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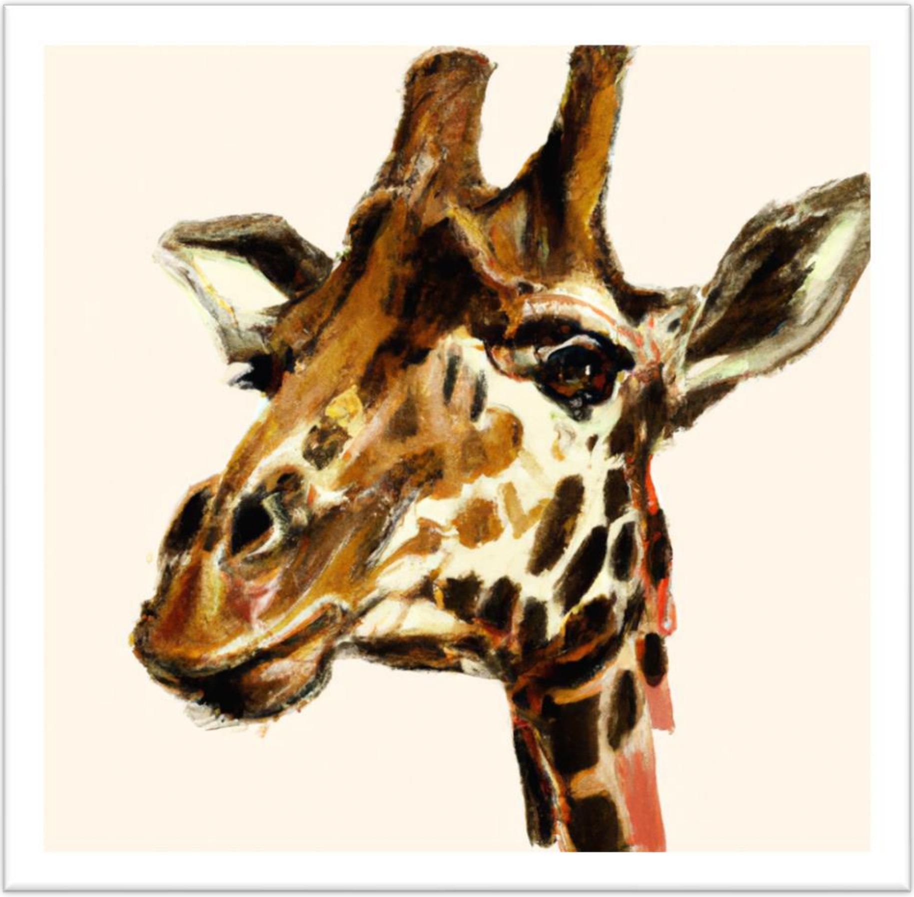
a new perspective in the evolutionary field

Álvaro López Caicoya

COGNITION IN UNGULATES:
A NEW PERSPECTIVE IN THE EVOLUTIONARY FIELD



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Cognition in ungulates: a new perspective in the evolutionary field

Cognición en ungulados: una nueva perspectiva en el estudio evolutivo

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Abstract

The study of animal cognition has advanced greatly over the century. We now know that many cognitive processes are shared among several species in the animal kingdom. The interest over the evolution of behaviour and cognition of animals is growing among scientists and also among society and the study of animals now encompasses more species, but some are still greatly underrepresented. In this thesis, we have tested ungulates (i.e. hoofed animals) in cognitive tasks that are broadly used in this field, but that had never been employed in the study species of this thesis. Ungulates are very important animals for our society as they are the main type of species kept in farms, but we barely know anything about how they understand the world. Our better understanding of this animals' trough behavioural experimentation could improve animal welfare in the near future. Trough the experiments made in this thesis, we showed that giraffes have the ability to find hidden food after short periods of time, have quantity discrimination skills similar to species with much larger relative brain sizes, and are capable of making statistical inferences to find their preferred food, something that had only been shown in a handful of species. We also found notable differences between several ungulate species in cognitive abilities. For example, forest buffalos do not show giraffes' ability to find food after short periods of time. European bison are good problem solvers and can bring an experimenter the tool needed to be fed, when they see the experimenter approaching but not feeding them. What give us a clue that we should not treat all ungulate species in the same way and design enrichments specialized for each of them. On the other side, both domestic and non-domestic ungulates showed basic gaze following abilities. Moreover, in a study comparing more than 10 ungulate species, we found that the individuals less integrated in the group and less neophobic showed a greater ability to display innovative behaviours. Moreover, less neophobic individuals, individuals of domesticated species and having higher fission-fusion dynamics were more likely to participate in the task but not to solve it. Overall, ungulates appear a very interesting taxon to test evolutionary hypotheses on the emergence of cognition, due to the variety of their socio-ecological characteristics and the variation in how they respond to tests. This thesis represents an initial approach towards better comprehending the cognition of this diverse and underrepresented in behavioural science group of animals.

Resumen

El estudio de la cognición animal ha avanzado mucho a lo largo del siglo. Ahora sabemos que muchos procesos cognitivos son compartidos entre especies del reino animal. El interés por la evolución del comportamiento y la cognición de los animales está creciendo tanto entre los científicos como entre la sociedad, y el estudio de los animales abarca ahora a más especies, aunque algunas siguen estando muy poco representadas. En esta tesis, hemos hecho pruebas a ungulados (es decir, animales con pezuñas) en tareas cognitivas ampliamente utilizadas en nuestro campo científico, pero que nunca antes se habían empleado en las especies de estudio de esta tesis. Los ungulados son animales muy importantes para nuestra sociedad, ya que son el principal tipo de animal criado en granjas, pero apenas sabemos nada acerca de cómo entienden el mundo. Si comprendemos mejor a estos animales a través de la experimentación conductual, podríamos mejorar el bienestar animal en un futuro cercano. A través de los experimentos realizados en esta tesis, demostramos que las jirafas tienen la capacidad de encontrar alimentos escondidos después de períodos cortos de tiempo, tienen habilidades de discriminación de cantidad similares a las especies con tamaños relativos de cerebro mucho más grandes y son capaces de hacer inferencias estadísticas para encontrar su alimento preferido, algo que solo se había mostrado en un puñado de especies. También encontramos diferencias notables entre varias especies de ungulados en cuanto a sus habilidades cognitivas. Por ejemplo, los búfalos enanos no muestran la habilidad de las jirafas para encontrar alimentos después de períodos cortos de tiempo. Los bisontes europeos son buenos solucionadores de problemas y pueden llevarle a un experimentador la herramienta necesaria para ser alimentados cuando ven que el experimentador se acerca pero no los alimenta. Esto nos da una pista de que no debemos tratar a todas las especies de ungulados de la misma manera y diseñar enriquecimientos especializados para cada una de ellas. Por otro lado, tanto los ungulados domésticos como los no domésticos mostraron habilidades básicas de seguimiento de la mirada. Además, en un estudio que comparaba más de 10 especies de ungulados, encontramos que los individuos menos integrados en el grupo y menos neofóbicos mostraban una mayor capacidad para mostrar comportamientos innovadores. Además, los individuos menos neofóbicos, los individuos de especies domesticadas y aquellos con una dinámica de fisión-fusión más alta tenían más probabilidades de participar en la tarea pero no de resolverla. En general, los ungulados parecen un taxón muy interesante para probar hipótesis evolutivas sobre la evolución de la cognición, debido a la variedad de sus características socio-ecológicas y a la variación entre ellos en cómo responden a las pruebas. Esta tesis representa un acercamiento inicial para comprender mejor la cognición de este diverso y poco representado grupo de animales en la ciencia del comportamiento.

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Introduction

Charles Darwin can be considered the founder of the discipline of Comparative Psychology. In his book "On the Origin of Species" (Darwin, 1859), he stated the following: "In the distant future I see open fields for far more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Light will be thrown on the origin of man and his history." Darwin's theory of evolution, which encompassed mental processes, provided a rationale for studying the minds of other animals in order to understand the human mind, as well as the evolution of different cognitive characteristics.

Today, Comparative Psychology, Ethology, and Evolutionary Psychology are interwoven in order to better understand how these mental processes evolve and are distributed in the animal kingdom. Our field can be defined as "a subdiscipline of psychology that scientifically studies the behavior and cognition of human and non-human animals, with emphasis on how behavior relates to phylogeny, ontogeny, and adaptation. Rooted in evolutionary principles, the field of Comparative Psychology seeks to answer a multitude of questions on a variety of species, with particular interest in how it relates to human behavior." (Hall & Brosnan, 2017). The comparative study of psychology has undergone significant evolution, especially since the beginning of the 20th century, with the work of great scientists such as Skinner, Lorenz, Morgan and Tinbergen, just to name a few (Lorenz, 1981; Morgan, 1903; Skinner, 1938; Tinbergen, 1963).

Comparative Psychology, however, has always had important limitations, the first being that only few species have been studied. As early as 1950, F. A. Beach complained about this issue, stating "it is definitely disturbing to discover that 50 per cent of the experiments analysed here have been conducted on one one-thousandth of one per cent of the known species." (Beach, 1950). In this case, Beach was referring to rats, the species in which all studies on learning were based on and continued to be so until almost present day. However, if we want to gain a real comparative understanding of cognition and behaviour, and on the forces that shape their distribution across species and taxa, more species need to be included.

This problem has persisted to this day, but in a different form. In the Journal of Comparative Psychology, a long-standing journal in this field, between 1983 and 1987 over 40% of published articles used rodents as study subjects. Between 2010 and 2015, almost 50% of studies focused on primates (Stevens, 2017). Over time, studies have shifted away from focusing solely on rodents, but this has not resulted on a fair division across species as almost 50% of studies still focused on primates. We can also utilize "The Book of Evolutionary Psychology" authored by David M. Buss as an example (Buss, 2015). This book is widely recognized as a comprehensive manual in evolutionary psychology courses. In its first volume, the term "primate" is referenced a total of 179 times, while the second volume contains 85 occurrences. Conversely, the term "ungulate" is mentioned four times in volume 1 and only once in volume 2. This exemplification could be extended to almost all mammalian species, highlighting the emphasis placed on great apes. Therefore, the same problem persists, although there has been some improvement in the number and variety of species studied, there is still unluckily a heavy focus on few species. If we want to discover variation in behavioural traits and cognitive skills among animals to uncover the evolutionary processes at work, we cannot limit to a single taxon.

To address some of the limitations of current comparative research, we have implemented a series of measures specifically targeting these limitations (du Sert et al., 2020; Farrar et al., 2020; Stevens, 2017; Tecwyn, 2021). First, we have attempted to conduct multi-species studies, by using the same experimental protocol across different animal species. In this thesis, it can be observed how the first chapters include articles focusing on a single species, and how we have gradually tested more species in the same task. As a result, our latest articles include up to 13 species.

Second, we have conducted our studies through collaborations across multiple laboratories. This type of procedure allows different contexts to serve as replications of studies. If similar results are obtained at different facilities by different experimenters, the results can be considered more robust. There are some recent examples in this direction, with researchers trying to implement this type of procedure with the "Many" projects such as the Manyprimates, Manybabies, Mabydogs, Manybirds or more recently Manygoats projects (Byers-Heinlein et al., 2020; Primates et al., 2019). All these projects try to merge the efforts of multiple labs from all around the world to increase sample size and robustness of the results. In this thesis, we have collected data in 4 different zoos in Europe (Barcelona, Leipzig, Nuremberg, and Barben Zoos).

Third, we have used Bayesian statistics in all the articles presented here. It is a type of statistics that is becoming increasingly common in our field and addresses some of the inherent problems in our field, such as small sample sizes (Dobson & Barnett, 2008).

And last, a new sensibility is causing society to have ethical concerns regarding the use of animals bred for the purpose of studying them in laboratories (Stevens, 2017). In this regard, testing animals that have not been bred for research purposes may be ethically much more acceptable, also because experimental tests may be a form of enrichment for captive animals. For this reason, it is important to test animals that do not exist solely for research purposes. Research with domestic animals (primarily dogs and cats) is increasingly popular (Kelly & Lea, 2023). In our studies, we have therefore tested animals living in zoos. In a review by Hopper from 2017, right before the beginning of this thesis, only 2 studies on animal cognition had been conducted in Spanish zoos (one in Valencia and one in Barcelona) between 2006 and 2016. During this thesis, from 2019 to 2023, we have already published 8 articles including animals from the Barcelona zoo, making a significant improvement to this number (Hopper, 2017).

To ensure the well-being of farm and zoo animals, it becomes imperative to understand their cognitive and behavioural requirements and capacities (Broom, 2011; Dawkins, 1998; Nawroth et al., 2019). The understanding of how animals perceive and interact with their environment is something of great importance for veterinaries, researchers, vets and companies such as zoos or farms. In order to assess animal welfare practices, it is essential to recognize that animals possess intricate cognitive processes and emotional states. By understanding their cognitive needs and capacities, a more accurate assessment can be achieved, leading to informed decision-making and the implementation of strategies that prioritize the animals' well-being. Citizens are becoming more aware of ethical considerations surrounding animal welfare. This acknowledgment has transcended the boundaries of public concern and has piqued the interest of politicians (Broom, 2011). As a result, all the society is becoming increasingly interested in understanding the cognitive aspects of farm animals' lives, recognizing that animal welfare is not solely about physical conditions but also on mental well-being. Us as researchers, have a pivotal role to play in enhancing our knowledge of animals' cognitive processes. Our research sheds light on how animals perceive and interpret their environment, the ways in which they form social bonds, and their capacity for learning and problem-solving. This knowledge enables us to better comprehend the needs and preferences of animals, and subsequently, make informed decisions to promote their welfare. A recent review on farm animal welfare stated: “General knowledge of how farm animals perceive and address their physical and social environment is of interest for improving housing and management practices (…) Current evidence only scratches the surface of farm animal cognitive capacities, but it already indicates that livestock species possess sophisticated cognitive capacities that are not yet sufficiently acknowledged in welfare legislation” (Nawroth et al., 2019).

With our research we aim to better understand ungulate cognition, from those ungulates we can find in farms, but also from some others that we only can find in zoos. We believe that the research comparing all of them is very interesting also from an evolutive point of view, although the research on farm animal cognition and behaviour is more urgent. Given the society views and the number of animals kept in farms compared to those kept on zoos.

Theoretical background

Comparative Psychology studies are essential to understand the mechanisms underlying human and other animals’ cognition (everything related to the acquisition, processing, and retention of information), as they allow us to explain how evolution has led to the emergence of cognitive traits (Shettleworth, 2009). However, to understand animal cognition as a whole, we must consider both more complex and more basic cognitive processes, and investigate the role of different evolutionary pressures (challenges at the ecological and/or social level) that might have led to the emergence of these cognitive skills, also taking into account evolutionary convergence in various animal taxa, not just in primates (Dunbar, 2009; Dunbar & Shultz, 2017; Reader & Laland, 2012; Shettleworth, 2009).

To date, we still do not know why in humans and other animal species emerged cognitive skills related to an increase in brain mass, a tissue that is highly expensive, only second to heart tissue (Dunbar, 2009; Kaufman et al., 2003). Numerous hypotheses have been proposed to explain the reason for encephalization, but none of them explains all the existing variability (Dunbar, 2002; Dunbar & Shultz, 2017). These hypotheses can be grouped in ecological hypothesis (more classic ones) and social hypothesis (the most recent ones).

One of the main ecological challenges that might be linked to an increase in cognitive skills is dietary breadth. This hypothesis predicts that species that exploit a higher number of animal or plant resources will have higher cognitive skills, to better keep track of the different species used as resources. (Isler & van Schaik, 2006; Kotrschal et al., 2013; Martin, 1981). Another important ecological pressure that might be linked to enhanced cognitive skills is the presence of predators, as the emergence of anti-predatory strategies might require larger brains and higher cognitive skills to better respond to predators (Shultz & Dunbar, 2006b). Finally, the type of habitat is also considered a relevant aspect in cognitive evolution. It has been shown that animals that live in mixed habitats (those mixing open spaces and closed spaces) have larger brains than those living in only open or close spaces (Shultz & Dunbar, 2006a).

In contrast, social hypotheses identify challenges related to social interactions and group organization as the driving force behind the evolution of cognitive skills (Dunbar, 2009; Dunbar & Shultz, 2021; Whiten, 2018). One of the hypotheses having received most experimental support is the social brain hypothesis, which defends that large brains evolved to solve social problems, favouring individuals capable of anticipating, responding, and perhaps manipulating the behaviour of other members of their group (Dunbar, 2009). For instance, fission-fusion dynamics have been recently proposed as an important aspect of social complexity, which might require higher cognitive skills to keep track of all the individuals in the group (Amici et al., 2012; Aureli et al., 2008; Schubiger et al., 2020). When groups have high levels of fission-fusion, group members frequently join and separate into subgroups of different sizes and composition, which might represent a major cognitive challenge for animals, who must remember each group member and the relationships established with them and among them over long periods of time (Amici et al., 2008; Aureli et al., 2008).

Unfortunately, all these hypotheses have only been systematically studied in primates and corvids, with very few exceptions in other taxa. This is problematic because we do not know if the underlying evolutionary pressures on cognitive evolution are the same in other animal taxa (Shultz & Dunbar, 2006b, 2006a). For example, it could be that social pressures best explain cognitive emergence in primates, but ecological factors might be better predictors of cognitive skills in those taxa in which social challenges are not as complex. This lack of studies across diverse taxa is problematic since it limits the validity and generality of findings across the field of brain and cognitive evolution. Evolutionary theories can only be robust if they are validated in more taxa (Benson-Amram et al., 2016; Krasheninnikova et al., 2019, 2020; MacLean et al., 2012; Vonk & Leete, 2017).

Given these premises, this thesis aimed to use ungulates as a study model to test some of the main hypotheses currently used to explain cognitive evolution. In a recent entry on the Encyclopedia of Animal Cognition and Behavior we can find a summary on the last research on ungulates´ cognition and behaviour (Murdock, 2020). This entry concludes saying that ungulate cognition "(…) is in its infancy. There is much unrealized potential in using the comparative approach with this order" (Murdock, 2020). Ungulates are a diverse group belonging to the clade Ungulata, what means hoofed animals. They can be categorized into two orders: Perissodactyla, comprising odd-toed ungulates such as horses, rhinoceroses, and tapirs, and Artiodactyla, encompassing even-toed ungulates like cattle, bovids, pigs, giraffes, camels, sheep, deer, and hippopotamuses. In this thesis we will present mainly results on Artiodactyla, although we have also tested tapirs and zebras that are Perissodactyla (unpublished results). Although we tested primarly Artiodactyla, we will speak about ungulates in general during this thesis since we currently don´t have data stating that the behaviour or cognition of these two orders might be any different. Future data more precise might oblige to make this difference. Cetaceans are also considered ungulates taxonomically, since recent discoveries suggest their ancestry can be traced back to early artiodactyls, but in this thesis we will not consider them due to obvious differences in this group of marine mammals (Wilson, 2011). Terrestrial ungulates are typically herbivorous, and many have developed specialized gut bacteria to facilitate cellulose digestion. While certain contemporary species, such as pigs, exhibit omnivorous behaviour (Wilson, 2011).

Ungulates are an ideal group to evaluate cognitive skills from a comparative perspective. They show an impressive variety of socio-ecological characteristics, which allow contrasting different evolutionary hypotheses (Focardi & Paveri-Fontana, 1992; Pérez-Barbería & Gordon, 2005; Shultz & Dunbar, 2006a). In addition, they are often accessible in zoos and farms, where they live in large groups, and it is easy to meet the requirements of space and motivation to carry out experiments (e.g. Marino & Allen, 2017; Marino & Colvin, 2015; Nawroth, 2017; Nawroth et al., 2019; Nawroth & Langbein, 2019; Nawroth & Rørvang, 2022). Moreover, despite the prevalence of ungulates in our society, their cognitive abilities remain largely understudied and poorly understood (Nawroth & Langbein, 2019; Nawroth & Rørvang, 2022). Across species, ungulates show important socio-ecological differences. Their social systems range from solitary to large groups, and their mating systems can range from monogamous pair bonding to large mixed groups (Pérez-Barbería et al., 2007; Pérez-Barbería & Gordon, 2005; Shultz & Dunbar, 2006). Ungulates also vary in the stability of the groups they form, which can be either characterized by high levels of fission-fusion or highly cohesive (Shultz & Dunbar, 2006). Also, domestication might be linked to changes in ungulate cognitive skills (Zeder, 2006, 2012). Already Darwin, in the origin of species (Darwin, 1859), suggested to test how domestication affected behaviour: “The possibility, or even probability, of inherited variations of instinct in a state of nature will be strengthened by briefly considering a few cases under domestication. We shall thus also be enabled to see the respective parts which habit and the selection of so-called accidental variations have played in modifying the mental qualities of our domestic animals”. Recently there has been indeed a steady increase in the number of studies on pets, especially on dogs, but domestic ungulates are still much behind those (Kelly & Lea, 2023).

We should mention, that during the course of our research, we encountered a significant challenge. We encountered difficulties in obtaining socio-ecological data pertaining to the ungulates we intended to investigate. Such information either was inexistent or was of questionable quality. Several of the ungulate species we sought to examine had received limited attention in wild studies, leaving us gaps of crucial insights into their grouping patterns and dietary preferences. This gap of knowledge in the field of socio-ecology paralleled the gap observed in our field, in evolutionary psychology. Apparently there are other scientific fields studying some species more than others. Furthermore, we encountered scientific articles addressing the ecological aspects of certain animals of interest to us, which failed to meet the criteria for robust scientific research, exhibiting limitations such as small sample sizes or questionable methodologies. To mitigate these challenges, we conducted extensive and meticulous research, selecting the most suitable data for each species under scrutiny. However, it is important to note that future discoveries and updates regarding the species studied in this dissertation may necessitate revisiting and refining the interpretations derived from our research.

Objectives and structure of the thesis

The main objective of this thesis was to conduct a battery of cognitive tests across several ungulate species, in order to assess whether some individual and specific characteristics predict the ability to solve these tests. We will compare these differences with the data already available in primates and other species in each chapter. We want to assess if the differences found in ungulates match those of other mammals, or if there is any characteristic that is not that relevant in other species that maybe in ungulates is key to cognitive performance (for example predatory pressure in the wild). Each of the hypotheses explained in introduction (ecological and social hypothesis), presents its own set of predictions regarding the performance of each species within the test battery (refer to Table 1 for detailed predictions associated with each hypothesis for the species tested in the first 5 chapters). The selection of species, as presented in Table 2, is based on two key considerations. Firstly, these species encompass a socio-ecological spectrum significant for the study of cognitive evolution according to current evolutionary hypotheses. Secondly, these species are conveniently accessible at the Barcelona Zoo and other collaborating zoos. The outcomes derived from this battery of tests will allow us to discern the best explanatory hypothesis that accounts for cognitive evolution in ungulates. Moreover, it will yield valuable insights into the cognition of species that have remained unexplored in this particular domain, despite having substantial relevance within our society.

As shown in the data later on, we found important variation across individuals, species and tests: not all animals were able to pass all tests, including simple ones, but others were. For example, forest buffalos were not able to solve even the basic object permanence test, but giraffes were able to solve that one and much more complex tests. Moreover, the comparison of species allowed us to assess the factors that explain the distribution of cognitive skills within the taxon, and thus the socio-ecological challenges that might drive the evolution of their cognitive skills. In Table 2, I summarized the tests that I presented in each chapter, as well as the DOI to access the published articles. In Table 3, I provided detailed information on each of the study species that can be found in each chapter to facilitate the search for any species of interest to the readers.

Table 1. Hypothesis and its predictions. Green means that the hypothesis predicts good performance, yellow intermediate performance and red low performance. The socio-ecological data has been obtained from (Bekhuis et al., 2008; Bercovitch & Berry, 2013; Berry & Bercovitch, 2017; Blake, 2002; Korte, 2009; Kowalczyk et al., 2011, 2019; Melletti et al., 2007; Ramos et al., 2015, 2016; Wilson, 2011)

HYPOTHESIS	**GENERAL PREDICTION**	**SPECIES**		
		Giraffe *Giraffa camelopardalis*	**Forest buffalo** *Syncerus caffer*	**Europen bison** *Bison bonasus*
Type of diet (**H1**)	Browser > Grazer	Browser ++	Grazer --	Grazer -
Diet complexity (**H2**)	High > Low	High ++	Low --	High ++
Predatory level (**H3**)	High > Mid > Low	Mid -+	Low --	Low --
Habitat (**H4**)	Mix > Close > Open	Open --	Close -+	Open --
Type of group (**H5**)	Fission-Fusion > Fix groups > Solitary	F-F ++	Fix -+	F-F ++
Group size (**H6**)	Big > Small > Solitary	Small -+	Small-Solitary -+	Big ++

Table 2. Chapter, species, year of publication, cognitive task and DOI for each of the studies presented in the thesis.

Chapter	Species	Year published	Cognitive task	DOI
1	Giraffes	2019	Object permanence, short-term memory	10.1037/com0000142
2	Giraffes	2020	Quantity discrimination	10.1007/s10071-020-01442-8
3	Giraffes	2023	Use of statistics	10.1038/s41598-023-32615-3
4	Giraffes, European bison and forest buffalo.	2021	Object permanence, short-term memory (Same procedure has first article published)	10.1186/s12983-021-00417-w
5	European bison	2021	Innovation	10.1098/rsos.201901
6	Guanacos, mouflon, lama and goats	2020	Gaze following	10.3389/fpsyg.2020.604904
7	10 ungulate species	2021	Neophobia	10.1007/s00265-021-03041-0
8	13 ungulate species	2023	Innovation	10.3389/fpsyg.2020.604904

Table 3. For each species, chapters in which it was included as study species.

Species tested	**Scientific name**	**Chapters**
Giraffes	*Giraffa camelopardalis*	1, 2, 3, 4, 7, 8
European Bison	*Bison bonasus*	4, 5
Forest buffalo	*Syncerus caffer nanus*	4
Guanaco	*Lama guanicoe*	6, 7, 8
Mouflon	*Ovis orientalis orientalis*	6
Lama	*Lama glama*	6, 7, 8
Goat	*Capra aegagrus hircus*	6, 7, 8
Barbary sheep	*Ammotragus lervia*	7, 8
Dromedary	*Camelus dromedarius*	7, 8
Scimitar oryx	*Oryx dammah*	7, 8
Przewalski horse	*Equus ferus przewalskii*	7, 8
Red deer	*Cervus elaphus*	7, 8
Sheep	*Ovis aries*	7, 8
Impala	*Aepyceros melampus petersi*	8
Mhorr gazelle	*Nanger dama mhorr*	8
Dorcas gazelle	*Gazella dorcas osiris*	8

The different chapters of this thesis can be summarized as follows:

- Chapter 1: In this study, we tried to determine if a simple task such as object permanence could be solved by giraffes. We also tested if they could do it with a small delay of 30 seconds, 60 seconds, and 120 seconds. Finally, we tested if they could use acoustic signals to find food. Giraffes proved to be capable of solving the object permanence test, as well as solving it after a 30s-delay.
- Chapter 2: Given the good performance of giraffes in the first study, we tested if they could solve another test on quantity discrimination. Giraffes demonstrated excellent discrimination skills when having to choose the larger of two quantities. Moreover, we did not find any bias towards food arrangement (i.e. preference for sparser versus dense arrangements of food pieces) or size (i.e. preference for smaller versus larger pieces).
- Chapter 3: Given the good performance of giraffes in the quantity discrimination task, we further tested whether they could use statistical cues to make inferences about the outcome of a sample. The results confirm that giraffes are also able to solve this task.
- Chapter 4: We extended the experimental protocol described in the first chapter to European bison and forest buffalo. We found that the bison were able to solve the object permanence task, but the forest buffalo could not solve any of the tests.
- Chapter 5: The results from the previous chapter with bison led us think that they may have advanced cognitive skills, and we thus studied them in two more complex innovation tasks. The bison did not solve the first task, in which they had to place a stump below a food source that was too high for them to be reached without the stamp. However, they did solve the second task, in which they had to push cubes towards the experimenter in order to be fed.

- Chapter 6: We conducted a task on social cognition, by comparing non-domesticated and domesticated ungulate species in their ability to follow the gaze of conspecifics and humans. Results showed that ungulates could reliably follow the gaze of both conspecifics and humans, with non-domesticated species also being successful.
- Chapter 7: In this study, we compared 10 different ungulate species in their reaction to novelty (i.e. neophobia), and analysed whether socio-ecological and/or individual characteristics predict the distribution of neophobia, when controlling for phylogeny. We found that individuals less integrated in the group more quickly approached novel objects, showing lower neophobia. Also, Barbary sheep were less neophobic than all the other species.
- Chapter 8: In the final chapter, we compare 13 different ungulate species in their ability to innovatively open cups containing food. We analysed whether socio-ecological and/or individual characteristics predict the distribution of innovation skills. We found that individuals who were less neophobic and less integrated into the group were also the best at solving the task. Whereas species with higher fission-fusion dynamics and domesticated species were more likely to participate in the task, although they were not better at solving it.

CHAPTER 1

Object permanence in *Giraffa camelopardalis*: first steps in giraffes' physical cognition

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Link to published videos in Supplementary material: **LINK**

Abstract

Although behaviour, biology and ecology of giraffes have been widely studied, little is known about their cognition. Giraffes' feeding ecology and their fission-fusion social dynamics are comparable to those of chimpanzees (*Pan troglodytes*), suggesting that they might have complex cognitive abilities. To assess this, we tested 6 captive giraffes on their object permanence (Condition 1), short-term memory (Condition 2) and ability to use acoustic cues to locate food (Condition 3). In Condition 1, we tested whether giraffes understand that objects continue to exist even when they are out of sight. Giraffes saw one of two opaque containers containing food, then containers were closed, and 2 seconds later giraffes could choose one. In Condition 2, we used the same procedure as in Condition 1, but with a delay of 30 seconds, 60 seconds or 2 minutes between closing the containers and subjects' choice. Condition 3 investigated whether giraffes could locate food inside one of two identical opaque containers, when the only cue provided was the sound made by food when shaking the baited container, or the lack of sound when shaking the empty container. Our results show that giraffes form mental representations of completely hidden objects, but may not store them for longer than 30 seconds. Moreover, they rely on stimulus enhancement rather than acoustic cues to locate food, when no visual cues are provided. Finally, we argue that giraffes and other ungulates might be a suitable model to investigate the evolution of complex cognitive abilities from a comparative perspective.

Key words: Object permanence, short-term memory, acoustic cues, giraffe, cognition, bayesian statistics.

Introduction

Previous studies have increased memory demands of object permanence tasks by introducing a delay between the baiting procedure and the moment in which subjects can retrieve the food: after the reward has been hidden, the subject waits for a specific period of time before selecting one of the containers (e.g. Barth & Call, 2006). In this way, memory demands are increased, and individuals have to remember the food location in the face of increasing delays. Unsurprisingly, performance declines with increasing delays across several species (see Cacchione & Rakoczy, 2017). Another modification that has been done to this paradigm is providing an acoustic cue (e.g. making the baited container produce a noise) instead of a visual one (e.g. showing the reward being hidden: Call, 2004). In this task, if subjects understand the causal connection between objects and the noise produced when they move, they should infer that the noisy container is the one that contains the reward. Moreover, when the empty container is shaken instead, subjects should use the absence of noise to infer by exclusion that the unshaken container must be baited. This paradigm has been already tested with children (e.g. Hill, Collier-Baker, & Suddendorf, 2012), all species of great apes (Call, 2004), corvids (Shaw, Plotnik, & Clayton, 2013), pigs and boars (Albiach-Serrano, Bräuer, Cacchione, Zickert, & Amici, 2012), among others. A similar inference-by-exclusion paradigm (with visual instead of acoustic cues) has also been used with two relatives of the giraffe, goats and sheep: subjects were shown either an empty or a full container, and then had to search for food (Nawroth, von Borell, & Langbein, 2014). Both species correctly solved the usual object permanence test (i.e. when the full container was shown), but only goats solved it when being provided with mere indirect information and inference by exclusion was needed (i.e. when the empty container was shown).

To our knowledge, none of these paradigms, nor any other paradigm assessing cognition, has so far been used to test giraffes. In this study, we therefore aimed to start exploring giraffes' cognition with an object permanence task. This task may be an ideal experimental tool, testing a basic cognitive skill (which is required for more complex skills to emerge) and having been widely used in comparative psychology, therefore also allowing comparisons across species. In giraffes, object permanence may play an essential role when dealing with social partners or predators, which may not always be visible but still exist. However, object permanence may be ecologically less relevant when considering their diet, as giraffes typically move from tree to tree to eat visible leaves (Leuthold & Leuthold, 1972). In this respect, testing object permanence in giraffes can be important to understand how cognitive skills really map the socio- and/or ecological challenges faced by giraffes in their every-day life and how modular brains are (Amici, Barney, Johnson, Call, & Aureli, 2012).

We conducted 3 different experiments on giraffes. Firstly, we tested stage 4 of object permanence by visibly hiding food in one of two opaque containers. Secondly, we tested their short-term memory skills, by increasing the delay between baiting and retrieval up to 2 minutes. Finally, we tested their inferential skills by testing their ability to use the presence or absence of acoustic cues to locate food. If giraffes' ecological (i.e. dietary breadth) or social characteristics (i.e. fission-fusion social dynamics) are linked to their cognitive skills, they should perform above chance across all experiments, similarly to other species with similar socio-ecological characteristics that have been shown to master these tasks (e.g. Barth & Call, 2006; Call, 2004).

Method

Ethics statement

The Barcelona Zoo and the Leipzig Zoo controlled and approved all the procedures. Given that giraffes participated on a completely voluntary basis, and no invasive procedures were used, no formal approval was required. During the task, moreover, individuals were never food deprived, and motivation to participate was ensured exclusively by the use of highly-preferred food (i.e. carrots, carob pellets and apples). Before testing started, we assessed participant’s food preferences by presenting them with two food types and making them choose one, with each possible comparison being repeated 12 times per individual. The experiments thus provided a form of enrichment for the subjects and did not present any risks or adverse effects.

Subjects and materials

We tested 6 giraffes (*Giraffa camelopardalis*) ranging from 1 to 21 years of age and housed at the zoos of Barcelona and Leipzig (see Table 1). All study subjects were consistently fed a diet of fruit and vegetables. None of the subjects had previous experience with the materials used in our experiments, and none had ever been tested in any cognitive task. The tests were carried out in the interior facilities, after isolating the participant giraffe from the group. Subjects kept visual, auditory and potentially tactile contact with the rest of the group in all cases. Only the experimenter remained in the enclosure during the tests.

Table 1
Subjects participating in the study.

Name	Sex	Age (years)	Zoo	Rearing history
Nuru	F	8	Barcelona	Mother
Yalinga	F	13	Barcelona	Mother
Nakuru	M	1	Barcelona	Mother
Max	M	21	Leipzig	Nursery
Andrea	F	9	Leipzig	Mother
Ashanti	F	16	Leipzig	Mother

All giraffes belonged to the subspecies *Giraffa camelopardalis rothschildi*. All of them were born in captivity.

For all the experimental conditions we used two identical opaque containers of approximately 15x15x3cm. Using only two containers allowed us to test naïve subjects with an easier set-up, as often is done in literature (e.g. Albiach-Serrano et al., 2012; Chiandetti & Vallortigara, 2011; Nawroth, von Borell, & Langbein, 2015). Depending on the result of previous individual preference tests, a piece of carrot or apple was used as a reward in case of a correct choice; in order to fill the container and facilitate visual discrimination, the food reward was laid on a bed of carobs or pellets, depending on the diet restrictions at the two facilities. Every trial was recorded from a video-camera fixed one meter behind the experimenter's back. All experimental conditions were administered in a pseudo-randomized order, except from the habituation phase, which was administered at the beginning to all subjects. Trials always started when the subject's head was in front of the experimenter, with its head approximately between the two containers.

Habituation phase

Only one container was used. The experimenter baited the container out of the subject's view, and then showed the container to the subject. After 5 seconds the experimenter closed the container and pushed it toward the subject. If the subject touched the container, the experimenter opened the lid and let the subject eat the food. After 4 successful retrievals out of 5 consecutive trials, the giraffe started the experimental phase.

Olfactory control condition

We used the same procedure as in the Habituation phase, but two containers were used. Out of the subject's view, the experimenter baited one of the two containers and closed both of them. Then, the experimenter showed both containers to the subject, holding each one in one hand, approximately at 80 cm from each other and around 50 cm from the subject. After 5 seconds, the experimenter simultaneously moved both containers toward the subject, and let the subject choose. The experimenter made this movement with his eyes closed to avoid providing inadvertent cues to the subject: he could notice the choice of the giraffe because both containers were light enough to be clearly moved by the giraffe during the election. If the subject touched the correct container, the experimenter opened the lid and let the subject eat the food, while removing the unchosen container. If the subject touched the wrong container, the experimenter opened its lid and showed its content to the subject, then showed the content of the correct container and removed both. In this condition, the subject had neither visual nor acoustic cues to locate the food, and could only rely on possible olfactory cues coming from the container containing the reward. Chance performance (50% of the trials) in this condition therefore indicated that subjects could not rely on olfactory cues to locate food.

Figure 1. (A) The experimenter shows the content of both recipients to one of the subjects. (B) The subject makes a choice.

Object permanence condition

We followed the same procedure as in the Olfactory control condition, but in this case the subject could see the baiting procedure. In full view of the subject, the experimenter showed the content of both containers, holding each one in one of his hands as above, and after 5 seconds he simultaneously closed the lids of both containers, making their content invisible. After 2 seconds, the experimenter closed his eyes and approached both containers to the subject, letting her choose (see an example in Video 1).

Memory condition

We used the same procedure as in the object permanence condition. The only difference was the time elapsed between closing the lid and letting the subject choose. Depending on the condition, the time elapse was 30 sec, 60 sec or 120 sec, instead of 2 sec. The experimenter stared at the ground during this time, observing his watch (see an example of the 30sec condition in Video 2).

Acoustic cues condition

We followed the same procedure as in the Object permanence condition, but this time the opaque lids were closed before being presented to the subject, so that no visual cue was given with regards to the food location. In the Shake full condition, the experimenter held both containers slightly beyond the subject's reach, and then shook 3 times the container containing the reward. In this way, the carob/pellets inside the container made a loud noise, similar to the sound of a rattle. After 2 seconds, the experimenter simultaneously pushed both containers toward the subject and let her choose (see an example in Video 3). In the Shake empty condition the procedure was identical, but this time the experimenter shook the empty container, which thus made no sound. In this last condition, a correct choice was coded when the giraffe selected the unshaken container, as this one contained the food reward.

Design

Each subject went first through a habituation phase. After this, each subject was administered 12 trials for each of the 7 conditions, in a pseudo-randomized order. Within each condition, the position of the food reward was also pseudo-randomized, being on the right side in half of the trials. There was always a 2 minute break between trials. Sessions continued until the subject stopped approaching the experimenter, usually around 30 minutes after the first trial.

Data analyses

An external observer coded 15% of all the trials from the video-recordings. This observer was naïve to the hypotheses: as soon as the subject made a choice, she stopped the tape and coded before seeing the experimenter's reaction to the subject's choice. Inter-observer reliability was excellent ($\kappa = 1$, $n = 75$).

We used Bayesian statistics to analyse the results, instead of the traditional null-hypothesis significance testing (NHST) (see NHST analyses in supplementary material 1). This was due to various reasons (see Kruschke, 2014). Firstly, Bayesian statistics provide more information about the analysed parameters, as compared to traditional hypothesis tests (Kruschke, 2013). Secondly, Bayesian statistics require no corrections for multiple comparisons and thus provide more statistical power, which is an advantage in case of multiple testing. Moreover, Bayesian analyses use the highest density interval (HDI) instead of the confidence interval employed for frequentist analysis. In particular, the HDI informs about the probability that a certain hypothesis is true, given the data, and does not simply accept or reject the null hypothesis, as NHST instead do. Therefore, the HDI reduces uncertainty, indicating the most credible values and covering 95% of data distribution.

To assess performance, we used the Bayesian alternative to a one-sample t-test and assessed whether each condition had its 95% HDI above chance (i.e. 6 out of 12 correct choices, 50%). Our dependant variable was the percentage of correct responses. A correct choice was scored if the subject chose the baited container by touching it with her lips or tongue. In those conditions resulting in a preference for the baited container, we repeated the analysis including only the first three trials, to assess performance before extensive learning could take place. If subjects in these conditions had simply learned to associate cups with food (e.g. the noisy cup and the food in the Acoustic cues condition), their performance should drop to chance levels in the first three trials. We applied a t distribution, as this has fatter tails than the normal distribution and can better accommodate outliers in the model. We used minimally informative priors as described by Kruschke (2013), i.e. normal priors with large standard deviation for (μ), broad uniform priors for (σ), and a shifted-exponential prior for (ν).

Since giraffes moved freely during the tests, we further controlled their body orientation in order to know if they used it as an aid to make their choices (e.g. by maintaining their head oriented toward the baited container throughout the trial). We thus counted the number of trials in which giraffes maintained their heads oriented towards the same container from the end of stimuli presentation (i.e. closing the lids in the visual conditions, or stopping containers' movements in acoustic conditions) until the choice was made.

Results

In the Olfactory control condition (95% HDI: .32 - .57) giraffes performed at chance level (50% correct choices), showing that they could not rely on olfactory cues to locate hidden food.

Subjects performed above chance level in the Object permanence condition (95% HDI: .67 - .75) and in the 30 sec Memory condition (95% HDI: .55 - .72). Equivalent results were obtained if only including the three first trials of these two conditions (95% HDI > .5). In the 60 sec Memory condition (95% HDI: .43 - .71) and in the 120 sec Memory condition (95% HDI: .4 - .82) giraffes performed at chance levels (Figure 2).

In the Shake full condition (95% HDI: .68 - .92) subjects performed above chance level but in the Shake empty condition giraffes performed below chance (95% HDI: .34 - .37). See supplementary material for the complete data (See Figure 2).

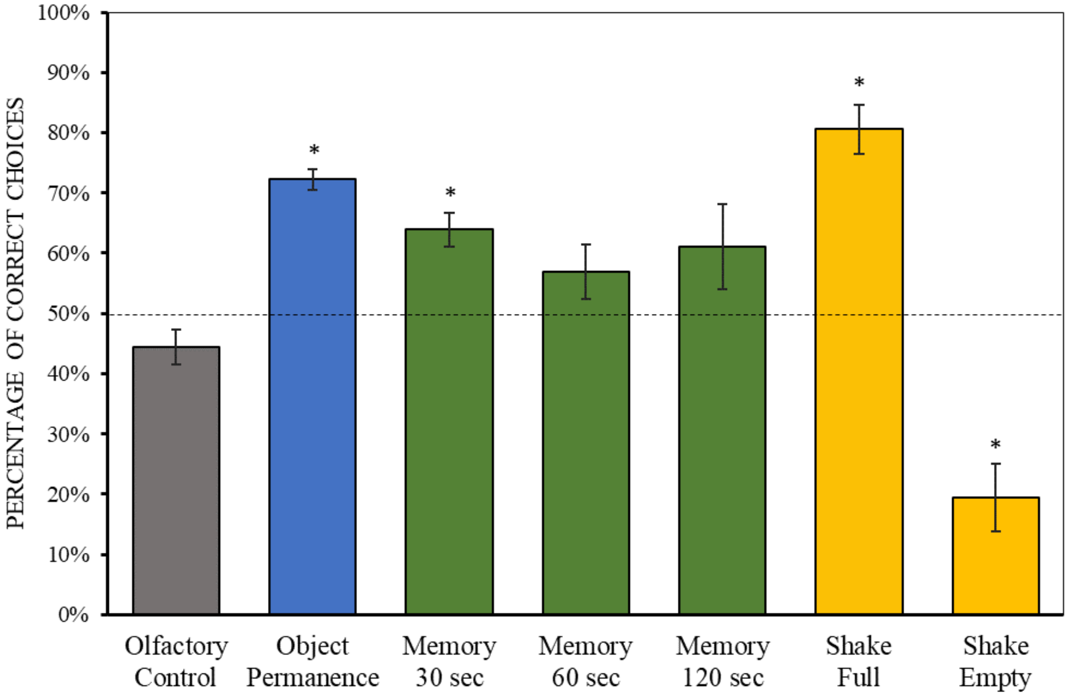

Figure 2. Mean ± SEM of correct choices in the forced-choice task. Values above 0.5 indicate a preference for the baited container. A 95% HDI above chance level (50%) is indicated by an asterisk. The percentage of trials in which giraffes maintained the head orientation toward the same container throughout the trial was relatively high in the Object permanence (43%), Shake full (58%) and Shake empty (76%) conditions, but much lower in the 30 sec (7%), 60 sec (1%) and 120 sec (0%) Memory conditions (Figure 3).

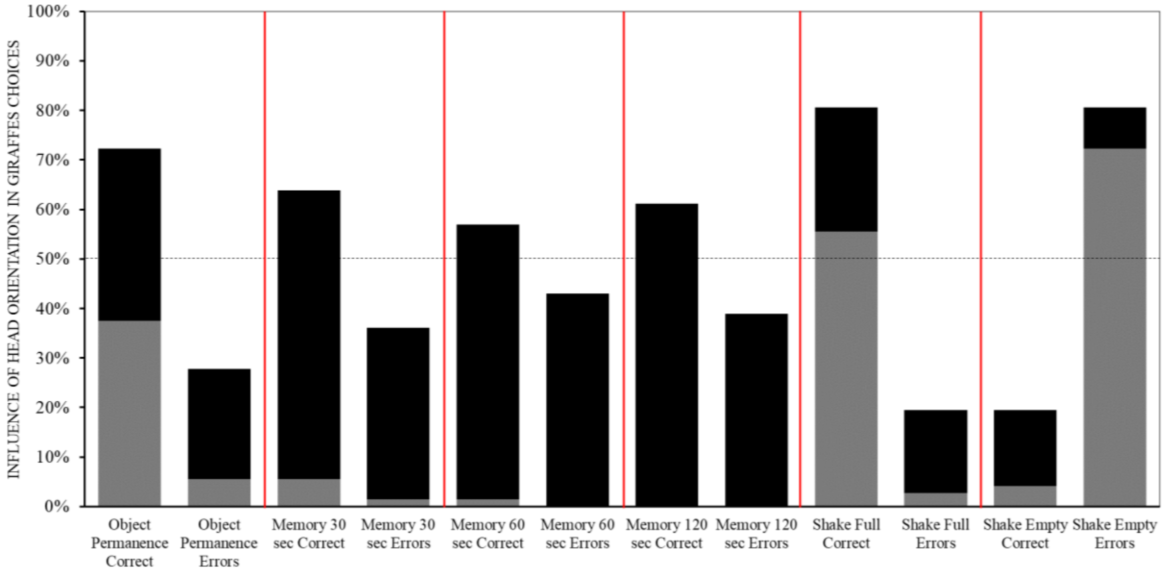

Figure 3. In grey, the percentage of trials in which giraffes maintained their heads oriented toward the correct (Correct) or the incorrect (Errors) container, from the end of the stimuli presentation, until their choice. In black, the percentage of trials in which giraffes did not maintain head orientation toward the container throughout the trial.

Discussion

Chance performance in the Olfactory condition confirmed that giraffes in the other conditions were not simply relying on smell to locate hidden food. Giraffes were able to locate food both in the Object permanence condition (2 sec delay) and in the 30 sec Memory condition, but not when delays were increased in the 60 sec and 120 sec Memory conditions, suggesting a memory or an attention limit. Giraffes could further use the presence of acoustic cues to locate food in the Shake full condition, but not the absence of acoustic cues to infer food location in the Shake empty condition.

Chance performance in the olfactory condition demonstrates that subjects failed to select the container containing food in the absence of visual and acoustic information. Therefore, our results in the other conditions cannot be attributed to giraffes' relying on inadvertent cues provided by the experimenter or by food smell to solve the task. Moreover, they are also not the result of learning, as giraffes either correctly solved the task from the very first trials (Object permanence, 30 sec Memory and Shake full conditions), and correctly performed also in the following trials, or failed to master a condition, even after being administered multiple trials (60 sec and 120 sec Memory, and Shake empty conditions).

Giraffes reached stage 4 of object permanence, as they consistently performed above chance level in our first condition. Understanding that objects exist even if being completely hidden may be the result of different socio-ecological pressures. In giraffes, for example, object permanence may be useful to track conspecifics – something important when living in groups (Zucca, Milos, & Vallortigara, 2007). However, object permanence is also a widespread ability in vertebrates (Cacchione & Rakoczy, 2017). Therefore, it is likely that this ability is shared with other species as a result of homology, and does not reflect specific selective pressures experienced since giraffes diverged from other taxa. Future studies should address whether giraffes also show further stages of object permanence. Goats, for instance, have been tested with a similar experiment, showing stage 6 of object permanence (i.e. being able to successfully track invisible displacements; Nawroth et al., 2015). Given the socio-ecological challenges faced by giraffes, it would come as no surprise if they could also reach stage 6.

The Memory conditions tested whether giraffes can use their short-term memory (Carruthers, 2013) to remember the location of hidden food. Their success in the 30 sec condition indicates that giraffes can store information for up to 30 seconds later. Their failure in the 60 sec and 120 sec conditions, however, indicates that their short-term memory might not last long when compared with other mammals (Lind, Enquist, & Ghirlanda, 2015). Dogs, for example, can store information for at least 240 seconds (Fiset, Beaulieu, & Landry, 2003), and cats for at least 60 seconds (Fiset & Doré, 2006). Even in the 30 sec condition, their accuracy (i.e. 72%) is far from the one shown by chimpanzees (i.e. 86%) with the same delay and three containers (Barth & Call, 2006). From an evolutionary perspective, however, this limit in short-term memory is surprising, as giraffes' fission-fusion social system would especially benefit from the ability to remember the position of others through time (see Aureli et al., 2008). Moreover, it is possible that giraffes may show a much better performance when tested in a long-term memory task. For instance, fights between bulls at first encounters are common, but these fights create dominance hierarchies and the same bulls rarely fight again (Shorrocks, 2016; but see Bercovitch & Berry, 2015). Given that adult bulls seldom encounter each other, this ability to recognize other individuals and remember the outcome of previous fights may indicate a good long-term memory.

Giraffes used their body orientation as a cue to choose in 52% of their correct trials in the Object permanence condition, but only in 9% of their correct trials in the 30 sec condition (see Figure 3). This indicates that, although body orientation may be used as a cue in these tasks, it is not necessary for giraffes to succeed. Also note that the most successful subject, Ashanti, barely used body orientation as a cue to solve Object permanence and Memory trials (only in 1 out of 48 trials), confirming that relying on body orientation is no key to success.

In the Acoustic cues condition we tested whether giraffes were able to make inferences about food position by relying on acoustic cues. Although they performed very well in the Shake full condition, performance in the Shake empty condition suggests that giraffes relied on stimulus enhancement (i.e. go toward the container being shaken) rather than acoustic cues to make their choices, and were not able to infer by exclusion the location of food. In these conditions, giraffes more heavily relied on body orientation to make their choice, keeping their head oriented toward the shaken container in 90% of the wrong Shake empty trials (Figure 3). This may indicate that their attention got trapped by the movement of the container. However, it is worth noting that this is an especially challenging test. For instance, not a single chimpanzee out of a sample of 12 performed significantly above chance levels when an empty container was shaken in an analogous experiment (Call, 2004). Only with larger sample sizes (e.g. 30 individuals) do primates start to achieve significant results in these tasks (Call, 2004). Similar patterns have been found in other primate species, being unusual to find individual performances above chance levels (Maille & Roeder, 2012; Marsh, Vining, Levendoski, & Judge, 2015; Sabbatini & Visalberghi, 2008). One of the possible explanations for our outcome is that giraffes have cognitive restraints: although they could use acoustic cues to locate food when the full container was shaken, inference by exclusion was cognitively too demanding to allow them success in the Shake empty condition. In contrast to apes, however, giraffes did not simply select the baited container at chance levels, in the Shake empty condition, but went for the empty shaken container significantly more than chance, showing evidence of stimulus enhancement (rather than simply lack of inference by exclusion). It is therefore likely that, even in the Shake full condition, subjects simply went for the baited container because it was shaken, and not because it made noise. This would also be in line with the leaf-based diet of wild giraffes: as leaves produce no sound when shaken, the ability to associate sound with food may have not been especially selected for.

Using stimulus enhancement to locate food, of course, need not be the result of evolutionary pressures, but may depend on our giraffes' captive condition. Being captive animals, they could have learned throughout their lives to associate food to human cues (e.g. shaking), rather/more than to physical cues (e.g. acoustic cues). Regarding this last explanation, it is usually thought that domesticated species are better able to understand human communicative cues (e.g. Kaminski, Riedel, Call, & Tomasello, 2005). Our results, however, would rather suggest that developmental experience may easily allow also wild animals to rely on human cues to locate food. Indeed, stimulus enhancement is traditionally considered an early indicator of social learning (Spence, 1937; Thorpe, 1956). Further experiments are needed to test these different possibilities, by for example testing giraffes' ability to use human cues, testing their abilities to make inferences by exclusion in the visual rather than acoustic modality, or providing them with acoustic cues while separately controlling for stimulus enhancement.

Overall, our results indicate that giraffes can successfully form mental representations of objects and store them in memory for short periods of time, and likely rely on stimulus enhancement to locate food, when only acoustic cues are provided. Our results are in line with recent, perhaps unexpected findings of complex cognitive capacities in other ungulates (e.g. Briefer, Haque, Baciadonna, & McElligott, 2014; Nawroth et al., 2014; Nawroth et al., 2015; Marino & Allen, 2017), and converge in suggesting that ungulates might have better cognitive skills than previously thought. Importantly, our results also show that giraffes are attentive and motivated enough to become valuable subjects in future cognitive tests. Given the variety of socio-ecological characteristics across ungulate taxa (see Shultz & Dunbar, 2006), this opens up to the possibility of comparing cognitive performance across ungulate species, to test evolutionary hypotheses about the emergence of complex cognitive abilities. Recently, evolutionary hypotheses have been mainly contrasted by comparing performance across primates and corvids: extending this approach to other taxa may not only provide an easier alternative, but also allow us to better understand the limits of evolutionary theories that have so far only been tested across few species. Such investigations may help to reconstruct the evolution of cognitive skills and to gain a real comprehensive view of their socio-ecological foundations.

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CHAPTER 2

Giraffes go for more: a quantity discrimination study in giraffes (*Giraffa camelopardalis*)

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Abstract

Many species, including humans, rely on an ability to differentiate between quantities to make decisions about social relationships, territories, and food. This study is the first to investigate whether giraffes (*Giraffa camelopardalis*) are able to select the larger of two sets of quantities in different conditions, and how size and density affect these decisions. In Task 1, we presented five captive giraffes with two sets containing a different quantity of identical foods items. In Tasks 2 and 3, we also modified the size and density of the food reward distribution. The results showed that giraffes (i) can successfully make quantity judgments following Weber's law, (ii) can reliably rely on size to maximize their food income, and (iii) are more successful when comparing sparser than denser distributions. More studies on different taxa are needed to understand whether specific selective pressures have favored the evolution of these skills in certain taxa.

Key words: Quantity discrimination, numerical abilities, giraffe, ungulate cognition, density

Introduction

In behavioural and cognitive studies there is an imperative necessity to broaden the number and diversity of species included (Stevens 2017). This is not only necessary to understand how other species perform in different cognitive tasks, but also to better test the strength and limits of current evolutionary hypotheses on the emergence of cognition. However, while most research focuses on mammals and birds with high encephalization quotient, other taxa are neglected in science (Stevens 2017).

Among these understudied taxa, ungulates represent a very interesting group of species, with social and ecological characteristics that are more varied and complex than traditionally thought (Shultz and Dunbar 2006). For instance, giraffes form fission-fusion groups (Deacon and Bercovitch 2018; Wolf et al. 2018; Bond et al. 2019), a social characteristic that has been linked to the evolution of complex cognition (Aureli et al. 2008). Moreover, giraffes have a wide dietary breadth, which is comparable to chimpanzees' (Berry and Bercovitch 2017). According to some authors, relying on a wide range of food items might have also been a primary driver of cognitive evolution in primates and other species (MacLean et al. 2014). Despite their relatively low encephalization quotient (0.64, similar to other ungulates; Graïc et al. 2017), therefore, giraffes and other species may show complex cognitive skills, as the result of specific selective pressures experienced in certain socio-ecological conditions.

Clearly, ungulates are thus a promising taxa to test how cognitive skills are distributed. Nonetheless, very few studies have so far tested ungulate cognition, for spatial cognition (Osthaus et al. 2013; Abramson et al. 2018), object permanence (Nawroth et al. 2015a; Caicoya et al. 2019), categorization skills (Meyer et al. 2012), ability to use human cues (Nawroth et al. 2015b, 2016) and a few other capacities (Nawroth et al. 2014; Knolle et al. 2017; Pitcher et al.

2017). The field of quantity discrimination is no exception, with three times more studies on primates than on all other mammals altogether (Agrillo and Bisazza 2018). Revealing the cognitive mechanism underlying quantity discrimination, however, is an important challenge for those interested in understanding the ontogeny and evolution of cognition (Dehaene 1992; Beran 2017; Agrillo and Bisazza 2018; Butterworth et al. 2018; Nieder 2020). The ability to reliably discriminate quantities provides clear evolutionary advantages, by for instance allowing individuals to select more abundant food sources (Perdue et al. 2012), to assess the quantity of potential mates (Lemaître et al. 2011), or to select the larger social subgroup, which can offer better protection against predators when hunting pressure is high (Gómez-Laplaza and Gerlai 2011). In giraffes, in particular, quantity discrimination could allow individuals to select for the location with more trees, for the tree with more leaves or flowers (Berry and Bercovitch 2017), or perhaps even for the place with less predators. Moreover, their fission-fusion dynamic may make it very important for them to assess how many group members are present, when making decisions about splitting the group or joining one subgroup depending on the current circumstances (Aureli et al. 2008).

Quantitative abilities allow individuals to recognize the larger quantity, and do not necessarily imply any numerical abilities (see Beran 2017). The ability to discriminate quantities has been traditionally thought to rely on two different mechanisms: the Object-file system (OFS), also known as a Parallel Individuation System, and the Analogue Magnitude System (AMS). The AMS follows Weber’s law, so that accuracy varies as a function of the ratio of the set sizes compared, independently of their absolute quantity (Cantlon and Brannon 2006). Sets with a lower ratio (e.g. 1:4), in particular, are easier to discriminate than sets with a higher ratio (e.g. 3:4; Dehaene 1992; Gallistel and Gelman 1992). Moreover, when the absolute value of the magnitudes increases, sets become harder to discriminate (e.g. 14:16 is harder to discriminate than 7:8; Cordes et al. 2001; Barth et al. 2003; Cantlon 2012). While quantities in the AMS are only approximately represented, quantities in the OFS are thought to be individually represented as distinct entities, and can thus be encoded as separate object files (Kahneman et al. 1992; Gallistel and Gelman 2000; Sears and Pylyshyn 2000; Brannon and Roitman 2003), which are available for higher-level cognitive processes (Cacchione et al. 2014). In contrast to the AMS, the OFS would not follow the Weber's law, so that in sets smaller than four, accuracy would not vary depending on the ratio of the food quantities (Cantlon and Brannon 2006). More recently, this dichotomous view has been questioned. In particular, while small quantities would be encoded by default as object files and larger quantities as magnitudes (as the brain would not manage to encode them as object files), small quantities could also be encoded as magnitudes (e.g. when there are limits in the attentional or working memory resources available; see Hyde 2011). So far, however, experimental evidence has shown that, while most animal species rely on the AMS (see e.g. Cantlon et al. 2010; Beran and Parrish 2016; Beran 2017; Nieder 2020), very few species appear to use the OFS and only in spontaneous-choice tasks (Hauser et al. 2000; Hunt et al. 2008; Gómez-Laplaza and Gerlai 2011; Gómez-Laplaza et al. 2017), perhaps because of the cognitive and perceptual limits in which the OFS should operate (see Hyde 2011) or because only the representation of large numbers may exhibit sufficient variability to result in a ratio effect (Nieder 2020).

However, quantities may not only vary in terms of the items they contain (Gallistel and Gelman 2000). Sets of food, for instance, may vary in the size of the food items presented, or in the density/sparsity of items within each set (Boysen et al. 2001; Beran et al. 2008; Libertus et al. 2014; Bertamini et al. 2018; Wadhera et al. 2018). Therefore, it is important to also assess how these variables affect animals’ ability to maximize food income (Stevens et al. 2007; Uller et al. 2013; Leibovich et al. 2017; Parrish et al. 2020). Giraffes, for example, would benefit from the ability to compare food patches with a different item distribution (i.e. sparser or denser). Moreover, even when the food patches overall contain identical food quantities, giraffes may still prefer denser food patches over sparser ones (e.g. because denser food allows individuals to more easily monopolize the food patch, and/or decrease the energy required to move between food items; see e.g. optimal foraging models in MacDonald and Agnes 1999; Hauser et al. 2000; Feigenson et al. 2002; Uller et al. 2003; Uller and Lewis 2009). Alternatively, giraffes might prefer sparser food over denser food patches, as the former covers a wider area and may thus either appear to contain more food (for a similar bias in humans, see e.g. Krueger 1972; Allïk and Tuulmets 1991; Allik and Tuulmets 1993), or may better allow individuals to disperse, reducing competition and gaining a better view of possible predators. Similar preferences may be present for food quantities with items of different size, as one single larger food may better allow food monopolization than many smaller food items.

The current study represents the first attempt to examine food quantity discrimination in a non-domesticated ungulate species, by systematically assessing the effect of quantity, size and density on the ability to discriminate food sets. To our knowledge, studies on quantity discrimination in ungulates have so far been conducted only on a domesticated species, horses (Uller and Lewis 2009; Petrazzini 2014). Through domestication, however, species might have increased their social cognitive skills (for which they have been directly or indirectly selected for: Hare and Tomasello 2005; Bräuer et al. 2006; Zeder 2006) while decreasing both their physical cognitive skills (as they are largely fed by humans and thus exposed to less foraging challenges than their wild counterparts: Bräuer et al. 2006) and their brain size (between 14%

and 24%; Zeder 2012). In this respect, the inclusion of a non-domesticated species like giraffes is especially interesting, because their physical cognitive skills, including their ability to discriminate food quantities, may be higher than in the domesticated ungulate species tested so far. For example, wolves performed better than dogs in these tests (Range et al. 2014; but see Rivas-Blanco et al. 2020). In this study, we thus assessed whether giraffes can spontaneously select the larger of two food quantities across different conditions, to shed light into the cognitive mechanisms of quantity discrimination and their evolutionary origins.

We presented individuals with two food quantities, which could vary in the quantity of identical food items (Task 1), in the quantity and/or size of the items (Task 2), or in the quantity and/or density of the items (Task 3). We predicted that giraffes would successfully select the larger quantity in all three tasks, reliably using the AMS in Task 1, relying on both quantity and size in Task 2, and successfully discriminating quantities independently of their spatial distribution in Task 3. Moreover, we predicted that giraffes would show an irrational bias when food patches overall contained identical food quantities. In particular, in line with optimal foraging models, giraffes should show a bias for sets including larger items (rather than more items; Task 2), and items with a denser distribution (rather than a sparser one; Task 3), as these facilitate monopolization and reduce the energy required to forage.

Methods

Participants. We tested two male and three female giraffes (*Giraffa camelopardalis*) ranging from 1 to 21 years of age, housed at the zoos of Barcelona and Leipzig. All study participants were fed a regular diet of fruit and vegetables, and had limited experience with experimental tasks (see Caicoya et al. 2019). Participants were never food or water deprived during this study, and participation was on a completely voluntary basis.

Procedures. Tests were carried out after isolating the subject from the group, but maintaining visual, auditory, and potentially tactile contact with the others. The experimenter (A.L.C.) was situated in a private area for keepers that giraffes could not reach with their whole body, but they could reach with their heads. In all three tasks, the experimenter baited two identical trays with different food quantities (i.e. carrot pieces, a preferred food reward for the study subjects) out of their view, and presented them to the subject once this oriented the face towards the experimenter. While the subject was in this position, both trays were in its view, because giraffes and ungulates, unlike primates, have a binocular field of vision of 88º and a total field of vision of approximately 280º (Mitchell et al. 2013). The experimenter extended both arms (with the trays approximately 50 cm from each other), while closing his eyes and orienting his face toward the ground, to avoid providing any cue. In this position, the trays were still without the subject's reach. After four seconds the experimenter advanced 10 cm towards the subject, coming within its reach, and still maintaining his eyes closed and his face oriented to the ground. The subject could thus select one of the trays by touching it with the tongue or muzzle. The giraffe ate the selected food, while the other one was removed, giraffes always ate all the food from the selected tray. The inter-trial interval was approximately 45 seconds, but sometimes giraffes would stroll around the enclosure after a trial, so that the inter-trial could be longer.

In Task 1, the two trays contained a different quantity of identical food items (each food piece was weighted on a kitchen scale before each experimental session, and weighted 6 grams). We varied both the ratio and the overall quantity of items in the two sets (see Table 1), as they both could affect performance. In particular, we included trays containing quantities above and below four pieces of food, to assess whether giraffes rely on an Analogue Magnitude System (AMS) or on a Object-file system (OFS; see Table 2). In particular, if giraffes rely on the AMS, their performance should decrease when the ratio between two items increases, in all sets of food. In contrast, if giraffes rely on the OFS, performance should only decrease when the ratio increases in trays containing more than four food items. We administered a total of 36 experimental trials per subject (i.e. 4 for each of the following 9 sets: 1:6, 2:8, 4:6, 6:8, 0:1, 1:4, 1:2, 2:3, 3:4). See an example of 2:3 on Video Task 1 in the electronic supplemental materials.

In Task 2, the two trays contained food items that could differ in size and/or quantity of items. The smaller piece of carrot (S) weighted 6 g, the intermediate one with double size (2S) weighted 12 g, and the largest one (4S) weighted 24 g. The pieces of carrot were weighted on a kitchen scale before each experimental session. In some trials (Only Size condition), subjects had to take only size into account to maximize food income, and not the quantity of items presented (i.e. the overall larger quantity consisted in the tray with the larger item, but the smaller quantity of items, e.g. 4S vs S+S+S). In other trials (Only Quantity condition), subjects had to take only the quantity of food items into account, and not their size (i.e. the overall larger quantity consisted in the tray with the larger quantity of items, but the smaller size of the items, e.g. S+S+S vs 2S). In other trials (Size condition), subjects received no contrasting information and only had to take size into account to maximize food income (i.e. the overall larger quantity consisted in the tray with the larger item, as the quantity of items on the two trays was always one, e.g. 2S vs S). Finally, in other trials (Irrational Bias condition), the food quantity was identical in the two trays, although one tray contained items with a larger size, and the other tray a higher quantity of items (e.g. 2S vs S+S). If subjects could rely on size as a cue to maximize food income, they should have selected the larger quantity in the Size condition (when size provided a reliable cue to the larger tray), and to a lesser extent also in the Only Size and Only Quantity conditions (when size and quantity of items provided conflicting information, and either size or quantity of items had to be used to reliably select the larger tray). Finally, if subjects preferentially relied on size (rather than quantity of items) to maximize food income, they should have selected the tray with the larger item also in the Irrational Bias condition. We administered a total of 32 experimental trials per subject (i.e. 4 for each of the following 8 sets: S:2S, S:4S, 2S:4S, S+S+S:2S, S+S+S+S+S:4S, S+S+S:4S, S+S:2S, 2S+2S:4S). For more details on the conditions, see Table 1 and Table 2. See an example of S:4S on Video Task 2 in the electronic supplemental materials.

In Task 3, the two trays contained food that could differ in the quantity of food items and/or in their distribution (i.e. denser or sparser), to assess whether the distribution of food interferes with the ability to discriminate larger trays. In some trials, subjects could maximize their food income by selecting the tray with more food items, with food on the two trays being either densely distributed (Both Dense condition: e.g. Dense4:Dense6) or sparsely distributed (Both Sparse condition: e.g. Sparse4:Sparse6). In other trials, subjects had to maximize food income by selecting from two sets with different distributions, in which the largest amount of food could be either the denser (Denser condition: e.g. Sparse4:Dense6) or the sparser one (Sparser condition: e.g. Dense4:Sparse6). Finally, in some trials, subjects had to choose between sets with an overall identical quantity of food, but with a different distribution (Irrational Bias condition: e.g. Dense4:Sparse4). If subjects could maximize food income through different distributions, they should have selected the larger quantity both when items were densely distributed (Both Dense condition) and sparsely distributed (Both Sparse condition). If subjects preferred denser food patches over sparser ones, they should have preferentially selected denser distributions in the Irrational Bias condition, and performance should have decreased in the Sparser condition (as preference for the denser distribution conflicted with food maximization). In contrast, if subjects preferred sparser food patched over denser ones, they should have preferentially selected sparser distributions in the Irrational Bias condition, and performance should have decreased in the Denser condition (as preference for the sparser distribution conflicted with food maximization). Each food piece weighted 6 g and had approximately a 3 cm diameter. The surface area covered by the denser and sparser sets was a square of approximately 12 and 26 cm diagonal. We administered a total of 24 experimental trials per subject (i.e. 4 for each of the following 6 sets: Dense4:Dense6, Sparse4:Sparse6, Sparse4:Dense6, Dense4:Sparse6, Dense4:Sparse4, Dense6:Sparse6). For more details on the conditions, see Table 1 and Table 2. See an example of 4 Sparse:4 Dense on Video Task 3 in the electronic supplemental materials.

Twelve further 12 trials were administered to check for side biases (see Table 1). In all tasks, the position of the trays and the order of the trials were counterbalanced and pseudorandomized across and within individuals. All trials were video-recorded. In each trial, we coded the tray selected by the subject. All subjects ate all the food from the tray they had selected.

Statistics. We run multilevel-ordered logit models, always including a varying intercept by subject identity to correct for repeated observations. A first set of models assessed variation in correct response (excluding Irrational Bias and Side Bias trials; see Table 1). In Task 1, we assessed the effect of ratio and quantity of items on model fit, by comparing a null intercept-only model (M1.0) to models obtained by adding fixed effects (i.e. first the set ratio: M1.1; then the interaction between set ratio and condition: M1.2; and finally the total quantity of items: M1.3).

In Task 2, we compared a null intercept-only model (M2.0) to a model (M2.1) including condition as fixed effect. Similarly, in Task 3, we compared a null intercept-only model (M3.0) to a model (M3.1) including condition as fixed effect. A second set of models assessed the existence of irrational preferences for size (over quantity; Task 2) or sparser arrays (over denser ones; Task 3), also including Irrational Bias trials. In Task 2, we used the selection of the larger size as dependent variable and compared a null intercept-only model (M2.2) to a model (M2.3) including condition as fixed effect. In Task 3, the selection of the sparser array was the dependent variable, and the null intercept-only model (M3.2) was compared to a model (M3.3) including condition as fixed effect.

Statistical analyses were run with a Bayesian approach, using the rethinking package (McElreath 2018) in R (version 3.2.3). In all models, we standardized continuous variables and we used weakly informative priors and estimated parameters with RStan (Stan Development Team, 2016), running 3 Hamiltonian Monte Carlo chains in parallel (with 10000 samples, half of which were warm-up). Convergence was suggested by a high effective number of samples (>1300) and Rhat estimates of 1.00 (McElreath 2018). We selected models based on the lowest Widely Applicable Information Criteria (WAIC) and the highest Akaike weights.

Finally, for each individual and task, we also used Bayesian binomial tests to assess whether subjects performed above chance level, and whether they showed side bias.

Results

In set 1, M1.1 had the lowest WAIC and the highest model weight, showing that ratio contributed to model fit in Task 1 (see Table 3), but not its interaction with condition (M1.2), nor the quantity of items presented (M1.3). In particular, higher ratio predicted worse performance (β

= −0.28, 89% Prediction Interval [PI] = −0.57 to 0.02; in the probability scale: β = 0.73; see Figure 2), and this was true both for quantities below and above four. Bayesian binomial tests confirmed that each subject performed above chance level in Task 1. Finally, Bayesian binomial tests showed that no subject had side biases in this task (see Table 4).

In set 2a, M2.1 had the lowest WAIC and maximum model weight, indicating an effect of condition on performance (see Table 3). In particular, the probability to be correct was higher in Size (β = 1.25, 89% PI = 0.54 to 1.96; in the probability scale: β = 0.87) than Only Quantity ((β = 0.63, 89% PI = 0.10 to 1.19; in the probability scale: β = 0.65), and Only Size (β = −0.54, 89% PI = −1.32 to 0.25; in the probability scale: β = 0.52; see Figure 3). Bayesian binomial tests confirmed that three subjects performed above chance level in Task 2, while two subjects performed at chance level (Table 4).

In Set 2b, M2.3 had the lowest WAIC and maximum model weight, indicating an effect of condition on performance (see Table 3). The probability to select the food item with a larger size was higher in Size (β =2.22, 89% PI = 1.52 to 2.94; in the probability scale: β = 0.87), as compared to Only Size (β = 0.29, 89% PI = −0.47 to 1.09; in the probability scale: β = 0.49) and both Irrational Bias (β = 0.01, 89% PI = −1.53 to 1.61; in the probability scale: β = 0.42) and Only Quantity (β = -0.32, 89% PI = -1.00 to 0.36; in the probability scale: β = 0.42; see Figure 3). Finally, Bayesian binomial tests showed that no subject had side biases in Task 2 (Table 4).

In set 3a, M3.1 had lower WAIC and higher model weight, indicating an effect of condition on performance (see Table 3). The probability to be correct was higher in Sparser (β = 0.90, 89% PI = 0.02 to 1.76; in the probability scale: β = 0.67), as compared to Both Dense (β = 0.00, 89% PI = −1.56 to 1.59; in the probability scale: β = 0.45), Both Sparse (β = −0.01, 89% PI = −1.65 to 1.60; in the probability scale: β = 0.45), and Denser (β = -0.20, 89% PI = -0.90 to

0.56; in the probability scale: β = 0.45; see Figure 4). Bayesian binomial tests showed that all subjects performed at chance level in Task 3 (Table 4).

Finally, in Set 3b, M3.2 had the lowest WAIC and the highest model weight, suggesting that the effect of condition was only marginal (see Table 3; Figure 4). Finally, binomial tests showed that no subject had side biases in Task 3 (Table 4).

Discussion

Here we present the first quantity discrimination study on a non-domesticated ungulate species. Overall giraffes' performance was good, being above chance in most tasks. Giraffes' performance in quantity discrimination followed Weber's law, increasing as the ratio between food items decreased. This held true also when quantities contained less than four items. Giraffes could also reliably use size cues to maximize their food income, although performance decreased when size of food items and quantity of food items provided contrasting information. Changes in the distribution of items made the task difficult for giraffes, which performed better with sparser than denser sets, despite showing no irrational preference for sparser distributions.

Giraffes relied on the Analogue Magnitude System (AMS) to discriminate quantities. In Task 1, the probability to make correct choices was affected by the ratio between the two food quantities in the tray, and this was true for both quantities below and above four. These findings are in line with most research on other non-human animals (Boysen and Berntson 1995; Beran 2017; Rivas-Blanco et al. 2020), including great apes (Cacchione et al. 2014), showing that most species rely on the AMS to discriminate quantities (but see e.g. Gómez-Laplaza and Gerlai 2011; Agrillo et al. 2014 for evidence of the Object-file System, OFS, in non-human animals). Whether giraffes lack the OFS, or the high cognitive and perceptual demands of the task prevented its use in our study, is a topic for further investigations, although our experimental approach was kept as simple as possible (e.g. simultaneous presentation of two visible food quantities in absence of training).

All giraffes performed above chance in Task 1, although we also included food sets with a higher ratio, which are harder to process (e.g. 3:4, 6:8). These results may suggest that performance in giraffes is as good, and perhaps even better, than other domesticated ungulate species that have been tested so far. Horses, for instance, performed above chance with 1:2 ratios (Uller and Lewis 2009; Petrazzini 2014; Henschel et al. 2016), but not always with other sets. For example, only 83% of the horses selected the larger set in the 2:3 trials and 56% of the horses in the 4:6 trials (Uller and Lewis 2009), while giraffes succeeded in 90% and 70% of the trials, respectively. However, direct comparisons must be taken cautiously since the presentation method varied between studies. If these results are confirmed by studies including more individuals and species, they may suggest that horses, despite being domesticated and thus likely having an advantage when interacting with humans (Kaminski and Nitzschner 2013), may not have faced the same evolutionary forces that led to the emergence of complex quantity discrimination skills in giraffes (or these might have gone lost through the process of domestication; see e.g. Lampe et al. 2017). For instance, it is possible that horses, being usually food provisioned by humans and thus facing lower food competition, may not require the same ability to discriminate quantities, as it also seems to happen with dogs, performing worse than wolves in a similar task (Utrata et al. 2012; Range et al. 2014; Miletto Petrazzini and Wynne 2017). Comparisons with other ungulate species, both domesticated and non-domesticated, and the inclusion of more subjects will be necessary to better understand these potential inter-specific differences in quantity discrimination, and whether brain reduction in domesticated species played a role in the emergence of these differences (Zeder 2012).

All the tested giraffes could successfully rely on size to maximize food income in Task 2, reliably selecting the item with the larger size (in the Size condition). However, performance decreased when size and quantity of items provided contrasting information on the best option. In particular, giraffes decreased performance (i) when the best option was the set containing more, smaller food items (Only Quantity condition), and even more (ii) if the best option was the set with less, larger food items (Only Size condition). In other words, when the largest item was in one set, but the most numerous tray was in the other set, giraffes still correctly preferred the set with more, smaller food items in the Only Quantity condition (but less than in the Size condition), while they randomly chose between S+S+S and 4S in the Only Size condition (see Figure 3). Clearly, the use of contrasting cues (size versus quantity of food items) increased the cognitive complexity of the task, and only 3 giraffes performed above chance in this task. The fact that giraffes’ performance especially decreased when the only reliable cue was size (rather than quantity of food items) is in line with findings in horses (Uller and Lewis 2009) and other species (Boysen et al. 2001; Vonk and Beran 2012; Leibovich and Ansari 2016; Leibovich et al. 2017; Agrillo and Bisazza 2018), which showed a similar difference between performance with quantity and size cues. As giraffes, for instance, other species can successfully rely on size to maximize food income, like for example chimpanzees (*Pan troglodytes*) (Boysen et al. 2001), dogs (*Canis lupus*) (Miletto Petrazzini and Wynne 2016) and different fish species (Lucon-Xiccato et al. 2015; Gómez-Laplaza et al. 2019). Notoriously, horses shown a strong tendency to choose the set with the biggest item when there was no difference in total amount of food between sets that giraffes didn´t show (Uller and Lewis 2009), further studies are necessary to explain this difference.

Giraffes had more problems to maximize food income when food was distributed with different densities in Task 3. Overall, giraffes had a higher probability of selecting the best option when food was sparsely distributed (as compared to when it was densely distributed). Therefore, larger food quantities are more easily detected when they are also more sparsely distributed. However, if food is more, but densely distributed, giraffes may wrongly encode it as being less abundant. Bayesian binomial tests showed that this task was pretty difficult, with giraffes overall performing around chance level. These results suggest that, although giraffes performed well in Task 1 (where the density of the food distribution was intermediate between the ones used in Task 3), and although giraffes have an excellent visual acuity (Mitchell et al. 2013), increasing the distance between food items may further enhance their ability to discriminate between different food quantities. In line with this, a recent study on angelfish (*Pterophyllum scalare*) showed that increasing the distance between items in a quantity discrimination task facilitates the discrimination in this species (Gómez-Laplaza and Gerlai 2020).

Furthermore, the analysis of Irrational bias trials in Tasks 2 and 3 allowed us to investigate whether giraffes preferred specific food items or food distributions, when this did not affect their food income. Please note that we use the term “irrational” only to refer to the fact that the preference for a certain tray was not functional (as both trays contained an identical quantity of food), having no implication about potential evolutionary reasons that might have led to the emergence of these preferences. In particular, our results suggest that giraffes may have an irrational bias for sets including more items (as compared to larger items; see Task 2), but no clear irrational bias for denser or sparser food distributions (see Task 3). In the Irrational bias trials in Task 2, giraffes preferentially selected the size with more food items (rather than the one with few larger ones). Therefore, not only did giraffes better discriminate quantities when food items differed in quantity (rather than size), but they also preferred the trays with a higher quantity of smaller items (rather than trays with a lower quantity of larger items). In contrast, even though they could better discriminate sparser trays (as compared to denser ones), giraffes showed no irrational bias for either of the two. Optimal foraging models suggest that several species prefer denser food patches than sparser ones, as the former would better allow food monopolization and reduce the energy required to move between food items (Parrish et al. 2020). If confirmed, however, our results would suggest that giraffes do not follow this pattern, while neither showing a bias for sparser distributions (which has instead been shown in humans: see e.g. Krüger, 1972; Allik & Tuulmets, 1991, 1993).

Taken together, the results of Task 2 (i.e. giraffes better discriminated and also preferred many smaller patches of food over larger ones only varying in size) and Task 3 (i.e. sparser food distributions were more easily discriminated than denser ones) suggest that giraffes may preferentially feed on smaller, more numerous food patches, and that this selection is facilitated by sparser food distributions. This contrasts for example with results in chicks (*Gallus gallus*), angelfish (*Pterophyllum scalare*), capuchin monkeys (*Sapajus apella*) and human infants preferring clustered items (Gómez-Laplaza and Gerlai 2013; Uller et al. 2013; Bertamini et al. 2018; Parrish et al. 2020), but is in line with chimpanzees (*Pan troglodytes*) preferring sparser arrays (Boysen and Berntson 1995; Boysen et al. 2001) and rats preferring multiple smaller pieces of food (Capaldi et al. 1989; Wadhera et al. 2018). Studying irrational biases in further conditions may be especially interesting in the future, to better understand possible cues that giraffes may preferentially use in the wild to select food patches, and evolutionary reasons for these preferences. For instance, it is possible that preferences for denser distributions, which are easier to monopolize, may only emerge in species which preferentially feed on highly caloric densely distributed food, like fruit or meat, but not in the ones feeding from widely distributed food like leaves. Finally, we found no side bias, in any of the tasks.

This study was the first one we are aware of to assess quantity discrimination in a non-domesticated ungulate species, and one of the few studies in mammals with low encephalization quotient. Giraffes performed well in most conditions, confirming them as a promising model to study animal cognition (see e.g. Caicoya et al. 2019, finding evidence of object permanence, and short term memory in this species). However, our study had a very small sample size. In the future, studies should include more individuals and trials to confirm our results, and better account for inter-individual differences in performance. Ideally, these studies should also better disentangle aspects of quantitative cognition that we did not explicitly address here (e.g. whether OFS would emerge with different cognitive and perceptual task demands; whether individuals relied on the visual pattern of items across the grid in Task 1, rather than on the quantity of food items presented). Moreover, the inclusion of more species with different socio-ecological characteristics and domestication levels should allow us to better understand (i) which evolutionary forces shaped the distribution of quantity discrimination skills, (ii) the effect of domestication on these skills, and (iii) the link between non-numerical cues (like food size and density) and the ecological characteristics of the species.

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Declarations

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Conflicts of interest/Competing interests

Authors declare no conflicts of interest or competing interests

Availability of data and material

Supplementary material

Code availability

Supplementary material

Ethics approval

The methodology for this study was approved by the welfare managers of the zoos of Barcelona and Leipzig.

Fig. 1 Image A shows a 6:4 comparison in Task 1. Image B shows a 4-sparse:4-dense in Task 3.

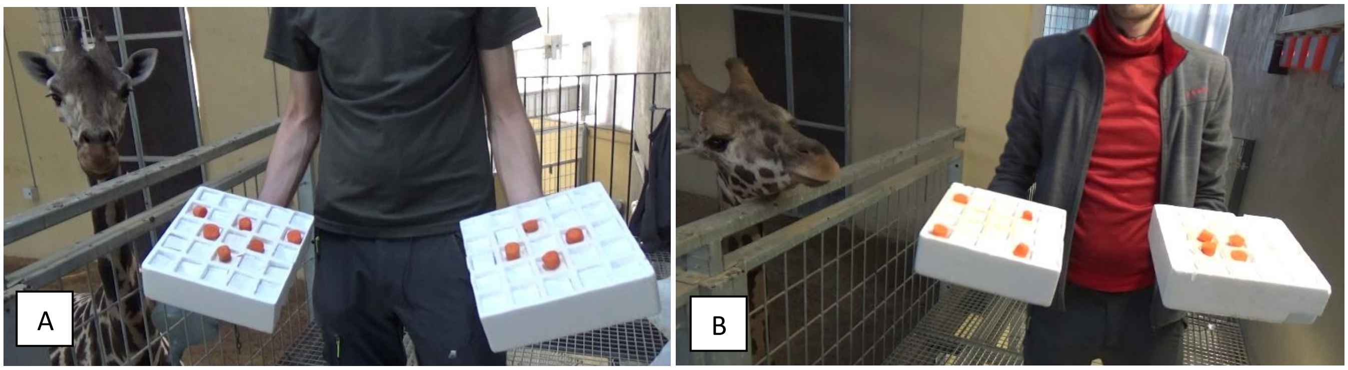


Fig. 2 Mean ± SE of the percentage of correct choices in Task 1, values above 0.5 indicate a preference for the bigger set. Bars follow a decreasing order following Weber´s law (increasingly difficult). For each experimental condition, the ratio between food quantities is expressed between parenthesis.

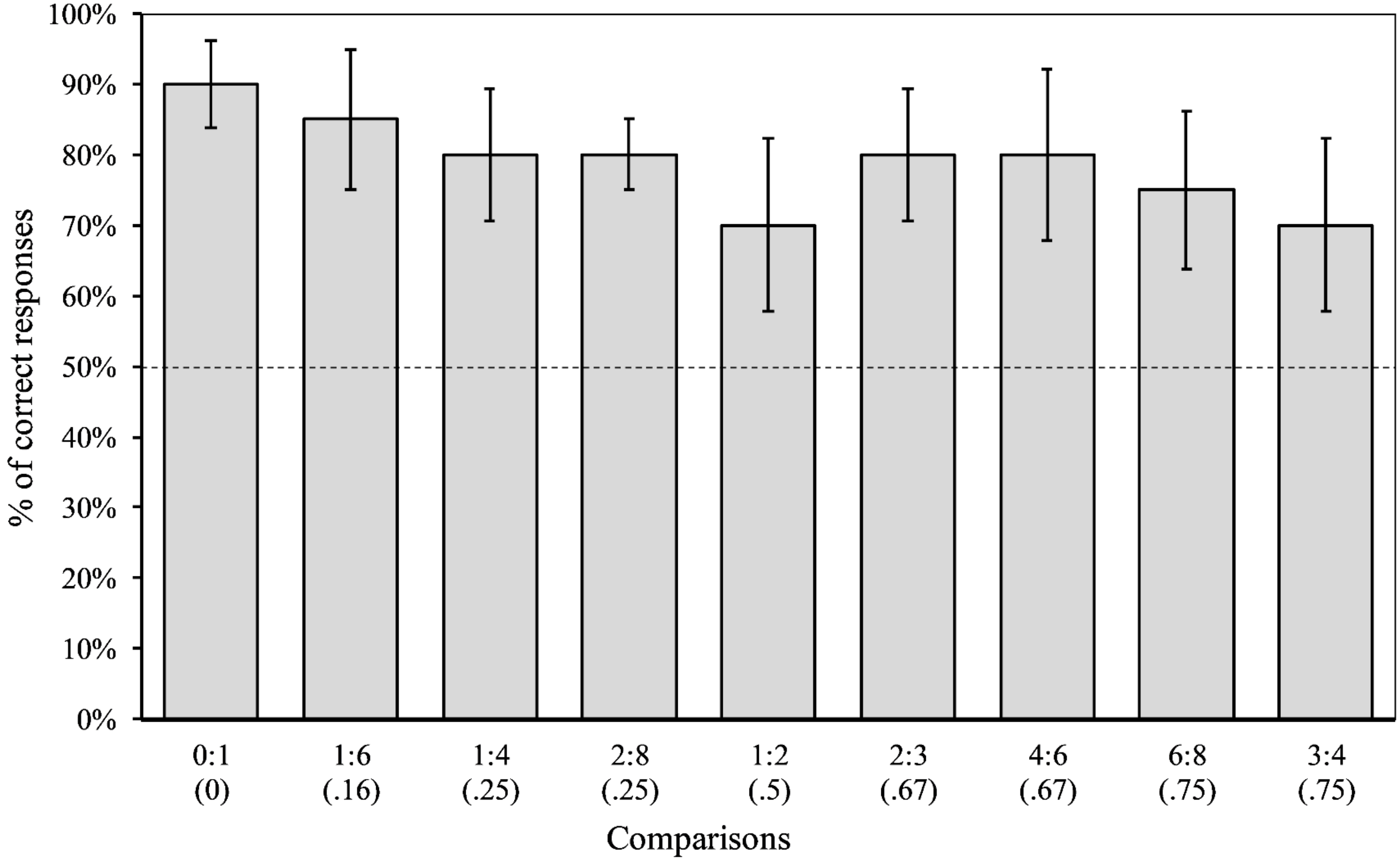


Fig. 3 Mean ± SE of the percentage of correct choices in Task 2. Values above 0.5 indicate a preference for the bigger set, except for the two experimental conditions evaluating irrational biases (no possible correct choice). In this case bars represent preference for quantity over size in dark grey stripped bars. Bars follow a decreasing order following Weber´s law (increasingly difficult). For each experimental condition, the ratio between food quantities is expressed between parenthesis.

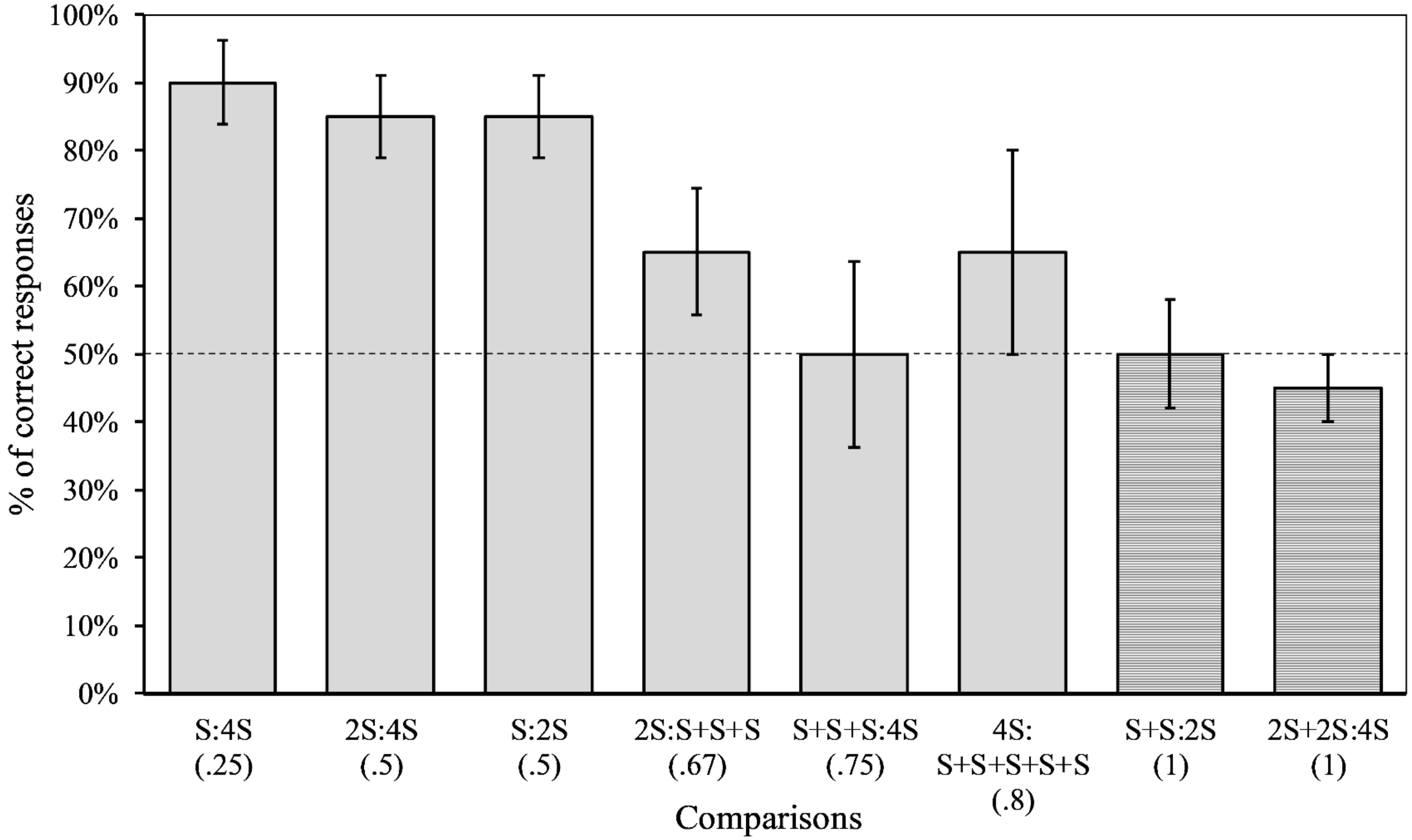


Fig. 4 Mean ± SE of the percentage of correct choices in Task 3. Values above 0.5 indicate a preference for the bigger set, except for the two experimental conditions evaluating irrational biases (no possible correct choice). In this case bars represent preference for sparse over dense in black dotted bars. Bars follow a decreasing order following Weber´s law (increasingly difficult). For each experimental condition, the ratio between food quantities is expressed between parenthesis.

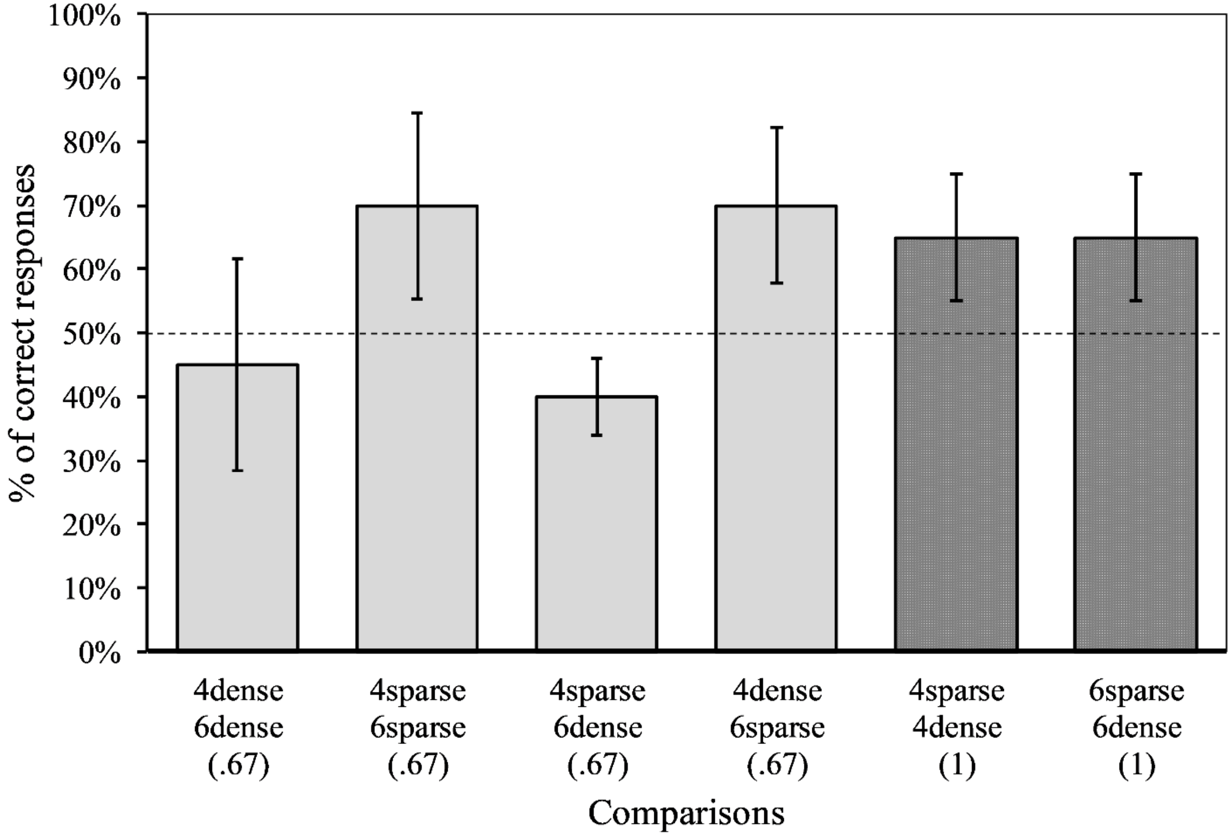


Table 1. Tasks and conditions administered, the aim of the condition, number of trials and the dependent variables used in the models.

Task & models	**Condition and food arrays shown**	**Aim of the condition**	**Number of trials per food array**	**Binomial dependent variables**	
				Correct response	**Irrational bias**
Task 1	“Above Four” 1:6, 2:8, 4:6, 6:8	Discrimination of quantities?	4	… for 6, 8, 6, 8	-
	“Below Four” 0:1, 1:4, 1:2, 2:3, 3:4	Object-file System?	4	… for 1, 4, 2, 3, 4	-
	“Side Bias T1” 1:1, 2:2, 4:4	Side bias? → binomial tests	2	-	-
Models				**M1.0 to M1.3**	**-**
Task 2	“Size” S:2S, S:4S, 2S:4S	Discrimination of size?	4	… for 2S, 4S, 4S	… for 2S, 4S, 4S
	“Only Quantity” S+S+S:2S, S+S+S+S+S:4S	Reliance on quantity (if size provides the wrong cue)?	4	… for S+S+S, S+S+S+S+S	… for 2S, 4S
	“Only Size” S+S+S:4S	Reliance on size (if quantity provides the wrong cue)?	4	… for 4S	… for 4S
	“Irrational Bias for Larger Size” S+S:2S, 2S+2S:4S	Irrational bias for larger size or quantity of items?	4	-	… for 2S, 4S
	“Side Bias T2” S:S, 2S:2S, 4S:4S	Side bias? → binomial tests	2	-	-
Models				**M2.0, M2.1**	**M2.2, M2.3**
Task 3	“Both Dense” Dense4:Dense6	Discrimination of quantities with denser arrays?	4	… for Dense6	-
	“Both Sparse”’ Sparse4:Sparse6	Discrimination of quantities with sparser arrays?	4	… for Sparse6	-
	“Denser” Sparse4:Dense6	Discrimination of larger quantity, if denser?	4	… for Dense6	… for Sparse4
	“Sparser” Dense4:Sparse6	Discrimination of larger quantity, if sparser?	4	… for Sparse6	… for Sparse6
	“Irrational Bias for Sparser Set” Dense4:Sparse4, Dense6:Sparse6	Irrational bias for density or sparsity?	4	-	… for Sparse4, Sparse6
Models				**M3.0, M3.1**	**M3.2, M3.3**

Table 2. Examples of the trays used in each condition. Each square grid represents the trays used in the experiment (Figure 1). An isosceles triangle represents a standard (S) carrot piece (6 g of weight), a scalene triangle represents twice a standard carrot piece (2S), and a square represents four times a standard carrot piece (4S).

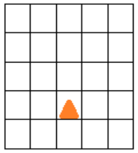
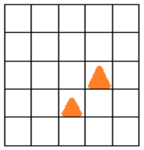
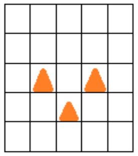
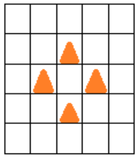
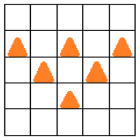
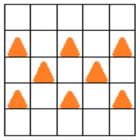
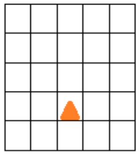
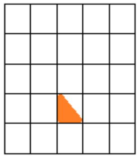
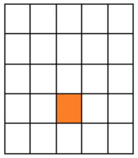
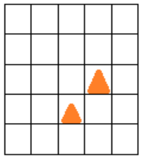
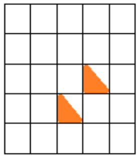
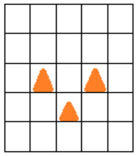
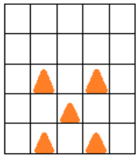
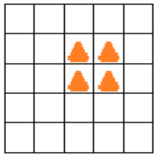
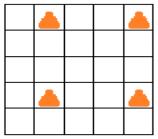
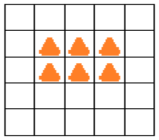
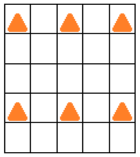
Task 1	1	2	3	4	6	8	
Quantity discrimination							
Task 2	S	2S	4S	S+S	2S+2S	S+S+S	S+S+S+S+S
Size vs Quantity							
Task 3	4 dense	4 sparse	6 dense	6 sparse			
Sparse vs Dense configurations							

Table 3. Sets of models, ordered with the smallest WAIC (Widely Applicable Information Criteria) first. The best models in each set are presented in bold, and for each model, we present the fixed effects included (apart from the intercept and an intercept by subject identity, which were included in all models), the WAIC, and the Akaike weight.

Set	**Model**	**Fixed effects included**	**WAIC**	**weight**
1	**M1.1**	**Ratio**	188.5	0.40
	M1.0	-	188.8	0.34
	M1.2	ratio, ratio*condition	189.9	0.19
	M1.3	ratio, ratio*condition, sum	191.8	0.07
2a	**M2.1**	**condition**	129.2	1.00
	M2.0	-	140.2	0.00
2b	**M2.3**	**condition**	125.0	1.00
	M2.2	-	157.3	0.00
3a	**M3.1**	**condition**	56.1	0.73
	M3.0	-	58.1	0.27
3b	**M3.2**	**-**	55.0	0.61
	M3.3	condition	55.9	0.39

Table 4. Bayesian factor values for each task, for both the number of correct choices (**Success**) and the number of choices on the right side (**Side bias**). Two-tailed Bayes factor with a beta prior of 1.

Subjects	**Task 1 Success**	**Task 1 Side bias**	**Task 2 Success**	**Task 2 Side bias**	**Task 3 Success**	**Task 3 Side bias**
Yalinga	41.55	1	31.5	0.7	0.3	0.9
Nuru	445	0.28	0.9	0.24	1.6	0.9
Nakuru	39	0.4	3.7	0.317	0.12	0.3
Max	122	0.28	126	0.21	4.1	0.3
Andrea	6360	0.28	9	0.45	0.4	0.5

CHAPTER 3

Giraffes make decisions based on statistical information

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ABSTRACT

The ability to make inferences based on statistical information has so far been tested only in animals having large brains in relation to their body size, like primates and parrots. Here we tested if giraffes (*Giraffa camelopardalis*), despite having a smaller relative brain size, can also rely on relative frequencies to predict sampling outcomes. We presented them with two transparent containers filled with different quantities of highly-liked food and less-preferred food. The experimenter covertly drew one piece of food from each container, and let the giraffe choose between the two options. In the first task, we varied the quantity and relative frequency of highly-liked and less-preferred food pieces. In the second task, we inserted a physical barrier in both containers, so giraffes only had to take into account the upper part of the container when predicting the outcome. In both tasks giraffes successfully selected the container more likely to provide the highly-liked food, also integrating physical information to correctly predict sampling information. By ruling out alternative explanations based on simpler quantity heuristics and learning processes, we showed that giraffes can make decisions based on statistical inferences.

Introduction

Reasoning about probabilities has long been considered a complex ability, traditionally ascribed only to adult humans (1–3). When reasoning about probabilities, individuals deal with a situation of uncertainty in which not all the information is available, and statistically infer which option might lead to the best possible outcome. This kind of decision making is very important in the real world, where only limited information is often available and not all possible outcomes are known with certainty (4). In the last decade, experimental evidence has shown that statistical inference is not limited to adult humans, but it emerges early on during human development. Twelve-month old infants, for instance, can predict outcomes from a sampling event and make decisions based on the comparison of relative quantities (5), whereas 4.5-month-olds can even account for the presence of physical constraints that could affect the sampling process (6). Other authors suggest that reasoning about probabilities might appear much later in development, from around 5 years of age (7,8).

The ability to make statistical inferences might be important for species other than humans, to make decisions in the face of uncertainty and/or to deal with unpredictable environments. To date, however, evidence of complex statistical skills in non-human animals (hereafter, animals) is extremely scant (9,10). One reason for that is that statistical reasoning (i.e. predicting the probability of rewards based on the relative frequencies of objects (11))can only be reliably demonstrated after ruling out alternative explanations based on simpler quantity heuristics (e.g. “select the container with a higher number of highly-liked food”, or “avoid the container with a higher number of less-preferred food” (12).

Great apes, long-tailed macaques (*Macaca fascicularis*) and keas (*Nestor notabilis*) have shown statistical reasoning, using relative frequencies of items to predict sampling events (11,13–16).

Moreover, keas could also combine information across different domains, integrating physical and social information when making statistical decisions (11), in contrast to chimpanzees that succeeded in integrating social information, but failed to integrate physical information when predicting sampling outcomes (17). In other species, evidence of statistical skills is yet missing, as individuals may have used simpler quantity heuristics to solve the task. Capuchin monkeys (*Sapajus apella*), for instance, successfully predicted sampling outcomes that could not be inferred by simply comparing the number of highly-liked items, but failed to do so when they could not simply avoid the container with a higher number of less-preferred items, thus suggesting that, at least in some contexts, capuchin monkeys use simpler quantity heuristics to make decisions (8). Similarly, it is not clear yet whether rhesus monkeys (*Macaca mulatta*), African grey parrots (*Psittacus erithacus*) and pigeons (*Columba livia*) really use quantity heuristics or relative frequencies to predict sampling outcomes, as controls for the use of quantity heuristics are usually missing (18–20); see (11).

The fact that both primates and keas show evidence of statistical reasoning suggests that statistical skills can convergently evolve in different taxa, despite differences in brain structure and neural density (11,14,15,21). Given that both primates and keas have brains with a large relative size (22,23), however, also raises the question of whether large brain sizes are a necessary prerequisite for the emergence of complex statistical skills. Here, we tested this hypothesis by studying statistical reasoning in an ungulate species, giraffes (*Giraffa camelopardalis*). Giraffes are an ideal model for this study: they perform well in different tasks of physical cognition (e.g. object permanence (24), memory (25), quantity discrimination (26)), and are characterized by high fission-fusion levels (27,28) and large dietary breadth (29) – two features that have been linked to the emergence of complex cognition (30,31) . Moreover, in contrast to primates and keas, giraffes have a relatively small brain size, with an encephalization quotient of 0.64 (32), which is quite small in comparison to the 2.48 of chimpanzees (22) or the 1.42 of keas (23). Therefore, giraffes may show complex cognitive skills as the result of specific selective pressures experienced in certain socio-ecological conditions, although they might not have especially large brains.

In this study, we followed the procedure used by previous studies on this topic (5,11,14). In Experiment 1, giraffes were presented with two transparent containers with different frequencies of highly liked (i.e. carrots) and less-preferred food (i.e. zucchini). The experimenter simultaneously took one piece from each container with his hands, without the giraffe seeing which piece was actually taken (Figure 1). The giraffe could then select one of the two outcomes by touching one of the two closed fists. Task 2 was identical, except that the two food containers were divided in two parts by a physical barrier, so that only the food in the upper part of the containers was accessible to the experimenter and had to be accounted for while making decisions (see video in Supplementary Information). We hypothesized that, if large brains are necessary for the emergence of statistical skills, giraffes would not be able to make statistical inferences and combine information across different domains.

RESULTS

In the first experimental task, we tested if giraffes were able to make decisions based on the relative frequencies of food items in the containers. We included three different conditions aimed to rule out the use of simpler quantitative heuristics (Table 1). In condition 1, subjects were expected to preferentially choose the container with 100 carrots + 20 zucchinis over the one with 20 carrots + 100 zucchinis if they were comparing relative frequencies. In condition 2, we expected that subjects would prefer the container with 20 carrots + 4 zucchinis over the one with 20 carrots + 100 zucchinis. In Condition 3, subjects were expected to choose more the container with 57 carrots + 63 zucchinis over the one with 3 carrots + 63 zucchinis. All study subjects (N=4) could solve the three conditions of the first task already in the first session (i.e., 17 out of 20 trials selecting the expected container), except for one subject in condition 2 and one in condition 3, who required two sessions to solve the condition.

The second experimental task was harder to master, because subjects had to also integrate physical information about the barrier internally dividing the container, in order to correctly predict sampling information (Table 1). Depending on the condition, we expected subjects to preferentially choose the container with 20 carrots + 4 zucchinis above the partition, and 20 carrots + 36 zucchinis below it (over the one with 20 carrots + 20 zucchinis above the partition, and 20 carrots + 20 zucchinis below it), and the one with 20 carrots + 20 zucchinis above the partition, and 20 carrots + 20 zucchinis below it (over the one with 4 carrots + 20 zucchinis above the partition, and 36 carrots + 20 zucchinis below it). In this task, three of the four subjects failed to pass the first condition after four sessions (Table 1). Only one subject passed the first condition (in the second session), and was therefore tested also in the second condition, which was solved in the first session.

Finally, we administered three control conditions to rule out that giraffes solved the task by using information other than relative frequencies (i.e. olfactory cues, inadvertent visual cues by the experimenter when sampling or holding the food, absolute quantities visible in the upper part of the containers; Table 1). In the first condition, giraffes could only rely on olfactory cues (but not on relative frequencies) to locate the carrot. In the second condition, giraffes relying on relative frequencies (rather than inadvertent visual cues by the experimenter) should have chosen the hand with the zucchini sampled from the container with a higher relative frequency of carrots. In the third condition, giraffes relying on relative frequencies (rather than visible absolute quantities) should have chosen the carrot sampled from the container with a higher relative frequency of carrots, although both containers were first presented with an equal number of carrots each.

We used Generalized Linear Mixed Models to assess whether the probability of making the correct choice (i.e. choosing the container more likely to provide the preferred food) differed across conditions and trials, when controlling for the side chosen. The full model significantly differed from the null one (GLMM: $\chi^2 = 35.96$, $df = 15$, $p < 0.001$). Condition had a significant effect as main term on the probability to choose the correct container ($p < 0.001$). In particular, with regards to the experimental conditions, subjects performed significantly worse in the first condition of the second task, than in the first and third conditions of the first task (vs. condition 1: $p = 0.046$; condition 3: $p = 0.033$). With regards to control conditions, subjects performed significantly worse in the first control condition (i.e. olfactory cues) than in most of the other conditions (vs. conditions 1, 2 and 3 of the first task: $p = 0.005$, $p = 0.011$ and $p = 0.004$, respectively; second control condition, i.e. inadvertent visual cues: $p = 0.025$). The second and third control conditions (i.e. inadvertent visual cues and visible absolute quantities, respectively), in contrast, did not significantly differ from any experimental condition (all $p > 0.005$). Finally, neither trial number ($p = 0.910$) nor side chosen ($p = 0.315$) had a significant effect on the response, suggesting no important learning effects and side biases in our study (Table 2).

DISCUSSION

In this study, giraffes could reliably make statistical inferences based on the relative frequencies of two different food types. Like chimpanzees and keas (11,14), giraffes spontaneously selected the container more likely to provide the preferred food in the experimental conditions, even when subjects could not rely on simpler quantity heuristics (e.g. because the correct container did not contain a higher number of highly-liked food, and the wrong container did not contain a higher number of less-preferred food). The relative brain size of giraffes is small, and smaller than the one of keas and primates (22,23,32), the only species for which statistical reasoning has been shown so far (11). Therefore, these results suggest that large relative brain sizes are not a necessary prerequisite for the evolution of complex statistical skills, and that the ability to make statistical inferences may be widespread in the animal kingdom.

Giraffes were surprisingly fast at solving the first experimental task, requiring on average 1.2 sessions to reliably select the correct container in at least 17 out of 20 trials. In contrast, keas tested with the same procedure required an average of 3.9 sessions, and up to 11 sessions, to solve the task (11). Although it is possible that the specific socio-ecological pressures faced by giraffes (27,28) might be linked to the evolution of complex cognitive skills, including enhanced statistical abilities, it is also possible that the use of tokens might have made the procedure more complex for keas (33); but see (34). Compared to great apes and long-tailed macaques, giraffes showed a similar performance, but giraffes were administered more trials than the other species (e.g. 23 trials on average in the first task; 12,13). Although it is possible that this might have facilitated performance in giraffes, it should be noted that we detected no learning effects in our study.

In the second task, only one giraffe could successfully integrate physical information when making statistical inferences, suggesting that the physical barrier greatly increased the difficulty of the task. In contrast to the first task, keas appeared to be more proficient than giraffes, with five out of six individuals solving the task after an average of only 1.9 sessions (11). Given that this task requires the ability to integrate information across multiple cognitive domains (11), the lower performance of giraffes in this task might suggest that, whereas they can reliably make inferences based on the relative frequencies of objects, their ability to integrate information across cognitive domains may be more limited. However, one should also note that, in contrast to keas, our study subjects did not go through a training phase to acquire knowledge about the physical properties of the barriers in the container. Future studies should therefore explore whether giraffes really have a limited ability to integrate information across domains. Moreover, the fact that one individual reliably solved both conditions of the second task, without previous training and after no more than two sessions, suggests that at least some individuals may be able to spontaneously integrate information from different domains to make decisions under uncertainty.

Finally, several control conditions confirmed that giraffes really made their choices based on the relative frequencies of food in the containers, and not on other information. When giraffes could only rely on olfactory cues to locate the carrot (but not on relative frequencies), their performance significantly decreased, suggesting that the use of olfactory cues could not explain their successful performance in the experimental conditions. Moreover, when we sampled zucchini from the container with a higher relative frequency of carrots, giraffes still preferentially selected the container with a higher relative frequency of carrots. Finally, when an equal quantity of carrots was visible in both containers at the beginning of the trial, and then covered with zucchini, giraffes could still successfully solve the task, and their performance did not decrease from the one shown in the other experimental conditions. Overall, these results therefore suggest that the use of olfactory cues, inadvertent visual cues by the experimenter and the amount of visible absolute food quantities cannot explain the successful performance of the giraffes in the experimental conditions.

In evolutionary terms, statistical abilities might provide crucial fitness benefits to individuals when making inferences in a situation of uncertainty, and it should, therefore, not be surprising if these abilities are widespread across animal taxa. In the future, it would be interesting to test more species with these experimental procedures, and use a comparative approach to assess whether the specific socio-ecological challenges faced by different species reliably predict the distribution of statistical skills across animals. Very likely, statistical skills may be present in several other taxa.

METHODS

Ethics. This research was approved and supervised by the staff of the Zoo of Barcelona. This study strictly adhered to the legal guidelines and regulations of the country in which it was conducted (Spain), and in accordance to the ARRIVE guidelines (35). The study was considered a form of enrichment for the giraffes and no further permits were required.

Subjects. Our study subjects were two male and two female giraffes (*Giraffa camelopardalis*) housed at the zoo of Barcelona. All study subjects were fed a regular diet of fruit and vegetables, and had limited experience with experimental tasks (19–21). Participants were never food or water deprived during this study, and participation was on a completely voluntary basis. The individuals could approach the experimenter at any time to participate in the study.

Experimental procedures. The procedure consisted of one food-preference task, two experimental tasks (for a total of 5 conditions), and three control conditions. In the food-preference task, we assessed individual food preferences by presenting each subject with two out-of-reach identical transparent containers, one with 120 pieces of zucchini and the other one with 120 pieces of carrots, all of the same size and form. We selected zucchini and carrots based on previous observations of the same subjects during a pilot study. In full view of the subject, the experimenter simultaneously put one hand in each of the two containers, grabbed one piece of food with each hand (making sure that the choice was not visible), and simultaneously presented the closed fists to the subject to make a choice. Subjects were tested in 20 trials and moved to the experimental tasks only if selecting the preferred food (i.e. carrots) in at least 17 trials. All individuals passed the criterion in the preference test.

The two experimental tasks largely followed the procedures used by Bastos and Taylor (11), but we reduced all training phases to minimize learning effects. The first experimental task consisted of three conditions, aimed to assess whether subjects could reliably select the preferred food based on the relative frequencies of the two food types, rather than on the absolute quantities presented (see Figure 2). In the first condition, the procedure was identical to the food-preference task, but the two containers had 20 carrots + 100 zucchinis, and 100 carrots + 20 zucchinis, respectively. In the second condition, the two containers had 20 carrots + 100 zucchinis, and 20 carrots + 4 zucchinis. In this condition, we predicted that giraffes would preferentially select the second container if comparing relative frequencies, but show no preference if comparing absolute quantities of the preferred food. In the third condition, the two containers had 57 carrots + 63 zucchinis, and 3 carrots + 63 zucchinis. As above, we predicted that giraffes would preferentially select the first container if comparing relative frequencies, but show no preference if comparing absolute quantities of the less-preferred food. In each condition, subjects could obtain the preferred food by comparing relative frequencies and selecting the container more likely to provide carrots (i.e. 100 carrots + 20 zucchinis, 20 carrots + 4 zucchinis, and 57 carrots + 63 zucchinis, respectively). If they did so in at least 17 out of 20 consecutive trials, they proceeded to the next condition, otherwise they received another session of the same condition, up to a maximum of 4 sessions (see Supplementary Information for a video example).

In the second experimental task, we tested whether giraffes can integrate physical information when making statistical inferences. We followed the same procedure as in the previous task. In the first condition, both containers had 40 carrots + 40 zucchinis. However, both containers were internally divided by a horizontal partition, so that only the food rewards above the partition could be sampled by the experimenter, and giraffes had to make their decision by only assessing the content in the upper part of the containers. Following Bastos and Taylor (11), we presented individuals with a container with 20 carrots + 20 zucchinis above the partition, and 20 carrots + 20 zucchinis below the partition, and with a second container with 20 carrots + 4 zucchinis above the partition, and 20 carrots + 36 zucchinis below it. We predicted that, if giraffes could also use their understanding of physical barriers when making statistical inferences, they should have preferentially selected the second container. The second condition was identical, but the number of carrots and zucchinis was inverted. In all tasks and conditions, we pseudo-randomized and counterbalanced the side of each container across trials. In both experiments, the experimenter always drew from the containers a piece of food belonging to the majority food type, as in previous studies (11,14)

Finally, we ran three control conditions to rule out alternative explanations based on simpler quantity heuristics and learning processes. First, we ran a condition to determine if giraffes relied on olfactory cues rather than relative frequencies to locate carrots. The procedure was similar to the food-preference task, but subjects did not see the containers from which food was sampled from. They had to choose between the two closed fists without watching which piece of food the experimenter held in each hand. Subjects were expected to be successful in this condition (i.e. selecting the hand with the carrot) if they relied on olfactory cues to locate the food, but not if they relied on their vision, as they could not see which piece of food the experimenter had sampled. Second, we ran a condition to rule out the possibility that the experimenter inadvertently provided visual cues to the giraffes when sampling the food and/or holding the food in the hands. We followed the same procedure as in the first condition of the first experimental task, but the experimenter always retrieved from the containers the least probable piece of food for that population. Subjects were expected to be successful in this condition (i.e. selecting the food sampled from the container with a higher relative frequency of carrots, which in this case were zucchini) if they relied on the relative frequencies of food, but not if they relied on inadvertent visual cues provided by the experimenter during the sampling procedure (in which case, subjects should have preferentially selected the container with a lower relative frequency of carrots, from which carrots were sampled). Third, we ran a condition to determine if giraffes relied on the overall absolute quantity of visible preferred food (as this food was partially covering the less-preferred food, and could have been visually more salient) rather than relative frequencies of the food in the containers. We followed the same procedure as in the second condition of the first experimental task, but the experimenter first showed the containers with only the carrots (having identical absolute quantities), and then added the zucchini in both containers, in full view of the subject. Subjects were expected to be successful in this condition (i.e. selecting the hand with the carrot sampled from the container with a higher relative frequency of carrots) if they relied on the relative frequencies of food, but not if they relied on the absolute quantities visible in the upper part of the containers (in which case, performance should have dropped at chance levels). For each of the three control conditions, we respectively ran 12 trials, 20 trials and 12 trials for each individual. We ran less trials for the olfactory condition because we had already tested this in previous experiments already with negative results (24). In the third control condition, we ran less trials due to time constraints.

Statistical analyses. We assessed individual performance in each experimental condition as the number of trials in which the subject made the correct choice (i.e. selecting the carrot in the first control condition C1; selecting the zucchini sampled from the container with a higher relative frequency of carrots in the second control condition C2; and selecting the carrot sampled from the container with a higher relative frequency of carrots in all the other conditions; see Table 1). To compare performance across conditions, and assess possible learning effects, we further run a generalized linear mixed model (36) in R (R Core Team, version 4.0.1), using the "glmmTMB" package (37). We used a binomial distribution to assess whether the probability to make the correct choice varied across trials and conditions, when controlling for the side chosen, including subject identity as random factor. Trial number and condition were first entered in interaction as test predictors, and then only entered as main effects as the interaction term was not significant. This final model was then compared to a null model which only included controls and random effects, using likelihood ratio tests (38). In case of significant categorical test predictors (i.e. condition), we ran post-hoc tests with Tukey corrections to compare the different levels of the predictor. We detected no problems when checking residual diagnostics and overdispersion using the “DHARMa” package (39).We further checked multicollinearity with the “performance” package (40) , which was no issue (maximum variance inflation factors = 1.40 (41)).

Data availability. Our dataset and code are available in Supplementary Information.

Table 1. Performance of the study subjects in all tasks and conditions (nominators represent the number of correct choices out of the total trials of each session, i.e. the number of trials in which subjects selected the carrot or, in C2, the food sampled from the container with a higher relative frequency of carrots). Below each condition (C) we report the different quantities presented to the animal (one line for each container: the first number of each line indicates the number of preferred food pieces, and the second one the number of less preferred food pieces). For task two we also report (in parenthesis) the number of food pieces below the partition.

Subjects	**Sex**	**Task 1**			**Task 2**		**Controls**		
		C1	**C2**	**C3**	**C1**	**C2**	**C1**	**C2**	**C3**
		100+20 **20+100**	**20+100** **20+4**	**3+63** **57+63**	**20+4 (20+36)** **20+20 (20+20)**	**20+20 (20+20)** **4+20 (36+20)**	**-**	**100+20** **20+100**	**20+100** **20+4**
Nakuru	M	17/20	18/20	18/20	9/20 + 15/20 + 11/20 + 2/20	-	8/12	13/20	11/12
Njano	M	17/20	17/20	3/20 + 17/20	10/20 + 2/20 + 1/20 + 8/20	-	7/12	16/20	10/12
Nuru	F	17/20	4/20 + 17/20	18/20	5/20 + 17/20	18/20	7/12	17/20	9/12
Yalinga	F	17/20	17/20	17/20	3/20 + 4/20 + 7/20 + 2/20	-	4/12	17/20	12/12

Table 2. Results of the full model run, with estimates, standard errors (SE), confidence intervals (CIs) and p values for test predictors (significant values are marked with an asterisk).

Predictors and controls	**Estimate**	**SE**	**2.5% to 97.5% CIs**	***p***
Intercept	1.86	0.35	1.17 to 2.56	-
Task 1, Condition 2	-0.17	0.42	-1.00 to 0.66	< .001*
Task 1, Condition 3	0.00	0.43	-0.85 to 0.85	
Task 2, Condition 1	-1.15	0.37	-1.88 to -0.41	
Task 2, Condition 2	0.46	0.81	-1.22 to 2.05	
Control condition 1	-1.62	0.43	-2.46 to -0.77	
Control condition 2	-0.43	0.41	-1.24 to 0.39	
Control condition 3	0.03	0.51	-0.98 to 1.04	
Trial number	0.00	0.01	-0.02 to 0.02	0.910
Side chosen	-0.20	0.20	-0.60 to 0.19	0.315

Figure 1. An example of a trial in Experiment 1, condition 2. Picture 1, the experimenter presents the two containers to the subject. Picture 2, the experimenter simultaneously takes one food piece from each container, without the giraffe seeing which piece is taken. Picture 3, the giraffe selects one of the two outcomes by touching it with the tongue.

Figure 2. A picture with the stimuli used in each condition of Experiment 1 (from left to right: condition 1, condition 2 and condition 3).

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AUTHOR CONTRIBUTIONS

A.L.C. conceived and designed the study, collected the data, participated in the data analysis and drafted the manuscript; M.C. participated in designing the study, coordinated the study and helped drafting the manuscript. F.A. designed the study, carried out the statistical analyses and helped drafting the manuscript. All authors gave their final approval for publication and agree to be held accountable for the work performed therein.

COMPETING INTERESTS

The authors declare no competing interests.

DECLARATION

The person appearing in photos and videos is myself, Alvaro Lopez Caicoya, first author of the manuscript. I consent the videos and photos included in the manuscript to appear at any form in the journal Scientific reports.

CHAPTER 4

Comparative cognition in three understudied ungulate species: European bison, forest buffalos and giraffes

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ABSTRACT

Background

Comparative cognition has historically focused on a few taxa such as primates, birds or rodents. However, a broader perspective is essential to understand how different selective pressures affect cognition in different taxa, as more recently shown in several studies. Here we present the same battery of cognitive tasks to two understudied ungulate species with different socio-ecological characteristics, European bison (*Bison bonasus*) and forest buffalos (*Syncerus caffer nanus*), and we compare their performance to previous findings in giraffes (*Giraffa camelopardalis).* We presented subjects with an Object permanence task, Memory tasks with 30 and 60 second delays, two inference tasks based on acoustic cues (i.e. Acoustic inference tasks) and a control task to check for the use of olfactory cues (i.e. Olfactory task).

Results

Overall, giraffes outperformed bison and buffalos, and bison outperformed buffalos (that performed at chance level). All species performed better in the Object permanence task than in the Memory tasks and one of the Acoustic inference tasks (which they likely solved by relying on stimulus enhancement). Giraffes performed better than buffalos in the Shake full Acoustic inference task, but worse than bison and buffalos in the Shake empty Acoustic inference task.

Conclusions

In sum, our results are in line with the hypothesis that specific socio-ecological characteristics played a crucial role in the evolution of cognition, and that higher fission-fusion levels and larger dietary breadth are linked to higher cognitive skills. This study shows that ungulates may be an excellent model to test evolutionary hypotheses on the emergence of cognition.

Keywords

ungulate, object permanence, acoustic cues, cognition, bovids, bison, buffalo, giraffe, test battery, memory

BACKGROUND

Throughout the history of comparative cognition, there has been a general bias to focus on a few specific species [1,2], although the inclusion of more diverse taxa can be essential to test specific hypotheses [3,4]. Such a bias in the selection of study species has often reflected practical considerations (e.g. availability of subjects, maintenance costs) rather than clear research needs. In the 1950s, for example, few species other than rodents were tested in experimental studies [5]. At the end of the last century, however, the focus has largely shifted on other taxa like primates and corvids [1]. In more recent years, the number of species studied and the research methods used has steadily increased, opening up exciting new possibilities for research in comparative psychology and animal cognition research [6–12]. Despite these recent advances, there is still a long way to go to ensure a fair representation of different taxa in comparative animal cognition research [13].

First of all, the inclusion of species from different taxa can provide important information on the limits of specific evolutionary hypotheses. The fission-fusion hypothesis, for example, predicts that species which frequently split and merge in subgroups of variable size and composition may face enhanced cognitive challenges that might have led to the evolution of specific cognitive skills, like memory, inhibition or analogical skills [14]. However, this hypothesis has mainly been tested in primates, by comparing cognitive performance in a series of species with different degrees of fission-fusion dynamics [15,16]. Is the fission-fusion hypothesis only valid for primates, or can we extend it to other taxa which also show a similar variation in social dynamics? Including other taxa is therefore a powerful tool to test the limits of specific evolutionary hypotheses and understand whether different selective pressures are at work in different taxa.

Moreover, the study of several species and taxa in cognitive test batteries might provide us with valuable information on how the mind is structured. For example, it has long been debated whether the mind consists of independently evolving modules or if there is a general factor explaining much of the variation in performance observed across different cognitive domains [17,18]. Several approaches can be used to address this question, and one of these includes comparing the performance of multiple species across different cognitive domains using comparable batteries of cognitive tasks [13]. If some species perform better than others in some domains, but not in all of them, it means that the mind is at least partially modular, with domain-specific cognitive skills probably undergoing different evolutionary pressures in response to specific socio-ecological challenges. Therefore, comparing the performance of several species across several domains allows assessing the extent to which the mind is modular, and also allows indirectly testing which different evolutionary pressures might have selected for specific cognitive skills [19–21].

Ungulates are one of many neglected taxa in comparative cognition, although they are an ideal model to test cognitive skills from a comparative perspective, as demonstrated by several recent studies [22–31]. Although most of these studies have focused on domesticated ungulate species (but see [27,32]), ungulates also include many non-domesticated species with an impressive variety of socio-ecological characteristics [33], allowing the reliable contrast of different evolutionary hypotheses. Moreover, there are very few studies that have explored the link between cognition and socio-ecological characteristics in ungulates, and all have used neuroanatomical measures as cognitive proxies [33–35]. These studies are promising, and suggest inter-specific differences in cognitive skills: large brains, for instance, are found in species with higher sociality and mixed habitats, while relative neocortex size is usually associated with social (but not ecological) factors [33]. However, neuroanatomical proxies cannot replace direct comparisons of actual cognitive performance [13]. Finally, ungulates are economically crucial for humans and some laboratories have started to study farm animal cognition to improve their welfare, demonstrating how changes in management or facilities can improve animal welfare and economic return [28,36–44].

In this study, we aimed to test two ungulate species that might prove a valid model to test evolutionary hypotheses on the emergence of cognitive skills in this taxon: European bison (*Bison bonasus*) and forest buffalos (*Syncerus caffer nanus*). These species belong to the same family (Bovidae) and tribe (Bovine), and are therefore phylogenetically very close, although they have very different socio-ecological characteristics. European bison, for example, live in East European forests [45], and although they have physiological adaptations to grazing, they also often browse, so that they are generally considered as mixed feeders [46,47]. European bison have not been domesticated, and live in herds of about 30 individuals, characterized by high levels of fission-fusion dynamics [48]. In contrast, forest buffalos are a subspecies of the African buffalo that live in dense rainforests in Africa, and feed primarily on grasses [49]. Although high levels of fission-fusion dynamics have been observed in another African subspecies (*Syncerus caffer caffer*), forest buffalo groups are rather cohesive [50], living in small groups of around 15 individuals with stable group size and composition [51,52]. Moreover, we compared the performance of these two species to giraffes (*Giraffa camelopardalis)*, which we had previously tested with the same experimental protocol (see below [27]). Giraffes are browsers with a remarkable dietary breadth [53] that live in open habitats, in fission-fusion societies [27]. By comparing European bison, forest buffalos and giraffes, it is therefore possible to assess whether socio-ecological characteristics (i.e. dietary breadth, fission-fusion dynamics [14,33,54]) predict the distribution of certain cognitive skills in ungulates (see below for detailed predictions)

We conducted several tasks in physical cognition on these species, to assess their understanding of objects. Indeed, the ability to segment the world into discrete objects that exist independently of us through space and time is one of the most fundamental conceptual structures, and therefore a widely studied area in comparative cognition [55]. By studying how animals understand objects, for instance, we can gain insight into their ability to deal with several daily physical and social challenges [16]. Object permanence, for example, is a cognitive ability that allows individuals to understand that objects continue to exist even when they are out of sight [56]. This ability is widespread across taxa, and appears to have deep evolutionary roots [56]. In a typical Object permanence task, one of several containers is baited, and once the food is out of view, the subject has to retrieve the food by selecting the container under which the food had been hidden (see [56]). Variations of these tasks include the introduction of a delay between the baiting procedure and the moment in which subjects can retrieve the food, to test subjects' memory [57]. Another variation of this task provides subjects with an acoustic cue instead of a visual one to locate the baited container [58]. In this task, subjects are presented with two containers, only one having been baited. If subjects understand the causal connection between objects and the noise produced when they move, they should infer that (i) when a container is shaken and produces noise, it likely contains the reward, but (ii) when a container is shaken and produces no noise, the non-shaken container likely contains the reward [22,58–61].

In this study, we tested European bison and forest buffalos in a series of tasks that were previously conducted in giraffes [27]. These tasks included an Object permanence task, two Memory tasks with 30 and 60 second delays (see Figure 1 and Figure 2), two Acoustic inference tasks (in which either the container with food rewards or the one without food rewards were shaken), and an Olfactory task (to control that individuals do not use olfactory cues to locate the food). Given that fission-fusion dynamics (e.g. [14]) and dietary breadth (e.g. [7]) have been linked to enhanced cognitive skills (including memory and inferential skills), we predicted that giraffes (forming fission-fusion groups and having a large dietary breadth) would show the best performance in the Memory and Acoustic inference tasks, followed by European bison (which also show a high degree of fission-fusion dynamics but shorter dietary breadth) and lastly by forest buffalos (which live in more cohesive groups and also have shorter dietary breadth). Object permanence, instead, is a rather basic cognitive ability, which appears to emerge relatively early through development and is widespread across animal taxa [56]. Therefore, we predicted that all study species would perform similarly well in the Object permanence task.

RESULTS

We used a Bayesian approach to assess how performance varied across species depending on the tasks (i.e. Object permanence task, Memory tasks with 30 and 60 second delays, Shake full and Shake empty task, and Olfactory task), whether the position of the food affected performance (i.e. whether individuals showed a side bias, preferentially selecting one side over the other), and whether there was a learning effect (i.e. performance increased across trials). For this reason, we compared a null intercept-only model (M0) to models obtained by adding the following fixed effects: tasks (M1), tasks and species (M2), the 2-way interaction of tasks with species, including their main effects (M3), and the 2-way interactions of tasks with species and food side with species, including their main effects, and trial number (M4; see Table 1).

When comparing models M0 to M4, M4 had the lowest WAIC and the highest model weight (see Table 1). Overall, giraffes were more likely to select the baited container (see Figure 3), as compared to bison (β = 0.72, 89% Prediction Interval [PI] = 0.22 to 1.22**)** and buffalos (β = 1.20, 89% PI = 0.69 to 1.69), while bison were more likely to make the correct choice than buffalos (β = 0.55, 89% PI = 0.05 to 1.08). As compared to the Object permanence task, performance in all three species was lower in both Memory tasks (with 30 second delay: β = −0.52, 89% PI = −1.00 to -0.04; with 60-second delay: β = −0.60, 89% PI = −1.06 to -0.12), in the Shake empty task (β = −0.54, 89% PI = −1.00 to -0.04) and also in the Olfactory task (β = −0.67, 89% PI = −1.14 to -0.19). However, such effect was especially strong for giraffes in the Shake empty task (β = −1.67, 89% PI = −2.36 to -1.01). Giraffes were also the only species performing better in the Shake full than in the Object permanence task (β = 0.70, 89% PI = 0.05 to 1.40). Finally, also the position of the food predicted individuals' performance, but this effect was weaker in giraffes as compared to both bison (β = -0.89, 89% PI = -1.34 to -0.44) and buffalos (β = −1.43, 89% PI = −1.90 to -0.97), and also weaker in bison than buffalos (β = −0.50, 89% PI = −0.96 to -0.03). In contrast, we found no clear effect of trial number, suggesting no increase in performance across trials.

Table 1.

Model	**Fixed effects included**	**WAIC**	**Weight**
M4	task*species + side*species + trial	1488.7	1.00
M3	task*species	1538.1	0
M2	task + species	1561.3	0
M1	task	1561.9	0
M0	-	1594.7	0

List of the models run, ordered with the smallest WAIC (Widely Applicable Information Criteria) and the highest Akaike weight first. For each model, we further present the fixed effects included (main effects were always included in the interactions). Intercept and intercept by subject identity were included in all models. The best model is the first one.

DISCUSSION

Our study showed important differences in the performance of three ungulate species in a series of tasks on the understanding of objects. In line with our predictions, giraffes showed overall the best performance, followed by European bison and lastly forest buffalos. For all species, performance was highest in the Object permanence task (except for giraffes, that performed better in the Shake full task), which was likely the easiest task, and lower in the two Memory tasks and in the Shake empty task. Importantly, no species relied on olfactory cues to solve the tasks. In contrast to the other species, giraffes performed better in the Object permanence task than in the Shake empty task, but worse than in the Shake full task. Finally, our results showed an effect of food position on individuals' performance (i.e. side bias), which was strongest in buffalos and intermediate in bison.

Overall, our study provided support to our prediction that the species socio-ecological characteristics predict their cognitive performance, since giraffes showed overall the best performance, followed by bison and lastly by buffalos (see Figure 3). Giraffes are characterized by large dietary breadth (which has been compared to the dietary breadth of chimpanzees, as both species feed on around 100 different plant species), and high levels of fission-fusion dynamics [62–66]. European bison, in contrast, show high levels of fission-fusion dynamics but short dietary breadth [48], while forest buffalos live in rather cohesive groups and also have short dietary breadth [50]. Therefore, our results would suggest that dietary breadth and/or fission-fusion levels may both contribute to the enhancement of cognitive skills, in line with studies in taxa that have higher encephalization rate (e.g. [15][7]).

However, these results are only preliminary. To confirm them, we would first need to include (i) individuals from more groups, to ensure that our results are independent of the study site, and (ii) larger samples, to better account for inter-individual differences and the possible effect of factors like sex, age or personality [67]. Our bison sample, for instance, only included females, while none of the study species included young individuals. Moreover, we only tested one study group for species (except for giraffes, which were tested in two different zoos). In the future, however, it would be important to include individuals from more groups, as inter-group differences are another important source of variation in the animal kingdom [68]. Therefore, although our results can be easily explained by inter-specific differences in socio-ecological factors, it is not possible to rule out other explanations, especially with our small sample size. Furthermore, we would need to include more species with a wider variety of socio-ecological characteristics (e.g. different predatory pressure, different type of habitat) that might also be linked to inter-specific variation in cognitive skills [33,69]. Ideally, one should also test a wider range of cognitive skills, as some socio-ecological challenges may be linked to the enhancement of specific cognitive skills. Fission-fusion levels, for instance, have been originally proposed to predict an increase in specific skills, like inhibition and analogical skills, and not to an overall enhancement of cognitive abilities [14]. Testing more cognitive skills would also be essential to understand the extent to which the mind is modular. In this study, all species generally performed better in the Object permanence task than in the other tasks. Therefore, it is not possible to make any inference on intra-specific variation across cognitive domains [17,18], unless data on more cognitive skills are collected.

Among the study species, buffalos showed the lowest performance, being close to chance levels in all tasks (Fig. 3). Such low performance may be explained by the lack of cognitive skills to solve these tasks, but it may also be due to other reasons, like low motivation or attention during the experiments. To control for that, all species had to pass a habituation phase before being tested (see Methods). This phase ensured that all study subjects (i) were motivated to participate (i.e. they approached the experimenter as soon as he entered in the facilities, and they retrieved all the food during the habituation trials), (ii) were attentive during the experimental procedures (i.e. they observed the experimenter during the baiting procedure) and (iii) understood the basic set-up. Also during the experimental phase, buffalos promptly approached the experimenter when testing started, observed the experimenter during the baiting, and quickly ate the food when choosing the correct side. Furthermore, the average number of sessions (days with experimental trials) required was similar for all the species, subjects required on average 10.1 (±2.5 SD) sessions to complete the tasks (giraffes: 9.3 ± 2.25 SD; bison: 10.4 ± 2.7 SD; buffalos: 10.8 ± 3 SD). Therefore, we doubt that lack of motivation or lack of attention can explain the inter-specific differences evidenced by our results. Future studies with more individuals should explore whether different set-ups might lead do different performance in this species, as even small procedural changes can importantly affect performance in cognitive tasks [70,71].

In line with their low performance, buffalos were also more likely to develop side biases, as the position of the food reward had a stronger effect on the choices they made. It is possible that side biases emerged through trials in this species as a response to the difficulty of the tasks, but also that they were the reason why the subjects failed in the tasks. In the first two trials of each task, most subjects showed no side bias (i.e. two subjects selected the right and left container 6 times each, one selected the left container 8 times and the right one 4 times), while two subjects showed a clear initial preference for the left container (which they selected 10/12 times). Through time, however, even the subjects initially showing no side bias developed a preference for one side. Future studies should better assess the tasks triggering the emergence of side biases, and the evolutionary role that these biases play in different species [13,72].

In the Acoustic inference tasks, giraffes responded differently from bison and buffalos. In particular, giraffes located the baited container in both tasks by reliably choosing the container shaken by the experimenter, regardless of the sound it produced (i.e. likely relying on stimulus enhancement). This turned out in a high number of correct responses in the Shake full task, but in a low number of correct responses in the Shake empty one (see Figure 3). These results suggest that giraffes might be better than the other study species at attending to humans to locate food. This might depend on the different relationship that giraffes might have with humans at the zoo, although the care given by the keepers to the study subjects was very similar across all study species, and all individuals had undergone the same habituation to the experimenter and the setup. In the future, inter-specific comparisons may benefit from further inclusion of behavioural observations (e.g. to assess personality traits and their effect on cognitive performance) and direct measures of individual reactions to humans, which may also predict cognitive performance [58]. In contrast, these results cannot be explained in terms of giraffes having a better ability to perceive acoustic cues. In the Shake empty task, giraffes performed worse than both other species, suggesting that they relied on the movement of the containers (i.e. stimulus enhancement) rather than on the noise caused by the shaking (i.e. causality), in order to make their choice. If movement (rather than sound) was the criterion that giraffes used to select a container in these tasks, it seems very unlikely that inter-specific differences in the perception of sounds might explain our results. Deeper knowledge about differences in the ability to understand these cues or other human cues could improve the welfare and management of these species in zoos and other facilities.

CONCLUSION

Overall this study confirms that ungulates may be an excellent model to test evolutionary hypotheses on the emergence of cognition, complementary to the studies in birds or primates. Despite only including captive individuals, our study revealed important inter-specific differences, suggesting that socio-ecological challenges mainly work in an evolutionary time frame. In the future, it would be necessary to (i) include more ungulate species to confirm these results and contrast more evolutionary hypotheses; (ii) test more individuals to have more robust results and better control for inter-individual variation in performance (e.g. sex, age, rank and personality); and (iii) use larger test batteries to assess a wider range of ungulate cognitive skills (e.g. [73]), and thus contribute to filling the current gaps in our understanding of cognitive evolution.

METHODS

Aim of the study

We tested three phylogenetically close species in a battery of tasks that measured different cognitive skills (i.e. object permanence, memory and inference skills). We aimed to test whether current evolutionary hypothesis on the link between cognition and socio-ecology (i.e. dietary breadth and fission-fusion) can also explain the distribution of these skills across species with a relatively small encephalization quotient.

Subjects

We tested five female European bison ranging from 6 to 30 years of age, and two male and three female forest buffalos ranging from 5 to 14 years of age, all housed at the Barcelona zoo, in Spain. Giraffes had already been tested by Caicoya and colleagues [27], and included 6 individuals from 1 to 21 years of age, housed at the zoos of Barcelona, Spain, and Leipzig, Germany (see Table 2). Each study group was housed in enclosures with different size (i.e. giraffes in Barcelona 1.580 m^2, giraffes in Leipzig 12.260 m^2, buffalos in Barcelona 835 m^2 and bison in Barcelona 617 m^2). In each species, individuals were socially housed with their conspecifics (i.e. social group size for giraffes in Barcelona: N=3, in Leipzig: N=7, for buffalos: N=5, for bison: N=5). They were all fed on a similar diet based on dry hay, fruit and vegetables. None of the study subjects had previous experience with experimental tasks, and none of them was ever food or water deprived.

Table 2.

Subjects participating in the study.

Species	Name	Sex	Age (years)	Zoo	Rearing history
Forest buffalos (*Syncerus caffer nanus*)	Suza	F	11	Barcelona	Parent
	Joan	M	6	Barcelona	Parent
	Xufa	F	14	Barcelona	Parent
	Canela	F	5	Barcelona	Parent
	Albert	M	14	Barcelona	Parent
European bison (*Bison bonasus*)	Estrella	F	8	Barcelona	Parent
	Verde	F	6	Barcelona	Parent
	Estaca	F	30	Barcelona	Parent
	Espiga	F	14	Barcelona	Parent
	Elipse	F	13	Barcelona	Parent
Giraffes (*Giraffa camelopardalis rothschildi*)	Nuru	F	8	Barcelona	Parent
	Yalinga	F	13	Barcelona	Parent
	Nakuru	M	1	Barcelona	Parent
	Max	M	21	Leipzig	Nursery
	Ashanti	F	16	Leipzig	Mother
	Andrea	F	9	Leipzig	Parent

All subjects were born in captivity

Procedures

The experimenter approached the fence of the enclosure from a place only accessible to zoo workers, and waited until one subject approached him. Individuals were always tested in the same area of their enclosure. The first animal approaching the experimenter was tested first, until completion of all the tasks and trials. When more individuals simultaneously approached the experimenter, all but one were made to move in another side of the enclosure by a research assistant using small food baits. In the same way, other group members were prevented from approaching the study subject during testing. Food rewards were always small pieces of carrots (i.e. approximately 5 pieces of 8 g each), which were highly liked food rewards in all study groups. Trials started when the subject's head was in front of the experimenter, approximately between the two containers.

Before being tested, all individuals and species underwent a habituation phase, to get them used to the experimenter and the set-up. In this phase, we only used one container. The experimenter baited the container out of the subject's view, turning around to bait it, and then showed the opened container (and its content) to the subject. After 5 seconds the experimenter closed the lid, waited for 2 seconds, and pushed the container towards the subject. If the subject touched the container, the experimenter opened the lid and let the subject eat the food. After 4 successful retrievals out of 5 consecutive trials, the subject started the experimental phase. In this way, we ensured to test in the experimental phase only those subjects that were motivated and attentive during the habituation phase, approaching and observing the experimenter during the baiting procedure, and promptly eating the food after having selected the correct container. All the individuals participating in the habituation phase successfully completed it and moved to the next phase.

Upon successful completion of the habituation phase, we started the experimental phase, which consisted of 12 trials for each task. All tasks and trials were administered in a pseudo-randomized order, so that (i) the order of tasks varied across individuals of each species in a similar way, (ii) the right and left container in each task were baited an identical number of times, and (iii) the same side was not baited in more than three consecutive trials. Trials were conducted as long as the subject stayed motivated, and were stopped if the subject failed to approach the experimenter for more than 30 minutes. In that case, the session was interrupted and testing was resumed on the next possible day, so that the daily number of trials administered varied within and across subjects. We recorded all trials with a video camera (SONY HDR-CX405) fixed on a tripod at one side of the experimenter. The procedures and experimental design used with bison and buffalos exactly matched the ones we had already used with giraffes [27], with the only exception that the opaque containers used for bison and buffalos (i.e. 60 x 40 x 8.4 cm) were larger than the ones used for giraffes (15 x 15 x 3 cm). This change was necessary to ensure that bison and buffalos could retrieve the selected food on their own, as both species are mainly grazers and are not as skilful as giraffes to retrieve food with their tongues.

Object permanence task. Out of the subject's view, the experimenter baited one of the two containers and showed them to the subject, keeping them opened so that their content was visible. The experimenter held both containers approximately 20 cm from each other and around 50 cm from the subject, on the other side of the fence (see Figure 1 and Figure 2). After 5 seconds, the experimenter simultaneously closed the lids of both containers, waited for 2 seconds and then moved both of them toward the subject, who could make a choice. A choice was recorded when the animal touched a box, and the touched box was considered as the one selected by the subject. If the subject touched the correct container, the experimenter opened the lid and let the subject eat the food, while moving the unchosen container out of the subject's reach. If the subject touched the unbaited container, the experimenter opened its lid and showed its content to the subject, then showed the content of the correct container and removed both. See a video example in Supplementary material "Object Permanence (incorrect trial)".

Memory task. We used the same procedure as in the Object permanence task. The only difference was the time that elapsed between closing the lid and letting the subject choose. Depending on the task, the time delay was 30 or 60 seconds, instead of 2 seconds. See a video example in Supplementary material "Memory 60s (incorrect trial)".

Acoustic inference tasks. In these tasks, the experimenter baited one of the two containers out of the subject's view, so that no visual cues were provided to the subject as to which container was baited. In the Shake full task, the experimenter held both closed containers slightly beyond the subject's reach, and then shook 3 times the baited container vertically. In this way, the carrots inside the container made a loud noise. After waiting for 2 seconds, the experimenter simultaneously pushed both containers toward the subject to choose. In the Shake empty task, the procedure was identical, but this time the experimenter shook the empty container, which thus made no sound. If subjects understood that empty containers produce no sound when shaken, they should have inferred that the unshaken container contained food, and preferentially selected it. If subjects instead failed to understand the causal link between the objects and the noise produced when they moved, they might have relied on stimulus enhancement to solve the task (i.e. selecting the shaken container, regardless of whether it produced a sound). See a video example in Supplementary material "Shake Full (correct trial)".

Olfactory task. We used the same procedure as in the Object permanence task. However, the experimenter never showed the opened containers to the subjects, who could therefore only rely on olfactory cues to locate the food. This task therefore controlled that olfactory cues could not be used to locate the food. See a video example in Supplementary material “Olfactory (incorrect trial)”.

The experimenter coded the trials on the spot. An observer who was not present during the sessions coded 15% of all the trials from the video-recordings, which had been randomly selected from the whole pool of trials. Inter-observer reliability was excellent ($\kappa = .98$, $n = 162$ trials).

Statistical analyses

We ran multilevel-ordered logit models, always including a varying intercept by subject identity to correct for repeated observations. We included all the administered trials in the data-set, and then assessed variation in correct response. Statistical analyses were run with a Bayesian approach, using the rethinking package [74] in R (version 3.2.3). The Bayesian approach combines prior information about population parameters with sampled data to obtain posterior plausibilities. In all models, we therefore used weakly informative priors to assign the initial plausibilities, and then estimated parameters with RStan (Stan Development Team, 2016). In order to obtain the posterior distribution, we run 3 Hamiltonian Monte Carlo chains in parallel (to reduce autocorrelation within chains), using 10000 samples, half of which were warm-up. Convergence was suggested by a high number of effective samples (a measure of the extent of autocorrelation of the samples within a chain) and Rhat estimates (measuring convergence of the chains to the target distribution) of 1.00 [74]. We selected models based on the lowest Widely Applicable Information Criteria (WAIC) and the highest Akaike weights. [32]

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DECLARATIONS

Ethics approval and consent to participate

The Barcelona Zoo and the Leipzig Zoo controlled and approved all the procedures. Given that subjects participated on a completely voluntary basis, and no invasive procedures were used, no formal approval was required. During the tasks, moreover, individuals were never food deprived, and motivation to participate was ensured exclusively by the use of highly-preferred food (i.e. carrots). The experiments thus provided a form of enrichment for the subjects and did not present any risks or adverse effects on the animals.

Consent for publication

Not applicable

Availability of data and materials

All data generated during the study are included in this article as supplementary information file.

Competing interests

We declare we have no competing interests

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government.

Authors' contributions

ALC carried out the field work with the help of bachelor and master students, conceived the study, participated in data analysis, participated in the design of the study and drafted the manuscript; MC participated in designing the study, coordinated the study and helped draft the manuscript. CE participated in design and coordination of the study. FA designed and conceived the study, carried out the statistical analyses and helped draft the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Additional files

- Dataset
- Video 1. Object permanence (incorrect trial)
- Video 2. Memory 60s (incorrect trial)
- Video 3. Shake full (correct trial)
- Video 4. Olfactory (incorrect trial)

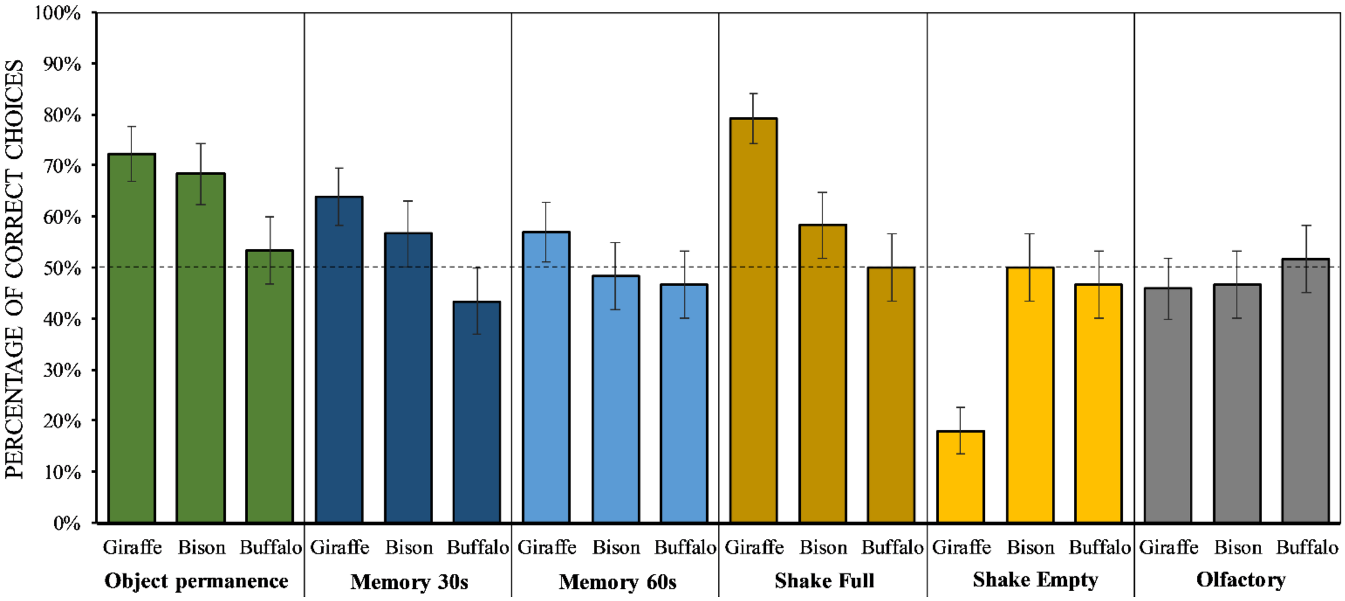
Fig. 1

A European bison awaiting in a 30s Memory trial.

Fig 2.

A forest buffalo awaiting in a 30s Memory trial

Fig. 3



Mean ± SEM of correct choices in the forced-choice tasks for each species. Values above 0.5 indicate a preference for the baited container.

CHAPTER 5

Problem solving in European bison (*Bison bonasus*): two experimental approaches

Short title: **Problem solving in European bison (*Bison bonasus*)**

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ABSTRACT

The ability to solve novel problems is crucial for individual fitness. However, studies on problem solving are usually done on few taxa, with species with low encephalization quotient being rarely tested. Here, we aimed to study problem solving in a non-domesticated ungulate species, European bison, with two experimental tasks. In the first task, 5 individuals were presented with a hanging barrel filled with food, which could either be directly accessed (control condition) or which could only be reached by pushing a tree stump in the enclosure below it and stepping on it (experimental condition). In the second task, 5 individuals were repeatedly fed by an experimenter using a novel bucket to retrieve food from a bag. Then, three identical buckets were placed in the enclosure, while the experimenter waited outside with the bag without feeding the bison, either with a bucket (control condition) or without it (experimental condition). In the first task, no bison moved the stump behind the barrel and/or stepped on it to reach the food. In the second task, two individuals solved the task by pushing the bucket within the experimenter's reach, twice in the experimental and twice in the control condition. We suggest that bison showed a limited ability to solve novel problems, and discuss the implications for their understanding of the functional aspects of the tasks.

Keywords: European bison, insight, Köhler, problem solving, ungulates, Bison bonasus.

INTRODUCTION

The ability to spontaneously solve novel problems plays a crucial role in the survival and fitness of individuals, by facilitating the exploration of new resources, the use of novel strategies and the invasion of new niches (1,2). Such an ability might be especially relevant in complex dynamic environments, or when socio-ecological conditions rapidly change, as the result of biotic and abiotic factors, and anthropogenic disturbance (3–5).

The study of problem solving has fascinated scientists for at least a century (6). However, experimental studies on problem solving have so far only included few taxa. To date, most studies have been conducted on primates (7–11), birds (12–15), canines (16–18) and rodents (19). Some notable exceptions include elephants (20), dolphins (21) and different carnivore species (22–25).

In recent years, however, some researchers have started investigating problem solving also in taxa with low encephalization quotient, such as ungulates (26–30). These studies have shown that ungulates can solve novel problems (e.g. such as detour tasks) and even learn from humans how to solve them (28). These studies are especially interesting, because they confirm that, even in mammals, the ability to solve novel problems is not limited to species with large brains (31,32). However, it is possible that other species might perform differently. To date, for instance, problem solving tasks have been only conducted on domesticated ungulate species. Through domestication, however, the ability to solve novel problems might have dramatically changed. On the one hand, as an adaptive consequence of human selection, domestic species might show a preference for novelty (33,34), which is linked to higher exploration and ability to innovate (7,35–38). On the other hand, domestication have led to a reduction in brain size (which, in ungulates, ranges from 14% to 24% (39)). Therefore, the inclusion of non-domesticated species is especially important to better understand the socio-ecological conditions that might favour the emergence of problem-solving skills.

To fill this gap, we tested problem solving in a non-domesticated species, European bison (*Bison bonasus*). Nowadays, bison live in Eastern Europe forests (40), although historically they were distributed throughout Europe (41). Despite many physiological adaptations to grazing, like their teeth microwear (42), European bison are mainly browsers, and this ability to adapt to a novel diet might have been crucial for their survival, as they are now the largest living herbivores in Europe (43). This species is an ideal candidate to study problem solving, because bison live in relatively complex social systems: herds include up to 30 individuals and are characterized by high levels of fission-fusion (44), which has been proposed as a major driver of enhanced cognition (45). Bison often migrate and form hierarchical groups which are maintained over many years, whose social structure flexibly changes across seasons (46). Moreover, bison might engage in solitary and social play relatively often (as we observed by comparing more than 20 ungulate species during a set of studies; Caicoya, pers. observ.), a behaviour that has been linked to behavioural innovation (47). The genus bison has an encephalization quotient (EQ) of 0.85, which is slightly higher than their close relatives like *Bos grunniensis* (EQ = 0.76), *B. javanicus* (EQ = 0.78), *B. taurus* (EQ = 0.55) or even *Equus caballus* (EQ = 0.78) (48,49), but clearly lower than other species usually tested in problem solving studies, such us chimpanzees (*Pan troglodytes*, EQ = 2.48) or *Homo sapiens* (EQ = 6.62) (49).

In this study, we aimed to assess if a non-domesticated ungulate species with relatively low encephalization quotient (50,51), would spontaneously innovate in an experimental context. For this reason, we presented a group of captive bison with two different problem solving tasks. In the first task, we adapted a classic experimental protocol (6) to ensure ecological relevance.

Bison were presented with a familiar plastic barrel hanging from a branch: the barrel was filled with carrots, from which they regularly fed by shaking it with the muzzle or horns, letting carrots fall out of its holes and on the ground. In the experimental condition, however, the barrel was too high to be reached, but bison could access it by moving a tree stump in the enclosure and climbing on it to shake the barrel. As bison have adapted to browse and can feed on food hanging from relatively high branches, this task should be ecologically relevant for them. When tested with a similar set-up, one elephant (20) and several chimpanzees could successfully solve the task (6), while seven sloth bears failed despite being provided with several social and non-social cues (25). In the second task, bison went through a training phase in which the experimenter repeatedly fed them with small pieces of dry carob, using a novel bucket as a scoop to retrieve the carob from a bag. In the experimental condition, the experimenter approached the bison with the bag, but the bucket had been previously placed in the enclosure, so that bison had to push it within the experimenter's reach to be fed. We hypothesized that, if bison understood the relevant aspects of the tasks (i.e. return a bucket to the experimenter to feed on carob and get on a tree stump in order to reach a barrel filled with carrots), they should have more frequently interacted with the tree stump/bucket and moved them towards the barrel/fence when this was needed to access the food (as compared to control conditions in which the objects were not functional).

MATERIALS AND METHODS

Ethics statement.

The Barcelona Zoo controlled and approved all the procedures. Given that bison participated on a completely voluntary base, and no invasive procedures were used, no formal approval was required. During the task, individuals were never food or water deprived, and motivation to participate was ensured exclusively by the use of highly preferred food (i.e. carrots and carob). The experiments thus provided a form of enrichment for the individuals and did not present any risks or adverse effects.

Subjects

We tested 5 European bison (*Bison bonasus*) housed at the zoo of Barcelona, ranging from 6 to 30 years of age. All study individuals were habitually fed on a diet of grasses. Individuals had little experience with experimental procedures, having only been tested in an object permanence task. Crucially, none of the individuals had ever been trained by the experimenters or by the zookeepers to return objects in the enclosure. The tasks were carried out in the external facilities of the bison, and their usual management was not changed due to our tasks. The bison enclosure size was 617m^2 and did not include many visual barriers (see Fig. 1, 2 and 3 for photos of the enclosure). The bison were not separated during the tasks, as testing took place while all bison could freely move inside their enclosure.

Task 1. Setup and procedure

In Task 1 we used a plastic barrel of approximately 100 cm height and 60 cm diameter, and a tree stump of 34 cm height, 46 cm diameter and 14 kg. Bison had extensive experience with the barrel, since it was a common enrichment in their facilities. The barrel habitually hanged from a branch, and individuals shook it with their muzzle/horns to let carrots fall out of its holes and on the ground, where they were eaten. In contrast, bison had no experience with the stump used for the experiment, although their facilities contained bigger tree trunks, which bison easily moved around the enclosure. Every morning, when bison were moved in the internal facilities in order to clean the external ones, the experimenter hung the stump 5 m from the barrel and filled the barrel with carrots. In the experimental condition, the barrel hanged approximately 20 cm higher than usually, so that bison could only reach it by moving the stump below it and standing on it (see Fig 1). Crucially, before this study was conducted, all bison had been repeatedly observed putting their front paws on the feeders in their facilities and stand on them for apparently no reason, suggesting that standing on objects belonged to their natural repertoire (see Fig 2). In the control condition, the barrel was hanging as usually, so that the stump, despite being also present in the enclosure, was not functional to retrieve the carrots (Fig 3). If bison did not solve the experimental condition after 6 sessions, the same condition was repeated, but placing the stump under the barrel, so that individuals only had to get on the stump to hit the barrel and retrieve the food. Each session lasted for 24 hours or until the barrel ran out of carrots. We administered a total of 20 experimental and 13 control sessions in a pseudo-randomized order (i.e. ensuring that no more than two identical conditions were administered in a row). The number of sessions differed between the two conditions to meet the management needs of the zoo.

Fig 1. **Experimental set up for task 1**. The second bison from the left is moving the stump, while the barrel is low enough to be reached without the stump (i.e. control condition).

Fig 2. A bison with its front paws on the feeder. Bison habitually stood on objects.

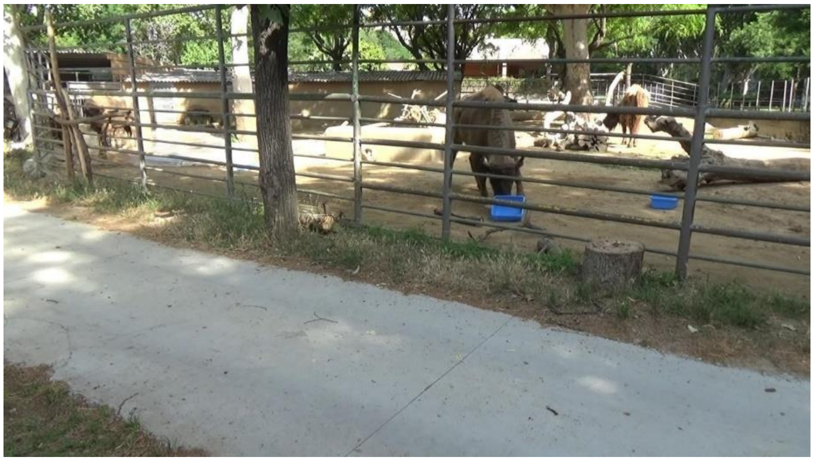
Fig 3. Set-up of the (1) control and (2) experimental conditions. The barrel hangs within and without reach, respectively.

Task 2. Setup and procedure

In Task 2, all bison first went through a training phase of 10 days, in which the experimenter repeatedly used a novel 35x28x18 cm blue bucket to feed individuals with small pieces of dry carob – a highly preferred food item (Fig 4). The bucket was ostensibly used as a scoop, with the experimenter retrieving the carob from a filled bag directly with the bucket, and never doing it in any other way, so that the bison could associate that the bucket was essential to be fed with the carob. In the experimental condition, the experimenter placed 3 identical buckets (to avoid monopolization by single individuals) in the internal facilities, when the bison were out of view in the external facilities. The buckets were placed three meters from the fence and three meters from each other. When the bison entered the internal enclosure, the experimenter approached the fence, stopped 2m from it, placed the bag with carob on the floor and then strolled around like if looking for something (i.e. the bucket) for 5 minutes. After that, the experimenter left the area for 5 further minutes (leaving the bag filled with carob visible on the ground), and then came back and repeated the procedure for 5 more minutes. If one bison pushed the bucket within the experimenter's reach during these 15 minutes, the experimenter immediately reached for it through the fence and gave the carob to the bison (Fig 5). If the bucket was not returned, the experimenter took the bag with the carob and left. Buckets were then collected from the enclosure by the keepers, after the experimenter had left. In the control condition, we repeated the same procedure as in the experimental one, with the only exception that the experimenter also had a bucket. We administered a total of 3 experimental and 4 control sessions, starting with the control condition and alternating them. In this way, we could compare performance in experimental sessions to performance in control sessions which were administered both before and after the experimental ones. Watch S1 File for a trial of a bison returning the bucket in an experimental trial.

Figure 4. Experimental set up for task 2 in a control trial. There are three buckets inside the facilities (red arrows), at three meters from the fence. The experimenter had another bucket outside the bison enclosure (green arrow).

Figure 5. A bison returning a bucket. This occurred while the experimenter was in his 5-minute leave of an experimental trial. Please refer to S1 File to see the complete video of a bison returning the bucket.



Coding

All sessions were video-recorded. In Task 1, we used two camera traps, one filming the whole area and one focusing on the barrel from 2m-distance. In Task 2, we used a video-camera standing on a tripod 3m behind the experimenter's back, filming the fence with the three buckets on the bison's side. In Task 1, we watched the videos to code: (i) whether individuals solved the task (i.e. climbed on the stump and got the carrots); (ii) the latency to first approach (i.e. stand below) the barrel (as a measure of motivation); (iii) the latency to first interact with the stump (i.e. touching, moving or sniffing it); (iv) the exact duration of time spent moving the stump, or (v) otherwise interacting with it. In Task 2, we watched the videos to code: (i) whether individuals solved the task (i.e. pushed the bucket within the experimenter's reach and got the carob); (ii) latency to first interact with the bucket (i.e. touching, moving or sniffing it); (iii) the exact duration of time spent interacting with the bucket, (iv) moving it in the correct direction (i.e. toward the fence) or (v) in any other direction.

Statistical analyses

Analyses were conducted using generalized linear mixed models (52) with the glmmTMB package (version 1.0.1 (53)) in R (R Core Team, version 3.5.0). In all models, we entered one line per individual and session. Models 1-4 assessed performance in Task 1. In particular, we assessed whether condition (i.e. Experimental or Control) predicted the latency to first approach the barrel (Model 1), the latency to first interact with the stump (Model 2), whether they moved the stump (Model 3) or otherwise interacted with it (Model 4). In all models, we controlled for the distance between stump and barrel (i.e. 5m or 0m) and session number, we included individual identity as random factor and (in Models 3-4) session duration as offset term. Models

5-7 assessed performance in Task 2. In particular, we assessed whether condition (i.e. Experimental or Control) predicted the latency to first interact with the bucket (Model 5), the probability of moving the bucket (Model 6) or otherwise interacting with it (Model 7). In all models, we included individual identity as random factor and session duration as offset term. Finally, as there were no instances of success in Task 1 and only few ones in Task 2, no statistical analyses were run for this variable.

All models were run with a binomial structure, except for models 1, 2 and 5, which had a Gaussian distribution. We used likelihood ratio tests (54) to compare full models containing all predictors with null models containing only control predictors, offset terms and random factors. When full models significantly differed from null models, likelihood ratio tests were conducted to obtain the *p* values for each test predictor via single-term deletion using the R function drop1 (55). We detected no convergence issues. To rule out collinearity, we determined the Variance Inflation Factor (VIF) (56), which were minimal (maximum VIF across all models = 1.35).

RESULTS

None of the individuals solved Task 1. In Task 2, however, individuals pushed the bucket within the experimenter's reach in 4 of the 30 administered trials: one individual (Elipse) did it twice, in two Experimental sessions, while another individual (Verde) did it twice, in two Control sessions.

Models 1 to 4 assessed performance in Task 1. For Model 1, the full-null model comparison was significant (GLMM: $\chi^2 = 22.48$, df = 1, $p < 0.001$), with latency to approach the barrel being significantly higher in the Experimental than in the Control condition (see Table 1).

In contrast, there was no significant difference between full and null model for Model 2 (GLMM: $\chi^2 = 0.08$, df = 1, $p = 0.778$), Model 3 (GLMM: $\chi^2 = 0.62$, df = 1, $p = 0.430$) and Model 4 (GLMM: $\chi^2 = 0.02$, df = 1, $p = 0.886$). In particular, condition neither predicted the latency to first interact with the stump (Model 2), nor the probability of moving it (Model 3) or otherwise interacting with it (Model 4; see Table 1).

Models 5 to 7 assessed performance in Task 2. There was no significant difference between full and null model for Model 5 (GLMM: $\chi^2 = 0.28$, df = 1, $p = 0.598$), Model 6 (GLMM: $\chi^2 = 1.42$, df = 1, $p = 0.233$) and Model 7 (GLMM: $\chi^2 = 0.01$, df = 1, $p = 0.978$). In particular, condition failed to predict the latency to first interact with the bucket (Model 5), and the probability of moving the bucket (Model 6) or otherwise interacting with it (Model 7; see Table 1).

Table 1. Summary of results. Results of the models run, including estimates, standard errors (SE), confidence intervals (CIs) and *p* values for each test and control predictor (in parentheses, the reference category). Significant test predictors are in bold, control predictors in italics. All models included individual identity as random effect, and Models 3, 4, 6 and 7 also included session duration as offset. The asterisks denote significant p values for the test predictors. All models had a binomial distribution, except for models 1, 2 and 5, which had a Gaussian distribution.

MODEL	**Estimate**	**SE**	**2.5% CI**	**97.5% CI**	***P***
M1: Latency to first approach the barrel (Task 1)					
Intercept	714.80	181.30	359.46	1070.14	-
Condition	439.90	89.54	264.40	615.40	<0.001*
Distance	9.69	96.47	-179.40	198.77	0.920
Session number	-19.17	13.51	-45.65	7.30	0.157
M2: Latency to first interact with the tree stump (Task 1)					
Intercept	1175.03	83.28	1011.81	1338.25	-
Condition	-21.96	77.86	-174.57	130.65	0.778
Distance	-207.80	83.89	-372.22	-43.38	0.013
Session number	38.67	11.75	15.64	61.69	<0.001
M3: Probability of moving the tree stump (Task 1)					
Intercept	-13.43	0.89	-15.18	-11.68	-
Condition	-0.73	0.94	-2.58	1.11	0.436
Distance	-0.94	0.97	-2.84	0.96	0.335
Session number	-0.11	0.18	-0.47	0.25	0.547
M4: Probability of otherwise interacting with the tree stump (Task 1)					
Intercept	-12.15	0.47	-1.31	-1.12	-
Condition	0.06	0.43	-7.75	8.97	0.887
Distance	0.41	0.46	-4.85	1.3	0.371
Session number	-0.21	0.08	-3.62	-6.15	0.006
M5: Latency to first interact with the bucket (Task 2)					
Intercept	14	1.96	10.15	17.85	-
Condition	0.74	1.39	-1.98	3.46	0.597
Session number	-1.68	0.85	-3.34	-0.01	0.049
M6: Probability of moving the bucket (Task 2)					
Intercept	-8.94	2.42	-13.69	-4.2	-
Condition	-1.46	1.31	-4.04	1.1	0.264
M7: Probability of otherwise interacting with the bucket (Task 2)					
Intercept	-8.76	1.17	11.07	-6.46	-
Condition	-0.03	1.13	-2.25	2.19	0.978

DISCUSSION

In our study, bison showed a limited ability to solve novel problems. In the first task, none of the five study individuals moved the tree stump behind the barrel with food and/or stepped on it to reach for the food when it was out of reach (experimental condition). Bison approached the barrel significantly later when the barrel was out of reach, as compared to when it was accessible (control condition). However, the latency to first interact with the stump and the probability of moving it or otherwise interacting with it did not significantly change across conditions. In the second task, two individuals solved the task by pushing the bucket within the experimenter's reach: one individual did it twice, when the experimenter had no bucket (experimental condition), and one did it twice, when the experimenter had the bucket but still refrained from feeding the bison (control condition). As in task 1, the latency to first interact with the bucket and the probability of moving it or otherwise interacting with it did not change across conditions. Please refer to S1 File to see the complete video of a bison returning the bucket in an experimental trial.

In the first task, none of the study individuals mastered the task. Individuals interacted in a similar way with the stump in the experimental and control condition, suggesting that they did not understand the functional value of the stump to solve the task and access the food in the experimental condition. Bison only differed between conditions in their latency to approach the barrel, which was higher in the experimental condition. This suggests that bison were less motivated to approach the barrel when it was out of reach, and could be interpreted in at least three different ways. First, it is possible that the motivation to approach the barrel in the experimental condition decreased through time, as bison could not retrieve food and therefore learned that food was not accessible when the barrel was hanging higher on the tree. However, this explanation is unlikely, in that the latency to approach the barrel did not vary through time (i.e. session had no significant effect on the latency to approach the barrel in Model 1; see Table 1). Second, it is possible that the motivation to approach the barrel was lower in the experimental condition from the very beginning, because bison understood that food could not be reached when the barrel was hanging higher, despite failing to understand how to reach for it. Third, it is possible that bison simply required longer to approach the barrel when it was hanging higher, because they were not used to see the barrel in that position and were thus simply reacting fearfully to the novel situation (57,58). In the future, further studies should better assess the role played by neophobia in the bison' behaviour, to contrast these different hypotheses.

In the second task, two individuals spontaneously pushed the bucket within the experimenter's reach. Crucially, none of the study individuals had been previously trained to return objects in the enclosure. Moreover, the zookeepers in Barcelona reported having never asked bison to give back objects left in their enclosures, nor having rewarded them in any way for pushing objects in the enclosure, and were indeed highly surprised by the behaviour of the animals. While one individual pushed the bucket within reach twice in the experimental condition (i.e. when the experimenter had the bag with carob, but no bucket, so that the bucket was functional to solve the task), another individual did it in the control condition (i.e. when the experimenter had the bag and the bucket, but still refrained from feeding the bison). These results may be explained in two different ways. First, it is possible that bison failed to understand the contingencies of the task, and then simply pushed the bucket toward the observer, without understanding its function. However, the bison did not simply interact with the bucket, but directly pushed it toward the experimenter for three meters, until the experimenter could reach for it through the fence. Therefore, this suggests that the bison understood that the bucket was required to obtain the food. Second, it is possible that the bison, despite understanding the functional value of the bucket, failed to differentiate between experimental and control condition. In particular, bison could have simply reacted to the experimenter providing no food by pushing the functional object to food retrieval, regardless of whether the experimenter had it already. Indeed, our study subjects had “nothing to lose” by trying to push the bucket toward the experimenter. If this is true, our results show that bison can successfully solve novel tasks by showing a general basic understanding of object functionalities. Future studies should ideally include more control conditions to better disentangle which task contingencies are taken into account by bison when solving novel problems, by for instance including control sessions in which novel but non-functional objects are placed in the enclosure. Finally, it is also possible that the bison pushing the bucket twice in the control session did it after socially learning to do it (i.e. after observing the other individual pushing the bucket in the experimental sessions). However, this explanation is unlikely, because the bucket was first returned in a control session (the first one), then in an experimental one (the fourth), then again in a control session (the fifth) and finally in an experimental one (the sixth). See S1 File for an example of bucket returning in an experimental trial.

Our study should clearly be considered as a first preliminary step in the investigation of problem solving in non-domesticated ungulate species. Overall, it confirms ungulates as a promising model to study innovation and, more generally, cognition (28,30,59–62). Despite their relative small brain size (50,51), bison showed some ability to solve novel problems, although their exact understanding of the functional aspects of the tasks is unclear. Whether specific socio-ecological characteristics, rather than brain size, are linked to specific cognitive abilities, and/or to a more general attitude toward novelty, remains a question to address.

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CHAPTER 6

Gaze following in ungulates: domesticated and non-domesticated species follow the gaze of both humans and conspecifics in an experimental context

SHORT TITLE: Gaze following in ungulates

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ABSTRACT

Gaze following is the ability to use others' gaze to obtain information about the environment (e.g., food location, predators, social interactions). As such, it may be highly adaptive in a variety of socio-ecological contexts, and thus be widespread across animal taxa. To date, gaze following has been mostly studied in primates, and partially in birds, but little is known on the gaze following abilities of other taxa and, especially, on the evolutionary pressures that led to their emergence. In this study, we used an experimental approach to test gaze following skills in a still under-studied taxon, ungulates. Across four species (i.e., domestic goats and lamas, and non-domestic guanacos and mouflons), we assessed individual ability to spontaneously follow the gaze of both conspecifics and human experimenters in different conditions. In line with our predictions, species followed the model's gaze both with human and conspecific models, but more likely with the latter. Except for guanacos, all species showed gaze following significantly more in the experimental conditions (than in the control ones). Despite the relative low number of study subjects, our study provides the first experimental evidence of gaze following skills in non-domesticated ungulates, and contributes to understanding how gaze following skills are distributed in another taxon – an essential endeavor to identify the evolutionary pressures leading to the emergence of gaze following skills across taxa.

INTRODUCTION

Gaze following is the ability of looking where others are looking (Butterworth and Jarrett, 1991; Emery et al., 1997). This ability is often considered one of the most basic forms of social cognition, as it allows individuals to socially acquire relevant information about the environment (e.g., about food location, presence of predators, occurrence of social interactions among group members; Tomasello et al., 2001; Tomasello et al., 1998), and also about others' interests and goals (Baron-Cohen, 1995). Therefore, gaze following might be highly adaptive for humans and other animals (Brooks and Meltzoff, 2002).

To date, gaze following has indeed been reported in a variety of taxa, including dogs (*Canis familiaris*: Téglás et al., 2012; Duranton et al., 2017; Miklösi et al., 1998; Range and Virányi, 2011; Met et al., 2014), birds (Nawroth et al., 2017; Kehmeier et al., 2011; Loretto et al., 2010; Schloegl et al., 2007; Bugnyar et al., 2004; Tornick et al., 2011; Jaime et al., 2009; Goossens et al., 2008; Schmidt et al., 2011; Watve et al., 2002), reptiles (Wilkinson et al., 2010; Simpson and O'Hara, 2019) and several primate species (e.g. Anderson and Mitchell, 1999; Emery et al., 1997; Burkart and Heschl, 2006; Scerif et al., 2004; Shepherd and Platt, 2008; Tomasello et al., 1998; Bräuer et al., 2005; Liebal and Kaminski, 2012; Itakura, 1996; Drayton and Santos, 2017; Sandel et al., 2011; Ruiz et al., 2009; Chen et al., 2017; see Rosati and Hare, 2009, for a review).

Clearly, gaze following does not necessarily imply complex cognition. Povinelli and Eddy, 1996, for instance, distinguished a low-level from a high-level form of gaze following in animals (also referred to as gaze following into space versus geometrical gaze following; see Loretto et al., 2010). In particular, low-level gaze following would be an innate response triggered by a shift in the individual's attention toward an external target: when a conspecific turns the head, for instance, the individual attention would be caught by this movement, and the individual would simply look in that direction, without any cognitive skills being involved. In contrast, high-level gaze following would also imply the ability to take others' perspective, and thus understand what others see from their location: if the individual sees a conspecific looking in another direction, for example, it might use the conspecific's gaze as a cue to obtain information about the environment, eventually moving around barriers to gain the conspecific's perspective (Povinelli and Eddy, 1996).

Although gaze following appears to be widespread across taxa, at least in its lower-level form, some studies have shown important differences in gaze following behaviour even among closely related species (Kano and Call, 2014). In particular, species can differ from each other in two main ways. Firstly, they can differ in their general sensitivity to gaze following: while some species reliably follow others' gaze, others might be less sensitive to the gaze of others, and less reliably follow it. Stump-tailed macaques (*Macaca arctoides*), for instance, follow the gaze of conspecifics more frequently than other macaque species (Tomasello et al., 1998), while bonobos (*Pan paniscus*) are more likely to follow others' gaze, as compared to chimpanzees (*Pan troglodytes*; Herrmann et al., 2010; Kano and Call, 2014). Similarly, some species might avoid direct gaze and gaze following (see Kaplan & Rogers, 2002). Secondly, species can specifically differ in their ability to follow the gaze of individuals of other species (i.e. allospecifics). While the gaze of a conspecific might provide relevant information to individuals in most species (so that they would benefit from following it), allospecifics' gaze might less likely trigger gaze following behaviour (see Kano and Call, 2014).

The reasons for these inter-specific differences, however, are yet unclear. Some researchers, for instance, have proposed that differences in gaze following skills might depend on differences in motivation and/or selective interest in certain models (Kano and Call, 2014). Other researchers have rather highlighted the role of domestication in the emergence of gaze following skills (see Kamiski et al., 2005; Hemmer, 1990). On the one hand, domestication might reduce sensitivity to predators (because humans protect domesticated animals against other predators; Hemmer, 1990), so that gaze following might be less frequent in domesticated species, if its main function is the acquisition of information about the presence of predators (see Kaminski et al., 2005). On the other hand, domestication might have selected for especially tame and socially skilled individuals (e.g. Hare et al., 2002; Hare and Tomasello, 2005), which might have enhanced social cognitive skills, and also be better at following others' gaze. However, while some studies have suggested that domestication has a positive effect on species' ability to follow others' gaze (e.g. Kaminski et al., 2004), other researchers have found no positive effect of domestication on gaze following skills (e.g. Werhahn et al., 2016). Therefore, the effect of domestication on gaze following is yet unclear, and more comparative studies are required to better understand which factors best predict inter-specific variation in gaze following (Kano and Call, 2014).

In this study, we aimed to compare species in their ability to follow the gaze of conspecifics and allospecifics and, in particular, the effect of domestication on these skills. For this purpose, we tested four different ungulate species: two domesticated ones (i.e. goats, *Capra aegagrus hircus*, and lamas, *Lama glama*), and two non-domesticated ones (i.e. mouflons, *Ovis orientalis orientalis*, and guanacos, *Lama guanicoe*). We selected ungulates for two main reasons. Firstly, ungulates are a still largely under-studied taxon, with only one species yet having been tested for its gaze following skills (Kaminski et al., 2005), to our knowledge. Therefore, testing these species can significantly increase the range of species on which we have information, and help to shed light on the selective pressures that might affect the emergence of gaze following skills in different taxa. Secondly, ungulates include a variety of domesticated and non-domesticated species, with an impressive variety of socio-ecological characteristics (see Shultz and Dunbar, 2006). Therefore, they constitute an ideal model to contrast different evolutionary hypotheses on the emergence of gaze following skills.

Here, we used a consolidated experimental approach in which subjects observed either a conspecific or a human experimenter suddenly turning the head toward a distant location. We monitored whether subjects followed the conspecific's and the human's gaze, by turning the head in the same direction of the model, and whether species differed in their performance. We predicted that (1) all species would more likely follow the gaze of a conspecific (rather than a human), as individuals in all species should have more interest/motivation to obtain information from conspecifics than allospecifics (see Kano and Call, 2014). Moreover, we predicted that (2) both domesticated and non-domesticated species would show gaze following skills, as also shown in other taxa (e.g. Loretto et al., 2010; Wilkinson et al., 2010; Werhahn et al., 2016).

METHODS

Ethics. The Barcelona and Leipzig Zoos controlled and approved all the procedures. We used no invasive methods, individuals were never separated from their group and participated on a completely voluntary basis. During the task, individuals were never food or water deprived, and the tasks did not present any risks or adverse effects. Therefore, no formal approval was required.

Subjects. We tested 17 goats (*Capra aegagrus hircus*) and 3 lamas (*Lama glama*) housed at the Leipzig Zoo, and 4 guanacos (*Lama guanicoe*) and 4 mouflons (*Ovis aries musimon*) housed at the Barcelona Zoo. Lamas and guanacos are phylogenetically closely related, and so are goats and mouflons, with lamas and goats having been domesticated approximately 5 000-3 800 and more than 10 000 years ago, respectively (see Goñalons, 2008; Vigne et al., 2005).

Study subjects included both males and females, and were all adults (i.e. older than one year), except for the goat sample, which also included 4 infants (for more details on the study subjects, see Table 1). The study subjects had little experience with experimental procedures: the lamas and some of the goats had been previously tested in a neophobia test (i.e. in which individuals were provided with food close to a novel object), while the guanacos and mouflons had never been taken part in any experiment. The tasks were carried out in the external facilities of the species, and their usual management was not changed due to our tasks. While goats and lamas are commonly considered domesticated species (Zeder and Hesse, 2000; Diaz-Lameiro, 2016; Dong et al., 2015), mouflons and guanacos are not (Chessa et al., 2009; Lincoln, 1990; Yacobaccio and Vilá, 2016; Cartajena et al., 2007).

Procedures. We administered two tasks, one using as a model a conspecific (Conspecific task), and one a human experimenter (Human task). We originally aimed to administer 6 to 12 trials per task and condition (i.e. Experimental and Control), but as subjects differed in their motivation to participate, the number of trials administered in each task and condition varied across them (see Table 1). Subjects were tested when they were approximately 1 to 4 meters from the experimenter. All trials were video-recorded with a video-camera positioned just outside the ungulate enclosure, so that the subject was clearly visible. Subject responses were later coded from the videos (see below).

In the Experimental condition of the Conspecific task, we opportunistically waited for two individuals facing each other, one giving its back to the experimenter (i.e. subject) and one having the experimenter in his visual field (i.e. model; see Fig. 1a). The experimenter tried to catch the model's attention (e.g. holding a piece of food in the air), so that the model would visibly move his head in another direction (e.g. raising or turning his head toward the experimenter), while the subject looked toward the model (i.e. so that the subject could see the model move his head). When the model moved the head toward the experimenter and the subject looked at the model, a trial was started. The Control condition of the Conspecific task was identical, except that no model was present, and the trial was started when the subject was giving his back to the experimenter (so that the subject was provided no gaze cue; see Fig. 1b). Trials were scored as successful if the subject turned his head in the same direction (i.e. at least 45 degrees) in which the model looked at (for Control trials, in the direction in which the model looked at in the corresponding Experimental trial).

In the Experimental condition of the Human task, we opportunistically waited for an individual (i.e. subject) to look at the experimenter (i.e. model; see Fig. 1c). The model then suddenly raised his/her head toward a distant upper corner of the enclosure (either on the right or on the left, randomizing the side across subjects and trials), and a trial was started. The Control condition of the Human task was identical, except that the model raised his/her head toward the body of the subject (see Fig. 1d). Trials were scored as successful if the subject turned his head toward the same upper corner of the enclosure (i.e. at least 45 degrees) in which the model looked at (for Control trials, in the direction in which the model looked at in the corresponding Experimental trial).

In both the Conspecific and the Human tasks, we first tested goats and lamas with 10-second trials. However, the greatest majority of subjects turned their head in the first 3ss of the Experimental trials (i.e. 75% in lamas, 79% in goats). When testing guanacos and mouflons, therefore, we preferred to administer shorter trials (i.e. 3-second trials) to be more conservative (i.e. to avoid coding trials as positive when subjects moved the head for other reasons). Clearly, in order to ensure comparability across species, trials were coded as successful in all species and conditions if the response (see above) was given in the first 3 seconds. As all trials were video-recorded and later scored from the videos (see above), the 3-second-interval could be accurately measured from the videos.

Statistical analyses. Analyses were conducted using generalized linear mixed models (Baayen et al., 2008) with the glmmTMB package (version 1.0.1; Brooks et al., 2017) in R (R Core Team, version 3.5.0). Our models were run with a binomial structure, entering one line per subject and trial, and further specifying whether the trial was successful (see above), the task and condition administered, the trial number, and the species, sex and age of the subject. A second observer independently coded 20% of the videos (i.e. whether the trial was successful), and inter-observer reliability was excellent (Cohen’s kappa = 0.94).

We then assessed whether the 3-way interaction of species (as categorical predictor with 4 levels), task (2 levels: Conspecific and Human) and condition (2 levels: Experimental and Control) predicted subject’s response (i.e. whether they would direct their gaze in the direction of the model’s gaze, as explained above). In the model, we further included all the 2-way interactions between species, task and condition, and their main effects. We also included subject age and sex as controls (as in some species gaze following skills are known to completely develop only by the end of infancy; e.g. Teufel et al., 2010; Rosati et al., 2016; and to be higher in females; e.g. Rosati et al., 2016). We finally included trial number as control (as response to others’ gaze may vary through time, either increasing as a result of learning, or decreasing as a result of habituation: Loretto et al., 2010; Schloegl et al., 2007, and subject identity as random factor.

We used likelihood ratio tests (Dobson et al., 2001) to compare the full model containing all predictors with the null model containing only control predictors and random factors. When the full model significantly differed from the null model, likelihood ratio tests were conducted to obtain the *p* values for each test predictor via single-term deletion, using the R function drop1 (Barr et al., 2013). If the 3-way interaction was not significant, we removed it from the full model and re-run the comparison with the null model by only including the 2-way interaction of condition with species and condition with task, their main effects, control predictors and the random factor. We detected no convergence issues. To rule out collinearity, we determined the VIFs (Field, 2005), which were minimal (maximum VIFs = 2.01).

RESULTS

The full-null model comparison was significant (GLMM: $\chi^2 = 76.61$, df = 15, $p < 0.001$). The 2-way interactions between condition and task ($p < 0.001$) and condition and species ($p = 0.005$) were both significant. In particular, the study subjects looked in the model's direction more in the Experimental than in the Control condition in both tasks, although this difference was stronger in the Conspecific task (Conspecific task: $p < 0.001$; Human task: $p = 0.016$; see Table 2). Moreover, while all species overall followed the model's gaze more in the Experimental than in the Control condition (see Fig. 2), goats ($p < 0.001$), lamas ($p = 0.002$) and mouflons ($p < 0.001$) did it significantly so, but not guanacos ($p = 0.638$).

DISCUSSION

Our study provides the first experimental evidence of gaze following skills in non-domesticated ungulates. In line with our predictions, ungulates followed the model’s gaze both with human and conspecific models, but were more likely to do so when the model belonged to the same species. Moreover, while all species followed the model’s gaze more in the Experimental than in the Control conditions, non-domesticated guanacos failed to significantly do so (but see below for a better discussion on the relatively low sample size).

The main finding of our research is that gaze following skills are present in ungulates, even in non-domesticated species (i.e. mouflons). This is in line with previous studies in other taxa, which have already shown that non-domesticated species can reliably follow others’ gaze (e.g. Loretto et al., 2010; Wilkinson et al., 2010), sometimes even better than their domesticated counterparts (e.g. Werhahn et al., 2016). Therefore, our study provides no support to the hypothesis that domesticated species show different gaze following skills than non-domesticated ones. Indeed, domesticated species do not seem to have a general advantage over non-domesticated species when following others’ gaze (as expected if close co-evolution with humans during domestication had selected for socially skilled individuals; see Hare et al., 2002). Similarly, non-domesticated species do not seem to outperform domesticated ones (as expected if gaze following skills were less adaptive in domesticated species, which receive extensive protection from predators by humans; see Kaminski et al., 2005). In contrast, gaze following appears to be really widespread across taxa, at least in its simple forms.

In contrast to non-domesticated mouflons, however, non-domesticated guanacos failed to reliably follow the model’s gaze, showing the same probability of gaze following in both experimental and control conditions. As visible in Figure 2, these results are mainly due to the low performance of guanacos (i.e. a higher proportion of successful trials in the Control rather than Experimental condition) when being tested with the human model. At the moment, it is not possible to understand why guanacos performed worse than the other species (including mouflons), especially with allospecific models. One reason might be that guanacos, for some yet unknown reason, show more selective attention toward their conspecifics, as chimpanzees also do (see Kano and Call, 2014). However, it is also simply possible that these results depend on our small sample size, as we could only test four guanacos. Although a larger sample size might have therefore provided different results, it is important to note that other species in our study showed evidence of gaze following skills, despite also having a small sample size (e.g. lamas, N=3). Moreover, while the inclusion of more study subjects might show that also guanacos can follow the gaze of humans and conspecifics, this study already provides evidence that domestication is no necessary prerequisite for the emergence of gaze following skills in ungulates.

While it is true that guanacos performed especially poorly when tested with a human model, all species performed significantly worse when tested with humans rather than conspecifics. This seems to confirm that animals, either domesticated or not, generally have more interest and/or motivation to follow the gaze of conspecifics, as these can more likely provide relevant information (see Kano and Call, 2014). These findings have important implications for the study of interactions between humans and other animals. On the one side, they suggest an astonishing ability of most animal species (also non-domesticated ones) to use human gaze in the same way as conspecific gaze. On the other side, they suggest some limits in this ability, even in domesticated species.

Incidentally, sex, age and trial number had no effect on individual performance in our study. These results are also largely in line with previous studies, which suggest that gaze following skills, at least in its lower-level form, emerge early on through development (see e.g. Range and Virányi, 2011; Kaminski et al., 2005). Moreover, as in previous studies (e.g. Kaminski et al., 2005), performance did not increase through time, suggesting that individual response was not the result of a learning process during the study.

Clearly, this study must be considered as a first attempt to study gaze following skills in ungulates. From a cognitive point of view, for instance, further research is needed to understand the psychological underpinnings of gaze following skills in the different species. By administering further conditions in which individuals need to take others' perspective to follow their gaze, we might be able to better understand whether ungulate species show high- or low-level forms of gaze following (see e.g. Amici et al., 2009; Loretto et al., 2010). Furthermore, future studies should include more individuals and species, to have more power, to better control for inter-individual differences and also to test other evolutionary hypotheses on the emergence of gaze following skills (e.g. high-level forms of gaze following are more likely to emerge in species with complex sociality; see e.g. Dunbar, 2009; Aureli et al., 2008). In the future, it will be especially important to also test other non-domesticated species. The ancestors of both guanacos and mouflons, for instance, have also been domesticated (i.e. into lamas and sheep; see e.g. Alberto et al., 2018; Chessa et al., 2009; Goñalons, 2008). Therefore, it is still possible that gaze following skills in these species are linked to the favourable pre-adaptive characteristics possessed by their ancestors, which might have favoured their domestication, but also the emergence of social cognitive skills like gaze following (see e.g. Zeder, 2012). Finally, future studies should assess whether ungulate species differ in their sensitivity to the gaze of humans and conspecifics, depending on the context (e.g. competitive or cooperative; see Castellano-Navarro et al., in review). Overall, our study confirms ungulates as a promising taxon to study comparative cognition, and zoo-housed animals as ideal subjects to extend the range of tested species, also including those that have long been neglected in cognitive research (Nawroth et al., 2017).

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Figure 1. Experimental set-up for the two tasks and conditions: A. Conspecific experimental trial. B. Conspecific control trial. C. Human experimental trial. D. Human control trial. Continuous lines indicate the model’s gaze direction, while dotted lines indicate subjects´ gaze direction when trials were coded as positive.

Figure 2. For each species, task and condition, mean proportion (+SD) of trials in which subjects followed the model's gaze.

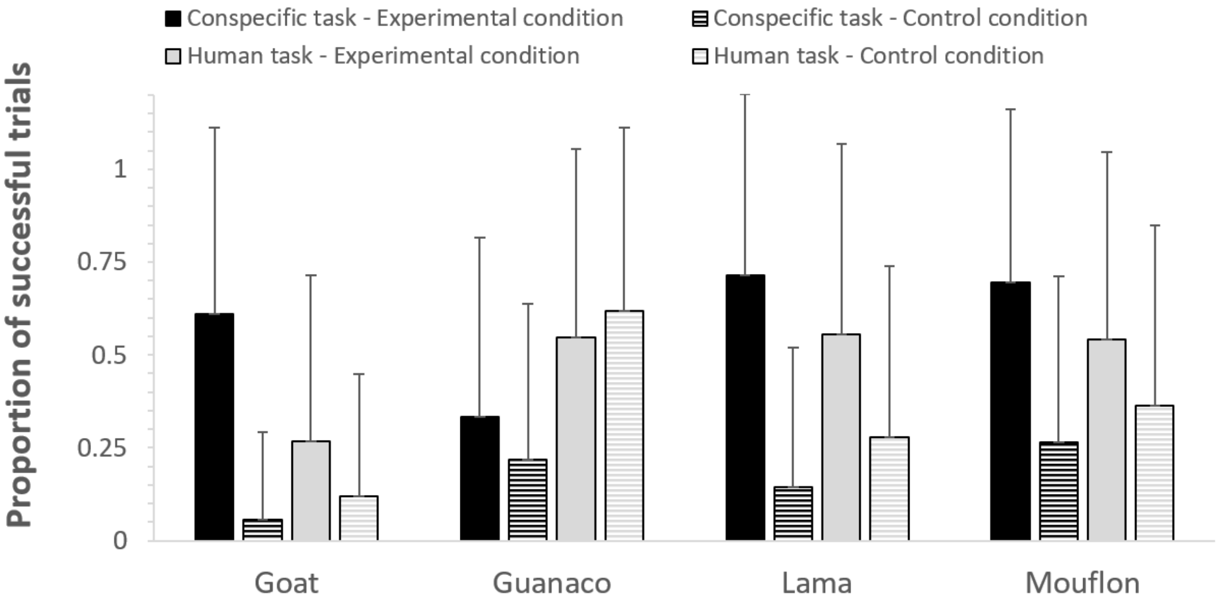

Table 1. For each species, subjects participating in the task, including their sex and age class, and the number of trials in which they participated, for each task (Conspecific and Human) and condition (Experimental and Control).

Species	**Subject**	**Age class**	**Sex**	**Number of administered trials**			
				Consp. (Exper.)	**Consp. (Control)**	**Human (Exper.)**	**Human (Control)**
Goat	1	Adult	Female	3	3	4	6
	2	Adult	Female	0	0	3	2
	3	Adult	Female	0	0	5	5
	4	Adult	Female	0	0	4	4
	5	Infant	Female	0	0	6	6
	6	Infant	Female	0	0	5	2
	7	Adult	Female	1	1	5	6
	8	Adult	Female	0	0	6	6
	9	Adult	Female	1	1	6	6
	10	Adult	Female	6	3	6	5
	11	Infant	Male	0	0	2	2
	12	Adult	Female	0	0	6	6
	13	Adult	Female	4	4	5	5
	14	Infant	Male	0	0	4	5
	15	Adult	Female	1	3	3	5
	16	Adult	Female	1	2	6	6
	17	Adult	Male	1	1	6	6
Guanaco	Hembra abajo	Adult	Female	7	6	6	8
	Hembra arriba	Adult	Female	5	13	10	10
	Rojo	Adult	Male	6	7	8	8
	Verde	Adult	Male	6	6	7	8
Lama	Flax	Adult	Male	3	2	6	6
	Krümel	Adult	Male	3	3	6	6
	Sancho	Adult	Male	1	2	6	6
Mouflon	Circulo amarillo	Adult	Female	6	7	8	6
	Circulo naranja	Adult	Female	1	2	9	9
	Cuadrado blanco	Adult	Female	9	11	8	11
	Cuadrad orojo	Adult	Female	8	6	7	7
	Cuadrado verde	Adult	Female	6	4	9	12
	Macho	Adult	Male	6	4	7	10

Table 2. Summary of the results for the full model, including the reference category for categorical predictors, estimates, standard errors (SE), z-values (*z*), confidence intervals (CIs) and *p* values for each test predictor (in bold, when significant) and control predictor (in italics).

Predictors	**Reference category**	**Estimate**	**SE**	***z***	**2.5% CI**	**97.5% CI**	***P***
Intercept	-	-2.95	0.48	-6.13	-3.89	-2.01	-
Species	Guanaco	2.17	0.52	4.15	1.15	3.20	-
	Lama	1.05	0.72	1.46	-0.36	2.45	
	Mouflon	1.63	0.47	3.48	0.71	2.54	
Condition	Experimental	2.77	0.55	5.01	1.69	3.85	-
Task	Human	1.08	0.34	3.15	0.41	1.75	-
Species*Condition	Guanaco, Experimental	-1.82	0.56	-3.23	-2.93	-0.71	0.005*
	Lama, Experimental	0.00	0.75	0.00	-1.47	1.47	
	Mouflon, Experimental	-0.60	0.52	-1.16	-1.63	0.42	
Task*Condition	Human, Experimental	-1.54	0.45	-3.44	-2.42	-0.66	<0.001*
Age class	Infant	-0.86	0.64	-1.35	-2.11	0.39	0.160
Sex	Male	-0.07	0.36	-0.21	-0.77	0.63	0.834
Trial	-	-0.02	0.04	-0.40	-0.10	0.07	0.693

The model had a binomial distribution, and included subject identity as random effect. The asterisks denote significant *p* values for the test predictors.

CHAPTER 7

Neophobia in 10 ungulate species – a comparative approach

SHORT TITLE: Neophobia in ungulates

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ABSTRACT

Neophobia (the fearful reaction to novel stimuli or situations) has a crucial effect on individual fitness, and can vary within and across species. However, the factors predicting this variation are still unclear. In this study, we assessed whether individual characteristics (rank, social integration, sex) and species socio-ecological characteristics (dietary breadth, group size, domestication) predicted variation in neophobia. For this purpose, we conducted behavioral observations and experimental tests on 78 captive individuals belonging to 10 different ungulate species - an ideal taxon to study inter-specific variation in neophobia given their variety in socio-ecological characteristics. Individuals were tested in their social groups by providing them with familiar food, half of which had been positioned close to a novel object. We monitored the individual latency to approach and eat food, and the proportion of time spent in its proximity. Using a phylogenetic approach and social network analyses, we showed that across ungulate species, neophobia was higher in socially more integrated individuals, as compared to less integrated ones. In contrast, rank and sex did not predict inter-individual differences in neophobia. Moreover, species differed in their levels of neophobia, with Barbary sheep being on average less neophobic than all the other study species. As group size in Barbary sheep was larger than in all the other study species, these results support the hypothesis that larger group size predicts lower levels of neophobia, and confirm ungulates as a highly promising taxon to study animal behavior and cognition with a comparative perspective.

KEY WORDS: neophobia, ungulates, personality, dietary breadth, social integration, social group size

SIGNIFICANCE STATEMENT: In several species, individuals may respond fearfully to novel stimuli, therefore reducing the risks they may face. However, it is yet unclear if certain individuals or species respond more fearfully to novelty. Here, we provided food to 78 individual ungulates with different characteristics (e.g., sex, rank, social integration, group size, domestication, dietary breadth), in different controlled conditions (e.g., when food was close to novel or to familiar objects). Across species, we found that socially integrated individuals responded more fearfully in all species. Moreover, being in larger groups decreased the probability of fearfully responding to novelty.

INTRODUCTION

Neophobia has been defined as the fearful reaction to novel stimuli or situations (Greenberg and Mettke-Hofmann 2001; Mettke-Hofmann 2017). In several taxa, neophobia is known to provide crucial fitness benefits (e.g., Wilson et al. 1994; Boissy 1995; Gosling and John 1999; Wolf et al. 2007). More neophobic individuals, for instance, are less likely to consume novel food which could be toxic, and may have a lower chance of encountering predators and competitors, as they are less explorative (e.g., Robertson 1982; Greenberg and Mettke-Hofmann 2001; Crane et al. 2020). However, neophobia also comes with costs, as it may reduce competitive abilities by for instance decreasing exploration of novel food sources (Cole and Quinn 2012) and the probability of innovation (Greenberg 2003; Carere and van Oers 2004; Smith and Blumstein 2008; Cole and Quinn 2012; Ferrari et al. 2015). Furthermore, neophobia may increase stress-related mortality, as neophobic individuals are more easily stressed in novel situations (Carere and van Oers 2004) and might have higher energetic costs for vigilance (see Crane et al. 2020). Therefore, neophobia may have complex implications for individual fitness (Smith and Blumstein 2008; Ferrari et al. 2015), and different individuals and species may find different ways to balance the benefits and costs linked to neophobia (Greenberg 2003).

At the individual level, for instance, neophobia might be linked to individual dominance rank. In social species, more dominant individuals usually have better access to resources (e.g., space, food, mates) as compared to subordinates (Arave and Albright 1976; Ellis 1995; Clarke and Faulkes 1997). Therefore, dominant individuals may gain lower potential payoffs from novelty, and might be more neophobic than subordinates (Hegner 1985; Greenberg-Cohen et al. 1994; Lahti 1998; Laland and Reader 1999; Greenberg and Mettke-Hofmann 2001; Wolf et al. 2007). However, while some studies have found evidence that subordinates are less neophobic than dominant conspecifics (Katzir 1982; Di Bitetti and Janson 2001; Stahl et al. 2001; Boogert et al. 2006), at least in some contexts (e.g., Dingemanse and Goede 2004), other studies have not (e.g., Boogert et al. 2006; Mettler and Shivik 2007; Moretti et al. 2015).

Similarly, social integration in the group might be linked to differences in neophobia. Strong social bonds, for instance, enhance individual fitness (e.g., Silk et al. 2003; Cameron et al. 2009; Silk et al. 2009; Schülke et al. 2010; Silk et al. 2010; Archie et al. 2014), and integration in the social group increases others' tolerance over food (Amici et al. 2020; Dell'Anna et al. 2020). Therefore, individuals that are better integrated in the social network might also gain lower potential payoffs from novelty (as compared to less integrated group members), and thus be more risk-aversive and less prone to explore novelty (see Wolf et al. 2007).

Furthermore, neophobia might also differ between sexes. On the one hand, males show higher variance in reproductive payoff than females, so that males should thus be less risk aversive and less neophobic than females (Cornwell-Jones and Kovanic 1981; Clutton-Brock 1988; Laviola and Loggi 1992; Schuett et al. 2010; Crane et al. 2020). On the other hand, males are often dominant over females, at least in mammals, and the positive link between rank and neophobia may be confounded by more specific sex effects (see Wingfield et al. 1987; Crane et al. 2020).

At the species level, less neophobic species may also be characterized by more generalist diets (Glickman and Sroges 1966; Clarke and Lindburg 1993), extractive foraging (Day et al. 2003), higher environmental variability (Greenberg 1984, 1990; Mettke-Hofmann et al. 2002; Martin and Fitzgerald 2005; Bergman and Kitchen 2009) and lower predation pressure (Crane and Ferrari 2017). More generalist species, for instance, feed on a higher number of food items with highly variable quality, so that being less neophobic would allow them to more easily switch across resources and explore novel ones (Greenberg 1983; Greenberg and Mettke-Hofmann 2001; Visalberghi et al. 2002; Day et al. 2003). Furthermore, domesticated species might be less neophobic. By having been selected for their ability to live in close association with humans, domesticated animals might show less fearful responses to novel stimuli, as also suggested by recent studies in dogs and rats (Sheppard and Mills 2002; Kaulfuß and Mills 2008; also see Modlinska et al. 2015; Moretti et al. 2015).

Finally, group size may also explain differences in levels of neophobia. In species with larger group size, for instance, individuals are usually less vulnerable to predation and more easily benefit from social facilitation when interacting with novel food, so that they might be overall less neophobic (Pulliam and Caraco 1984; Beck and Galef 1989; Galef et al. 1990; Visalberghi and Addessi 2000; Addessi and Visalberghi 2001; but see Stöwe et al. 2006; Addessi et al. 2007). However, group size might not necessarily have an impact in evolutionary terms. Several studies, for instance, suggest a direct effect of group size on neophobia in developmental terms, through direct experience (Brown et al. 2013; Modlinska and Stryjek 2016). Ravens (*Corvus corax*), for example, show different reactions to novel objects depending on whether they are tested alone or in groups (Stöwe et al. 2006). Some studies have indeed found a link between living/being tested in larger groups and showing reduced neophobia within different species (Heinrich and Marzluff 1991; Visalberghi and Addessi 2000; Lonsdorf 2006; Tarnaud and Yamagiwa 2008; Costa et al. 2014; Moretti et al. 2015). However, others have found little to no evidence (Ryer and Olla 1991; Brown and Laland 2001; Brown and Laland 2002; Stöwe et al. 2006; Apfelbeck and Raess 2008; Dardenne et al. 2013).

In this study, we aimed to study inter-individual and inter-specific variation in neophobia in ungulates. Ungulates are a largely neglected taxon in comparative psychology, despite their high variation in socio-ecological characteristics, which makes them an ideal candidate to test how specific socio-ecological conditions may favor the emergence of certain traits or behaviors (Caicoya et al. in review; see Shultz and Dunbar 2006; Schaffer et al. 2020). In this study, we tested neophobia toward novel objects (see Greenberg 1992; Mettke-Hofmann et al. 2002; Greenberg 2003; Brown and Jones 2016) by providing ten ungulate species with familiar food, half of which had been positioned close to a novel object. Our study species differed in their socio-ecological characteristics and in particular in terms of dietary breadth, group size and domestication (see Methods; see TABLE 1). All species were tested in captivity: while captive individuals are usually expected to be less neophobic than their wild counterparts (Bergman and Kitchen 2009; van de Waal and Bshary 2010; Benson-Amram et al. 2013; but see Crane and Ferrari 2017), neophobia is also known to have a strong genetic component (Mettke-Hofmann 2017). Hence, testing captive individuals should reproduce “consistent and meaningful differences among species according to their evolutionary history” (see Crane et al. 2020 , p.220). Based on existing literature, we expected differences in neophobia both within and across species. In particular, we predicted that neophobia should be higher in more dominant individuals (Prediction 1), in individuals that are better integrated in their social group (Prediction 2) and in females (Prediction 3). Moreover, we predicted that neophobia should vary across species, being higher in species with lower dietary breadth (Prediction 4), living in smaller groups (Prediction 5), and/or having been domesticated (Prediction 6).

METHODS

Ethics. The study was approved by the welfare managers at the zoos of Barcelona, Barben, Nuremberg and Leipzig, who controlled and approved all the procedures. The study was mainly observational, all the animals participated on a completely voluntary basis, individuals were not separated from their social groups and no invasive procedures were used. Therefore, no formal approval was required. During the task, individuals were never water or food deprived, and motivation to participate was ensured exclusively by the use of highly preferred food belonging to their natural diets. The experiments thus provided a form of enrichment for the subjects and did not present any risks or adverse effect. The study was carried out in accordance with the national regulations of all the countries in which the study took place.

Subjects. We studied 78 subjects belonging to 10 ungulate species across three years. Subjects were housed in their natural groups at the zoos of Barcelona (Spain), Barben (France), Nuremberg and Leipzig (Germany), and were all individually recognizable. We tested one group of 5 oryx (*Oryx dammah*) in Barcelona; one group of 7 dromedaries (*Camelus dromedarius*) and one group of 7 red deer (*Cervus elaphus*) in Barben; one group of 15 barbary sheep (*Ammotragus lervia*) in Nuremberg; one group of 6 giraffes (*Giraffa camelopardalis rothschildi*), 2 groups of goats (*Capra aegagrus hircus*), one with 9 and one with 7 individuals, one group of 4 guanacos (*Lama guanicoe*), one group of 4 lamas (*Lama glama*), one group of 4 Przewalski horses (*Equus ferus przewalskii*) and one group of 10 sheep (*Ovis aries*) in Leipzig. For the analyses we had to remove four subjects (i.e., two goats and two sheep) for which we had no behavioral information (as the individuals were removed from their groups during the study and observations could not be completed). Therefore, the final study sample was N=74. None of the study subjects had ever been tested in a neophobia test before and none had, to the best of our knowledge, come in contact with objects with the same shape and color as the ones used in this study, although all species occasionally participated in enrichment activities. None of the study subjects had ever participated in an experimental task, except for 3 of the 6 giraffes, which had participated in (i) a task on physical cognition in which they had been exposed to two small plastic containers (~15x15x3 cm) that could contain food (Caicoya et al. 2019), (ii) a quantity discrimination task in which they had been tested with two white trays containing food (Caicoya et al. 2020) and (iii) an inhibition task in which they had been exposed to a plastic cylinder with food (data unpublished).

All groups included males and females of different age and ranks (see Online Resource, TABLE S-1), and differed in their socio-ecological characteristics, including dietary breadth, social group size and domestication (see TABLE 1). To classify our study species according to their dietary breadth, social group size and domestication, we used data from literature (see references in TABLE 1). However, these studies were conducted with different procedures and in very different conditions, so that we considered inappropriate to calculate species-specific indexes and use them as direct test predictors in the models (see below), as they were not strictly comparable. Dietary breadth, for instance, may be measured in terms of how many plant species are eaten (i.e., taxonomic dietary diversity), or how many plant lineages (i.e., phylogenetic dietary diversity), but these measures are not positively correlated (Kartzinel & Pringle, 2020). Moreover, even if the same index is used, methodological differences in the way data are collected (e.g., observational effort, sampling areas) can importantly affect the results of these categorizations. In the models, we therefore tested for inter-specific differences (including species as test predictor), and then interpreted the results based on the socio-ecological information on the species, as available from literature. Furthermore, as group size might affect neophobia independently of evolutionary history (see above), we also included the actual size of our study groups as a possible explanation of differences in neophobia (see TABLE 1).

Behavioral observations. We conducted behavioral observations on each study group to determine the dominance rank and the social integration of each individual. Throughout the study period, we recorded via *all occurrence sampling* all dyadic agonistic interactions with a clear winner-loser outcome (i.e., threat, chase, fight), for each species (Altmann 1974). We assessed dominance hierarchy using the Elo method (Neumann et al. 2011) and, in particular, the EloRating package, version 0.43 in R (R Core Team, version 3.5.0). We set 1000 as the individual start values, and 100 as the k factor, which is a weighted constant based on winning probability (Albers and Vries 2001; Sánchez-Tójar et al. 2018). We then averaged these values through the study periods, and standardized them to range from 0 (i.e., lowest rank) to 1 (i.e., highest rank). Below, we refer to these values simply as Elo-ranks (TABLE S-1). For more studies using the Elo method, see for instance Gomez-Melara et al. 2021 or Langos et al. 2013. For the giraffes and two of the red deer, we observed no agonistic interactions throughout the study period. For these individuals, rank was assessed by the experimenter together with the animal keepers, based on observations of priority of access to food (i.e., ranking all the giraffes from 1 to 6, and the two red deer from 1 to 7, and then rescaling the ranks to be between 0 and 1).

In each group, we further assessed Eigenvector centrality as a measure of individual social integration. For this reason, we determined the spatial proximity network in each study group, based on observational data collected with 100 *instantaneous scans* per group. Scans were made every 15 minutes across several days, and recorded the spatially closest individual (“nearest neighbor”) of each group member (Altmann 1974). We built an undirected weighted matrix for social network analyses, which were run using the following packages in R: vegan (version 2.5-3; Oksanen et al. 2018), asnipe (version 1.1.10; Farine 2013), and igraph (version

1.2.1; Csardi and Nepusz 2006). Social network analyses assessed individuals' Eigenvector centrality (TABLE S-1), which is a measure proportional to the sum of the centralities of each individual's neighbors, and measures the importance of individuals as "social hubs" (Farine and Whitehead 2015; Farine 2017). As multiple researchers conducted behavioral observations, we ensured inter-observer reliability by starting data collection only after reaching inter-observer reliability >90%, as estimated by comparing multiple random samples of behavior (Kaufman and Rosenthal 2009).

Neophobia test. In all species, we administered the neophobia task in a familiar environment, testing all subjects together in their study group, in their outer enclosure. In the neophobia task we included two different phases, the habituation phase (consisting of two sessions) and the experimental phase (consisting of two further sessions). All sessions were administered in different days, to reduce the effect of other contingencies on individual response. In the habituation phase, we placed preferred familiar food in two familiar locations, approximately 2m from each other (although this distance was slightly increased/reduced depending on the animal size). The position of the two food locations was the same through all trials in each species, but we waited to place all items (and therefore to start the trial) until all animals were further than 1m from both locations. As animals in all study groups had visual access to the set-up, sessions started when the food (and the novel object) had been positioned. To ensure high motivation, we used familiar food that was highly preferred by the study subjects. In the experimental phase, we repeated exactly the same set-up, but close to one of the two food locations (i.e., approximately 1m, although this distance was increased/decreased depending on the animal size), we also positioned one visible novel object (i.e., either a plastic red bucket or a plastic blue bowl, either right or left, depending on the session, approximately 20 x 20 x 40 cm and 30 x 30 x 20 cm, respectively). We administered two sessions for each phase and study group, starting with the same object for all species to increase comparability. Each session lasted 10 minutes or until the food in one of the two locations was consumed. We used two different novel objects instead of two repeats of the same object, to create more accurate measures of novelty response (see Greggor et al. 2015), and we applied short sessions to avoid habituation to the novel object (Greenberg and Mettke-Hofmann 2001). For Barbary sheep, we used other objects instead (i.e., a plastic red ball and a plastic blue bucket, with the same dimensions as the objects above), as the keepers already used objects similar to the ones used for the other species during their daily feeding routine. For oryx, we administered only one experimental session (as the coronavirus outbreak did not allow us to complete testing). Although we originally aimed to use novel food to measure individual levels of neophobia, we had to use familiar food and novel objects in order to comply with the procedural recommendations of the zoos in which data were collected.

Coding. We video-recorded all sessions. From the videos, we coded the identity of each individual approaching the food (i.e., individual latency to approach with the muzzle within 1m from the food), the time spent in proximity of the food (i.e., from the time approaching the food to the time moving more than 1m away from the food), and the latency to eat the food (i.e., from the moment the subject first approached it). In the experimental phase, we also further specified the food approached (i.e., familiar or novel). We then prepared our datasets, entering six lines per individual, one for each of the two sessions of the habituation phase, and two for each of the two sessions of the experimental phase (for each session, one line for the familiar food, and one for the food close to the novel object). For each line, we entered the individual latency to approach food for the first time in the session, the individual latency to eat the food for the first time in the session, the total time the individual spent in proximity of the food in the session, and the time the individual did not spend in proximity. We further specified the subject identity, its species, sex, rank and centrality (i.e., social integration, see above), the session number, trial duration and whether the food approached was familiar or novel. If subjects never approached the food in one session, we assigned them the total duration of the trial as latency (i.e., 600 seconds), as often done in literature on neophobia (e.g., Greggor et al. 2016). By simultaneously presenting food close to a novel object or not, we could avoid order effects and reduce the possibility that our measure was an artefact of motivation (as both kinds of food were available close to each other and at the same time). To calculate inter-observer reliability, the last author recoded 20% of the recorded videos (i.e., 9 of the 44 sessions recorded in the 11 study groups). Inter-observer reliability was excellent (i.e. Spearman exact correlation for latency to approach food: N = 97, rho = 0.999, $p < .001$; for latency to eat food: N = 97, rho = 0.984, $p < .001$; for time spent in proximity: N = 97, rho = 0.995, $p < .001$).

Statistical analyses. Analyses were conducted using generalized linear mixed models (Baayen et al. 2008) with the MCMCglmm package (version 1.0.1; Hadfield and Nakagawa 2010) in R (R Core Team, version 3.5.0). To control for phylogenetic relationships across study species, we used the package ape (Paradis and Schliep 2019) to build a consensus tree from 10 000 trees, which had been subsampled and pruned from the mammal tree of life to match our study species (Upham et al. 2019). In all models, we then included a covariance matrix with the phylogenetic relationship between species, as based on the consensus tree (for a similar approach, see e.g. Lukas and Clutton-Brock 2017; Lukas and Huchard 2019; Lukas and Clutton-Brock 2020). All models were run with a Gaussian distribution and non-informative priors, using 1 000 000 iterations, a burn-in of 100 000 and a thinning interval of 300, to facilitate convergence and minimize autocorrelation (see e.g. Lukas and Clutton-Brock 2017; McElreath 2020). We repeated all the analyses three times, visually inspected the models for convergence and found no evidence of convergence issues. We considered terms to be statistically significant when the pMCMC values were lower than 0.05 (see e.g. Lukas and Clutton-Brock 2017).

We conducted three different models, assessing whether latency to approach food (Model 1), latency to eat food (Model 2) and time spent in proximity of food (Model 3) varied across species and individuals, depending on the side approached (i.e., close/opposite to the novel object; hereafter, novelty). In particular, we assessed whether latency to approach food (Model 1), latency to eat food (Model 2) and time spent in proximity of food (Model 3) were predicted by the 2-way interactions of novelty with individual rank (Prediction 1), novelty with individual centrality (Prediction 2), novelty with sex of subject (Prediction 3) and novelty with species (Predictions 4-6). Two-way interactions also included interaction terms as main effects. In all models, we further controlled for session number and duration (in Model 3, as offset term), and included subject identity as random factor. In case of significant categorical predictors with more than two categories (i.e., when the interaction between novelty and species was significant), we conducted post-hoc tests with the emmeans package (version 1.5.0, Lenth et al. 2020).

RESULTS

In Model 1, after accounting for phylogeny, we only found a reliable effect of the 2-way interaction of novelty with centrality on the latency to approach food (posterior estimate: 267.4 [95% confidence intervals, CIs: -1.6 to 511.8], $p = 0.046$). In particular, more central individuals had a higher latency to approach the novel side (as compared to the familiar one), while the pattern reversed for less central individuals, which had a much higher latency to approach the familiar side. Rank and sex had no effect on the latency to approach food (neither in interaction with novelty, nor as main effects), and none of the species differed in the latency to approach the novel versus the familiar side. Session number had no significant effect on the latency to approach food.

After accounting for phylogeny in Model 2, we found no significant effect of rank, centrality or sex on the latency to eat food (neither in interaction with novelty, nor as main effects). Moreover, none of the species differed in the latency to eat food on the novel versus the familiar side. Session number had no significant effect on the latency to eat food.

Finally, after accounting for phylogeny in Model 3, we found a significant effect of rank (posterior estimate: 84.8 [95% CIs: 19.7 to 146.6], $p = 0.013$) and centrality (posterior estimate: 201.4 [95% CIs: 41.0 to 354.2], $p = 0.017$), with time spent in food proximity being higher for higher-ranking and more central individuals, independently of novelty. Moreover, none of the species differed in the time spent close to the novel versus the familiar side, except for Barbary sheep, which spent significantly more time close to the novel than to the familiar side (post-hoc tests, posterior estimate: -124.1 [highest posterior-density intervals: -190.8 to -56.8]). Finally, session number had no significant effect on the time spent in food proximity.

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DISCUSSION

In this study, we tested neophobic responses to novel objects in 74 subjects of 10 different ungulate species, and found differences both within and across species that partially supported our predictions. In particular, more socially integrated (i.e., central) individuals were more neophobic than less central ones, showing a higher latency to approach food closer to novel objects (in line with Prediction 2). However, rank and sex did not predict inter-individual differences in neophobia (in contrast to Predictions 1 and 3). Moreover, species differed in their levels of neophobia, with Barbary sheep being less neophobic than all the other species, and spending a higher proportion of time close to novel objects. Given their socio-ecological characteristics (see below and TABLE 1), these results support the hypothesis that actual group size is the main driver of group differences in neophobia (in line with Prediction 5), while dietary breadth and domestication played little to no role (in contrast to Predictions 4 and 6).

Our results showed clear inter-individual differences in levels of neophobia. Less central individuals had a lower latency to approach the novel side (as compared to the familiar one), suggesting that individuals being less integrated in their social group are also less neophobic, or perhaps more likely to overcome neophobia to increase their food intake. These results are in line with recent studies on primates showing that less central individuals have a lower probability of retrieving food (Amici et al. 2020; Dell'Anna et al. 2020), and are also more likely to overcome neophobia when access to food is uneven across group members (Amici et al. 2020). Across species, less central individuals may more often have to rely on novel food sources to get a share of resources, so that lower neophobia might be selected for. Alternatively, it is possible that different personalities may have complementary functions at the group level, with more neophobic individuals contributing to the maintenance of group cohesion (thus also being more central), and less neophobic individuals contributing to the exploration of novel resources and the spread of the group (see Michelena et al. 2009). In both cases, social integration in the group appears to have a complex encompassing effect on individual fitness, in line with other studies in human (Smith and Christakis 2008; Holt-Lunstad et al. 2010) and nonhuman primates (Silk et al. 2003; Silk et al. 2009; Schülke et al. 2010; Silk et al. 2010; Archie et al. 2014; Dell'Anna et al. 2020).

Our results also showed inter-specific differences in neophobia. In particular, Barbary sheep showed a significant preference for the side with the novel object, as compared to the familiar side. In contrast, all the other species were equally likely to select the novel and the familiar side. Which socio-ecological differences best explain these differences? Barbary sheep are not a domesticated species, they show relatively high levels of dietary breadth in the wild (although lower than other species like goats and red deer), and in the wild they usually live in social groups with an intermediate size (see TABLE 1). However, the group size of Barbary sheep in the zoo was larger than all the other study species (see TABLE 1). Therefore, our results provide support for the hypothesis that neophobia might decrease when individuals live in larger groups. These results are in line with findings in other taxa, including birds (Heinrich and Marzluff 1991; Stöwe et al. 2006), primates (Visalberghi and Addessi 2000; Lonsdorf 2006; Tarnaud and Yamagiwa 2008; Gustafsson et al. 2011; Masi et al. 2012), cows (Costa et al. 2014), dogs and wolves (Moretti et al. 2015). However, more studies are needed to confirm these results. First, it would be especially important to confirm these findings by comparing conspecifics living in similar conditions, but having groups of different size. Second, it would be interesting to compare how individuals living in larger groups (as Barbary sheep in our study) perform when being tested alone. In this way, we could better disentangle whether differences in individual neophobic levels are predicted by the group size in which individuals grow, or rather by the group size in which they are tested. Such an approach would be especially interesting considering the ongoing debate over the benefits of individual and group testing of personality in social species (e.g., Magnhagen and Bunnefeld 2009; Webster and Ward 2011).

Overall, our findings confirm sociality as a crucial driver of neophobia in animals. On the one hand, social integration in the group may provide key fitness benefits and thus reduce the potential payoffs that individuals might gain by overcoming neophobia and exploring novelty. On the other hand, larger group sizes may provide more opportunities for social learning, reduce stress levels and ultimately decrease neophobia. Therefore, sociality appears to provide individuals with significant plasticity in their neophobic responses. Further exploring the link between fitness, sociality and neophobia in other taxa is surely a rewarding endeavour for future studies. For instance, the inclusion of solitary species or eusocial species might reveal further important effects of other aspects of sociality on individual neophobic responses.

In contrast, we find no support for the hypotheses that neophobia is higher in species that have a wider dietary breadth in the wild (Prediction 4) or that have been domesticated (Prediction 6). At the moment, however, these results should be taken with caution, for several reasons. First, there are yet no standardized methods to collect socio-ecological data across ungulate species: in general, even when the same indexes are used (e.g., Simpson's index of diversity, number of species fed on), methods to collect data often differ across studies due to objective difficulties when collecting data in the wild. Therefore, direct comparisons across species should always be taken with caution, because different methodological approaches might account for much variation in the results. Second, socio-ecological characteristics may also vary strongly within species, across different groups or populations, so that generalizations should be taken with caution (see e.g., Des Roches et al. 2018). This is no trivial issue, as it is still unclear to what extent socio-ecological factors affect behavior in evolutionary or developmental terms (see e.g., Waal and Johanowicz 1993; Boesch 2012; Brown et al. 2013). Third, inter-specific differences linked to domestication might have been masked by the fact that all our study animals lived in captivity, and have therefore had extensive contact to humans through development, causing a general decrease in neophobia in the study subjects. Several studies have shown that captive individuals are often less neophobic, more explorative and/or innovative than wild conspecifics, likely because they are more often exposed to novel objects, and/or have more time and energy to devote to these activities (Benson-Amram et al. 2013; Forss et al. 2015; Lazzaroni et al. 2019; but see e.g., Crane and Ferrari 2017 for evidence that neophobia may actually be higher in captive than wild conspecifics). Fourth, factors other than dietary breadth, group size or domestication might (also) account for inter-specific differences in neophobia. Predation pressure or environmental variability, for instance, might also predict differences in neophobia. By testing captive individuals, we could control for predation risk in this study, but future studies in the wild should ideally test how differences in predation pressure across and within species might affect individual neophobic response. Finally, it should be noted that different measures of neophobia might provide very different results. For this reason, our study relied on different measures (i.e., latency to approach and eat food, time spent in proximity), and indeed, these provided complementary but not identical results. For instance, the presence of more group members in our study appeared to decrease neophobia when measured as time spent in object proximity, but not when measured as latency to approach or eat food, in line with a previous study on ravens (*Corvus corax*; Brown et al. 2013). In the future, studies using a larger variety of novel stimuli (including acoustic or olfactory ones) and directly manipulating food novelty (e.g., changing food taste and texture) will be especially important.

Overall, our study showed a link between low neophobia and low centrality and also larger group size. More studies on more individuals and species are surely needed to confirm these preliminary results. First, future studies should better control for a variety of potentially confounding factors (e.g., previous exposure to human-made objects, enclosure size, group structure, previous life history of the study animals). Second, our study revealed no significant effect of sex on individual levels of neophobia. In the future, it would be interesting to explore whether the inclusion of more ungulate species would lead to different results, as sex might predict differences in neophobia only in species with larger sexual dimorphism (see e.g., Amici et al. 2019, showing that individuals of the larger sex are more likely to innovate than those of the smaller sex). Third, our study only included captive individuals that had spent their whole life in captivity. Captive conditions, however, might increase individual exposure to novel stimuli during lifetime, perhaps decreasing individual neophobic responses and degrading potential inter-individual and inter-specific differences in neophobia. Therefore, future comparative studies should ideally also include individuals from wild groups, whose socio-ecological characteristics should be directly measured with standardized protocols. Fourth, our study measured neophobic response in two different sessions, and found no effect of session number on individuals' neophobic response. While this suggests that our study subjects consistently responded to the stimuli in this study, future research would especially benefit from including more trials and more stimuli to better measure repeatability of the neophobia responses across trials and contexts, for longer time frames. In line with this, this study explored individual reaction to novel objects, which has been correlated to food neophobia and risk taking in other studies (Coleman and Wilson 1998; Bókony et al. 2012; Greggor et al. 2015). However, neophobia might also strongly vary across contexts (e.g., in foraging versus antipredator contexts, toward physical versus social stimuli; e.g., Coleman and Wilson 1998; Boogert et al. 2006; see Greggor et al. 2015). Therefore, future studies should also better disentangle how these different forms of neophobia are linked to each other and distributed within and across species. These studies will not only be important to understand how neophobia responses are distributed between and within species, but will also have an essential role in conservation and animal welfare, to better predict resilience to human changes, success during reintroduction programs, and/or the effect of enrichment activities in captivity (e.g., Lee 1991; Dukas and Bernays 2000; Nicolakakis et al. 2003; Reader and Laland 2003; Sol et al. 2005b; Sol et al. 2005a; Ramsey et al. 2007; Lefebvre 2011; Griffin 2016).

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Conflicts of interest/Competing interests

Not applicable

Availability of data and material

Data and script are made available as supplementary information

Code availability

The models are described in details in the text, including the packages used, and the script is provided as supplementary information.

Authors' contributions

Not applicable

Ethics approval

The study was approved by the welfare managers at the zoos of Barcelona, Barben, Nuremberg and Leipzig, who controlled and approved all the procedures. The study was mainly observational, all the animals participated on a completely voluntary basis, individuals were not separated from their social groups and no invasive procedures were used. Therefore, no formal approval was required. During the task, individuals were never water or food deprived, and motivation to participate was ensured exclusively by the use of highly preferred food belonging to their natural diets. The experiments thus provided a form of enrichment for the subjects and did not present any risks or adverse effect. The study was carried out in accordance with the national regulations of all the countries in which the study took place.

Consent to participate

Not applicable

Consent for publication

Not applicable

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Fig 1 For each species, mean proportion of time spent (+ SE) close to food on the familiar side (i.e., with no object: white bars) and on the novel side (i.e., with the novel object: grey bars)

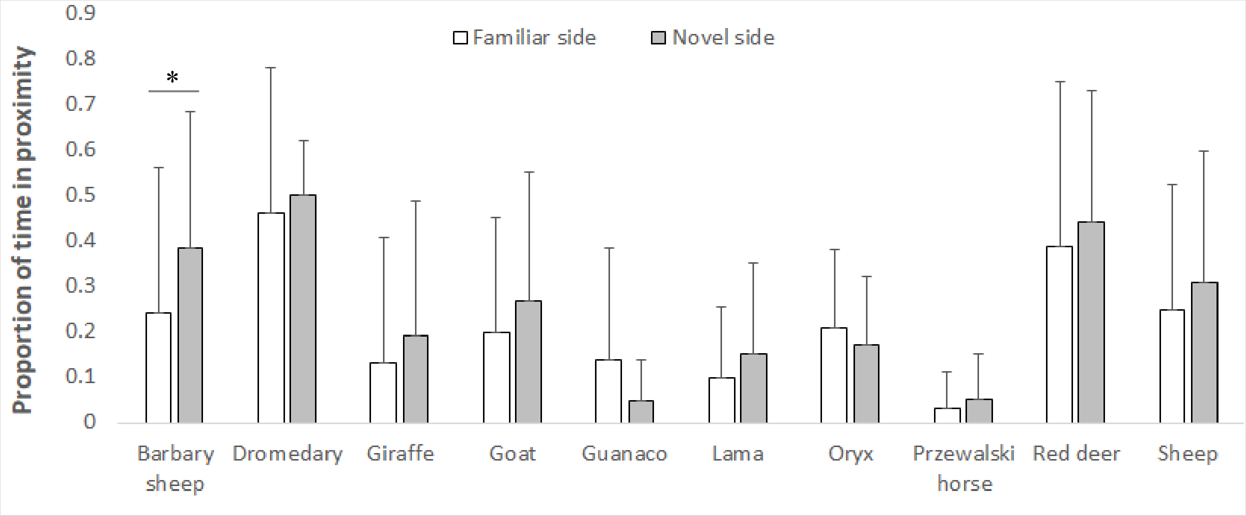

TABLE 1 Socio-ecological characteristics of the species tested (in bold, those showing a significance preference for the novel side).

SPECIES	**Dietary breadth (wild)**	**Group size (wild)**	**Actual group size**	**Domestication**
Barbary sheep	69-79[1]	5-25[2]	15	No
Dromedary	17-58[3]	2-20[4]	7	Yes
Giraffe	93[5]	1-46[6]	6	No
Goat	33-126[7]	5-100[8]	7-9	Yes
Guanaco	35-76[9]	2-20[10]	4	No
Lama	>35[11]	16[12]	4	Yes
Oryx	45[13]	10-30[12,14]	5	No
Przewalski horse	52[15]	<10[16]	4	No
Red deer	145[17]	4-10[18]	7	No
Sheep	29-79[7,8,19]	2-60[20,21]	10	Yes

Ogren 1962; Ramsey and Anderegg 1972, [2] Gray and Simpson 1982, [3] Elmi et al. 1992; Am Abbas et al. 1995, [4] Gauthier-Pilters and Dagg 1981, [5] Berry and Bercovitch 2017, [6] Muller et al. 2018, [7] González-Pech et al. 2015; Mellado 2016, [8] Nowak and Paradiso 1983, [9] Puig et al. 2001; Baldi et al. 2004, [10] Bank et al. 2002; Marino and Baldi 2008, [11] Posse and Livraghi 1997, [12] Nowak and Walker 1999, [13] Gilbert and Woodfine 2004, [14] Newby 1984, [15] Slivinska and Kopij 2011, [16] Grum-Grzhimailo 1889, [17] Gebert and Verheyden-Tixier 2001, [18] Gibson and Guinness 1980; Clutton-Brock et al. 1982, [19] Fox and Streveler 1986, [20] McClelland 1991, [21] Maisels 1993.

CHAPTER 8

Innovation across 13 ungulate species: problem solvers are less integrated in the social group and less neophobic.

SHORT TITLE: Innovation in ungulates

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ABSTRACT

Innovation is the ability to solve new problems or find novel solutions to familiar problems, and it is known to provide animals with crucial fitness benefits. Although this ability has been extensively studied in some taxa, the factors that predict innovation within and across species are still largely unclear. In this study, we used a novel foraging task to test 111 individuals belonging to 13 ungulate species - a still understudied taxon. To solve the task, individuals had to open transparent and opaque cups with food rewards, by removing their cover. We assessed whether individual factors (neophobia, social integration, sex, age, rank) and socio-ecological factors (dietary breadth, fission-fusion dynamics, domestication, group size) predicted participation and performance in the task. Using a phylogenetic approach, we showed that success was higher for less neophobic and socially less integrated individuals. Moreover, less neophobic individuals, individuals of domesticated species and having higher fission-fusion dynamics were more likely to participate in the task. These results are in line with recent literature suggesting a central role of sociality and personality traits to successfully deal with novel challenges, and confirm ungulates as a promising taxon to test evolutionary theories with a comparative approach.

KEY WORDS

Innovation, Problem solving, Ungulates, Neophobia, Fission-fusion, Social integration

INTRODUCTION

Innovation can be defined as the ability to solve new problems or find novel solutions to familiar problems (1,2). In humans, innovative behaviour has played a crucial role for the success of our species (3–5). However, innovation is thought to also provide fitness benefits in species other than humans, especially in complex dynamic environments where socio-ecological challenges often vary (1,2,6–10). Innovation, for instance, can be highly adaptive to exploit new food sources, to innovatively reduce predation pressure, or to effectively cope with environmental changes by better adapting to novel ecological conditions (1,2,9,11–17). From great tits (*Parus major*) opening milk bottles (18) to chimpanzees (*Pan troglodytes*) using new tools to solve novel foraging problems (19), experimental evidence has clearly shown that innovation is widespread in the animal kingdom (3,13,20,21). To date, however, it is still unclear which factors predict the distribution of innovation across species and individuals (22).

At the species level, several studies have assessed the link between the ability to innovate and specific socio-ecological characteristics of the species (e.g. 23–29). In birds, for instance, species that exploit a larger variety of habitats (23,30) or have a more urbanized lifestyle (24) also show a higher innovation rate. Similarly, the frequency of proto-tool use predicts innovation rate in primates (25) and birds (26), whereas group living is linked to the innovative exploitation of novel food sources in both birds (28,29, but see 31) and fish (27). To date, the largest majority of comparative studies on innovation have been conducted in birds and primates, with few exceptions (fish: 11; carnivores: 32; meerkats: 33; rodents: 2). However, different evolutionary pressures may be at play across species, and the inclusion of other taxa is essential to understand the limits and generalizability of specific evolutionary hypotheses (see 34–36). Some species, for instance, show high levels of fission-fusion dynamics (i.e. individuals frequently split into subgroups of varying size and composition), and may require higher cognitive skills (e.g. analogical skills, inhibition) to deal with such complex sociality (37–41). Similarly, complex cognitive skills may be linked to a wider dietary breadth, to facilitate the recognition and processing of different food types (42–44), or to social group size, to allow individuals to more effectively deal with a high number of different social partners (45–47). Fission-fusion dynamics, dietary breadth and social group size may therefore be linked to higher cognitive skills and better innovation skills. Finally, domestication might also affect the ability to innovate, as domesticated species have been selected for traits and skills that facilitate interactions with humans, and may thus be more likely to interact with anthropogenic stimuli and innovate (48,49). For some authors, however, it is also possible that domestication reduces the ecological challenges that individuals in these species face (50–52), leading to an overall reduction of cognitive skills and brain size (53).

At the individual level, innovation has been linked to an excess of energy, and it is thought to be more common in individuals who have a higher daily food intake and can thus devote more time and/or energy to innovation (20). More recent work, however, suggests that innovative behaviour, by entailing important risks, may be more common in individuals that have more limited access to resources and need to rely on innovative behaviour to survive (2,11,54). Therefore, innovation should be more common in lower-ranking individuals, who usually have little access to resources, but also in females and younger individuals, as they generally have higher metabolic costs (for a review, see 22). Moreover, other factors may explain inter-individual variation in innovation. Neophobia, for instance, is the fearful reaction to novel stimuli or situations (55), and might decrease the likelihood that individuals take part in novel tasks and solve novel problems (12, 56,57). However, although little neophobia is likely to facilitate interaction with novel set-ups, its link to innovation is still debated (22,58). Moreover, also social integration may explain inter-individual variation in innovation. Across taxa, social integration is known to provide crucial fitness benefits to individuals (primates: 59, 60; humans: 61, 62; horses: 63), and this may affect the potential payoffs when responding to novelty, with more integrated individuals being less likely to interact with novel stimuli or situations than less integrated ones (see 57).

In this study, we aimed to assess the factors that predict inter- and intra-specific variation in ungulate innovation. Ungulates offer an exceptional model for comparative research, as they show a remarkable variety of socio-ecological characteristics, including differences in fission-fusion dynamics, dietary breadth and sociality (from non-social to monogamous and large mixed stable groups) (41,57,64–67). Moreover, ungulates show important variation in terms of cognitive skills (57,66), which might be linked to the socio-ecological variation that characterizes them. Finally, ungulates have already shown complex problem-solving skills in novel foraging tasks (68), making them an ideal candidate taxon for the study of inter- and intra-specific variation in innovation. Here, we tested 111 individuals of 13 ungulate species by providing them with novel transparent and opaque cups, which they had to open to retrieve food. We then assessed whether innovation (i.e. participating and solving the task, latency to solve the task, variety of behaviours used for this purpose) differed across species and subjects depending on their socio-ecological and individual characteristics. Based on existing literature, we focused on the following socio-ecological traits, which might be linked to higher cognitive skills and/or greater ability to innovate: fission-fusion dynamics (37–40), dietary breadth (42–44), social group size (45–47) and domestication (48,49). We therefore predicted that innovation should be more likely in species with higher fission-fusion dynamics (Prediction 1), with a wider dietary breadth (Prediction 2), living in larger groups (Prediction 3) and/or having been domesticated (Prediction 4). In terms of inter-individual variation, we followed literature suggesting that innovative behaviour should be more common in individuals who have more limited access to resources (2,11,54), in those who more positively react to novelty and in those who are less integrated in their social group (see 57). We therefore predicted that innovation should be more likely in more subordinate individuals (Prediction 5), in females (Prediction 6), in younger individuals (Prediction 7), in less neophobic ones (Prediction 8) and in individuals that are less integrated in the social group (Prediction 9).

METHODS

Ethics statement. The study was carried out in accordance with the national regulations of all the countries in which the study took place. The experimental procedures were approved by the research coordinators at the zoos of Barcelona (Spain), Barben (France), Nuremberg and Leipzig (Germany), where the study was conducted. The risk assessment was conducted together by the research coordinators and the keepers working with each study group, and permission was only granted if they considered that the experimental procedures posed no risks to the animals (e. g. in terms of increased competition over food resources), and instead provided them with clear benefits in terms of enrichment. The study was mainly observational, all the animals participated on a completely voluntary basis and they were not separated from their social groups. During the task, individuals were never water or food deprived, and motivation to participate was ensured exclusively by the use of highly preferred food belonging to their regular diets. The experiments were thus considered to provide no risks or adverse effect for the subjects, and were regarded as a form of enrichment. The ethical approval by the zoos has been submitted to the Journal together with the manuscript, and can be accessed upon request to the Editor of the Journal.

Subjects. We studied 111 subjects belonging to 13 ungulate species, including 6 impalas (*Aepyceros melampus petersi*), 13 mhorr gazelles (*Nanger dama mhorr*), 13 dorcas gazelles (*Gazella dorcas osiris*), 7 scimitar oryx (*Oryx dammah*), 7 dromedaries (*Camelus* *dromedarius*), 7 red deer (*Cervus elaphus*), 15 Barbary sheep (*Ammotragus lervia*), 6 giraffes (*Giraffa camelopardalis rothschildi*), 4 guanacos (*Lama guanicoe*), 4 lamas (*Lama glama*), 4 Przewalski horses (*Equus ferus przewalskii*), 9 sheep (*Ovis aries*) and two groups of goats (*Capra aegagrus hircus*), one with 9 and one with 7 individuals. All subjects were housed with conspecifics of different sex and age at the zoos of Barcelona, Barben, Nuremberg and Leipzig, and were all individually recognizable. None of the study subjects had ever been tested in an innovation test before, although all species occasionally participated in enrichment activities, and 3 of the 6 giraffes had previously participated in other cognitive tasks (69,70). Based on existing literature, we further classified the study species according to their socio-ecological characteristics, including dietary breadth, presence of fission-fusion dynamics and domestication (for more details on the study subject and the species classification, see Supplementary Material).

Behavioural observations. In each study group, we conducted behavioural observations to assess individuals' dominance rank and social integration in the group. First, we assessed dominance hierarchy by using *all occurrence sampling* to record all dyadic agonistic interactions in each group, with a clear winner-loser outcome (i.e., threat, chase, fight). We then used the Elo method (71) with the EloRating package (version 3.5.0; 69), setting 1000 as the individual start values and 100 as the k factor - a weighted constant based on winning probability (72,73). Finally, we averaged these values through the study period, and standardized them to range from 0 (i.e., lowest rank) to 1 (i.e., highest rank). For 21 individuals (3 dorcas gazelles, 6 giraffes, 2 goats, 1 impala, 5 mhorr antelopes, 1 scimitar oryx, 2 red deer, 1 sheep) we observed no agonistic interactions throughout the study period, and their rank was therefore assessed by the experimenter together with the animal keepers, based on observations of priority of access to food (57). Second, we assessed Eigenvector centrality as a measure of individual social integration. We assessed spatial proximity networks in each study group, by conducting 100 *instantaneous scans* per group. Scans were conducted every 15 minutes across several days, recording the spatially closest individual (“nearest neighbor”) of each group member (73). We then built an undirected weighted matrix for social network analyses and used the vegan (version 2.5-3; 74), asnipe (version 1.1.10; 75) and igraph packages (version 1.2.1; 76) in R to assess individuals’ Eigenvector centrality (i.e. a measure proportional to the sum of the centralities of each individual’s neighbors, which assesses the importance of individuals as “social hubs”; 77, 78). As we had no social network data for 7 individuals (2 goats, 1 impala, 3 mhorr antelopes and 1 sheep), we conventionally assigned them the average centrality value for that study group (57). To ensure that this conventional attribution of centrality did not bias our results, we also repeated all the analyses after removing these 7 individuals, and found identical results for all the models (see below).

Neophobia. All of our study subjects were previously tested with a neophobia task in which individuals were exposed to familiar food, part of which was positioned close to a novel object (57). We used these data to calculate a neophobia index, as the proportion of time in which individuals approached the side with no object, out of the total time they spent in proximity of the food from either side. More detailed analyses on neophobia for most individuals (N=78) have been already published (57). Out of the 111 study subjects, 15 individuals (1 barbary sheep, 4 dorcas gazelles, 1 giraffe, 4 goats, 1 scimitar oryx, 1 Przewalski horse, 1 red deer and 2 sheep) did not participate in the task when the novel object was present. If they participated in previous sessions where no novel object was present (N=8; 1 giraffe, 4 goats, 1 scimitar oryx, 1 Przewalski horse and 1 red deer), we assumed that it was the presence of the object that prevented them from participating, and assigned them the highest possible score for neophobia (i.e., 1). We assigned a neutral value of 0.5 to all the individuals that did not participate neither in the presence nor in the absence of the novel object (N=7), as the presence of the novel object had no effect on their behaviour in the task.

Innovation task. We tested all study groups with an innovation task. The task was conducted in a familiar environment (i.e. the external enclosures), when all group members were present. During the task, we presented the group with identical plastic cups, which had an opaque cover on top and were inserted on a long rigid board. All cups were filled with a highly favorite food reward (i.e. carrots, alfalfa, fodder or food pellets, depending on the species), which could be reached with the muzzle after removing the cover . The number of cups was proportional to the study subjects in the group. The board was positioned in an area of the enclosure often used by the study groups. A session started when the board was in place and the experimenter left the enclosure, and lasted up to 20 minutes or until all the food was gone. All study groups received two sessions, on two different days: a first session with transparent cups (i.e. transparent condition), in which food was visible, and a second session with completely opaque cups (i.e. opaque condition), in which food was not visible. Impalas, however, only received the first session, because the covid pandemics prevented us from finishing the task, and the group composition changed when testing was again possible. We video-recorded all sessions, and we later coded from the videos: (i) whether subjects participated in the task (i.e. whether they approached with the muzzle within 1 m from the cups), (ii) whether they solved the task (i.e. whether they successfully opened the cup and retrieved the food), (iii) the individual latency to solve the task for the first time (i.e. the total amount of time spent in proximity of the cups before first opening one), (iv) the strategy used to open each cup (e.g. opening the lid with the lips, nose, muzzle or tongue), and (v) the exact duration of the session (see Figure 1 for a picture of the set-up).

Statistical analyses. We used the MCMCglmm package (version 1.0.1; 79) in R (version 3.5.0; 79) to run generalized linear mixed models (80) with phylogenetic controls. To control for phylogenetic relationships across study species, we prepared a consensus tree with the package ape (81), based on 10,000 trees that we subsampled and pruned from the mammal tree of life to match the species included in our study (82). From the consensus tree we obtained a covariance matrix with the phylogenetic relationship between species, which we then included in the models (for a similar approach, see e.g. 57,83–85).

We conducted 3 sets of models, to assess whether participation (as binomial dependent variable: Model 1), success (as binomial dependent variable: Model 2) and probability of using more than one strategy to solve the task (as binomial dependent variable: Model 3) varied across species and individuals. In Models 1 and 2 we included a line for each study subject and condition, whereas in Models 3 we only included individuals who solved the task. In all the models, we included as test predictors whether the species has fission-fusion dynamics, whether it is domesticated, whether it has low or high dietary breadth, and the group size of the study groups. As test predictors, we also included the individual's sex, age, rank, Eigenvector centrality and neophobia index, as defined above. Finally, in the first two models we controlled for condition (i.e. transparent or opaque) and session duration, including subject identity as random factor, whereas in the last model we only controlled for the overall number of trials solved by each individual.

We then used AIC values to compare each of the three models above to an identical model including phylogenetic controls, controls and random factors, but no test predictors. If this comparison suggested that the more complex model provided a better fit to the data, we assessed the posterior mean, 95% confidence intervals (CIs) and pMCMC of the single test predictors. Terms with pMCMC values lower than 0.05 were considered statistically significant (see e.g. 85). All models included non-informative priors, 1 000 000 iterations, a burn-in of 100 000 and a thinning interval of 300 to minimize autocorrelation and facilitate convergence (see 85,86). We repeated the analyses three times, and visual inspection of the models suggested no convergence issues (data and script are available in Supplementary Material).

RESULTS

On average, 62% of the study subjects participated in at least one condition of the task. However, participation largely varied across species, with 100% of the dromedaries approaching the cups, but only 33% of the sheep. Overall, only 36% of the study subjects were successful in retrieving food at least once. The species with a higher percentage of successful individuals were dromedaries and goats, with 86% and 69% of the individuals opening the cups. Among the individuals who solved the task, latency to open the cup for the first time was on average 51 seconds, ranging from an average of 6 seconds for Prewalski horses to more than 5 minutes for mhorr gazelles. Finally, we found that only 9 out of 40 successful individuals used more than one strategy to solve the task, including 3 of the 6 successful dromedaries and both successful scimitar oryx.

After accounting for phylogeny, the more complex model for Model 1 provided a better fit to the data than the simpler one (complex model, AIC: 124.8, weight: 0.993; simple model, AIC: 134.7, weight: 0.007). Participation was higher in species with fission-fusion dynamics (posterior estimate: 7.2 [95% CIs: 0.5 to 14.5], $p = 0.010$), in domesticated species (posterior estimate: 6.7 [95% CIs: 0.9 to 13.7], $p = 0.005$), and in individuals with lower neophobia (posterior estimate: -12.8 [95% CIs: -24.5 to -3.3], $p = 0.001$). For Model 2, the more complex model provided a better fit to the data than the simpler one (complex model, AIC: 110.4, weight: 0.871; simple model, AIC: 114.2, weight: 0.129). The probability of success was predicted by lower levels of neophobia (posterior estimate: -23.0 [95% CIs: -41.2 to -7.1], $p < 0.001$), and by lower integration in the social network (posterior estimate: -13.4 [95% CIs: -32.7 to 1.8], $p = 0.047$). Finally, the simpler models provided a better fit to the data than the more complex ones for Model 3 (simple model, AIC: 13.0, weight: 1; complex model, AIC: 28.7, weight: 0), suggesting that none of the test predictors we included reliably predicted inter-individual and inter-specific variation in the probability of using more than one strategy to solve the task.

DISCUSSION

Our study showed inter-and intra-specific variation in innovation, in our study sample. In particular, we found differences in the probability that ungulates participated in the task and solved it. Domesticated species and species with higher fission-fusion dynamics were more likely to participate in the task, and so were individuals who were less neophobic to novel objects. Moreover, less neophobic individuals and socially less integrated ones were more likely to solve the task. In contrast, we found no differences across individuals or species in the latency to solve the task or in the probability of using more than one strategy to retrieve food (see Supplementary Material for a video clip with an individual of each species solving the task using different strategies).

Species with higher fission-fusion dynamics and domesticated species were more likely to participate in the task, although they were not better at solving it. Domestication may facilitate interaction with novel set-ups and be linked to an increased interest in anthropogenic objects, as suggested by studies in other taxa (e.g. in captive canids 87, and birds 88). However, this would not necessarily lead to an increase in problem solving skills, as the domestication process might have specifically selected for traits and skills that facilitate interactions with humans (and human artefacts), but not for cognitive skills that allow more efficient problem solving (e.g. in captive dogs and wolves 89). Moreover, also species that show higher fission-fusion dynamics in the wild were more likely to participate in the task, but not to solve it. Fission-fusion dynamics have been linked to enhanced cognitive skills, like inhibition and analogical reasoning (41), which may increase behavioural flexibility and problem solving abilities (e.g. in humans 90, and wild birds 91). However, our study failed to find a link between fission-fusion dynamics and innovation, and there are at least two reasons for that. First, it is possible that fission-fusion dynamics need to be experienced during ontogeny to drive variation in cognitive skills (but see 37, in captive primates). As our study subjects were all captive, this might have prevented us from finding a relationship between the two variables (see below). Second, not all forms of fission-fusion dynamics might be linked to an increase in cognitive skills. Aureli and colleagues (2008), for instance, highlighted how the emergence of higher socio-cognitive skills may be limited to some of the different phylogenetic routes by which fission-fusion dynamics evolved. In particular, when fission-fusion dynamics evolve in group-living species, individuals already rely on a set of complex skills that are necessary for living in a group, and they might thus evolve more complex ones – something that would not be possible when fission-fusion dynamics emerge in solitary species (41). Therefore, more detailed ecological data will be necessary to better quantify fission-fusion dynamics in ungulates and identify the phylogenetic routes by which they emerged.

Dietary breadth failed to significantly predict inter-specific variation in innovation. These results are in contrast with other studies, which have shown a significant link between dietary breadth and cognitive skills (e.g. in captive and wild birds: 92, 93; in wild primates: 43, 94). These differences may be explained in at least three ways. First, it is possible that different evolutionary pressures are at play across different taxa. Therefore, whereas dietary breadth might play a crucial role in the emergence of complex cognitive skills in birds or primates (43,94), other socio-ecological characteristics may be more relevant in ungulates for the emergence of problem solving skills. Moreover, it is possible that our limited sample size, which only included captive individuals, did not allow us to detect inter-specific variation, because sample size was too small and captive individuals may not be representative of their wild counterparts (see below for a better discussion). Finally, it is possible that our current socio-ecological classification should be improved by the inclusion of more precise socio-ecological data, because it is currently based on studies that used very different methods (see below).

In terms of intra-specific variation, less neophobic and socially less integrated individuals were more likely to solve the innovation task. Individuals with lower neophobia were indeed more likely to participate and successfully open the cups. Little neophobia may facilitate interaction with novel set-ups, without necessarily being linked to higher innovation (58). However, when the set-up is relatively easy and does not require subjects to have a complex understanding of the contingencies of the task, as in our study, non-causal manipulation of the set-up might be sufficient to solve the task. Future studies should therefore ideally test how performance changes with more complex tasks. Our results are also in line with other studies showing a link between higher innovation rate and lower neophobia in wild (12,23,56,95–98) and captive animals (12,56,99–101). Moreover, our study showed that little integration in the social network was linked to higher innovation. These findings provide support to the hypothesis that, also in ungulates, socially less integrated individuals may be more likely to interact with novelty and to innovate (see example in captive ungulates 57). Less integrated individuals may more likely overcome neophobia and deal with novel socio-ecological challenges to get a better share of resources, likely because they have to overcome the lower fitness benefits of low social integration (in humans, see: 61,62, in wild primates 59,60,102–104), and/or because their social position does not allow them to adequately rely on social information (see e.g. 105, for a negative relationship between individual innovation and social learning in primates). Our findings are also in line with recent literature in wild (106) and captive (107) primates, showing that socially less integrated individuals are less likely to obtain resources and more likely to overcome neophobia when food is unevenly distributed in the group. Finally, it should be noted that, in this study, we measured social integration in terms of spatial proximity between group members. In ungulates, greater distance from other group members may have direct consequences for individual survival, especially when facing high predatory pressure (108). Therefore, low social integration may be especially important in this taxon as a predictor of problem solving skills, by posing a real challenge for individual fitness.

No other factors included in the analyses predicted intra-specific variation in innovation (i.e. individual's sex, age, rank). These results are in line with a recent meta-analysis of studies on intra-specific variation in innovation (22), which provides no clear support to evolutionary hypotheses linking innovation to these individual traits, either because they would predict excess of energy (20) or a limited access to resources (2,11,54). Instead, variation in innovation seems to vary across individuals depending on differences in sociality or in traits related to personality, like neophobia (22).

Finally, we did not find a link between the test predictors included in this study and the probability of using more than one strategy to solve the task. This is in contrast with previous studies showing a link between higher motor flexibility (i.e. using more than one technique to solve the task) and higher innovation rate (in wild birds 110). However, it is possible that other set-ups allowing more variation in the behavioural strategies used to innovate might evidence different patterns. Here, for instance, most individuals opened the cups by using their nose, muzzle or lips, and only 9 of the 111 study subjects used more than one strategy. Still, some individuals explored alternative behaviours to open the cups, by for instance gently lifting the lid with the lips, or throwing the cups on the floor to retrieve the food.

Current limitations of this study include the fact that we could only test a limited number of subjects for each species, and that we only included captive individuals, which may not be representative of their wild counterparts. Socio-ecological constraints experienced during ontogeny (110), continuous exposure to human cultural milieu (111,112), reduced predation risk, high food availability and extensive exposure to novel objects may affect the development of cognitive skills in captive individuals (113), and mask potential differences across individuals and species. Moreover, previous studies suggest that captive animals may more likely interact with new objects and solve novel problems than their wild counterparts (12,22). Therefore, more studies including wild individuals are required before our findings can be generalized. Another important limitation of our study is that we assessed inter-specific variation based on socio-ecological characteristics of the study species as described in literature. However, the studies we used to categorize species often used different methods, were conducted under very different conditions and had different quality. In the future, it will be essential to bring together experts of ungulate socio-ecology to make a more quantitative categorization of species according to their socio-ecological traits. Finally, we could not include brain size measures as test predictors in our models, because there are no data in literature for all the species we included. Future studies should ideally target species for which these measures are available, to assess whether different brain size measures and innovation rate are linked in ungulates, as it also happens in other taxa (13,32,114).

Overall, we showed that personality traits and social integration play an important role in ungulates, by reliably explaining variation in problem solving skills. These results are only partially in line with findings in other species, and despite important limitations in our study, they suggest that different evolutionary pressures may be at work in different taxa. Therefore, ungulates constitute a valid model for the comparative study of cognition, and the inclusion of still understudied taxa appears a powerful tool to test the limits of current evolutionary hypotheses.

Figure 1. A Dorcas gazelle retrieving food after removing the cover from a cup.

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Discussion

In this section, I will attempt to briefly summarize the main findings of the previous chapters. Each chapter already references and make comments about the chapters that were published earlier, so I will try not to repeat too many things already discussed in those chapters.

The rationale for the choice of tests and study species might not always be straightforward, due to the largely exploratory nature of this thesis. We encountered species that were difficult to work with, tests that did not work, groups that could not be tested as planned due to logistic reasons, and much of this depended on the fact that we know so little about these animals. But in the end, all the tests make up a cohesive body of research that I will try to synthesize now.

The first three chapters are the most exploratory ones, as we only tested one species (giraffes) in three tasks (object permanence, quantity discrimination and statistics inferences). In these chapters, we were attempting to determine whether giraffes could perform well in tasks widely used in the field of evolutionary psychology. The positive results obtained in the first chapter, in fact, were the driving force behind the realization of the present doctoral thesis.

The first chapter revealed that giraffes had the ability to find hidden objects after up to 30 seconds after having been hidden and follow experimenter cues to find food. This was key to begin this line of research, as this was our first contact with ungulates in cognitive tests. Also, this was the very first ever made cognitive test on giraffes, so the results were key for us to continue working on this research line. Even though the results were very relevant for us, they were not that surprising when compared with the results already existing in the literature of other species. Goats for example could solve an even more complex object permanence task (Nawroth et al., 2015). Boars and pigs showed also similar abilities in a previous study (Albiach-Serrano et al., 2012). In another study, pigs showed good object permanence abilities and difficulties in the shake empty task, just as giraffes (Nawroth & von Borell, 2015). In general object permanence is a widespread ability in vertebrates (Cacchione & Rakoczy, 2017). The memory task yielded a not very impressive results, being the giraffe results below results in similar tasks in dogs or cats for example (Fiset et al., 2003; Fiset & Doré, 2006).

Giraffes could discriminate quantities with a precision comparable to species with a much larger relative brain size in the second chapter. There is not much research on the quantity abilities of related species to compare with (Murdock, 2020). Indeed, this was the first quantity discrimination study published in a non-domesticated ungulate species. We know that pigs are able to discriminate the place with more food in a simple paradigm (Held et al., 2005), but we don’t know about their capacity to discriminate different food ratios (Nawroth et al., 2022). The most relevant studies on quantity discrimination in ungulates are probably in horses. We found that giraffes were clearly better, only 83% of the horses selected the larger set in the 2:3 trials and 56% of the horses in the 4:6 trials, while giraffes succeeded in 90% and 70% of the trials, respectively (Uller & Lewis, 2009). Unpublished data on other species confirm that giraffes have also better quantity discrimination abilities than European bison, forest buffalos and common zebras (unpublished results).

In the third chapter giraffes could use statistical information to find their preferred food. It appears that they exhibit levels of cognitive performance comparable to species with much larger relative brain sizes, despite our limited understanding of their cognitive abilities. Only a handful of species, primates and corvids, had previously correctly passed this test

(Bastos & Taylor, 2020; Eckert et al., 2018, 2018; Placì et al., 2019). The fact that giraffes passed this test is quite surprising if you compare them to the animals that correctly solved the test before. This could mean that giraffes may be superlative in statistical abilities. But it may also mean that many more species than we previously thought are capable of solving this task. A third explanation that we cannot discard, although we made several control conditions to get rid of this possibility, is that maybe this test is not measuring statistical capabilities, but a simpler way of discriminating between foods or even colours.

It seems that giraffes may possess impressive cognitive abilities even when compared to other ungulate species, as demonstrated in Chapter 4, where they outperformed both bison and forest buffalo. Moreover, recent data we have collected, indicate that giraffes also outperform common zebras (*Equus burchelli chapmanni*) in the cognitive tasks performed in this chapter. These results suggest that giraffes may represent an underexplored species with the potential to reveal new insights into the evolution of cognitive abilities in animals. Given these findings, giraffes appear to be an incredibly promising species for the field of evolutionary psychology. From this fourth chapter, we used a more comparative approach, applying the same experimental protocol across different species. This allowed us to further test whether ungulates are really a good model to test evolutionary hypotheses. We found that forest buffaloes, as predicted, performed worse than other species in a series of tests on object permanence. Crucially, as we had predicted, buffaloes were also the study species with the simplest sociality and lowest dietary breadth (Bekhuis et al., 2008; Blake, 2002; Korte, 2009). It seems unlikely to be due to differences in facilities or environment, as European bison have the same keepers and environment, and they performed well in the object permanence task. This study is essential for this thesis as it is the first one to demonstrate that the species we worked with yield very different results, therefore they are highly interesting for conducting comparative studies. Furthermore, it is worth noting that the mere fact of finding such big performance differences between species, where for instance, giraffes respond quite well to the 30-second memory test while buffaloes perform at chance, is already significant. It shows that there are significant differences in cognitive ability within this group of animals, and that our tests serve well to reveal those differences, this makes ungulates very much worth studying.

In the fifth chapter of our study, we aimed to investigate whether European bison possess the cognitive ability to solve complex problems by understanding the functions of different objects. This task was designed to be novel and required bison to employ a range of cognitive skills to complete successfully. Despite our efforts to ensure the task was appropriately challenging, the bison were able to succeed in only one of the two tasks presented to them. They failed to replicate a simplified version of one of the first studies in problem solving of science, the task that Köhler did with chimpanzees in Tenerife (Köhler, 1925). While this outcome was not entirely positive, it provided valuable information regarding the cognitive abilities of the species under investigation. It is important to note that negative results, such as these, are just as significant as positive ones and can contribute to increasing the transparency of scientific research (Parker et al., 2016). Therefore, we believe that sharing these findings is crucial for the advancement of our understanding of animal cognition. Anyway, the mere fact that bison were able to solve the task of returning the cubes to the experimenter is truly remarkable. Even the zookeepers at the Barcelona Zoo who work with bison daily did not expect them to succeed in this task. These results are in line with a few previous studies on problem solving abilities in ungulates (Abramson et al., 2018; Nawroth, Baciadonna, et al., 2016).

In the sixth chapter, we showed that both domesticated and non-domesticated ungulates are also skilled at gaze following, a social ability traditionally associated with domestic animals or animals living in complex societies (Drayton & Santos, 2017; Téglás et al., 2012). This is the only study on social cognition that we conducted in this thesis, and while we would have liked to further explore this area, we did not come up with any feasible ideas. Nonetheless, the finding that even non-domesticated ungulates are capable of gaze following with humans is very interesting, until this study we only had research on domestic ungulates (Kaminski et al., 2005; Nawroth, Ebersbach, et al., 2016). Further research should be conducted to investigate whether gaze following between human and ungulates also differs in any way between animals that are closely related to the wild ancestors of our current domesticated animal and those who not.

In the seventh chapter, we included multiple species of ungulates to compare their performance in the same task. We found that individuals less integrated in the group more quickly approached novel objects, showing lower neophobia. These results are in line with recent studies on primates (Amici et al., 2020; Dell'Anna et al., 2020). Also, Barbary sheep were less neophobic than all the other species, even preferring the novel side to the familiar side. We argue that this might be due to be the larger group tested, what might decrease neophobia as already stated in the literature (Gomez-Melara et al., 2021; Moretti et al., 2015; Visalberghi & Addessi, 2000)

Finally, in the eighth chapter, we compared 13 species in their ability to solve a novel task (i.e. innovation task). Through the collaboration of several zoos and many collaborating students, we could show that both individual and specific characteristics reliably predict whether subjects solve a novel task. In particular, we found that individuals who were less neophobic and less integrated into the group were also the best at solving the task. Low levels of neophobia might let animals explore better the new problem and therefore have more opportunities of solving it (Griffin & Guez, 2014). Also, less integrated into the group might innovate more because they have to overcome the lower fitness benefits of low social integration (Schülke et al., 2010; Silk et al., 2010). Whereas species with higher fission-fusion dynamics and domesticated species were more likely to participate in the task, although they were not better at solving it. The domesticated species participating more in the task came with no surprise as domesticated species are more accustomed to human objects and are also selected to interact with our materials (Moretti et al., 2015; Suzuki & Okanoya, 2021; Zeder, 2012). But domesticated animals are not selected due to high cognitive skills, indeed domestication is demonstrated to reduce relative brain size (Zeder, 2012). More surprising was the fact that fission-fusion dynamics didn´t predict more innovation rate as previous studies suggested (Amici et al., 2008; Aureli et al., 2008; Taylor et al., 2007), we don´t have a clear answer to this question, but it might be due to animals not experience fission-fusion themselves due to live in captivity or because the data we have about which species have fission-fusion dynamics in the wild is not precise.

At a practical level, investigating the cognitive abilities of these animals, can provide vital insights for developing more effective conservation strategies while ensuring the welfare of individual by designing better methods to enrich their environment (Nawroth et al., 2022). Understanding the cognitive capacities of individuals, including their capacity for innovation, is important as it enables them to adapt to new and changing environments, especially when reintroduced into their natural habitat or relocated to unfamiliar settings.

Differentiating between individuals with greater potential for adaptation to novel environments, which could be assessed through cognitive testing, can aid in selecting and forming more successful groups for reintroduction programs, leading to better outcomes for the individuals and the environment. Additionally, understanding the social and hierarchical dynamics of groups is crucial in ensuring that the group chosen for relocation or reintroduction is as balanced as possible, which can further enhance the chances of a successful reintroduction.

Our objective for the future is to use cognitive testing to generate species, group, and individual profiles that can be used to improve the effectiveness of various conservation interventions. By doing so, we aim to maximize the welfare of individuals involved and contribute to the long-term survival of these species. Indeed, as Jordi Sabater Pi once said, "To conserve, first one must know, and from that knowledge arises the esteem and the necessity to protect" and it is from such knowledge that we can develop a deeper appreciation of these species and the need to protect them.

To this end, we plan to collaborate with the Zoo of Barcelona on several reintroduction plans they have, including the current program on reintroduction of Dorcas gazelle in the Sahel (see Figure 1). Currently, the selection of individuals for reintroduction is based solely on genetic information. However, we believe that incorporating our knowledge of for example group integration and innovation capacity of each individual could improve the selection process. In particular, the data presented in the seventh and eighth chapter of this thesis could be very useful for this purpose.

In addition, we also recognize the importance of conducting in-situ studies of reintroduced groups to correlate our findings from ex-situ cognitive testing with the individuals' behaviour in their natural habitats. This approach can provide additional insights into how cognitive abilities correlate with ecological pressures and ultimately help us to further refine our conservation strategies. If we got to collaborate with a reintroduction process and to get data from, for example, which individuals are the most successful in the destination areas, we believe we could greatly improve the survivability ratio.

In conclusion, investigating the cognitive abilities animals is a critical area of research for developing more effective conservation strategies. Our approach can provide insights into how to select and form more successful groups for reintroduction programs and lead to better outcomes for the individuals and the environment. By maximizing the welfare of the individuals involved, we hope to contribute to the long-term survival of these species.

Figure 1. A photogram of a Dorcas gazelle being reintroduced in the Sahel by the Zoo of Barcelona and the CSIC (video in Zoo Barcelona, Youtube).

The use of cognitive tests with captive animals, such us the ones we used in this thesis, is a topic that has been subject to ethical debates. However, these tests were not only enrichments for the animals but also serve as essential tools for scientific research and conservation purposes. This method of testing we believe has been shown to be an effective form of environmental enrichment for captive animals, as it provides them with new stimulation and encourages natural behaviours.

Moreover, cognitive testing with captive animals is essential for scientific research. Many species in zoos and wildlife sanctuaries are not found in the wild, or are threatened by habitat loss, or maybe are too neophobic to approach new things, making it difficult to conduct field studies. In these cases, zoos and sanctuaries serve as the only viable option for studying these animals. For example, the scimitar oryx, that participated in chapter 7 and 8 of this thesis, is extinct in the wild (see Figure 2). Cognitive tests provide researchers with valuable information about the cognitive abilities of animals, which can be used to develop better conservation strategies.

It is also worth noting that cognitive testing with captive animals such as zoos and farms is ethically sound. Unlike animal testing in labs, which often involves invasive procedures, cognitive testing with captive animals only involves providing treats to already captive animals. These animals are not forced to participate in the tests, and they can choose to opt-out at any time (see Figure 2). As we saw in the introduction, not many scientists are currently working in zoos of Europe, and big opportunities for research might be being lost. We hope that the results presented in this thesis will encourage new scientist to tests these kinds of animals.

On the other side, in our experience, being a scientist in a zoo can present unique challenges that may not be encountered in a traditional laboratory setting. One of the biggest challenges that scientists may face in a zoo is the issue of priority. As zoos are often large and complex institutions, there may be many different departments and staff members who are vying for resources and attention. This can make it difficult for scientists to get the support and resources they need to conduct their research, as this kind of work is never something to prioritize over everyday duties.

Another issue that scientists may encounter in a zoo is the difficulty of doing any task that modifies the everyday management in any way. Zoos have strict protocols in place for the management of animals, and any changes to these protocols must be carefully considered and approved by multiple stakeholders. This can make it challenging for scientists to conduct experiments that involve modifying the animals' living conditions or routines.

Despite these challenges, being a scientist in a zoo can also be highly rewarding. Zoos provide a unique opportunity to conduct research on animals in a naturalistic setting, and the results of this research can have important implications for conservation efforts. Moreover, scientists in zoos have the opportunity to work closely with zoo staff and other experts in the field, which can lead to valuable collaborations and partnerships. By working together to overcome the challenges inherent in conducting research in a zoo setting, scientists can make important contributions to our understanding of animal behaviour, cognition, and welfare.

Figure 2. A scimitar oryx has food in cups in the first photo. In the second photo the oryx has taken out almost all cups and tries to retrieve all the food.

The main goal of this thesis was to assess if current hypotheses about the evolution of cognition are also valid in ungulates. I consider this objective to have been partially achieved.

Overall, we faced two main problems during this work. Firstly, the lack of time to finish a more comprehensive battery of tests in a greater number of ungulates. The inclusion of more species and tasks, however, likely exceeded the normal time and effort allocated to a PhD thesis, especially considering that little work has been so far done on this taxon.

The second major problem we faced was the lack of information about the socio-ecology of some species. There are some species, especially those included in the last two chapters of the thesis, for which we have little information about the variety of plants they ingest in nature, their sociality type or mean group size. Therefore, although individuals in several species are available and motivated to work, the lack of information about their socio-ecology does not allow to properly interpret our results. In the future, it would be crucial to have better data on these species, which might also allow to better interpret our findings. In all of these species, we did find some articles describing their socio-ecology, but not all of them had the same quality, so that our conclusions should be taken with caution.

In chapter 4, we found clear differences between the tested species, which were in line with what expected based on the socio-ecology of the studied species. We stated in chapter 4: "Overall, our study provided support to our prediction that the species socio-ecological characteristics predict their cognitive performance, since giraffes showed overall the best performance, followed by bison and lastly by buffalos. Giraffes are characterized by large dietary breadth (which has been compared to the dietary breadth of chimpanzees, as both species feed on around 100 different plant species), and high levels of fission-fusion dynamics. European bison, in contrast, show high levels of fission-fusion dynamics but short dietary breadth, while forest buffalos live in rather cohesive groups and also have short dietary breadth. Therefore, our results would suggest that dietary breadth and/or fission-fusion levels may both contribute to the enhancement of cognitive skills, in line with studies in taxa that have higher encephalization rate”. The classification of these three species is based on high-quality socio-ecological studies, so we are confident that our conclusions are quite robust.

Our work further shows the tremendous potential of giraffes as study subjects in the future. Giraffes showed a very high level of attention and motivation when being tested, and an ability to solve a variety of novel problems which is comparable to animals with a much higher encephalization index. It would be interesting to test other species of ungulates in all those tasks in which giraffes performed successfully, to verify to what extent the capacity of giraffes is exceptional. Some unpublished preliminary data including other species already point to this.

The chapter 7 and chapter 8 are highly related since they are done in almost the same animal species. Also, the results of neophobia in chapter 7 were used as a predictor for chapter 8. These two chapters on neophobia and innovation in ungulates have revealed some important factors that predict variation in cognitive abilities within and across species. In the neophobia study, chapter 7, we investigated whether individual characteristics (rank, social integration, sex) and species socio-ecological characteristics (dietary breadth, group size, domestication) predicted variation in neophobia across ten different ungulate species. Using a phylogenetic approach and social network analyses, we found that neophobia was higher in socially more integrated individuals, but not predicted by rank or sex. Additionally, we found that Barbary sheep were on average less neophobic than all the other species studied, possibly due to their larger group size.

In the innovation study, chapter 8, we used a novel foraging task to test the innovation abilities of 13 ungulate species. To solve the task, individuals had to open transparent and opaque cups with food rewards, by removing their cover. We assessed whether individual factors (neophobia, social integration, sex, age, rank) and socio-ecological factors (dietary breadth, fission-fusion dynamics, domestication, group size) predicted participation and performance in the task. Using a phylogenetic approach, we found that success in the task was higher for less neophobic and socially less integrated individuals, and that less neophobic individuals, individuals of domesticated species, and those with higher fission-fusion dynamics were more likely to participate in the task.

Our findings highlight the important role of social integration in predicting neophobia and subsequently, innovation in ungulates. These results suggest that low social integration is a crucial aspect of ungulate cognition that has been relatively unexplored in the literature. By shedding light on the cognitive abilities of ungulates, our studies could potentially provide valuable insights into the cognitive abilities of other animal species as well. Further research in this area could help us better understand the relationship between social integration, neophobia, and innovation in animals.

Conclusions

The chapters of this thesis have likely provided evidence that ungulates are a tremendously underrated group in terms of cognitive ability, which might instead be of great scientific interest. We believe this is the most important conclusion of this thesis and we hope it will encourage other research groups to focus more on these species. There are still many ungulate species whose cognition and behaviour have not been studied. Research groups could find a whole new area of research by systematically studying these species, and society could benefit from it.

We can also conclude that current hypotheses on the evolution of cognition might also work in ungulates (see chapter 4), as giraffes perform better than bison, and bison better than buffalos in a series of studies on object permanence. Also, giraffes perform better than zebras in this task. Giraffes is the species we tested that ranks higher in social and dietary complexity. In chapters 7 and 8, however, we did not find the same pattern, perhaps due to the weakness of the socio-ecological data of the species we based our analysis on. We believe that if we want to have a good quality science, we would ideally also need to collect data in the wild. These data could allow us better understanding also domestic animals that live in our farms, since we could better understand the evolutionary pressures that their wild ancestors likely experienced. That data could also help to understand the domestic animals that live in our farms, since we could understand better those wild ancestors they came from.

Our work also suggests that we should take the welfare and care of ungulates more seriously. Given the cognitive skills they show, it seems necessary to really encourage zoos and farms to make more efforts to offer these animals good living conditions, including enrichment activities and environments that properly stimulate them. The importance of ungulates in our society is unquestionable. We must learn that ungulates are not "just livestock", but sentient beings with complex abilities and skills. I truly hope that within few years, the field of comparative cognition will be enriched with many more studies on these species.

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