group dynamics in reindeer reveal an increase of cohesiveness at the beginning of the peak rut. *Acta ethologica* 18: 101–110.

Body, G.; Weladji, R.B.; Holand, Ø.; Nieminen, M. 2015b. Measuring variation in the frequency of group fission and fusion from continuous monitoring of group sizes. *Journal of Mammalogy* 96: 791–799.

Boivin, X.; Garel, J.P.; Mante, A.; Le Neindre, P. 1998. Beef calves react differently to different handlers according to the test situation and their previous interactions with their caretaker. *Applied Animal Behaviour Science* 55: 245–257.

Bondi, A.; Norton, S.; Pearman, L.; Dyson, S. 2020. Evaluating the suitability of an English saddle for a horse and rider combination. *Equine Veterinary Education* 32: 162–172.

Brown, G.E.; Ferrari, M.C.O.; Elvidge, C.K.; Ramnarine, I.; Chivers, D.P. 2013. Phenotypically plastic neophobia: a response to variable predation risk. *Proceedings of the Royal Society B: Biological Sciences* 280: 20122712.

Brown-Leonardi, C. 2016. Reindeer champions: culture, rituals and training race reindeer. *Polar Record* 52: 316–329.

Bürkner, P.-C. 2018. Advanced Bayesian Multilevel Modeling with the R Package brms. *The R Journal* 10: 395–411.

Cabrera, D.; Nilsson, J.R.; Griffen, B.D. 2021. The development of animal personality across ontogeny: a cross-species review. *Animal Behaviour* 173: 137–144.

Carlstead, K. 2009. A comparative approach to the study of Keeper-Animal Relationships in the zoo. *Zoo Biology*: n/a-n/a.

Carr, N.; Broom, D.M. 2018. The position of animals in tourism. *Tourism and animal welfare*: 26–44.

Carroll, J., Murphy, C.J., Neitz, M., Ver Hoeve, J.N. and Neitz, J., 2001. Photopigment basis for dichromatic color vision in the horse. Journal of Vision, 1(2), pp.2-2.

Clubb, R.; Rowcliffe, M.; Lee, P.; Mar, K.U.; Moss, C.; Mason, G.J. 2008. Compromised Survivorship in Zoo Elephants. *Science* 322: 1649–1649.

Cook, A.; Arter, J.; Jacobs, L.F. 2014. My owner, right or wrong: the effect of familiarity on the domestic dog's behaviour in a food-choice task. *Animal Cognition* 17: 461–470.

Coutellier, L. 2006. Are dogs able to recognize their handler's voice? A preliminary study. *Anthrozoös* 19: 278–284.

Crawley, J.A.H.; Lahdenperä, M.; Seltmann, M.W.; Htut, W.; Aung, H.H.; Nyein, K.; et al. 2019. Investigating changes within the handling system of the largest semi-captive population of Asian elephants. *PLOS ONE* 14: e0209701.

Crawley, J. 2021. The impact of human relationships on semi-captive Asian elephant health and welfare. Doctoral dissertation, University of Turku. ISBN: 978-951-29-8611-8

Dai, F.; Cogi, N.H.; Heinzl, E.U.L.; Dalla Costa, E.; Canali, E.; Minero, M. 2015. Validation of a fear test in sport horses using infrared thermography. *Journal of Veterinary Behaviour* 10: 128–136.

Dalmau, A.; Fabrega, E.; Velarde, A. 2009. Fear assessment in pigs exposed to a novel object test. *Applied Animal Behaviour Science* 117: 173–180.

Dorey, N.R.; Conover, A.M.; Udell, M.A.R. 2014. Interspecific communication from people to horses (Equus ferus caballus) is influenced by different horsemanship training styles. *Journal of Comparative Psychology* 128: 337–342.

Doyle, C. 2018. Elephants in Captivity. In: Linzey, A.; Linzey, C. (Eds.), *The Palgrave Handbook of Practical Animal Ethics*, Palgrave Macmillan UK, London, p.181–206.

Driscoll, C.A.; Macdonald, D.W.; O'Brien, S.J. 2009. From wild animals to domestic pets, an evolutionary view of domestication. *Proceedings of the National Academy of Sciences* 106: 9971–9978.

Dyson, S.; Martin, C.; Bondi, A.; Ellis, A.D. 2020. The influence of rider skill on ridden horse behaviour, assessed using the Ridden Horse Pain Ethogram, and gait quality. *Equine Veterinary Education*: eve.13434.

Escobar-Ibarra, I.; Mota-Rojas, D.; Gual-Sill, F.; Sánchez, C.R.; Baschetto, F.; Alonso-Spilsbury, M. 2021. Conservation, animal behaviour, and human-animal relationship in zoos. Why is animal welfare so important? *Journal of Animal Behaviour and Biometeorology* 9: 1–17.

FAO. 2014. The role, impact and welfare of working (traction and transport) animals. Animal Production and Health Report. : 54.

FEI .2023. THE EQUESTRIAN FEDERATION OF FINLAND. Available at: https://data.fei.org/NFPages/NF/Details/Federation/44/THE-EQUESTRIAN-FEDERATION-OF-FINLAND (Accessed: 03 June 2023)

Fortin, M.; Valenchon, M.; Lévy, F.; Calandreau, L.; Arnould, C.; Lansade, L. 2018. Emotional state and personality influence cognitive flexibility in horses (Equus caballus). *Journal of Comparative Psychology* 132: 130–140.

Fosbury, R.A.E.; Jeffery, G. 2022. Reindeer eyes seasonally adapt to ozone-blue Arctic twilight by tuning a photonic tapetum lucidum. *Proceedings of the Royal Society B: Biological Sciences* 289: 20221002.

Freeman, S.L. 2019. A scoping review of the current literature exploring the nature of the horse-human relationship. *Veterinary Evidence* 4.

Friard, O.; Gamba, M. 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution* 7: 1325–1330.

Gácsi, M.; Maros, K.; Sernkvist, S.; Faragó, T.; Miklósi, Á. 2013. Human Analogue Safe Haven Effect of the Owner: Behavioural and Heart Rate Response to Stressful Social Stimuli in Dogs. *PLoS ONE* 8: e58475.

Gácsi, M.; Gyoöri, B.; Virányi, Z.; Kubinyi, E.; Range, F.; Belényi, B.; et al. 2009. Explaining Dog Wolf Differences in Utilizing Human Pointing Gestures: Selection for Synergistic Shifts in the Development of Some Social Skills. *PLOS ONE* 4: e6584.

García-Rosell, J.-C.; Tallberg, L. 2021. 7 Animals as tourism stakeholders: Huskies, reindeer, and horses working in Lapland. In: *7 Animals as Tourism Stakeholders: Huskies, Reindeer, and Horses Working in Lapland*, De Gruyter Oldenbourg, p.103–122.

Greggor, A.L.; Thornton, A.; Clayton, N.S. 2015. Neophobia is not only avoidance: improving neophobia tests by combining cognition and ecology. *Current Opinion in Behavioural Sciences* 6: 82–89.

Hampson, B.A.; De LAAT, M.A.; Mills, P.C.; Pollitt, C.C. 2010. Distances travelled by feral horses in 'outback' Australia: Distance travelled by feral horses. *Equine Veterinary Journal* 42: 582–586.

Hart, L.A. 1994. The Asian elephants-driver partnership: the drivers' perspective. *Applied Animal Behaviour Science* 40: 297–312.

Hart L.A. and Locke P. 2007. Nepali and Indian Mahouts and their unique relationships with elephants. In: Encyclopedia of Human-Animal Relationships. Greenwood Publishing, Westport

Hartig, F. 2021. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.3.

Hartmann, E.; Rehn, T.; Christensen, J.W.; Nielsen, P.P.; McGreevy, P. 2021. From the Horse's Perspective: Investigating Attachment Behaviour and the Effect of Training Method on Fear Reactions and Ease of Handling—A Pilot Study. *Animals* 11: 457.

Hausberger, M.; Bruderer, C.; Le Scolan, N.; Pierre, J.-S. 2004. Interplay Between Environmental and Genetic Factors in Temperament/Personality Traits in Horses (Equus caballus). *Journal of Comparative Psychology* 118: 434–446.

Hausberger, M.; Roche, H.; Henry, S.; Visser, E.K. 2008. A review of the human–horse relationship. *Applied Animal Behaviour Science* 109: 1–24.

Hayward, A.D.; Mar, K.U.; Lahdenperä, M.; Lummaa, V. 2014. Early reproductive investment, senescence and lifetime reproductive success in female Asian elephants. *Journal of Evolutionary Biology* 27: 772–783.

Hedges S., Leimgruber P., Lynam A., Mar K.U., Riddle H., Thaw W.N., Tyson M. 2018. Myanmar Elephant Conservation Action Plan.

Hemsworth, L.M.; Jongman, E.; Coleman, G.J. 2015. Recreational horse welfare: The relationships between recreational horse owner attributes and recreational horse welfare. *Applied Animal Behaviour Science* 165: 1–16.

Henning, J.D.; Beck, J.L.; Scasta, J.D. . Spatial Ecology Observations From Feral Horses Equipped With Global Positioning System Transmitters. *Spatial ecology*: 10.

Hinde, R.A. 1976. Interactions, Relationships and Social Structure. *Man* 11: 1–17.

Hinde, R.A. 1987. *Individuals, Relationships and Culture: Links Between Ethology and the Social Sciences*. CUP Archive, 228p.

Hockenhull, J.; Creighton, E. 2014. Management practices associated with owner-reported stable-related and handling behaviour problems in UK leisure horses. *Applied Animal Behaviour Science* 155: 49–55.

Hogg, C.; Neveu, M.; Stokkan, K.-A.; Folkow, L.; Cottrill, P.; Douglas, R.; et al. 2011. Arctic reindeer extend their visual range into the ultraviolet. *Journal of Experimental Biology* 214: 2014–2019.

Horn, L.; Range, F.; Huber, L. 2013. Dogs' attention towards humans depends on their relationship, not only on social familiarity. *Animal Cognition* 16: 435–443.

Hosey, G.; Melfi, V. 2014. Human-animal interactions, relationships and bonds: A review and analysis of the literature. *International Journal of Comparative Psychology* 27: 117–142.

Ijichi, C., Griffin, K., Squibb, K. and Favier, R., 2018. Stranger danger? An investigation into the influence of human-horse bond on stress and behaviour. Applied animal behaviour science, 206, pp.59-63.

Irie, N.; Hiraiwa-Hasegawa, M.; Kutsukake, N. 2019. Unique numerical competence of Asian elephants on the relative numerosity judgment task. *Journal of Ethology* 37: 111–115.

Jackson, J.; Childs, D.Z.; Mar, K.U.; Htut, W.; Lummaa, V. 2019. Long-term trends in wild-capture and population dynamics point to an uncertain future for captive elephants. *Proceedings of the Royal Society B: Biological Sciences* 286: 20182810.

Jagoe, A.; Serpell, J. 1996. Owner characteristics and interactions and the prevalence of canine behaviour problems. *Applied Animal Behaviour Science* 47: 31–42.

Jardat, P.; Lansade, L. 2021. Cognition and the human–animal relationship: a review of the sociocognitive skills of domestic mammals towardshumans. *Animal Cognition*.

Jardat, P.; Liehrmann, O.; Reigner, F.; Parias, C.; Calandreau, L.; Lansade, L. 2023. *Horses discriminate between human facial and vocal expressions of sadness and joy*. (https://www.researchsquare.com). Accessed on 03 Jun. 2023.

Kalof, L. 2017. *The Oxford Handbook of Animal Studies | Oxford Academic*. (https://academic.oup.com/edited-volume/28022). Accessed on 03 Jun. 2023.

Kaminski, J.; Riedel, J.; Call, J.; Tomasello, M. 2005. Domestic goats, Capra hircus, follow gaze direction and use social cues in an object choice task. *Animal Behaviour* 69: 11–18.

Kelly, K.J.; McDuffee, L.A.; Mears, K. 2021. The Effect of Human–Horse Interactions on Equine Behaviour, Physiology, and Welfare: A Scoping Review. : 18.

Kerepesi, A.; Dóka, A.; Miklósi, Á. 2015. Dogs and their human companions: The effect of familiarity on dog–human interactions. *Behavioural Processes* 110: 27–36.

King, T.; Hemsworth, P.H.; Coleman, G.J. 2003. Fear of novel and startling stimuli in domestic dogs. *Applied Animal Behaviour Science* 82: 45–64.

Klingel, H. 1982. Social organization of feral horses. *Journal of reproduction and fertility Supplement* 32: 89–95.

Krause, M.A.; Udell, M.A.R.; Leavens, D.A.; Skopos, L. 2018. Animal pointing: Changing trends and findings from 30 years of research. *Journal of Comparative Psychology* 132: 326–345.

Krueger, K.; Flauger, B.; Farmer, K.; Maros, K. 2011. Horses (Equus caballus) use human local enhancement cues and adjust to human attention. *Animal Cognition* 14: 187–201.

Kuhl, G. 2011. Human-Sled Dog Relations: What Can We Learn from the Stories and Experiences of Mushers? *Society & Animals* 19: 22–37.

Lahdenperä, M.; Mar, K.U.; Lummaa, V. 2014. Reproductive cessation and post-reproductive lifespan in Asian elephants and pre-industrial humans. *Frontiers in Zoology* 11: 54.

Lahdenperä, M.; Mar, K.U.; Lummaa, V. 2016. Nearby grandmother enhances calf survival and reproduction in Asian elephants. *Scientific Reports* 6: 27213.

Lair, R. C. 1997. Gone Astray: The Care and Management of the Asian Elephant in Domesticity. UN FAO & RAP

Lambert, C.T.; Guillette, L.M. 2021. The impact of environmental and social factors on learning abilities: a meta-analysis. *Biological Reviews* 96: 2871–2889.

Lansade, L.; Bouissou, M.-F.; Erhard, H.W. 2008. Fearfulness in horses: A temperament trait stable across time and situations. *Applied Animal Behaviour Science* 115: 182–200.

Lansade, L.; Valenchon, M.; Foury, A.; Neveux, C.; Lévy, F.; Moisan, M.P. 2014. Enriching a horse's environment not only enables to improve its welfare, but also enables to reduce its emotions and

to increase its learning ability, while at the same time promoting the safety of handlers. *Équi-meeting Infrastructures, Horas national du Lion d'Angers, France, 6-7 October 2014. Proceedings*: 116–122.

Lansade, L.; Marchand, A.R.; Coutureau, E.; Ballé, C.; Polli, F.; Calandreau, L. 2017. Personality and predisposition to form habit behaviours during instrumental conditioning in horses (Equus caballus). *PLOS ONE* 12: e0171010.

Lansade, L.; Trösch, M.; Parias, C.; Blanchard, A.; Gorosurreta, E.; Calandreau, L. 2021. Horses are sensitive to baby talk: pet-directed speech facilitates communication with humans in a pointing task and during grooming. *Animal Cognition* 24: 999–1006.

Lazzaroni, M.; Range, F.; Backes, J.; Portele, K.; Scheck, K.; Marshall-Pescini, S. 2020. The Effect of Domestication and Experience on the Social Interaction of Dogs and Wolves With a Human Companion. *Frontiers in Psychology* 11.

Leavens, D.A.; Hopkins, W.D. 1999. The whole-hand point: The structure and function of pointing from a comparative perspective. *Journal of Comparative Psychology* 113: 417–425.

Lee, K.E.; Kim, J.G.; Lee, H.; Kim, B.S. 2021. Behavioural and cardiac responses in mature horses exposed to a novel object. *Journal of Animal Science and Technology* 63: 651–661.

Lenth R.V. 2021. emmeans: Estimate ± SEd Marginal Means, aka Least-Squares Means. R package version 1.6.3. https://CRAN.R-project.org/package=emmeans

Lesimple, C.; Fureix, C.; LeScolan, N.; Richard-Yris, M.-A.; Hausberger, M. 2011. Housing conditions and breed are associated with emotionality and cognitive abilities in riding school horses. *Applied Animal Behaviour Science* 129: 92–99.

Librado, P.; Khan, N.; Fages, A.; Kusliy, M.A.; Suchan, T.; Tonasso-Calvière, L.; et al. 2021. The origins and spread of domestic horses from the Western Eurasian steppes. *Nature* 598: 634–640.

Losey, R.J.; Nomokonova, T.; Arzyutov, D.V.; Gusev, A.V.; Plekhanov, A.V.; Fedorova, N.V.; et al. 2021. Domestication as Enskilment: Harnessing Reindeer in Arctic Siberia. *Journal of Archaeological Method and Theory* 28: 197–231.

Lynch, E.C.; Lummaa, V.; Htut, W.; Lahdenperä, M. 2019. Evolutionary significance of maternal kinship in a long-lived mammal. *Philosophical Transactions of the Royal Society B: Biological Sciences* 374: 20180067.

Maisonpierre, I.N.; Sutton, M.A.; Harris, P.; Menzies-Gow, N.; Weller, R.; Pfau, T. 2019. Accelerometer activity tracking in horses and the effect of pasture management on time budget. *Equine Veterinary Journal* 51: 840–845.

Mar K.U. 2007. The Demography and Life-History Strategies of Timber Elephants in Myanmar [PhD Thesis]. UCL, UK

Maros, K.; Gácsi, M.; Miklósi, Á. 2008. Comprehension of human pointing gestures in horses (Equus caballus). *Animal Cognition* 11: 457–466.

Mata, R.; Wilke, A.; Czienskowski, U. 2013. Foraging across the life span: is there a reduction in exploration with aging? *Frontiers in Neuroscience* 7.

McComb, K.; Moss, C.; Sayialel, S.; Baker, L. 2000. Unusually extensive networks of vocal recognition in African elephants. *Animal Behaviour* 59: 1103–1109.

McGreevy, P.; McLean, A.; Buckley, P.; McConaghy, F.; McLean, C. 2011. How riding may affect welfare: What the equine veterinarian needs to know: How riding may affect welfare. *Equine Veterinary Education* 23: 531–539.

McLean, A.N.; McGreevy, P.D. 2010. Horse-training techniques that may defy the principles of learning theory and compromise welfare. *Journal of Veterinary Behaviour* 5: 187–195.

Merkies, K., McKechnie, M.J. and Zakrajsek, E., 2018. Behavioural and physiological responses of therapy horses to mentally traumatized humans. Applied animal behaviour science, 205, pp.61-67.

Merkies, K.; Franzin, O. 2021. Enhanced Understanding of Horse–Human Interactions to Optimize Welfare. *Animals* 11: 1347.

Mota-Rojas, D.; Broom, D.M.; Orihuela, A.; Velarde, A.; Napolitano, F.; Alonso-Spilsbury, M. 2020. Effects of human-animal relationship on animal productivity and welfare. *Journal of Animal Behaviour and Biometeorology* 8: 196–205.

Mumby, H.S. 2019. Mahout Perspectives on Asian Elephants and Their Living Conditions. *Animals* 9: 879.

Nawroth, C.; Ebersbach, M.; von Borell, E. 2014. Juvenile domestic pigs (Sus scrofa domestica) use human-given cues in an object choice task. *Animal Cognition* 17: 701–713.

Nawroth, C.; Martin, Z.M.; McElligott, A.G. 2020. Goats Follow Human Pointing Gestures in an Object Choice Task. *Frontiers in Psychology* 11.

Notzke, C. 2019. Equestrian tourism: animal agency observed. *Current Issues in Tourism* 22: 948–966.

Pérez-Guisado, J.; Muñoz-Serrano, A. 2009. Factors linked to dominance aggression in dogs. *Journal of Animal and Veterinary Advances* 8: 336–342.

OIE. 2022. Welfare of working equids. Terrestrial Animal Health Code. Chapter 7.12.

Phuangkum P., Lair R.C., Angkawanith T. 2005. Elephant Care Manual for Mahouts and Camp Managers: FAO & FIO.

Plotnik, J.M.; de Waal, F.B.M.; Moore, D.; Reiss, D. 2010. Self-recognition in the Asian elephant and future directions for cognitive research with elephants in zoological settings. *Zoo Biology* 29: 179–191.

Plotnik, J.M.; Brubaker, D.L.; Dale, R.; Tiller, L.N.; Mumby, H.S.; Clayton, N.S. 2019. Elephants have a nose for quantity. *Proceedings of the National Academy of Sciences* 116: 12566–12571.

Polla, E.J.; Grueter, C.C.; Smith, C.L. 2018. Asian Elephants (Elephas maximus) Discriminate Between Familiar and Unfamiliar Human Visual and Olfactory Cues. *Animal Behaviour and Cognition* 5: 279–291.

van Praag, H.; Kempermann, G.; Gage, F.H. 2000. Neural consequences of enviromental enrichment. *Nature Reviews Neuroscience* 1: 191–198.

Pritchard, J.C.; Lindberg, A.C.; Main, D.C.J.; Whay, H.R. 2005. Assessment of the welfare of working horses, mules and donkeys, using health and behaviour parameters. *Preventive Veterinary Medicine* 69: 265–283.

R Core Team. 2023. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rankins, E.M.; Wickens, C.L. 2020. A systematic review of equine personality. *Applied Animal Behaviour Science* 231: 105076.

Ransom, J.I.; Kaczensky, P. 2016. *Wild Equids: Ecology, Management, and Conservation*. JHU Press, 244p.

Rault, J.-L.; Waiblinger, S.; Boivin, X.; Hemsworth, P. 2020. The Power of a Positive Human–Animal Relationship for Animal Welfare. *Frontiers in Veterinary Science* 7: 590867.

Reindeer Herders' Association. 2020. *reindeer*. Reindeer Herders' Association. (https://paliskunnat.fi/reindeer-herders-association/reindeer-info/brochures-guidelines/brochures/). Accessed on 03 Jun. 2023.

Riddle, H.S.; Stremme, C. 2011. Captive elephants - an overview. *Journal of Threatened Taxa*: 1826–1836.

Rouder, J.N.; Engelhardt, C.R.; McCabe, S.; Morey, R.D. 2016. Model comparison in ANOVA. *Psychonomic Bulletin & Review* 23: 1779–1786.

Ruet, A.; Arnould, C.; Levray, J.; Lemarchand, J.; Mach, N.; Moisan, M.-P.; et al. 2020. Effects of a temporary period on pasture on the welfare state of horses housed in individual boxes. *Applied Animal Behaviour Science* 228: 105027.

Sallet, J.; Mars, R.B.; Noonan, M.P.; Andersson, J.L.; O'Reilly, J.X.; Jbabdi, S.; et al. 2011. Social Network Size Affects Neural Circuits in Macaques. *Science* 334: 697–700.

Salmi, A.-K.; van den Berg, M.; Niinimäki, S.; Pelletier, M. 2021. Earliest archaeological evidence for domesticated reindeer economy among the Sámi of Northeastern Fennoscandia AD 1300 onwards. *Journal of Anthropological Archaeology* 62: 101303.

Salmi, A.-K.; Niinimäki, S.; Soppela, P.; Kynkäänniemi, S.-M.; Wallén, H. 2022. Working Reindeer in Past and Present Reindeer Herding. In: Salmi, A.-K. (Ed.), *Domestication in Action : Past and Present Human-Reindeer Interaction in Northern Fennoscandia*, Springer International Publishing, Cham, p.95–121.

Salter, R.E.; Hudson, R.J. 1979. Feeding Ecology of Feral Horses in Western Alberta. *Journal of Range Management* 32: 221.

Sankey, C.; Richard-Yris, M.-A.; Leroy, H.; Henry, S.; Hausberger, M. 2010a. Positive interactions lead to lasting positive memories in horses, Equus caballus. *Animal Behaviour* 79: 869–875.

Sankey, C.; Henry, S.; Górecka-Bruzda, A.; Richard-Yris, M.-A.; Hausberger, M. 2010b. The Way to a Man's Heart Is through His Stomach: What about Horses? *PLOS ONE* 5: e15446.

Scandurra, A.; Alterisio, A.; Marinelli, L.; Mongillo, P.; Semin, G.R.; D'Aniello, B. 2017. Effectiveness of verbal and gestural signals and familiarity with signal-senders on the performance of working dogs. *Applied Animal Behaviour Science* 191: 78–83.

Scopa, C.; Contalbrigo, L.; Greco, A.; Lanatà, A.; Scilingo, E.P.; Baragli, P. 2019. Emotional Transfer in Human–Horse Interaction: New Perspectives on Equine Assisted Interventions. *Animals* 9: 1030.

Serpell, J. 1996. *In the Company of Animals: A Study of Human-Animal Relationships*. Cambridge University Press, 320p.

Sheppard, V.A.; Fennell, D.A. 2019. Progress in tourism public sector policy: Towardsan ethic for non-human animals. *Tourism Management* 73: 134–142.

Sherratt, T.N.; Morand-Ferron, J. 2018. The adaptive significance of age-dependent changes in the tendency of individuals to explore. *Animal Behaviour* 138: 59–67.

Sherwen, S.L.; Hemsworth, P.H. 2019. The Visitor Effect on Zoo Animals: Implications and Opportunities for Zoo Animal Welfare. *Animals* 9: 366.

Skinner, J.; Hilly, L.; Li, X.; Cawdell-Smith, A.; Bryden, W. 2022. *EQUINE PRODUCTION SYSTEMS AND THE CHANGING ROLE OF HORSES IN SOCIETY*.

Smet, A.F.; Byrne, R.W. 2013. African Elephants Can Use Human Pointing Cues to Find Hidden Food. *Current Biology* 23: 2033–2037.

Sneddon, L.U.; Braithwaite, V.A.; Gentle, M.J. 2003. Novel object test: examining nociception and fear in the rainbow trout. *The Journal of Pain* 4: 431–440.

Søndergaard, E.; Ladewig, J. 2004. Group housing exerts a positive effect on the behaviour of young horses during training. *Applied Animal Behaviour Science* 87: 105–118.

SPANA. 2021. Annual report and financial statements.1: 3

Squibb, K., Griffin, K., Favier, R. and Ijichi, C., 2018. Poker Face: Discrepancies in behaviour and affective states in horses during stressful handling procedures. Applied animal behaviour science, 202, pp.34-38.

Srinivasaiah, N. M., Varma, S., & Sukumar, R. 2014. Documenting Indigenous Traditional Knowledge of the Asian Elephant in Captivity. ANCF Report.

Stépanoff, C. 2012. Human-animal "joint commitment" in a reindeer herding system. *HAU: Journal of Ethnographic Theory* 2: 287–312.

Sukumar R. 2003. The Living Elephants: Evolutionary Ecology, Behaviour, and Conservation. Oxford Unversity Press

Sukumar, R. 2006. A brief review of the status, distribution and biology of wild Asian elephants Elephas maximus. *International Zoo Yearbook* 40: 1–8.

Suter, I.C.; Hockings, M.; Baxter, G.S. 2013. Changes in Elephant Ownership and Employment in the Lao PDR: Implications for the Elephant-Based Logging and Tourism Industries. *Human Dimensions of Wildlife* 18: 279–291.

Swann, W.J. 2006. Improving the welfare of working equine animals in developing countries. *Applied Animal Behaviour Science* 100: 148–151.

Tallet, C.; Veissier, I.; Boivin, X. 2005. Human contact and feeding as rewards for the lamb's affinity to their stockperson. *Applied Animal Behaviour Science* 94: 59–73.

Thalmann, O.; Shapiro, B.; Cui, P.; Schuenemann, V.J.; Sawyer, S.K.; Greenfield, D.L.; et al. 2013. Complete Mitochondrial Genomes of Ancient Canids Suggest a European Origin of Domestic Dogs. *Science* 342: 871–874.

Thielke, L.E.; Udell, M.A.R. 2019. Characterizing Human–Dog Attachment Relationships in Foster and Shelter Environments as a Potential Mechanism for Achieving Mutual Wellbeing and Success. *Animals* 10: 67.

Trösch; Cuzol; Parias; Calandreau; Nowak; Lansade. 2019. Horses Categorize Human Emotions Cross-Modally Based on Facial Expression and Non-Verbal Vocalizations. *Animals* 9: 862.

Tyler, N.J.C.; Jeffery, G.; Hogg, C.R.; Stokkan, K.-A.; Giguère, N. 2014. Ultraviolet Vision May Enhance the Ability of Reindeer to Discriminate Plants in Snow. *Arctic* 67: 159–166.

UNData – FAO. 2020. UNData a world of information - Horses. Available at: http://data.un.org/Data.aspx?d=FAO&f=itemCode%3A1096 (Accessed: 15 June 2023)

Valenchon, M.; Lévy, F.; Moussu, C.; Lansade, L. 2017. Stress affects instrumental learning based on positive or negative reinforcement in interaction with personality in domestic horses. *PLOS ONE* 12: e0170783.

Valenchon, M.; Lévy, F.; Fortin, M.; Leterrier, C.; Lansade, L. 2013a. Stress and temperament affect working memory performance for disappearing food in horses, Equus caballus. *Animal Behaviour* 86: 1233–1240.

Valenchon, M.; Lévy, F.; Prunier, A.; Moussu, C.; Calandreau, L.; Lansade, L. 2013b. Stress Modulates Instrumental Learning Performances in Horses (Equus caballus) in Interaction with Temperament. *PLOS ONE* 8: e62324.

Vanitha, V.; Thiyagesan, K.; Baskaran, N. 2009. Socio-Economic Status of Elephant Keepers (Mahouts) and Human–Captive Elephant Conflict: A Case Study from the Three Management Systems in Tamil Nadu, Southern India.

Varma S, Abraham D, Hasbhavi R (2009) Database for Captive Elephants and Their Mahouts in Andaman: Protocol & Significance. Bangalore, India

Vehtari, A.; Gelman, A.; Gabry, J. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing* 27: 1413–1432.

Vidament, M.; Lansade, L.; Danvy, S.; Priest, B.D.S.; Sabbagh, M.; Ricard, A. 2021. Personality in young horses and ponies evaluated during breeding shows: Phenotypic link with jumping competition results. *Journal of Veterinary Behaviour* 44: 1–11.

Vidya, T.N.C.; Sukumar, R. 2005. Social and reproductive behaviour in elephants. *Current Science* 89: 1200–1207.

Wikman, I.; Hokkanen, A.-H.; Pastell, M.; Kauppinen, T.; Valros, A.; Hänninen, L. 2016. Attitudes of beef producers to disbudding and perception of pain in cattle. *Animal Welfare* 25: 429–438.

Wickham H. 2016. ggplot2: elegant graphics for data analysis. Springer-Verlag, New York (R package)

Wilkins, A.S.; Wrangham, R.W.; Fitch, W.T. 2014. The "Domestication Syndrome" in Mammals: A Unified Explanation Based on Neural Crest Cell Behaviour and Genetics. *Genetics* 197: 795–808.

Williams, J.; Tabor, G. 2017. Rider impacts on equitation. *Applied Animal Behaviour Science* 190: 28–42.

Wilson, R.T. 2003. The environmental ecology of oxen used for draught power. *Agriculture, Ecosystems & Environment* 97: 21–37.

Yokoyama, S., Takenaka, N., Agnew, D.W. and Shoshani, J., 2005. Elephants and human color-blind deuteranopes have identical sets of visual pigments. Genetics, 170(1), pp.335-344.

Zeder, M.A. 2012. The Domestication of Animals. *Journal of Anthropological Research* 68: 161–190.

Zuur, A.F.; Ieno, E.N.; Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems: Data exploration. *Methods in Ecology and Evolution* 1: 3–14.

Zuur, A.F.; Ieno, E.N.; Walker, N.; Saveliev, A.A.; Smith, G.M. 2009. *Mixed effects models and extensions in ecology with R*. In: *Statistics for Biology and Health*. Springer New York, New York, NY.

Suplementary Materials

Thesis supplementary information

Data are also available online with papers for **Chapters I, II, III** and **IV**.

Supplementary information for the novel objects experiments with reindeer:

The output of the Generalised Linear Mixed Models used to assess the effect of the handler familiarity and the training level on the success of reindeer at stepping on the novel surfaces or at crossing the arches.

1: Model: glmmTMB(Success to step on surface (1/0)~Handler familiairity + training level +(1|reindeer_ id), family=binomial)

Surfaces	**Estimate**	**standard error**	***Z value***	***P value***
Intercept	1.116	0.701	1.593	0.111
Familiarity: Unfamiliar	-0.704	0.854	-0.825	0.410
Training level: working	-0.290	0.285	1.017	0.309

2: Model: glmmTMB(Success to cross the arch (1/0)~Handler familiairity + training level +(1|reindeer_ id), family=binomial)

Arches	**Estimate**	**standard error**	***Z value***	***P value***
Intercept	0.767	0.865	0.886	0.335
Familiarity: Unfamiliar	-0.372	0.874	-0.426	0.670
Training level: working	-0.022	0.269	-0.083	0.933

We did not perform the planned statistical analyses with the novel object tests as only two individuals out of the 16 freely and very briefly approached the novel object (stuffed unicorn) and they all strictly refused to be touched with the object. Therefore, there was not enough variation in the behavioural response for it to be statistically analysed.

TURUN
YLIOPISTO
UNIVERSITY
OF TURKU

Painosalama, Turku, Finland 2023

ISBN 978-951-29-9428-1 (Print)
ISBN 978-951-29-9429-8 (PDF)
ISSN 0082-6979 (Print)
ISSN 2343-3183 (Online)