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**Exclusion by Donkey's Ears: Donkeys (*Equus asinus*) Use Acoustic Information to Find Hidden Food in a Two-Way Object-Choice Task**

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### Abstract

Once believed uniquely human, the capacity to reason is now investigated in a wide range of species. One component of this ability, inference by exclusion, has been traditionally explored through the cups task, where two containers are presented but only one covers a food reward (if cup A is empty, then choose cup B). Often based on low-level cognitive mechanisms (learning), performance on this task can also reflect reasoning processes in some individuals. Limited taxonomic investigation, however, has hindered our understanding of the factors that contribute to the evolution of reasoning in animals. Using the cups task, we first investigated the ability of 14 semi-wild donkeys to locate a food reward by using visual or acoustic cues alone (pre-test phase). While all subjects failed the task when provided with visual cues, 7 donkeys succeeded in the acoustic modality. We thus tested the capacity of donkeys to make choices by exclusion in the acoustic modality (test phase). Three conditions were presented, where subjects received information about either both containers (Full information condition), solely the empty container (Exclusion condition), or no information (Control condition). Most subjects chose the correct container in the Full information condition, while they chose randomly in the Control condition. Except for one individual, donkeys improved their performance across trials in the Exclusion condition. Our study contributes to the very small body of literature on exclusion based on acoustic cues in animals, and paves the way to further experiments on the cognitive processes underlying exclusion performance in donkeys.

*Keywords:* common donkey, cups task, *Equus asinus*, exclusion performance, two-way object-choice task

### **Exclusion by Donkey's Ears: Donkeys (*Equus asinus*) Use Acoustic Information to Find Hidden Food in a Two-Way Object-Choice Task**

The capacity to reason has long been considered one of the hallmarks of human intelligence (Watanabe & Huber, 2006). About half a century after the publication of Darwin's *On the origin of species* (Darwin, 1859), the first attempts emerged to unravel the nature of the suspected logical processes occurring inside the mind (the "black box": Manktelow & Chung, 2004). Animal research over the past few decades has been particularly flourishing, and has come to reveal analogues of typical forms of reasoning processes (transitive inference: e.g., Tromp et al., 2015; for a review see Guez & Audley, 2013; causal reasoning: e.g., Taylor et al., 2012; for a review see Schloegl & Fischer, 2017).

A well-known aspect of reasoning involves the ability to use logic based on inference by exclusion (reviewed in Völter & Call, 2017; see also Marsh et al., 2015). This mechanism allows for inferring the solution to a problem when fragmentary or no information is available, and can be advantageous in a range of biological contexts, such as foraging (Darmaillacq et al., 2018; Marsh et al., 2015). Imagine for instance a crow chasing a young rabbit. Suddenly, the prey swerves and disappears in a blackberry bush. After inspecting the bush, the crow decides to fly over it and stumbles upon a cul-de-sac that leads to a burrow with two cavities (A and B). Therefore, if the crow does not see anything inside the first cavity (not A), prey might be hiding in the other cavity (not A, then B). Depending on the individual/species tested, or the task employed, exclusion may require different levels of cognition (from basic learning processes to *true* inferences: Pepperberg et al., 2013). Inferential reasoning by exclusion uses logical representations of available information and is essential to making relevant decisions or judgments in our everyday lives (Zeithamova et al., 2012). Other cognitive processes have been suggested to contribute, or support, the emergence of this capacity in animals, such as object permanence, causal conditionals, and proto-negation (O'Hara et al., 2015; Völter & Call, 2017). Interest in the concept of exclusion has burgeoned through comparative studies targeting several nonhuman

animal species, with the aim of elucidating its nature and evolution (Völter & Call, 2017).

A generic approach to exploring inferential reasoning in animals is through the two-way object-choice task (Call, 2004; Jelbert et al., 2015; Mikolasch et al., 2012; Plotnik et al., 2014). In the visual version, two cups are presented, where the subject has previously learned that only one covers a food reward. In the critical phase, the experimenter lifts solely the empty cup. To solve the task, the individual must *exclude* this option (choosing the empty cup) and logically select the other, non-lifted, container. This task, however, does not allow differentiating between low- (mere *avoidance* of the empty cup) and high-level explanations (*true inference* of the location of the food in the non-lifted container: Call, 2004). Therefore, success in this task has been assigned the term 'exclusion performance' in a number of previous studies, which encompasses both explanations (e.g., Nawroth et al., 2014; Mikolasch et al., 2012; Schloegl et al., 2009; Schloegl, 2011).

Given its well-established and easy-to-administer aspects, the two-way object-choice paradigm (also called the cups task), has been widely used in comparative psychology to study exclusion (e.g., Call, 2004; Danel et al., 2021; Mikolasch et al., 2012; Pepperberg et al., 2013; Plotnik et al., 2014; Subias et al., 2019). Importantly, the paradigm can easily be modified to better suit the perceptual systems and ecological backgrounds of different species (Plotnik et al., 2014). Several studies have used the visual version of the task only, which requires animals to locate hidden food by sight when previously shown the content of the empty container (e.g., Darmaillacq et al., 2018; Plotnik et al., 2014). So far, successful exclusion based on visual cues has been found in various species such as dogs (e.g., *Canis familiaris*: Erdőhegyi et al., 2007; including through a computer-controlled two-choice procedure: Aust et al., 2008), goats (*Capra aegagrus hircus*: Nawroth et al., 2014), monkeys (e.g., *Cebus apella*: Paukner et al., 2009; *Papio hamadryas anubis*: Schmitt & Fischer, 2009), apes (e.g., *Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*: Call, 2004; *Symphalangus*, *Nomascus*, *Hylobates*, *Symphalangus syndactylus*, and *Ateles geoffroyi*: Hill et al., 2011), and birds (e.g., *Psittacus erithacus*, *Corvus corone*

*corone*, respectively: Mikolasch et al., 2011; Mikolasch et al., 2012; *Calyptorhynchus banksii*: Subias et al., 2019). In nonhuman primates, research has also been conducted in the auditory domain (Call, 2004), with some species showing better performance in auditory exclusion tests than in visual ones (e.g., lemurs, *Eulemur macaco* and *Eulemur fulvus*: Maille & Roeder, 2012; but see e.g., De Petrillo & Rosati, 2020; Sabbatini & Visalberghi, 2008), and others showing similar abilities in both modalities (e.g., great apes: Call, 2004; great apes, lesser apes, and spider monkeys: Hill et al., 2011). A few experiments within the auditory modality have also revealed exclusion abilities in nonprimates, namely birds (grey parrots: Schloegl et al., 2012; but see Shaw et al., 2013) and trained pigs (Nawroth & von Borell, 2015). The Asian elephant (*Elephas maximus*), on the other hand, which showed marked difficulties in both modalities (visual: Plotnik et al., 2013; acoustic: Plotnik et al., 2014), relied on olfactory information to solve exclusion tasks (Plotnik et al., 2014). These results indicate that testing distantly related species across sensory modalities and with different ecological backgrounds is essential to shed light on the taxonomic distribution of exclusion performance in animals (Völter & Call, 2017).

Recently, feeding ecology and foraging flexibility have been proposed to be the source of, or potential contributors to, variation in exclusion skills (respectively: De Petrillo & Rosati, 2020; Nawroth et al., 2014). More specifically, in a comparative study with small ruminants that differed in their feeding ecology, Nawroth et al. (2014) found that more flexible and highly selective foraging goats outperformed rather unselective sheep (*Ovis orientalis aries*) on the visual version of the cups task. Based on the predictions of the adaptive specialization hypothesis (De Kort & Clayton, 2006), the authors suggested that differences in exclusion abilities are predicted by the species' specific feeding ecology. Similarly to goats (Stuth, 1991), other species are highly flexible and selective in their food intake and can spend long periods of time searching for more profitable food patches, potentially indicating their capacity to choose by exclusion.

Long viewed, mistakenly, as “small horses” (Burden & Thiemann, 2015), domestic donkeys

(*Equus asinus*) possess a unique ecological background among equines for testing exclusion performance in foraging contexts. This species' diet and foraging needs are tied to the eating habits of its ancestor (the wild ass, *Equus africanus*: Beja-Pereira et al., 2004). The wild ass lives in arid and desert regions where food is sparse and of very low nutritional value (Izraeli et al., 1989; Kimura et al., 2013). As a result, the donkey is a highly flexible yet selective forager that feeds on grass, browse (woody shrubs, trees, and broadleaf plants), and forbs (flowering plants) as well (Grinder et al., 2006).

Similar flexibility is found in donkeys' complex social behavior (Murray et al., 2013; Proops et al., 2012), where social organization (e.g., solitary, small group, large group, or herd system: Grinder et al., 2006; Marshall & Asa, 2013) depends on environmental conditions (abundance of food resources). Acoustic information plays a significant role in this context (Grinder et al., 2006). Donkeys' large ears can process high frequency sounds and move 180° independently from each other, enabling them to receive various types of information from conspecifics located kilometres away (Burden & Thiemann, 2015; Lindsay & Clayton, 1986). Vocalizations occur when locating the position of others in space, meeting conspecifics, soliciting herd cohesion, or during antagonistic interactions. In terms of ecological relevance, acoustic abilities seem also particularly important in the predatory and foraging contexts. As potential prey, donkeys emit specific sounds when perceiving danger (sharp snort, bray) and exploit information about the presence of food conveyed indirectly through conspecifics' acoustic cues (e.g., chewing sounds; SD, personal observation). Their visual sense, on the other hand, allows them to perceive frontal and rear threat postures of differing intensity during social communication. Vision is also more adapted to ensure the animal's survival than to identifying (stationary) food during foraging (Miller & Murphy, 2010). For instance, due to the lateral position of their eyes, equids have a broad visual field, efficient peripheral vision and visual acuity, and adaptations to dim and bright light, which are crucial for predator detection.

First domesticated more than 5000 years ago, mainly for their ability to transport heavy loads in



mountainous and arid regions of Africa and Asia (Burden & Thiemann, 2015; Kimura et al., 2013; Marshall & Asa, 2013; Rossel et al., 2008), donkeys are now widely used for draught and production purposes all around the world. Beyond these significant roles, this species now fulfils additional functions in society (e.g., as a companion, or as ‘facilitator’ in assisted programs for child development: Rose et al., 2011). Investigating perception and cognition in this species is thus crucial in order to develop proper care and management programs (Mc Lean & Gonzalez, 2018). Indeed, despite their heavy economic use in many regions of the globe, donkeys are largely underrepresented in behavioral studies (Kimura et al., 2013). Among large domestic ungulates, most cognitive research has focused on horses (Baragli et al., 2011). A handful of experimental studies have compared donkeys with other equids on their ability to learn (Waring, 2003), discriminate objects (Proops et al., 2009), show object permanence, and retain short-term information (Baragli et al., 2011). Moreover, mules and donkeys were shown to be better than horses at solving a test of spatial cognition and at perseveration abilities (Osthaus et al., 2013).

The goal of this study was twofold. First, we investigated whether 14 semi-wild donkeys were able to use their visual and auditory senses to locate a hidden food reward in a two-way object-choice task. Second, on the condition that subjects succeeded to solve the task in one or both modalities, we aimed to assess the capacity of subjects to show exclusion performance (selecting the rewarded container when provided solely with information about the empty container). We predicted that donkeys would be able to transfer to other contexts their capacity to use visual and acoustic information in the social domain (Plotnik et al., 2014). If donkeys effectively rely on both modalities during the cups task, this might suggest meta-use of socio-cognitive skills to solve novel foraging problems. Furthermore, given the flexible yet selective aspects of their feeding habits, and the demands associated with their foraging ecology (rarity of food, potentially requiring the rapid avoidance of unprofitable food patches), we also predicted exclusion ability to be present in this species.

## Methods

### Subjects

Fourteen semi-wild common donkeys (*Equus asinus*) participated in this study (4 females: Ânoushka, Fânnette, Gudule, Nânou; 10 males: Albân, Bâbylone, Boucânet, Don Juan, Hurricâne, Mânti, Pânettone, Tac, Tic, Urbân). These subjects belonged to 'Provenc'Ânes', a professional donkey breeder in Rians (France), and were aged between 11 and 20 years. On its return from transhumance (Sep – Nov 2019), the herd was separated into two groups. Individuals from Group 1 ( $n = 5$ : Ânoushka, Bâbylone, Gudule, Pânettone, Tic) were allowed to move freely within an area of 40 hectares. Donkeys from Group 2 ( $n = 9$ : Albân, Boucânet, Don Juan, Fânnette, Hurricâne, Mânti, Nânou, Tac, Urbân) were located within a natural field of 20 hectares. The subjects were tested four times a week on average from 10 a.m. to 3 p.m. between Dec 2018 and May 2019 (the groups' running order alternated daily e.g., on day 1 individuals from Group 1 were tested first, then the reverse on day 2, etc.). For the pre-test and test phase, each subject was visually isolated from the others in an enclosure that covered 20 m<sup>2</sup> for both groups, and which was located 15 m (Group 1) and 30 m (Group 2) away from the donkeys' territory. All animals had access to natural grass and water *ad libitum*. Prior to this study, the subjects had never been tested in cognitive tasks.

The professional donkey breeder 'Provenc'Ânes', who was responsible for donkey husbandry and care, and the National Federation of Trekking Donkeys, provided the authorization to carry out experiments. The Ethics Committee of Department of Psychology of the University of Lyon 2 read and approved the study. The methods were carried out in accordance with the ASAB/ABS guidelines for the treatment of animals in behavioral research and teaching and met the requirements of the Guide to Ethical Information Required for Animal Behavior Papers.

### Experimental Setup and Materials

The apparatus consisted of a white-painted wood (OSB) box (height 57.5 cm x width 55 cm x

length 77.5 cm) elevated on two height-adjustable pine trestles (98.5 cm x 45 cm x 70 cm; Figure 1). The box front had 5 vertical wooden bars (45 cm in length) and a horizontal slot (77.5 cm in length) from which a sliding platform (8 mm x 33.6 cm x 67.9 cm) could be retracted or extended in order to, respectively, (i) allow the experimenter to put the containers in place out of the sight of the subjects (behind a curtain positioned on a rod, a distance of 15 cm from the box front), and (ii) give the subjects access to the reward if they succeeded. Each side of the sliding platform was fitted with metal ball bearing drawer runners (31.5 cm in length, ©DIAL), facilitating the sliding mechanism on the support wood plank. A wood bar was fixed in the center of the sliding platform (2 cm x 2.7 cm x 44 cm) that served as a push/pull handle. We used two types of containers: *Containers 1* consisted of two identical opaque Tupperware® boxes (17.7 cm x 17.7 cm x 5.8 cm) screwed on at either end (30 cm apart) of the sliding platform. A pair of detachable plastic containers was used as *Containers 2* (5 cm x 16 cm x 16 cm), which could be inserted in *Containers 1*. To control for residual olfactory cues, all receptacles (*Containers 1* and *2*) were in contact with the food and used interchangeably. Donkeys were not food-deprived but were kept motivated by using pieces of carrot (2 cm in diameter) and/or fibre pellets as rewards – both highly favoured food items that did not form part of the subjects' regular food. All test trials were recorded using a video camera (Samsung camera HMX-F90) mounted on a tripod.

< Insert Figure 1 about here >

## **Procedure**

### ***Habituation***

Three days prior to the start of the experiments, all individuals were given access to the apparatus to allow for habituation. The unrewarded apparatus was presented within each group's territory every day for 3 hours continuously. In an outside visually isolated test area, the donkeys were then individually trained to push the lids from both *Containers 1* by gradual shaping. Once they had learned to retrieve the food rewards (two pieces of carrot in total, one in each container) out of the

open containers, the lids were gradually added to cover the containers to an increasingly greater extent (depending on the subject's individual learning speed) until they were entirely closed. At the onset of a trial and behind the curtain, the subject waited in front of the test apparatus while the experimenter placed one piece of carrot inside both *Containers 2* and closed them with the lids of *Containers 1*. Then, the experimenter opened the curtain and pushed the wood bar, allowing the donkey to push both lids and feed from the containers. During this procedure, the experimenter stayed still and looked straight ahead. The distance between the experimenter and the subject was about 65 cm, with the exact distance depending on the position of the donkey. The next trial started as soon as the experimenter had closed the curtain. The inter-trial interval was set to at least 10 s, with the exact time dependent on the behavior of the subject. The donkeys had to remove the lids 15 times in a row (trials 1 min each) from each of the containers to move to the next pre-test phase.

### ***Pre-Test Phase***

In this phase, for both conditions, only one container covered a reward. Consequently, the subject had to locate visually or acoustically the correct rewarded container. The order in which donkeys were tested on any given day was based on the subjects' voluntary participation, and the food reward was not positioned on the same side consecutively more than 3 times in a row. If the subject chose the correct rewarded container, it was allowed to retrieve the food; if it removed the lid of the unrewarded container, the experimenter let the subject investigate the empty container for a maximum of 5 s. In order to prevent reliance on low-level enhancement effects (e.g., the tendency to choose the container that is manipulated last: Mikolasch et al., 2012), the experimenter always moved both hands in each modality (visual: when showing the reward, auditory: when lifting and shaking the containers, see below).

In the visual modality, just after having opened the curtain, the experimenter stretched both of her hands out towards the subject, each hand in front of one container, and waited 3 s with a reward (a

piece of carrot) located in only one palm. Subsequently, she inserted each of her hands in the respective containers, released the reward, and placed the lid on each container.

In the acoustic modality, fibre pellets were added to the usual piece of carrot. The rationale for this was that fibre pellets create a clear and loud noise. First, the experimenter shook both *Containers 2* for 3 s without interruption. Subsequently, she quickly and simultaneously put each *Container 2* within their respective *Containers 1*, put the lids on *Containers 1*, and gave the subject access to both containers.

For both modalities, each pre-test session consisted of 10 trials and the subjects were advanced to testing if they chose the rewarded container in 8 out of 10 trials in at least two successive sessions. A maximum of 40 trials in total was administered if subjects failed to reach criterion. If the individual succeeded in 8 out of 10 trials during its fourth session (40 trials), we allowed it to receive another session of 10 trials to give it a final opportunity to reach criterion.

### ***Test Phase***

Given that no subject passed the pre-test phase in the visual modality (see Results), only the acoustic modality was tested. Each subject received 30 trials in total for each condition (30 trials for Exclusion, 30 trials for Full information, and 30 trials for Control). Trials were administered using test sessions: one test session consisted of 6 trials (2 Exclusion trials, 2 Full information trials, and 2 Control trials). Thus, to reach 30 trials for each condition, each subject received 15 test sessions in total. The conditions were presented in a pseudo-randomized order within sessions. Here again, no side remained rewarded on more than 3 consecutive trials in any of the conditions. Each session lasted up to 15 min and a maximum of 4 sessions were administered per day. The inter-trial interval was typically approximately 1 min.

In the Full information condition, the food reward (a piece of carrot with fibre pellets) was hidden within one *Container 2* and then both *Containers 2* were lifted and shook simultaneously in front

of the subject for 3 s. After both containers were put down, the subject was allowed to choose between them. In the Exclusion condition, the same procedure as in the Full information condition was followed (both containers were simultaneously lifted), except that after lifting, only the empty container was shaken. Finally, in the Control condition, subjects had no acoustic information about the food location: the experimenter did not shake the containers but only lifted them simultaneously. This condition assessed whether the subjects' choices were influenced by the use of olfactory cues.

### ***Potential Non-Cognitive Confounding Factor: Motivation***

We assessed whether individual variation in interacting with the setup could be explained by differences in motivation. The test measured the latency (in s) for each subject to feed from a bucket. We conducted these tests over two consecutive days after the test phase (usually 2 trials per day, 10 min apart). Four trials were administered in total for each subject (each lasting 2 min maximum). Before each trial, the subject was brought to the visually isolated test area, allowing the experimenter to place the food in a bucket located about ten meters away from this location. Then, the experimenter allowed the donkey to go freely towards the bucket, and measured the time taken from when the donkey began to walk until it inserted its nose inside the bucket.

### **Data Analysis**

The experimenter reported results for each tested individual and after each trial, and subsequently verified the results by watching the videos. For every trial, direct observation and video analysis yielded identical results; in no case was there a mismatch.

Our first goal was to implement Generalized Linear Mixed Model trees to identify associations of variables that lead to different success rates. GLMM trees, described by Fokkema et al. (2019), are particularly well fitted to animal cognitive studies involving decision-type data (see Danel et al., 2021 and Romain et al., 2021 for a detailed description and examples). The GLMM tree algorithm identifies subgroups of observations (also called terminal nodes) that differ in success rate, taking into

consideration the nested structure of the dataset (subjects). Our second goal was to implement a GLMM analysis to determine which subgroup of observations, and thus testing conditions, significantly differed in terms of success rate.

In the GLMM tree analysis (goal 1), donkeys' success probability at trials was modelled as a variable following a binomial distribution, considering Condition (Control vs Full information vs Exclusion), Food Position (Right vs Left), and Trial Number (1 vs 2 vs...30) as splitting variables. To account for individual differences, we included subject identity as a random effect. We back transformed coefficients from the logit scale to obtain success probabilities on the response scale. In order to assess the significance of tree-based algorithms between nodes (goal 2), success probability was then modelled in a GLMM with a binomial distribution accounting for Condition (Control vs Full information vs Exclusion), Food Position (Right vs Left), and Trial Number (1 vs 2 vs...30).

At last, we conducted binomial tests to assess how individual performance was different from chance performance in each experimental condition and during the first 12 trials. Finally, we used Spearman's correlation tests to analyse the relationship (i) between mean latency to feed (motivation) and probability of success in the pre-test phase ( $n = 14$ ), and (ii) between mean latency to feed (motivation) and probability of success in the test phase (Full information and Exclusion;  $n = 7$ ).

All analyses were conducted in R Version 3.6 (R Core Team, 2019). We used the packages *glmertree* (Fokkema et al., 2019) and *lme4* (Bates et al., 2015) to implement the GLMM tree and the GLMM analyses, respectively, and the package *multcomp* (Hothorn et al., 2008) to perform the post-hoc tests.

## Results

### Pre-Test Phase

In the visual modality, none of the 14 individuals reached the success criterion, but continued to perform at chance level across all sessions (see Table S1, Supplemental Materials). On the other hand, in

the acoustic modality, 7 individuals (Ânoushka, Babylone, Gudule, Pânettone, Tac, Tic, Urbân) passed criterion and proceeded to testing (Table S1).

### Test Phase

The variable *Condition* was the first partitioning variable on the root node (the full set of observations) that yielded a p value below the pre-specified significance level ( $p \geq 0.05$ ; Figure 2 shows the resulting GLMM tree). The first split in the tree (Node 1,  $p < 0.001$ ) separated the data into two subgroups: the first subgroup included the Control condition (Node 2) and the second subgroup both the Exclusion and Full information condition. Observations in Node 3 (trial) were further split into two nodes: Node 4, which represented the Exclusion and Full information condition for trials  $\leq 11$ ; and Node 5 ( $p < 0.001$ ), which included the Exclusion and Full information condition for trials  $> 11$  (12-30). Node 5 then split into Node 6 (Exclusion condition) and Node 7 (Full information condition). We did not identify an effect of Food position (this was never a splitting variable in the GLMM tree), indicating the absence of any bias towards either side of the container. The intervals of trials provided (1-11, 12-30) are not arbitrary but specified by the GLMM tree analysis.

Post hoc tests from the GLMM showed that donkeys were significantly less successful in Control than in Exclusion  $> 11$  trials ( $1.38 \pm 0.26$ ,  $z = 5.29$ ,  $p < .001$ ), Full information  $> 11$  trials ( $2.86 \pm 0.41$ ,  $z = 6.92$ ,  $p < .001$ ), and Exclusion + Full information  $< 11$  trials ( $0.72 \pm 0.22$ ,  $z = 3.25$ ,  $p < .001$ ; Table 1).

Donkeys' success probability was lower in Exclusion + Full information  $< 11$  trials than in Full information  $> 11$  trials ( $2.14 \pm 0.43$ ,  $z = 5.01$ ,  $p < .001$ ). No significant difference was found between Exclusion + Full information  $< 11$  trials and Exclusion  $> 11$  trials ( $0.65 \pm 0.28$ ,  $z = 2.35$ ,  $p = .09$ ). Finally, subjects chose the correct container significantly more in Full information  $> 11$  trials than in Exclusion  $> 11$  trials ( $1.48 \pm 0.45$ ,  $z = 3.32$ ,  $p < .001$ ).

< Insert Figure 2 and Table 1 about here >

### Binomial Tests



At the individual level, the performance varied considerably between subjects (Table 2). Five out of 7 donkeys chose the correct rewarded container within the Exclusion condition (Ânoushka, Gudule, Tac, Tic, Urbân; binomial test:  $p < 0.05$ ), including 2 subjects on their first trial (Ânoushka, Tic). All individuals succeeded above the level expected by chance in the Full information condition, no subject selected the correct container above chance during the Control condition, and no donkey possessed or developed a preference towards the left or right container (side bias) in the experimental conditions (binomial test:  $p < 0.05$ ; Table S2).

< Insert Table 2 about here >

#### **Potential Non-Cognitive Confounding Factor: Motivation**

Mean latency to feed did not correlate with probability of success either in the pre-test phase and the test phase (Spearman correlation,  $n = 14$ , pre-test phase:  $r_s = .10$ ,  $p = .37$ ;  $n = 7$ ; test phase, Full information condition:  $r_s = -.22$ ,  $p = .64$ ; test phase, Exclusion condition:  $r_s = -.45$ ,  $p = .31$ ). Individual variation in performance during the pre-test phase and the test phase (Full information and Exclusion condition), therefore, cannot be explained by inherent differences in motivation.

#### **Discussion**

We tested 14 semi-wild donkeys' exclusion performance in a two-way object-choice task. Overall, while all donkeys were not able to use visual cues to track the location of a food reward, half of our subjects succeeded in using acoustic cues to select a rewarded container. Most donkeys also showed exclusion performance in the acoustic modality, by selecting the rewarded cup significantly more when provided with information about the empty cup only. Furthermore, given that subjects performed at the level expected by chance in the Control condition, our results in the Full information and Exclusion condition could not be explained by the use of olfactory cues to solve the task.

Although donkeys were readily able to remove the lids of the containers in the habituation phase, they had difficulties in choosing the rewarded container in the pre-test phase of the visual

modality. This negative result may be related to this species' blind spot (located under the nostril and behind the head) and visual capacities that are not as well as developed as those of other large mammals (Chapman & McLennan, 2017). On any given trial during the habituation phase, the visual cue was first presented about 30 cm away from the subject while, in the subsequent choice phase, the rewarded container was located just under the donkey's head. This close proximity may have prevented the subjects from selecting the correct container. Conversely, goats and sheep, which rely on similar food sources and also possess a narrow blind zone to the rear (Adamczyk et al., 2015), were able to select the correct baited container in the visual version of the cups task (Nawroth et al., 2014). In this latter study, the sliding platform supporting the containers was placed in front of the subjects. This slight methodological difference may explain why these two small ungulate species have been more capable of selecting the correct container in the visual domain (4 out of 6 sheep and 10 out of 11 goats chose the rewarded cup significantly more often when both cups were lifted in the experiment controlling for local enhancement). These results and considerations need to be taken into account when designing further cognitive studies using the two-way object-choice task with donkeys. So far, most studies on mammals and birds have focused on the visual domain. In these groups, more than one sensory modality may be exploited to receive and process information (including in the foraging context) and these must be investigated in order to more fully comprehend animals' cognitive capacities. For instance, sheep have failed in using indirect information in visual exclusion tasks (Nawroth et al., 2014), although we cannot rule out the possibility that the absence of noise (or smell) may be more relevant for this species.

Donkeys efficiently exploited their auditory sense to locate the reward in the pre-test phase. One may relate their performance to non-cognitive motivational factors (first possibility) or unintentional, spontaneous cues given by the experimenter (second possibility: Mikolasch et al., 2012; Schloegl, 2011). However, the performance of subjects did not correlate with the latency to feed in a foraging task (in the pre-test phase with all 14 individuals, but also later on in the test phase with 7

subjects). Thus, the variation in performance observed among subjects cannot be explained by differences in motivation to participate in the task.

Regarding the second possibility (social enhancement effects), the actions exhibited by the experimenter involved the simultaneous movement of both hands and containers (Mikolasch et al., 2012). Donkeys' performance is therefore unlikely to be due to social enhancement effects. Moreover, although horses reared and trained in anthropic environments are well known for their capacity to read human behavior (the 'Clever Hans phenomenon': e.g., Trestman, 2015), the latter suggestion also appears unlikely in the present study. If donkeys have been guided by unconscious experimenter-given cues, they should have chosen the rewarded container significantly more in the visual condition as well.

Some donkeys were adept at locating hidden food and excluding non-rewarding options within the acoustic domain, similarly to a handful of species, including some apes (Call, 2004; Bräuer et al., 2006; Hill et al., 2011), monkeys (Maille & Roeder, 2001; Sabbatini & Visalberghi, 2008), birds (Schloegl et al., 2012), and swine (Nawroth & von Borell, 2015). In order to prevent learning of the visual and acoustic cue, and similarly to other exclusion studies assessing the use of multiple sensory modalities in mammals, we did not administer more than 40 trials in the pre-test phase for each modality (e.g., Plotnik et al., 2014). However, during the test phase, we found a progressive improvement in subjects' performance over trials within the Full information condition. We thus cannot rule out the possibility that donkeys may have learned to associate acoustic cues with the reward over repeated exposure.

When only the empty container was shaken in the Exclusion condition, 6 out of 7 donkeys had a clear preference for selecting the rewarded container. Although our test setup does not allow differentiating between low- and high-level cognitive mechanisms (Marsh et al., 2015; Nawroth et al., 2014), some observations lead us to provide potential explanations about the cognitive processes at play. Among the 6 individuals that selected the correct container in the Exclusion condition, 5 donkeys improved their performance over trials. The use of a low-level strategy (associative learning) therefore

cannot be entirely excluded (Mikolasch et al., 2012). This learning mechanism, which represents an efficient cognitive strategy to solve the task, has been reported in other species (e.g., brown skuas, *Catharacta antarctica ssp. lonnbergi*; Danel et al., 2021; carrion crows, *Corvus corone corone*: Mikolasch et al., 2012; great apes: Call, 2006; olive baboons, *Papio hamadryas anubis*: Schmitt & Fischer, 2009; Tufted capuchin monkeys, *Cebus apella*: Paukner et al., 2009). One donkey (Ânoushka), however, did not gradually learn to solve the task in the Exclusion condition. This subject chose correctly from her first trial onward, which suggests the use of a strategy other than one learned by trial and error.

Future work may assess donkeys' performance through the use of additional controls (e.g., see the information seeking paradigm in Paukner et al., 2006; or the modified design of the tubes task used by Jelbert et al., 2015) or more than two cups (Grether & Maslow, 1937; Ferrigno et al., 2021; Mody & Carey, 2016; Pepperberg et al., 2019). For instance, in a study comparing the capacity to infer by exclusion in Old- and New World monkey species (Marsh et al., 2015), one of the tasks used 3 cups (one cup covering a food reward) in 4 experimental conditions, where across conditions experimenters revealed the content of either: a single empty cup (condition 1), both empty cups (condition 2), the baited cup (condition 3), and the baited cup and one empty cup (condition 4). Unlike the traditional two-cups task, such multiple-cups tasks control for the use of associative learning processes. Specifically, when only one empty cup was lifted in condition 1, subjects had to choose between the two other containers and thus could not obtain the reward by simply learning to avoid the empty cup. It is also possible to determine whether subjects truly represent the dependent relationship between the cups (A 'or' B), or rather use alternative searching strategies (maybe A and maybe B), by simultaneously presenting 4 containers (two sets of containers, with one container in each set covering a food reward; see Ferrigno et al., 2021; Mody & Carey, 2016; Pepperberg et al., 2019). Multiple-cups tasks thus discourage the use of non-deductive approaches (avoidance strategies), are more challenging at the cognitive level, and allow identifying the underlying cognitive processes utilised.

Future studies may also include an experimental condition in which only the baited container is shaken ('Baited' condition). This condition, which offers a direct comparison with the Exclusion condition (only the empty container is shaken vs only the baited container is shaken), will allow us to clearly determine whether donkeys choose the shaken baited container. Provided that inferential reasoning by exclusion is verified in donkeys in the future, further comparative experiments with horses and donkeys may be carried out in order to shed light on the evolutionary drivers behind this capacity. One of the most salient differences between the two species is that donkeys are both grazers and browsers while horses are mainly grazers (Burden & Thiemann, 2015). If highly flexible donkeys outperform less flexible horses on the two-way object-choice task, this would provide further support towards the role of feeding ecology in the emergence of exclusion abilities.

In conclusion, our experiment corroborates the importance of identifying and taking into account differences in perceptual abilities when comparing species' performance in the two-way object-choice task (Plotnik et al., 2013). Although most tested donkeys were able to choose by exclusion, these subjects likely solved the task by learning to avoid the empty cup over trials. Thus, albeit we have previously suggested that inferential exclusion abilities may have significant ecological benefits in donkeys, it would be premature to relate our results to inferential reasoning mechanisms. Nevertheless, one subject stood out from the crowd, and further tests are required to draw firm conclusions about her capacity - and the capacity of other donkeys more generally - to reason by exclusion.

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**Tables****Table 1***Post Hoc Tests of the GLMM Analysis for the Variable Condition*

Comparisons of subgroups	Estimate	SE	z	p
Exclusion + Full information < 11 trials - Control	0.73	0.22	3.26	0.01
Exclusion > 11 trials - Control	1.38	0.26	5.29	< .001
Full information > 11 trials - Control	2.86	0.41	6.92	< .001
Exclusion > 11 trials - Exclusion + Full information < 11 trials	0.65	0.28	2.33	0.09
Full information > 11 trials - Exclusion + Full information < 11 trials	2.14	0.43	5.01	< .001
Full information > 11 trials - Exclusion > 11 trials	1.48	0.45	3.32	< .001

**Table 2***Individual Performances*

Subjects	Conditions	First trial	First 12 trials	Correct choices/Total
Ânoushka	Exclusion	1	<b>10/12</b>	<b>26/30</b>
	Full information	1	<b>10/12</b>	<b>26/30</b>
	Control	1	5/12	14/30
Babylone	Exclusion	0	5/12	12/30
	Full information	0	7/12	<b>23/29</b>
	Control	1	8/12	14/29
Gudule	Exclusion	0	6/12	<b>21/30</b>
	Full information	1	<b>10/12</b>	<b>27/30</b>
	Control	1	7/12	16/30
Pânettone	Exclusion	1	7/12	20/29
	Full information	1	<b>12/12</b>	<b>29/30</b>
	Control	0	6/12	18/30
Tac	Exclusion	0	7/12	<b>23/30</b>
	Full information	1	8/12	<b>25/30</b>
	Control	1	5/12	15/30
Tic	Exclusion	1	9/12	<b>26/30</b>
	Full information	1	7/12	<b>23/30</b>
	Control	0	6/12	15/30
Urbân	Exclusion	0	8/12	<b>24/30</b>
	Full information	1	<b>12/12</b>	<b>30/30</b>
	Control	0	5/12	15/30

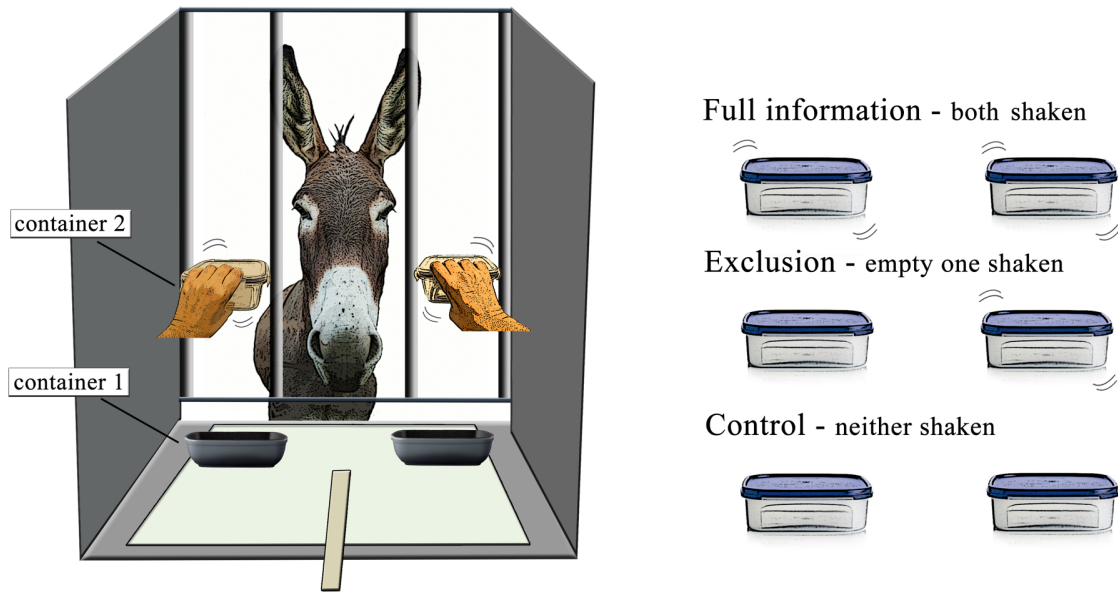
*Note.* First trial: 1 means successful, 0 means unsuccessful. Bold denotes significance (binomial tests;  $p < 0.05$ : 21 correct choices or more out of 30 trials).



Figures

Figure 1

*Schematic Representation of the Apparatus (A) and the Experimental Conditions (B) Used to Assess Donkeys' Exclusion Performance in the Acoustic Modality*



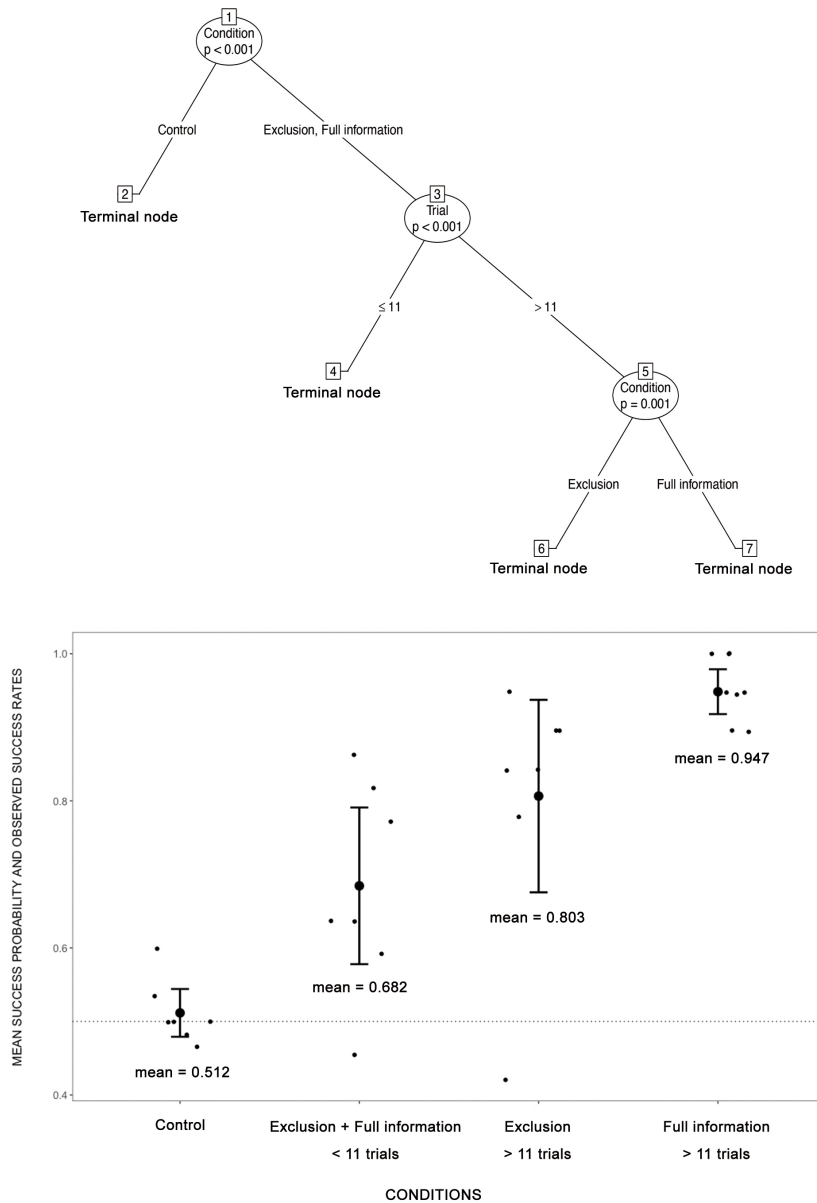
A Test trial - full information condition

B Experimental conditions

**Figure 2**

*Donkeys' Mean Success Probability to Choose Correctly in Each Terminal Node Specified by the GLMM*

*Tree Analysis*



*Note.* Error bars represent 95% confidence intervals associated with estimated means. Dots show the observed performance of each individual during the different tests between 0 and 1 (0 to 100% success).

**Supplemental Materials**

Data including subjects' performance during the pre-test phase in the visual and acoustic domain, and subjects' side bias during the pre-test and test phase, is available as Supplemental Materials.