

Aberystwyth University

Pulling the wool over their eyes?

Quail, Megan R.; Fraser, Mariecia D.

Published in:

Applied Animal Behaviour Science

DOI:

[10.1016/j.applanim.2023.106131](https://doi.org/10.1016/j.applanim.2023.106131)

Publication date:

2024

Citation for published version (APA):

Quail, M. R., & Fraser, M. D. (2024). Pulling the wool over their eyes? Object permanence, numerical competence and categorisation in alternative livestock species. *Applied Animal Behaviour Science*, 270, Article 106131. <https://doi.org/10.1016/j.applanim.2023.106131>

Document License

CC BY

General rights

Copyright and moral rights for the publications made accessible in the Aberystwyth Research Portal (the Institutional Repository) are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the Aberystwyth Research Portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the Aberystwyth Research Portal

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

tel: +44 1970 62 2400
email: is@aber.ac.uk



Pulling the wool over their eyes? Object permanence, numerical competence and categorisation in alternative livestock species

Megan R. Quail^{*}, Mariecia D. Fraser

IBERS, Aberystwyth University, Pwllpeiran Upland Research Centre, Cwmystwyth, Aberystwyth SY23 4AB, United Kingdom

ARTICLE INFO

Keywords:
Cognition
Behaviour
Alpaca
Sheep
Goat

ABSTRACT

The adaptive abilities of grazing livestock species are not well understood, despite the potential link between behaviour driven decision making and the overall productive efficiency of the animal through foraging strategy. This study aimed to assess and compare these adaptive behaviours, relating to i) object permanence, ii) numerical competence, and iii) categorisation capabilities of domesticated species that possess distinctly different digestive physiologies and backgrounds. Seven animals from each species, including sheep (*Ovis aries*) (avg. 5 years of age, 60 kg initial weight), goats (*Capra hircus*) (avg. 3 years, 45 kg initial weight), and alpacas (*Lama pacos* (Linnaeus, 1758)) (avg. 3 years, 70 kg initial weight), were presented with a total of nine choice tasks, grouped relative to the three abilities being tested (object permanence, numerical competence, and categorisation). Specifically, the stage of object permanence for each subject was tested based on their ability to solve simple visible displacement, to overcome perseveration error, and double invisible displacement tasks. Subjects were also presented with a two-choice task of different open-centre and filled shapes to assess the capacity for simple discrimination and open-ended categorisation. Lastly, numerical competence was compared across five trials consisting of different ratios and volumes of food reward. A basic awareness of object permanence was found in all subjects. Overall, the goats demonstrated the greatest capacity for object permanence across the three species, particularly when presented with more complex three-cup A-not-B tasks. This increase in complexity had no significant effect on goat performance as a group ($p = 0.13$), whereas alpaca ($p = 0.0005$) and sheep performance significantly declined ($p = 0.04$). We also found no evidence to demonstrate contrasting cognitive capabilities between these species in relation to spontaneous numerical cognition ($p > 0.05$), or in the use of perceptual cues in open-ended categorisation ($p = 0.246$). This study is the first instance of multiple direct comparisons of cognitive capability across domesticated livestock species. Furthermore, this work is the first account of object permanence, numerical competence and categorisation in alpacas, as well as object permanence in sheep and numerical competence in sheep and goats. This information could prove useful to predict the outcome of interaction between these species in a grazing context and for inferences relating to behaviour driven decision making, such as foraging strategy, and the overall productive efficiency of the animal. Here, we conclude that the three species tested possess comparable capacity for physical cognition in the tasks discussed.

1. Introduction

The cognitive capabilities of domesticated livestock species have been underrepresented within behavioural research (Nawroth et al., 2019). This lack of data is unexpected considering the population size of farmed animals across the globe and the projected growth of global demand for livestock products (60% increase by the year 2050) (FAO, 2014). Specifically, the adaptive abilities of livestock species are not well understood, despite the potential link between behaviour-driven

decision-making and the overall productive efficiency of the animal, through processes such as foraging strategy (Tomasello and Call, 1997).

There are several aspects of physical cognition (i.e., spatial awareness of objects) that may be connected to the foraging behaviour of livestock species. For instance, an understanding of object permanence has implications for the ability of animals to mentally track the location of conspecifics or food sources when no longer visible (Nawroth et al., 2019; Piaget, 1954). The degree of object permanence can be categorised according to the six stages of Piagetian classification (Piaget,

^{*} Corresponding author.

E-mail address: mrq2@aber.ac.uk (M.R. Quail).

<https://doi.org/10.1016/j.applanim.2023.106131>

Received 22 July 2023; Received in revised form 22 November 2023; Accepted 30 November 2023

Available online 2 December 2023

0168-1591/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

1954) (Table 1), ranging from simple visible displacement (single hiding location) (stage 4b of object permanence), to double invisible displacement (multiple hiding locations with cross transposition- stage 6b).

Limited research within domesticated animals to date indicates there could be variation in the stage that different species of livestock achieve (Nawroth et al., 2019). For instance, Nawroth et al., (2013a) reported that domesticated pigs (*Sus scrofa domestica*) were unable to solve object permanence transposition tasks, although human-given cues had a positive effect on performance (Nawroth et al., 2013b). Similar results were found when using canines (*Canis lupus familiaris*) (Rooijackers et al., 2009). In contrast, dwarf goats (*Capra hircus*) were able to use visual cues to solve transposition tasks (Nawroth, 2015). Other domesticated small ruminants may possess a similar level of object permanence, but this has not been tested. In the case of domesticated herbivores, researchers and farmers could use this information to better understand the role of object permanence in determining the spatial distribution of animals when grazing, as well as the potential interaction between different grazing species that possess contrasting grazing behaviours and dietary preferences.

Furthermore, the ability of domesticated livestock species to differentiate between two different quantities, also known as numerical competence, could also influence the grazing behaviour of domesticated herbivores. Evidence suggests that there are two mechanisms that form the basis of this capability in humans and other animals, such as the process of “subitizing” (recognising small quantities without counting, i. e., 4–5) and the approximate number system (ANS) (rapid representation of quantity, regardless of amount). Researchers have discussed the potential role of these mechanisms in the apparent numerical competence of primates, birds and small mammals (Nawroth et al., 2019). However, evidence of numerical competence in domesticated animals is as yet limited to canines and horses (*Equus caballus*). These animals have demonstrated spontaneous numerical cognition (i.e., an awareness of quantity, without prior training) (Nawroth et al., 2019). Based on this evidence, we hypothesise that similar numerical abilities may be present in other domesticated herbivores, particularly as the quantity of a food source can have direct implications for foraging decisions. If validated, this information could be used to predict how numerical competence may influence interactions between grazing species at pasture.

The capacity of domesticated livestock to group food sources based on physical similarities through categorisation may also influence foraging behaviour and adaptability to novel environments (Nawroth et al., 2019). There are five levels of categorisation, consisting of: (1) simple discrimination between two stimuli, (2) discrimination across a limited number of stimuli, (3) perceptual categorisation, (4) conceptual categorisation, and (5) abstract categorisation (Herrnstein, 1990). Evidence of categorisation across a limited number of stimuli has been found in several domesticated herbivores. Cattle (*Bos taurus*) and sheep (*Ovis aries*), for instance, have been shown to categorise familiar and unfamiliar conspecifics. Likewise, both sheep and dwarf goats can use

open-ended categories to solve perceptual tasks (Meyer et al., 2012), such as species-based categorisation during diet selection (Ginane and Dumont, 2010). Comparable findings have also been recognised in horses (Hanggi, 1999, 2003) and chickens (*Gallus gallus domesticus*) (Werner and Rehkämper, 1999). Based on this evidence, we hypothesised that similar categorisation abilities may be present in other domesticated herbivores. Again, if confirmed, there would be the potential to use this information to predict how the ability to categorise stimuli may inform interactions between grazers, particularly amongst alternative livestock species that are frequently overlooked in favour of conventional systems. Thus, the objectives of this study were to assess and compare i) object permanence, ii) numerical competence, and iii) categorisation capabilities of domesticated species that possess distinctly different digestive physiologies and backgrounds, namely sheep, goats and alpacas (*Lama pacos* (Linnaeus, 1758)).

2. Material and methods

The work described was conducted in accordance with the requirements of the UK Animals (Scientific Procedures) Act 1986 and with the approval of the Aberystwyth University Animal Welfare and Ethical Review Board.

2.1. Experimental design

Seven animals from each species, (alpacas, sheep and goats) participated in the experiments. Specifically, animals were male Huacaya alpacas, aged 2–6 years, male Welsh Mountain Sheep, aged 5 years, and female Cashmere x Boer goats, aged 3 years. The animals were selected following an initial three-week training and acclimation period prior to the commencement of the trials. Animals that demonstrated a disinterest in the experiments at this stage were subsequently excluded from participation in the main study. The animals were housed together in species groups when participating in the experiments. Experimental sessions occurred between the hours of 9:00–10.00, 11:00–13.00, and 14:00–15:00. The animals were allowed to graze freely outside of these times. Subjects always had access to water, with no additional feed offered during each experimental session to ensure motivation. All experiments were conducted across six-weeks between January– March 2023.

During experiments, single animals were separated from their species group through allocation to an individual pen (1 m x 2 m). The remainder of the species group were housed in an adjacent compartment (4.5 m x 7 m) that was visible to the test subject. The experimenter was positioned in an adjoining space to the test subject pen, separated from the animal by a gate with a centre partition. The partition allowed the animal to indicate their selection of stimuli based on head inclination and snout position in relation to this dividing line. A wooden board (50 cm x 65 cm) was used to present the stimuli to the animal across all of the experiments. Correct selection of the appropriate stimuli was rewarded with a food incentive (typically sugar beet pellets). A food reward was taped to the inside of all cups used in object permanence experiments to disregard olfactory input. A series of experiments were used to assess the stage of object permanence across all subjects (Fig. 1).

2.2. Experimental procedure

This study followed the methodologies described by Nawroth et al. (2015) for the assessment of object permanence, with the added introduction of different numbers of hidden locations and visual cues.

2.2.1. Object permanence: experiment 1: simple detection of visibly hidden stimuli

During Experiment 1, a food reward was positioned in the centre of the wooden sliding board and visibly covered with a single cup (black: 9 cm x 6.5 cm). The board was then immediately moved towards the

Table 1

The stages of object permanence (Piaget, 1954).

Stage	Explanation
1 and 2	Failure to search for hidden objects.
3	Solve a task involving a partly hidden object.
4a	Solve a simple visible displacement task, if the subject was allowed to commence search before the object was hidden.
4b	Solve a simple visible displacement task, but are unable to overcome perseveration error.
5a	Solve a simple visible displacement task and can overcome perseveration error.
5b	Solve double visible and single invisible displacement.
6a	Solve sequential invisible displacement.
6b	Solve double invisible displacement, using multiple hiding locations with cross transposition.

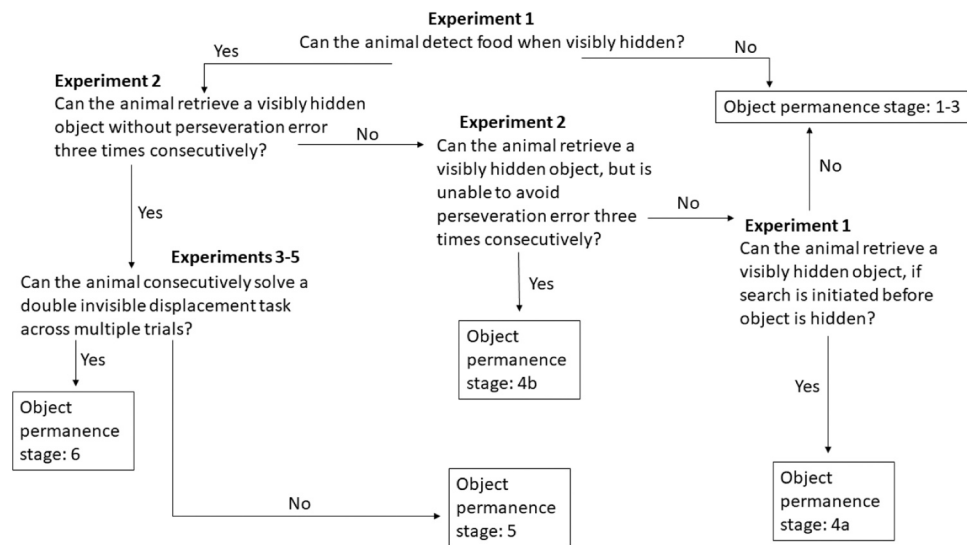


Fig. 1. Summary of the series of experiments used to determine the stage of object permanence (according to the Piagetian classification system) (Piaget, 1954).

gate that separated the experimenter from the subject. This allowed the animal to tap the cup with their snout to indicate an awareness that the food had been hidden. Subject responses were scored as “correct” after selection of the cup, or “incorrect” following a failure to make a choice. Each animal was required to replicate this indication on three consecutive training runs before a test trial was conducted. The test trial consisted of an identical format to the training trials. A maximum of six training runs were allowed per animal.

2.2.2. Object permanence: experiment 2: A-not-B task

Subjects were presented with two identical cups (black: 9 cm×6.5 cm) (Experiment 2 A). These cups were placed at either extreme of the wooden board (hereafter referred to as location 1 and location 2, respectively) at a distance of approximately 45 cm apart. Each subject received two motivation trials before the experimental session commenced. The reward was placed uncovered in location 1 and then in location 2, with the cups placed behind each reward.

The training runs were then conducted. In these sessions, the reward for each subject was randomly and visibly assigned to location 1 or location 2, and both locations were simultaneously covered with the cups. The location of the reward remained consistent across a maximum of six training runs and the subject was required to select the correct location on three consecutive occasions. A test trial was executed if these criteria had been met. During this test trial, the reward was visibly hidden in the opposite location to the position that had been used in the training runs. Selection of the previously rewarded location was considered as an incorrect response. This process was replicated three times to produce three test trials per subject. Three consecutive correct responses across the three test trials were designated as a successful demonstration of overcoming perseveration error.

The conditions reported above were then replicated using three cups (Experiment 2B), placed approximately 23 cm apart on the wooden board across locations 1, 2 and 3 (central position). The central cup (location 3) was never baited. The addition of third location was designed to test the subject’s ability to solve a double invisible displacement of a higher level of complexity.

2.2.3. Object permanence: experiment 3: cross transposition with identical visual cues

Each subject received two training runs to provide motivation to participate in the task. During training, a reward was visibly hidden beneath one cup at each location on the wooden board (locations 1 and 2; the alternative cup was not present during these training runs).

Following the training runs, two identical cups were used to conduct a transposition task (Experiment 3 A). The reward was randomly assigned to location 1 or 2, using a random number generator, and covered with the cup whilst in full view of the subject. Cup locations were switched, through crossing over from left to right, or right to left. This crossover was visible to the animal. Following crossover, the board was immediately presented to the subject for selection. Each subject received twelve test trials. The direction of transposition (moving the baited cup in front or behind the unrewarded cup) and hand position (moving the baited cup with the left or right hand) were randomised for each trial. A separate assessment using three cups of identical size and colour was also conducted (Experiment 3B). In this set of trials, the cup in the centre of the wooden board (location 3) was never baited during the training runs or subsequent trials.

2.2.4. Object permanence: experiments 4 and 5: cross transposition with different visual cues

The conditions of the cross-transposition task were then replicated using two cups of different sizes (brown: 9 cm×6.5 cm; brown: 5.5 cm×4.3 cm) (Experiment 4), and then of two different coloured cups of identical size (red: 9 cm×6 cm; blue: 9 cm×6 cm) (Experiment 5).

2.2.5. Numerical competence

Individual animals entered the test subject pen and were presented with two identical opaque plastic buckets (25 cm×15.5 cm) that were mounted approximately 15 cm apart on a wooden board (55 cm×65 cm). This wooden board was placed on top of a plastic box. Pieces of carrot (divided into identical circular sections and then quartered (1 cm×1 cm)) were individually dropped into each bucket in full view of the subject. The carrot pieces were allocated to each bucket in different ratios across four different test trials, including: one vs two, two vs three, two vs six, and four vs six pieces of carrot, in accordance with the methodology described by Uller and Lewis (2009). A fifth trial was also conducted to compare the response of the subject when presented with a volume of carrots that was equal to the number of pieces offered (two quarters vs one half). The bottom of each bucket had been removed and a hole had been cut into the board beneath. This allowed the pieces of carrot to fall through the bucket and into the box below, which ensured that the animal was unable to use olfactory cues to determine the location of the greater food quantity. The box was lined with cotton wool to prevent any auditory input.

Prior to each test trial, the food amounts were randomly allocated to each bucket across three training runs. The replication of the training

runs was designed to counteract the association between the reward and the bucket that had been baited last. Following allocation of the carrot pieces, the experimenter lifted the board (with buckets attached) away from the box beneath. The board was then lowered to the floor and immediately presented to the subject, allowing the animal to select a location through placing the snout inside the chosen bucket. A reward (sugar beet) was then placed in front of the bucket that had been allocated the larger quantity of carrot pieces. The use of a different food item as a reward was intended to avoid difficulty in differentiating between stimuli (carrot pieces) and reward, which has been shown to result in low accuracy in decision making amongst other animal species (primates) (Schmitt and Fischer, 2011).

2.2.6. Categorisation

Each subject was presented with two stimuli, in accordance with the methodology of Hanggi (1999). The stimuli consisted of a filled and unfilled circle of equal proportion (8 cm × 8 cm), printed on white paper of an equal size (10 cm × 10 cm). The filled shape was randomly assigned to location 1 or 2 on the wooden board, with the other shape positioned at the opposite location. The shapes were initially attached to the board using clear tape to avoid excessive movement, especially during training sessions when the subjects frequently displaced the stimuli before becoming acclimatised to the task. Selection of the filled shape (through touching of the stimulus with the snout or indication through head position) resulted in an immediate reward, which was placed directly in front of the stimuli. Following approximately 60 training runs, the subject became acclimatised to the stimuli and developed the ability to choose between the shapes. Twenty test trials were then conducted directly after this stage, as additional training sessions resulted in a progressive lack of interest in the task. Subjects were required to identify the correct stimulus across 95% of the test trials (nineteen out of twenty trials) to progress onto the next stage (modified from the ten correct responses described by Hanggi 1999).

Each subject was then randomly presented with a single filled and unfilled shape from 18 different sets of shapes, replicated across 20 test trials. Selection of the filled shape was rewarded by the experimenter. No prior training or familiarisation had been conducted with these new sets of stimuli. Successful categorisation of multiple sets of stimuli was recorded if each subject identified the correct stimulus across 95% of the test trials (19 out of 20 trials).

2.3. Data analysis

Statistical analyses were conducted in R-Studio version 4.2.2 (R-Studio Team, 2020), using the packages ‘stats’ (R Core Team, 2022) and ‘MASS’ (Venables and Ripley, 2002). The number of correct responses scored in each task were recorded on an individual basis in each trial, grouped according to species. A Poisson generalised linear model (GLM) with a log link function was fitted to predict the performance of subjects in relation to species and the number of cups that were used in the object permanence A-not-B task, and in the numerical competence trials. The Confidence Intervals (CIs) (95%) and probability values for all GLMs were computed using a Wald z-distribution approximation. Performance within species groups was assessed across the two and three cup A-not-B object permanence tasks using a Pearson’s Chi-squared test.

The number of “correct” responses within species groups during the transposition tasks were tested against a pre-established threshold of success (10 out of 12 trials) using a binomial test (Nawroth et al., 2015), and then compared to the chance level (50%) also using the ‘stats’ package. A negative-binomial GLM with a log link function was fitted to compare the performance of subjects in relation to species and the number of cups that were used in each object permanence transposition task. Independent two-group t-tests were used to compare performance between species groups in the cross-transposition task featuring three cups. Between-species differences in the transposition tasks with different visual cues were assessed using a one-way analysis of variance

(ANOVA). A two-way ANOVA with testing for interaction was used to compare performance between species in the categorisation experiment.

3. Results

3.1. Object permanence

All subjects across each species group scored a “correct” response for all test trials during experiment 1. In the A-not-B task, two subjects scored a correct response on three consecutive trials during the two-cup experiment (experiment 2) (one sheep and goat, respectively). A single alpaca, two sheep and three goats did not select the correct cup on any of the test trials. All other subjects recorded a minimum of one or two correct responses for the two-cup task.

During the three cup A-not-B task, two sheep were able to make a correct selection on one of the three test trials, whereas all other subjects across each species failed to record a single correct response (Fig. 2). The effect of species was not a statistically significant predictor of response across both the two and three cup A-not-B tasks ($p > 0.05$). However, a decrease in the number of cups (three cups versus two) resulted in a statistically significant and positive effect on performance ($p < 0.001$). Further analysis suggests that an increase from two to three cups resulted in a significant and negative effect on alpaca performance ($X^2(2, N = 14) = 10.5, p = 0.0005$) and on sheep performance ($X^2(3, N = 14) = 8.3, p = 0.04$), whereas no effect was found within the goat group ($X^2(3, N = 14) = 5.6, p = 0.13$).

A single subject (alpaca) selected the correct response on ten of twelve trials when presented with a two-cup cross transposition task ($p = 0.01$, compared to the chance level (50%)). In the three-cup cross transposition task, an individual goat scored a significant number of correct responses (ten out of twelve trials, $p = 0.01$) (Fig. 3). The effect of species was not a statistically significant predictor of response in the two-cup transposition task ($p > 0.05$). However, there was a significant difference in performance amongst species in the three-cup transposition task ($p = 0.02$), specifically between the goat (6.9 correct responses out of ten ± 2.52 (SE)) and alpaca species groups (4.0 correct responses out of ten ± 2.41 (SE)) ($t(12) = -2.16, p = 0.05$). A decrease in the number of cups (three cups versus two) also resulted in a statistically significant and positive effect on performance ($p < 0.001$). Further analysis suggests that an increase from two to three cups

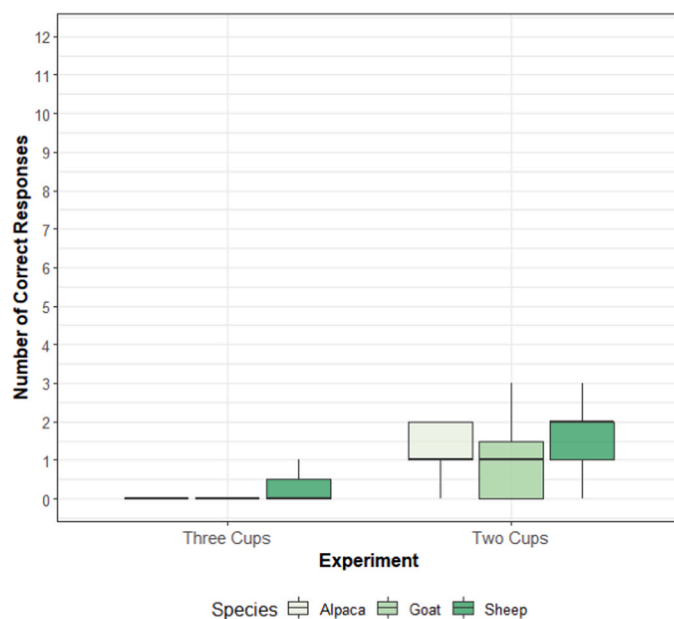


Fig. 2. A-not-B task: Comparison of the number of correct responses (maximum of three) across species (alpaca, goat, sheep) relative to two or three cups used.

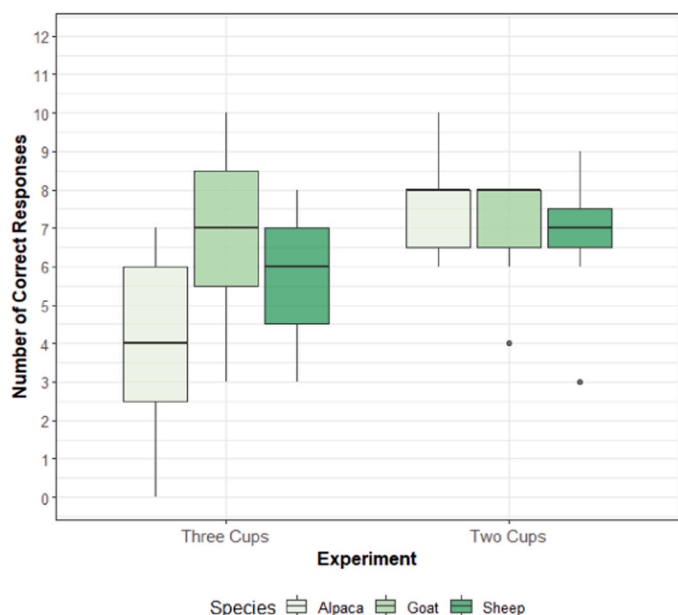


Fig. 3. The number of correct responses (maximum of twelve trials) across all three species (alpaca- green, goat- purple, sheep- orange) in relation to the number of cups that were used during cross transposition experiments (two cups versus three cups). Outliers (grey dots) in each group are shown where present.

resulted in a negative effect on alpaca performance ($p = 0.006$), whereas no effect was found within the sheep ($p = 0.33$) or goat species groups ($p = 0.89$).

A single subject (sheep) selected the correct response on ten of twelve trials when presented with a two-cup cross transposition task with different visual cues (cup sizes) ($p = 0.01$, compared to the chance level (50%)). In contrast, three subjects (one goat and two sheep) scored a significant number of correct responses during the cross-transposition tasks when using cups of different colours (ten out of twelve trials, $p = 0.01$) (Fig. 4). The effect of species was not a statistically significant predictor of response across all two cup transposition experiments ($p > 0.05$). Subject performance was also not significantly different across species when presented with identical or distinct visual cues during the cross-transposition experiments ($p > 0.05$). Within species group variability in performance was not detected across all two cup transposition tasks for goats ($p = 0.98$), sheep ($p = 0.42$), and alpacas ($p = 0.32$).

3.2. Numerical competence

As a group, the goats selected the larger quantity more frequently on average (2.8 correct responses out of four \pm 0.89 (SE)), than the sheep (2.4 correct responses out of four \pm 0.79 (SE)) and the alpacas (1.9 correct responses out of four \pm 1.07 (SE)). Two goats consistently selected the highest quantity across all four trials, whereas the sheep (four subjects) and alpacas (two subjects) chose the greater amount on a maximum of three trials. However, the effect of species was not a statistically significant predictor of response across the numerical competence experiments ($p > 0.05$) (Fig. 5).

Subject performance was also not significantly different across species when presented with an equal number and volume of carrot pieces ($p > 0.05$). As a group, the goats selected the volume of carrot pieces more often than the equivalent number (5 of 7 subjects), particularly when compared to the alpacas (1 of 7 subjects), as well as the sheep (3 of 7 subjects) (Fig. 6).

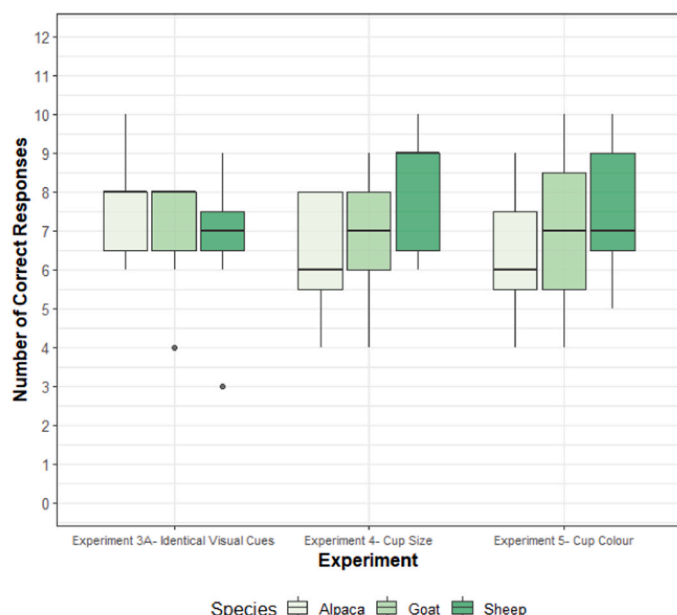


Fig. 4. The number of correct responses (maximum of twelve trials) across all three species in relation to the experimental conditions during cross transposition experiments (3A-5). Experiment 3 A: cross transposition of two cups with identical visual cues; experiment 4: cross transposition of two cups with different visual cues (cup size); experiment 5: cross transposition of two cups with different visual cues (cup colour). Outliers (grey dots) are shown where present.

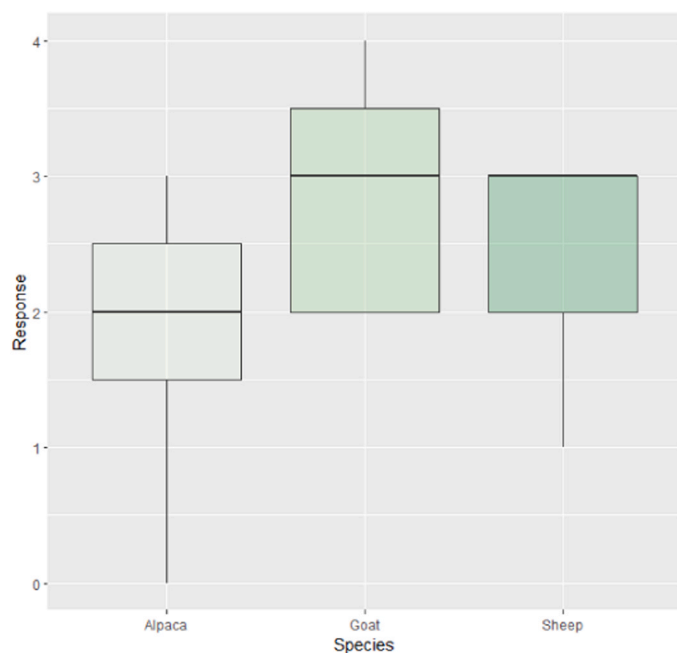


Fig. 5. Numerical competence experiment (trials 1–4). A correct response was scored when the subject selected the larger quantity within a given ratio: trial 1- one vs two pieces of carrot, trial 2- two vs three, trial 3- two vs six, and trial 4- four vs six.

3.3. Categorisation

Performance did not significantly differ between species groups in the categorisation experiment ($p = 0.246$), and no effect of number of stimuli was detected ($p = 0.94$) (Fig. 7). A single alpaca and one sheep achieved a 95% success rate when presented with a single set of stimuli,

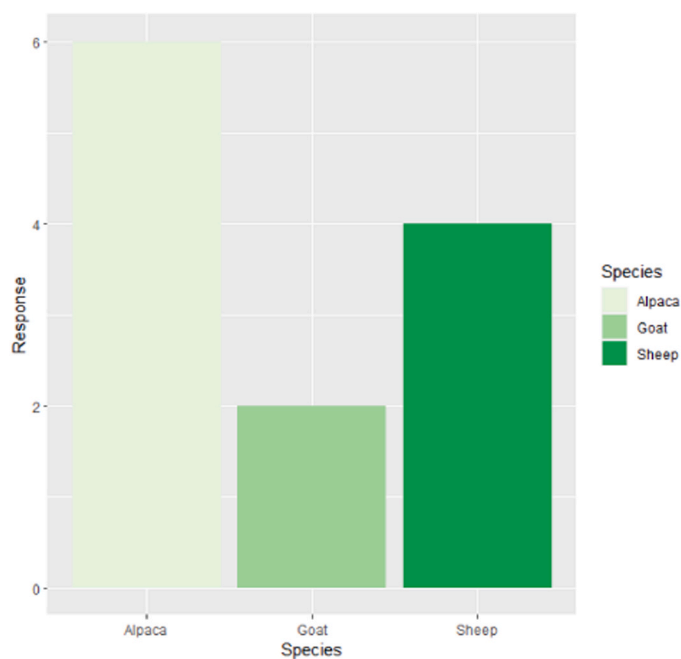


Fig. 6. Numerical competence experiment (trial 5). The subjects selected between an equivalent volume or number of carrot pieces. The response across alpacas, goats and sheep is shown as the number of animals that selected either category, with a maximum of seven subjects per species.

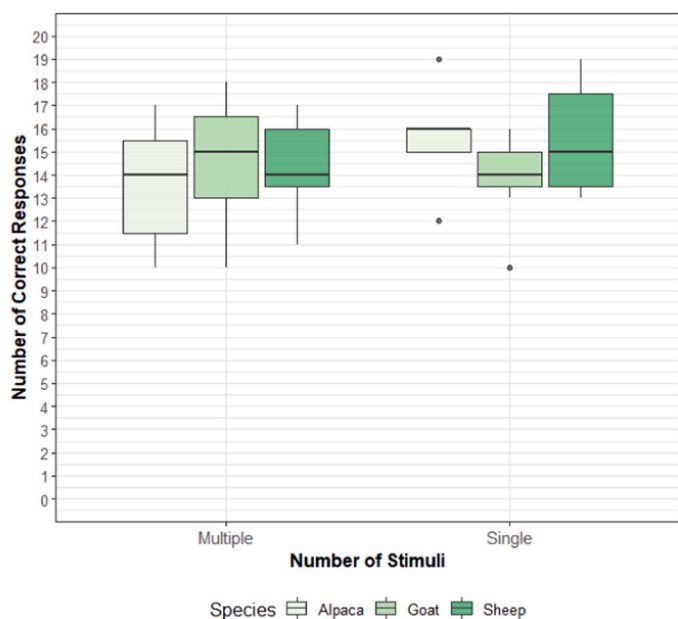


Fig. 7. The number of correct responses (maximum of 20 trials) across all three species (alpaca- green, goat- purple, sheep- orange) in relation to the number of stimuli that were used during the categorisation experiment. Outliers (grey dots) in each group are shown where present.

and subsequently met the criteria for simple discrimination. As a group, the alpacas scored an average of 15.6 ± 0.78 (SE) correct responses (range of 12–19, out of 20 trials) for the single set of stimuli. The goats and sheep achieved an average of 13.9 ± 0.74 (SE) (10–16), and 15.6 ± 0.92 (SE) (13–19) correct responses for the single set of stimuli, respectively.

None of the subjects were able to successfully categorise multiple sets of stimuli. The alpacas scored an average of 13.6 ± 0.99 (SE) correct

responses (out of 20 trials) (ranging from 10 to 17), whereas as the goat and sheep species groups averaged 14.6 ± 1.06 (SE) (10–18) and 14.4 ± 0.81 (SE) (11–17), respectively.

4. Discussion

This study presents the first instance of multiple direct comparisons of cognitive capability across domesticated livestock species. Furthermore, this work is the first account of object permanence, numerical competence and categorisation in alpacas, as well as object permanence in sheep and numerical competence in sheep and goats. The number of combined subjects in this study across all species also exceeds the minimum accepted sample size of a single species that has been applied in other studies of livestock cognition, including horses (Hanggi, 1999), pigs (Nawroth et al., 2013a; Nawroth and Borell, 2015), goats (Kaminski et al., 2005; Nawroth et al., 2015), and cattle (Rybarczyk et al., 2001). Equally, the combination of female and male subjects used in this study (female goats, male sheep and alpacas) are mirrored in these aforementioned studies, with no reported effect on performance between sexes. All animals also appeared to be equally motivated to participate in this study. It is therefore unlikely that sex influenced subject performance. As such, this work offers a comprehensive approach to a distinctive comparison across multiple species.

4.1. Object permanence

A basic awareness of object permanence was found in all subjects across the alpacas, goats and sheep. However, the majority of subjects failed to overcome the A-not-B error during the two-cup and three-cup tasks, resulting in allocation to stage 4a of object permanence (according to the Piagetian classification system (Piaget, 1954)). One sheep and goat, respectively, did not commit the A-not-B error during the two-cup experiment. These two subjects met the criteria for stage 4b of object permanence for this task. The performance of alpacas and sheep as a group in the A-not-B task was significantly improved when the number of hidden locations was reduced from three to two.

A single alpaca and one goat solved the double invisible displacement task above the chance level, and subsequently reached stage 6 of object permanence for this experiment. As a group, goats performed significantly better than alpacas in the three-cup task. Altogether, the capacity of the sheep to solve double invisible displacement tasks improved when presented with contrasting visual cues, rather than identical cues, such as different sizes (one sheep) and different colours (two sheep). Likewise, a single goat performed above the chance level when presented with different colour cues during the two-cup cross transposition experiment, indicating object permanence stage 6 according to this task. Overall, the goats demonstrated a greater capacity for object permanence than the other species when assessed as a group across all experiments, particularly when presented with more complex three-cup tasks.

A higher stage of object permanence amongst the goats may be indicative of a greater environmental awareness than in sheep or alpacas. Specifically, the ability to track conspecifics or predators may be a useful adaptation when navigating areas of dense browse whilst foraging (Noë and Laporte, 2014). A field-scale assessment of the extent of this capacity might be a useful step towards our understanding of behaviourally-driven foraging strategy, such as the physiological response of the animal to a series of changes in the position of conspecifics within a complex environment. Equally, the ability to track and mentally reconstruct the position of stimuli within a foraging context may be a useful adaptation for greater feeding efficiency.

There are several potential influencing factors that must be addressed in relation to the performance of those subjects that were unable to achieve a response above the chance level in the object permanence tasks. For instance, previous evidence has shown that the location and direction of transposition (towards the subject, rather than

away) had a significant effect on the performance of dwarf goats during similar double invisible displacement tasks (Kaminski et al., 2005; Nawroth et al., 2015). The effect of location bias and direction of movement was also noted in this study (M. Quail, pers. obs.), although never directly tested. Nawroth et al., (2015) hypothesised that this bias towards a single location could be attributed to the lateral placement of the eyes in goats, which is similar to sheep and alpacas, and subsequent hemispheric lateralisation- as has been observed in horses (Baragli et al., 2021). As such, we would expect to observe an equal influence of direction of transposition on each species, with no effect on between-species comparisons in performance.

Likewise, it is unlikely that the subjects had learned to select the opposite location to the baited cup through repeated experience (Albiach-Serrano et al., 2012), rather than tracking the hidden object, as no opposite-side bias was observed and the opportunity to learn the parameters of the experiment was limited through finite training runs. There is also currently no evidence to suggest that subtle cues from the experimenter, particularly direction of gaze, could have influenced goat or sheep behaviour (Kaminski et al., 2005; Beausoleil and Stafford, 2006), although further evidence is required for alpacas. However, there is the potential to apply promising new technologies, such as the tracking of facial features in animals using artificial intelligence (AI) systems (McLennan and Mahmoud, 2019), to detect the influence of these factors on the process leading to a correct or incorrect selection on a finer-scale.

4.2. Numerical competence

The ability to discriminate between two different quantities was observed in individual subjects across all species up to a maximum of six stimuli. Likewise, there was no significant difference detected between species in their preference for larger volumes of stimuli when offered an equal quantity of smaller stimuli. This suggests the potential for comparable spontaneous numerical cognition in these species. However, this study is the first evidence of numerical ability in sheep, goats, and alpacas. As such, a more expansive study of these species across a greater number of individuals would be useful to verify these initial conclusions, particularly using reaction time as an indicator of the mechanism that governs these behaviours (i.e., subitizing, and approximate number system (ANS)) (David and Pérusse, 2010; Gabor and Gerken, 2014).

Similar levels of numerical competence have been observed in the foraging behaviour of other domesticated livestock species in the wider literature. Juvenile pigs, for instance, have demonstrated the capacity to select a foraging site based on the quantity and value of food available (Held et al., 2005). Likewise, spatial grazing patterns in cattle have also been linked to an awareness of food source quantity (Howery et al., 2000). Thus, we can hypothesise that the numerical competence observed in this study is also a driving factor in the foraging strategy of sheep, goats and alpacas. This ability to discriminate between sites based on the quantity of preferred vegetation available may allow the animal to increase foraging efficiency, particularly across the vast grazing areas that are typically associated with alpaca and wild goat populations (Pfister et al., 1989; Wade et al., 2023). A field-scale comparison would be a logical next step to assess the role of numerical competence on the spatial distribution of these species within a natural pasture environment. There is also the potential to evaluate numerical competence in the context of horizontal and vertical social learning within a grassland setting (Nawroth et al., 2019).

4.3. Categorisation

Two subjects (a single sheep and alpaca) demonstrated the ability to successfully discriminate between stimuli in a two-choice task. No evidence of open-ended categorisation using perceptual cues was found in the sheep, goats or alpacas, however. These findings were unexpected given that open-ended categorisation of symbols has been reported in

Nigerian dwarf goats (Meyer et al., 2012). However, the effect of length of training time on the ability of a subject to reach the criterion for successful categorisation has been reported in goats and horses (Hanggi and Ingersoll, 2009; Meyer et al., 2012), facilitated through a learning curve of trial-and-error. Likewise, there is currently a lack of standardisation amongst these studies to determine the criteria for successful categorisation. As such, the findings of this study may be partially attributed to the comparatively shorter training period used and discrepancies between methodologies.

In a similar way, these findings contradict evidence that sheep have the ability to categorise sward species based on perceptual similarity (Ginane and Dumont, 2010). We would expect to observe comparable findings in the Welsh Mountain sheep used in this study, particularly as categorisation of food sources would be a useful tool for survival in environmentally challenging conditions on poorer quality indigenous grasslands, which are typical landscapes for this breed. This discrepancy may be related to the importance of local perceptual features for categorisation in different animal species (Marsh and MacDonald, 2008; Troje et al., 1999). For instance, Ginane and Dumont (2010) observed that certain perceptual cues, such as sward height, were not used for discrimination between food sources in spite of adverse conditioning to the sward species. This was suggestive of a compartmentalised approach to categorisation amongst sheep, divided into transient or intrinsic state, rather than a whole-object approach to discrimination (as might be observed in the shape stimuli used in this study). It would therefore be useful to further define the features that sheep use to categorise stimuli, particularly in relation to food source. For example, evidence suggests that sheep may selectively graze based partially on the green shade of the grass, which is usually associated with higher digestibility (Van der Merwe and Marshal, 2012). In the context of foraging, this information can be used to assess and potentially predict the grazing behaviour of sheep when presented with a heterogeneous grazing environment. A direct comparison can then be formed between the categorisation ability of species with contrasting foraging strategies such as alpacas (dietary preference for tall grasses and fewer forbs) and sheep (short grasses and forbs) (Quispe et al., 2021), particularly as the extent of categorisation in this species has not been explored beyond the scope of this study. A more expansive study of these species is now needed across a greater number of individuals to determine the mechanism that governs these behaviours on a finer-scale.

5. Conclusion

This study presents the first comparison of object permanence, numerical competence, and categorisation capabilities in livestock species with distinct foraging strategies; alpacas, sheep and goats. A basic awareness of object permanence was found in all subjects. Overall, the goats demonstrated the greatest capacity for object permanence between the three species. This may be linked with the need to mentally reconstruct the position of stimuli to facilitate a more selective browse diet than is typically found in preferential grazers, such as sheep and alpacas. We also found evidence to suggest comparable spontaneous numerical cognition in these species, and an equal inability to use perceptual cues in open-ended categorisation. The initial insight into the cognitive capabilities of alternative livestock species we have provided will prove useful in developing future research exploring the processes that drive grazing distribution in species with contrasting dietary preferences.

CRediT authorship contribution statement

Both MRQ and MDF contributed to the conception and design of the study, as well as the interpretation of the data. MRQ collected and analysed the data, then completed the first draft of the article. Both authors revised the manuscript and agreed on the final draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are available from the corresponding author upon request.

Acknowledgements

We thank Alys Fraser for assistance with data collection. We also thank Iolo Davies, Eirian Richards and Callum Doonan for their support with animal handling. This work was funded by an Aberystwyth University AberDoc studentship.

References

- Albiach-Serrano, A., Bräuer, J., Cacchione, T., Zickert, N., Cacchione, F., 2012. The effect of domestication and ontogeny in swine cognition (*Sus scrofa scrofa* and *S. s. domestica*). *Applied Animal Behaviour Science* 141, 25–35. <https://doi.org/10.1016/j.applanim.2012.07.005>.
- Baragli, P., Scopa, C., Felici, M., Reddon, A.R., 2021. Horses show individual level lateralisation when inspecting an unfamiliar and unexpected stimulus. *PLoS One* 5, 16. <https://doi.org/10.1371/journal.pone.0255688>.
- Beausoleil, N.J., Stafford, K.J., Mellor, D.J., 2006. Does direct human eye contact function as a warning cue for domestic sheep (*Ovis aries*)? *Journal of Comparative Psychology* 120 (3), 269–279. <https://doi.org/10.1037/0735-7036.120.3.269>.
- David, H., Pérusse, R., 2010. Numerical competence in animals: definitional issues, current evidence, and a new research agenda. *Behav. Brain Sci.* 11, 561–579. <https://doi.org/10.1017/S0140525x00053437>.
- Food and Agriculture Organisation of the United Nations. 2014. FAO Assistance Towards Feed Analysis. Increasing Incomes, Improving Food Safety and Safeguarding the Environment. Livestock Production Systems Branch Animal Production and Health Division FAO, Rome, Italy.
- Gabor, V., Gerken, M., 2014. Shetland ponies (*Equus caballus*) show quantity discrimination in a matching-to-sample design. *Anim. Cogn.* 17 (6), 1233–1243. <https://doi.org/10.1007/s10071-014-0753-0>.
- Ginane, C., Dumont, B., 2010. Do grazing sheep use species-based categorisation to select their diet? *Behav. Process.* 84, 622–624. <https://doi.org/10.1016/j.beproc.2010.01.022>.
- Hanggi, E.B., 1999. Categorisation learning in horses (*Equus caballus*). *J. Comp. Psychol.* 113, 243–252. <https://doi.org/10.1037/0735-7036.113.3.243>.
- Hanggi, E.B., 2003. Discrimination learning based on relative size concepts in horses (*Equus caballus*). *Appl. Anim. Behav. Sci.* 83, 201–213. [https://doi.org/10.1016/S0168-1591\(03\)00136-9](https://doi.org/10.1016/S0168-1591(03)00136-9).
- Hanggi, E.B., Ingersoll, J.F., 2009. Long-term memory for categories and concepts in horses (*Equus caballus*). *Anim. Cogn.* 12 (3), 451–462. <https://doi.org/10.1007/s10071-008-0205-9>.
- Held, S., Baumgartner, J., Kilbride, A., Bryne, R.W., Mendl, M., 2005. Foraging behaviour in domestic pigs (*Sus scrofa*): remembering and prioritizing food sites of different value. *Anim. Cogn.* 8, 114–121. <https://doi.org/10.1007/s10071-004-0242-y>.
- Herrnstein, R.J., 1990. Levels of stimulus control- a functional approach. *Cognition* 37, 133–166. [https://doi.org/10.1016/0010-0277\(90\)90021-B](https://doi.org/10.1016/0010-0277(90)90021-B).
- Howery, L.D., Bailey, D.W., Ruyle, G.B., Renken, W.J., 2000. Cattle use visual cues to track food locations. *Appl. Anim. Behav. Sci.* 67, 1–14. [https://doi.org/10.1016/S0168-1591\(99\)00118-5](https://doi.org/10.1016/S0168-1591(99)00118-5).
- Kaminski, J., Riedel, J., Call, J., Tomasello, M., 2005. Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. *Anim. Behav.* 69, 11–18. <https://doi.org/10.1016/j.anbehav.2004.05.008>.
- Lama pacos (Linnaeus, 1758) in GBIF Secretariat (2023). GBIF Backbone Taxonomy. Checklist dataset <https://doi.org/10.15468/39omei> accessed via GBIF.org on 2023-12-12.
- Marsh, H.L., MacDonald, S.E., 2008. The use of perceptual features in categorisation by orangutans (*Pongo abelli*). *Anim. Cogn.* 11, 569–585. <https://doi.org/10.1007/s10071-008-0148-1>.
- McLennan, K., Mahmoud, M., 2019. Development of an automated pain facial expression detection system for sheep (*Ovis aries*). *Animals* 9 (4), 196. <https://doi.org/10.3390/ani9040196>.
- Meyer, S., Nürnberg, G., Puppe, B., Langbein, J., 2012. The cognitive capabilities of farm animals: categorisation learning in dwarf goats (*Capra hircus*). *Anim. Cogn.* 15, 567–576. <https://doi.org/10.1007/s10071-012-0485-y>.
- Nawroth, C., Borell, E., 2015. Domestic pigs' (*Sus scrofa domestica*) use of direct and indirect visual and auditory cues in an object choice task. *Anim. Cogn.* 18, 757–766. <https://doi.org/10.1007/s10071-015-0842-8>.
- Nawroth, C., Borell, E., Langbein, J., 2015. Object permanence in the dwarf goat (*Capra aegagrus hircus*): perseveration errors and the tracking of complex movements of hidden objects. *Appl. Anim. Behav. Sci.* 167, 20–26. <https://doi.org/10.1016/j.applanim.2015.03.010>.
- Nawroth, C., Ebersbach, M., Borell, E., 2013a. A note on pigs' knowledge of hidden objects. *Arch. Anim. Breed.* 56, 861–872. <https://doi.org/10.7482/0003-9438-56-086>.
- Nawroth, C., Ebersbach, M., Borell, E., 2013b. Juvenile domestic pigs (*Sus scrofa domestica*) use human-given cues in an object choice task. *Anim. Cogn.* 17, 701–713. <https://doi.org/10.1007/s10071-013-0702-3>.
- Nawroth, C., Langbein, J., Coulon, M., Gabor, V., Oesterwind, S., Benz-Schwarzburg, J., Borell, E., 2019. Farm animal cognition- linking behaviour, welfare and ethics. *Front. Vet. Sci.* 6, 24. <https://doi.org/10.3389/fvets.2019.00024>.
- Noë, R., Laporte, M., 2014. Socio-spatial cognition in vervet monkeys. *Anim. Cogn.* 17, 597–607. <https://doi.org/10.1007/s10071-013-0690-3>.
- Pfister, J.A., Martin, F.S., Rosales, L., Sisson, D.V., Flores, E., Bryant, F.C., 1989. Grazing behaviour of llamas, alpacas and sheep in the Andes of Peru. *Appl. Anim. Behav. Sci.* 23, 237–246. [https://doi.org/10.1016/0168-1591\(89\)90114-7](https://doi.org/10.1016/0168-1591(89)90114-7).
- Piaget, J., 1954. *The Construction of Reality in the Child*. International Universities Press, New York.
- Quispe, C., Ñaupari, J., Distel, R.A., Flores, E., 2021. Feeding selection of sheep and alpaca on puna tussock rangelands grazed previously by cattle. *Small Rumin. Res.* 197. <https://doi.org/10.1016/j.smallrumres.2021.106349>.
- R Core Team, 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rooijakkers, E., Kaminski, J., Call, J., 2009. Comparing dogs and great apes in their ability to visually track object transpositions. *Anim. Cogn.* 12, 789–796. <https://doi.org/10.1007/s10071-009-0238-8>.
- Rybarczyk, P., Koba, Y., Rushen, J., Tanida, H., Passillé, A.M., 2001. Can cows discriminate people by their faces. *Appl. Anim. Behav. Sci.* 74, 175–189. [https://doi.org/10.1016/S0168-1591\(01\)00162-9](https://doi.org/10.1016/S0168-1591(01)00162-9).
- Schmitt, V., Fischer, J., 2011. Representational format determines numerical competence in monkeys. *Nat. Commun.* 29, 257. <https://doi.org/10.1038/ncomms1262>.
- Tomasello, M., Call, J., 1997. *Primate Cognition*. 1st ed. Oxford University Press, New York, NY.
- Troje, N.F., Huber, L., Loidolt, M., Aust, U., Fider, M., 1999. Categorical learning in pigeons: the role of texture and shape in complex static stimuli. *Vis. Res.* 39, 353–366. [https://doi.org/10.1016/S0042-6989\(98\)00153-9](https://doi.org/10.1016/S0042-6989(98)00153-9).
- Uller, C., Lewis, J., 2009. Horses (*Equus caballus*) select the greater of two quantities in small numerical contrasts. *Anim. Cogn.* 12, 733–738. <https://doi.org/10.1007/s10071-009-0225-0>.
- Van der Merwe, J., Marshal, J.P., 2012. Hierarchical resource selection by impala in a savanna environment. *Austral Ecol.* 37, 401–412. <https://doi.org/10.1111/j.1442-9993.2011.02297.x>.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S. Fourth Edition*. Springer, New York.
- Wade, C., Trotter, M.G., Bailey, D.W., 2023. Small ruminant landscape distribution: a literature review. *Small Rumin. Res.* 223. <https://doi.org/10.1016/j.smallrumres.2023.106966>.
- Werner, C.W., Rehkämper, G., 1999. Discrimination of multidimensional geometrical figures by chickens: Categorization and pattern-learning. *Anim. Cogn.* 2, 27–40. <https://doi.org/10.1007/s100710050022>.