



UNIVERSITY OF THE
WITWATERSRAND,
JOHANNESBURG

**Quantity Discriminatory Capacity and Choice Preference Between
Binary Rewards in African Elephants**

by

Elena Mariotti

(1077194)

Submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

in

Animal, Plant, and Environmental Science

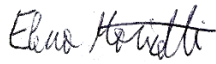
in the Faculty of Science,

University of the Witwatersrand, Johannesburg, South Africa

October 2024

DECLARATION

I hereby declare that this thesis is my own, unaided work, and that recognition has been given to the references used and assistance received. It is being submitted for the Degree of Doctor of Philosophy in the Faculty of Science at the University of the Witwatersrand. It has not been submitted for any degree or examination at any other University.



Elena Mariotti

2nd day of October 2024

ABSTRACT

The ability to quantitatively discriminate between different numbers of the same items is shared by most animals and pre-verbal humans, and it is a requirement for being able to do simple arithmetic operations. This thesis investigated African elephants' (*Loxodonta africana*) ability to do simple arithmetic by testing their quantity discrimination ability, potential drivers of it, and their learning ability, with a special focus on individual differences. The results from this thesis provide informative priors representing a necessary foundation to quantitatively estimate the risk preferences of elephants in further choice tasks, which is the aim of the larger project this thesis is part of.

Individual elephants were presented with binary choices over different quantities of the same food. All data analysis used a Bayesian framework, to allow informed inferences about individual elephants. First, the preference of the elephants for different fruits was measured. Subsequently, using game pellets and the preferred fruits, quantity discrimination choices were observed using olfactory-only or olfactory-and-sound as cues. Elephants were successful in discriminating between different quantities based on olfactory cues only, but only when they could smell directly on the top of the perforated buckets containing the rewards. A combination of olfactory information and sound reduced their discrimination ability. The absolute difference between the alternatives had a stronger effect on the choices made by the elephants when the difference between the alternatives was larger, while the ratio of the alternatives affected the choices mostly when the two alternatives were similar in size, regardless of the food used. This finding

suggests that elephant olfactory quantity discrimination was driven mainly by the numerosity of the rewards rather than by the idiosyncratic characteristics of the food.

Grouping the quantity discrimination evidence over each reward together, I was able to show that elephants can perform simple arithmetic operations, being more precise when the alternatives differ by at least two units. The learning ability of the elephants was affected by the order and difficulty of the tasks, with initial tasks, when elephants were not accustomed to the experimental set-up yet, showing clear indication of learning. The fact that the elephants in this study were able to successfully discriminate between different quantities of different fruits, that they were relatively precise when the difference between the alternatives was at least 2 units, and that they showed signs of learning over the course of novel tasks, allows one to infer that eliciting the risk preferences of elephants might be possible. In addition to representing the first step to a quantitative elicitation of the risk preferences of elephants, this thesis proves for the first time that African elephants can do simple arithmetic and also provides vital information to increase our understanding of how elephants make decisions in the wild.

DEDICATION

to

Nonna Lina

Questo studio sui Bao è dedicato a te.

Ti voglio bene. Manchi.

Buona Pasqua!

ACKNOWLEDGEMENTS

First and foremost I must thank my supervisors, Prof. Francesca Parrini and Prof. Don Ross, and my advisors Prof. Glenn W. Harrison and Prof. E. Elisabet Rutström for the constant guidance and support they provided throughout the research process. Although each of you is involved in many other important projects, you have always been there for me. Thank you.

I would like to express my gratitude to Prof. Neville Pillay and Prof. Ed T.F. Witkowski for the advice they shared during the committee meetings and for having been in my corner since when I was in their Honours class.

This project would not have been possible without funding from the Center for the Economic Analysis of Risk (CEAR) at Georgia State University, or without the ethical clearance released by the Animal Ethics Screening Committee of the University of the Witwatersrand and by the Animal Care and Use Committee of Georgia State University.

To Sean and Jenna Hensman, thank you for having hosted me in your cottage for the whole duration of the data collection. Thank you for all your help in carrying out this project, both from a working and a personal point of view. I will never forget the time I spent at Adventures with Elephants, where I had my first experiences with African elephants, lions, and cheetahs, and flying on Patches.

There is quite a large group of people who deserve my gratitude. Handlers, this project would have not been possible without you. You are a beautiful group of people who made me feel at ease from the first day. Your knowledge of elephants is invaluable, and your passion for your work is impressive. I have learnt a lot from each one of you,

on elephants and more. A big thank you goes to: David Mupupu, Edward Mabotha, Heritage Chauke, Jerico Kanobvurunga, Joseph Kamupambe, Lawrence Maako, Nathan Nyakapanda, Oscar Severino, Richard Thandane, Sydney Pondamare, Thabo Ramashia, and Weekend Nyakwete. In addition, I want to thank Cloudie Nyamasoka and Adele Smit for helping locate the team each day and for our numerous chats, Mathew Kachombo and Muchaneta Magriva for feeding me tasty sadza, and Phillip Ngwenya for the countless operations of building, moving, accommodating, and fixing he made for the project. Thank you all!

To Andrea C. Bouwer and Jaco E. Jacobs, thank you for everything. You both helped with the project, read my stuff to confirm it made sense, and suggested ideas, but most of all, you supported me, listened (often to Italian music too), cheered me up, and are real friends. You helped when times were tough. Thank you.

This project started in March 2020. If I made it through lockdown in Johannesburg without going totally insane it is only thanks to Paulo Henrique Pinheiro Ribeiro. You offered me a room at your place when I was in need, we learnt to cook our respective traditional dishes (and the difference between parsley and cilantro), and we spoke about any possible topic for months. Thank you P.

Also thank you to my Wits mates who understood and supported me during this journey: Kiara Haylock, Alexandra Turner, Kim Mordecai, Tamryn Hamilton, Dr Nikhail Arumoogum, Dr Zaara Kidwai, Dr Subhadeep Bhattacharjee, Dr Melinda Boyers, Dr Blair Cowie, and Dr Redae T. Tesfai.

Last but not least, thank you to my family and old friends, who have endured me for the whole project, who always believe in me especially when I do not do it, and who always welcome me when I come home. I love you.

*We cannot go back. That's why it's hard to choose.
You have to make the right choice. As long as you don't choose,
everything remains possible.*

Mr. Nobody

*If science teaches us anything, it teaches us to accept our failures,
as well as our successes, with quiet dignity and grace...*

Young Frankenstein

*Invece sotto l'occhi c'abbiamo solo ste cartacce senza senso,
che 'so proprio distanti d'a forma che avevamo pensato...
però se potemo comunque strigne intorno ar foco e ricordasse che
tanto alla fine, tutti i pezzi de carta so 'boni pe' scaldasse.*

Strappare lungo i bordi

TABLE OF CONTENTS

DECLARATION	I
ABSTRACT	II
DEDICATION	IV
ACKNOWLEDGEMENTS	V
LIST OF FIGURES	XII
LIST OF TABLES	XX
CHAPTER 1: GENERAL INTRODUCTION.....	1
MOTIVATION FOR THE STUDY	1
LITERATURE REVIEW	4
Decision theory, maximisation criterion and optimality	4
Quantity discrimination	7
Quantity discrimination, how it works	8
Accumulator model	10
Trained vs untrained discrimination tests	15
The effect of the sense and mode of presentation of the alternatives	20
The effect of side preference	21
Learning in quantity discrimination tasks	22
Quantity discrimination in elephants	24
AIM AND OBJECTIVES.....	26
GENERAL METHODOLOGY	27
Study species	27
Study subjects	30
Study design	32
Statistical analysis.....	34
ETHICAL APPROVAL	55
THESIS OUTLINE	55
OUTPUTS	56
REFERENCES.....	56

CHAPTER 2: FRUIT PREFERENCE OF SIX SEMI-TAME AFRICAN ELEPHANTS	63
INTRODUCTION	63
METHODS	67
Data collection.....	67
Data analysis.....	70
RESULTS	75
Illustrative Results	75
Detailed Results.....	78
DISCUSSION	84
REFERENCES.....	87
 CHAPTER 3: AFRICAN ELEPHANT NON-VISUAL REWARD QUANTITY DISCRIMINATION: A CHOICE EXPERIMENT	 90
INTRODUCTION	90
METHODS	94
Data collection.....	94
Data analysis.....	99
RESULTS	103
Effects on choice.....	105
The ROPE.....	109
Effect of magnitude when alternatives have fixed ratio of 0.5.....	112
Learning.....	114
DISCUSSION	117
REFERENCES.....	121
 CHAPTER 4: AFRICAN ELEPHANT OLFACTORY QUANTITY DISCRIMINATION OF FRUITS WITH OR WITHOUT DIRECT CONTACT WITH THE SOURCE OF SMELL	 123
INTRODUCTION	123
METHODS	127
Data collection.....	127
Data analysis.....	131
RESULTS	132
Choosing the larger alternative more than by chance.....	132

Learning.....	136
Effects on choice.....	141
The ROPE.....	147
DISCUSSION	151
REFERENCES.....	156
CHAPTER 5: CAN ELEPHANTS DO SIMPLE ARITHMETIC?.....	159
INTRODUCTION	159
METHODS	163
Measuring utilities for choice attributes	163
RESULTS	167
Boskos	168
Apples.....	168
Oranges.....	168
DISCUSSION	172
REFERENCES.....	173
CHAPTER 6: GENERAL DISCUSSION	175
NOVELTY AND RELEVANCE	175
STATISTICAL CONSIDERATIONS.....	178
CONCLUSION	181
REFERENCES.....	181
APPENDIX 1.....	183

LIST OF FIGURES

FIGURE 1.1: THE UTILITY CURVE OF FOOD REWARDS. THE MORE FOOD IS OBTAINED, THE HIGHER ITS TOTAL UTILITY, AND THE SMALLER THE MARGINAL UTILITY OF EACH EXTRA UNIT OF FOOD OBTAINED. FIGURE ADAPTED FROM HIRT ET AL. (2016).	5
FIGURE 1.2: THE LOCATION OF ADVENTURES WITH ELEPHANTS IN LIMPOPO PROVINCE, SOUTH AFRICA (A), AND AN AERIAL VIEW OF THE RESERVE (B).....	32
FIGURE 1.3: A GANTT CHART SHOWING THE TIMELINE OF THE DATA COLLECTED FOR THIS THESIS, FROM MARCH 2021 TO MARCH 2023.	33
FIGURE 1.4: A BETA PROBABILITY DENSITY FUNCTION (YELLOW) REPRESENTS THE PRIOR, THE SCALED BINOMIAL LIKELIHOOD FUNCTION (LIGHT BLUE) REPRESENTS THE LIKELIHOOD DISTRIBUTION OF THE OBSERVED DATA, AND THE BETA PROBABILITY DENSITY FUNCTION (GREEN) OBTAINED BY COMBINING THE PRIOR AND THE LIKELIHOOD REPRESENTS THE POSTERIOR.....	36
FIGURE 1.5: NORMAL CUMULATIVE DENSITY FUNCTIONS USED IN A PROBIT MODEL. THE FOUR INDIVIDUALS REPRESENT HYPOTHETICAL INDIVIDUALS HAVING DIFFERENT STRENGTHS OF PREFERENCE FOR THE LARGER ALTERNATIVE.	39
FIGURE 1.6: FOUR STANDARD GRAPHICAL DIAGNOSTIC PLOTS (TRACE, AUTOCORRELATION, HISTOGRAM, AND KERNEL DENSITY) FOR THE CONVERGENCE OF THE MCMC SIMULATION USED IN BHMS.	45
FIGURE 1.7: TWO WAYS OF VISUALISING A ROPE. IN PANEL A, THE PROBABILITIES THAT THE RATIO (GREEN) AND ABSOLUTE DIFFERENCE (LIGHT BLUE) OF THE ALTERNATIVES ARE INCLUDED IN ± 1 (TOP) OR ± 2 (BOTTOM) ROPES ARE INDICATED BY THE SHADED AREAS UNDER THE CURVES. IN PANEL B, THE SAME PROBABILITIES ARE SHOWN ON THE Y-AXIS, AND EACH ± 5 PP INDICATES AN AREA OF 10 PERCENTAGE POINT CHANGE, 5 BEING ON THE LEFT AND 5 ON THE RIGHT OF THE $B = 0$ USED AS THE REFERENCE. .	52
FIGURE 2.1: AN OVERVIEW OF THE “FRUIT PREFERENCE EXPERIMENT”. A) THE ELEPHANT (CHOVA) FACES THE TWO ALTERNATIVES FROM THE STARTING POSITION, BEFORE APPROACHING THEM; B) A VIEW OF ONE OF THE ALTERNATIVES FROM THE TOP; C) A VIEW OF THE ALTERNATIVE WHEN CHOVA SMELLS IT AND THE RESEARCHER KEEPS A FOOT ON TOP OF IT.	70

FIGURE 2.2: THE UTILITIES OF CHOVA FOR DIFFERENT FRUITS, ESTIMATED FROM A CONDITIONAL LOGIT BHM FROM CHOICES IN THE EXPERIMENT. THE BLACK VERTICAL LINE REPRESENTS THE UTILITY ZERO ASSIGNED TO THE UTILITY OF OPTION NONE.....	75
FIGURE 2.3: THE UTILITIES OF CHOVA FOR APPLES AND BANANAS ESTIMATED FROM A CONDITIONAL LOGIT BHM FROM CHOICES IN THE EXPERIMENT.	76
FIGURE 2.4: THE PROBABILITY OF EACH FRUIT BEING CHOSEN BY EACH ELEPHANT IN A BINARY CHOICE TASK ESTIMATED FROM THE BHM IN THE “FRUIT PREFERENCE EXPERIMENT”. THE DASHED RED LINE SHOWS THE 50% PROBABILITY FOR THAT FRUIT TO BE CHOSEN COMPARED TO THE ALTERNATIVES. THE VERTICAL BLUE LINES REPRESENT THE 50% HDI.....	80
FIGURE 2.5: THE PROBABILITY OF EACH ELEPHANT AND ALL OF THE ELEPHANTS CHOOSING EACH FRUIT IN A BINARY CHOICE TASK ESTIMATED FROM THE BHM IN THE “FRUIT PREFERENCE EXPERIMENT”. THE DASHED RED LINE SHOWS THE 50% PROBABILITY FOR THAT FRUIT TO BE CHOSEN COMPARED TO THE ALTERNATIVES. THE VERTICAL BLUE LINES REPRESENT THE 50% HDI.....	81
FIGURE 2.6: THE POSTERIOR DISTRIBUTION OF THE ELEPHANT PROBABILITIES OF CHOOSING APPLE ESTIMATED FROM THE BHM IN THE HEAD-TO-HEAD TEST OF THE “FRUIT PREFERENCE EXPERIMENT”. THE DASHED RED LINE REPRESENTS THE PROBABILITY OF CHOOSING APPLE BY CHANCE.	84
FIGURE 3.1: THE RESEARCHER PREPARING TO PLACE THE PERFORATED BUCKETS CONTAINING THE PIECES OF BOSKOS IN FRONT OF THE ELEPHANT IN THE “BOSKOS EXPERIMENT”.	95
FIGURE 3.2: THE GENERAL SET-UP OF THE TWO CONDITIONS OF THE “BOSKOS EXPERIMENT” SHOWING THE LOCATION OF THE RESEARCHER, HANDLERS, AND BUCKETS IN RELATION TO THE ELEPHANT.	96
FIGURE 3.3: A VIEW OF THE BEGINNING OF EACH TRIAL OF THE “BOSKOS EXPERIMENT”. THE ELEPHANT (CHOVA) IS WAITING ON THE MAT, THE BUCKETS HAVE BEEN LOADED WITH THE PREDETERMINED QUANTITIES OF BOSKOS, AND THE HANDLERS (EDWARD AND THABO) ARE READY TO PLACE ONE FOOT ON THEIR BUCKET AND WAIT FOR THE ELEPHANT TO WALK TOWARDS THEM, SMELL THE BUCKETS, AND CHOOSE ONE.	97

FIGURE 3.4: THE POSTERIOR DISTRIBUTION OF THE ELEPHANT PROBABILITIES OF CHOOSING THE LARGER ALTERNATIVE ESTIMATED FROM THE BHM WITHOUT COVARIATES IN THE “BOSKOS EXPERIMENT”. THE DASHED RED LINE REPRESENTS THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE BY CHANCE.	104
FIGURE 3.5: THE POSTERIOR DISTRIBUTION OF THE EFFECT OF THE RATIO BETWEEN THE ALTERNATIVES (TOP PANEL) OR THE ABSOLUTE DIFFERENCE OF THE ALTERNATIVES (BOTTOM PANEL) ON THE ELEPHANT PROBABILITIES OF CHOOSING THE LARGER ALTERNATIVE ESTIMATED FROM THE BHM _{RD} IN THE “BOSKOS EXPERIMENT”. THE DASHED RED LINE REPRESENTS THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE BY CHANCE.	105
FIGURE 3.6: THE AME OF THE MAGNITUDE OF THE ALTERNATIVES ON THE PROBABILITY OF EACH ELEPHANT CHOOSING THE LARGER ALTERNATIVE, ESTIMATED FROM THE BHM _{RM} IN THE “BOSKOS EXPERIMENT”. THE DASHED RED LINE, BEING THE REFERENCE, REPRESENTS THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE WHEN THE CUMULATIVE MAGNITUDE OF THE ALTERNATIVES IS 3.....	106
FIGURE 3.7: THE AME OF CHOOSING IN THE SMELL-PLUS-SOUND CONDITION ON THE PROBABILITY OF EACH ELEPHANT CHOOSING THE LARGER ALTERNATIVE, ESTIMATED FROM THE BHM _{RD} IN THE “BOSKOS EXPERIMENT”. THE DASHED RED LINE REPRESENTS A 0 EFFECT OF THE CONDITION ON THE PROBABILITY OF EACH ELEPHANT CHOOSING THE LARGER ALTERNATIVE.....	107
FIGURE 3.8: THE AME OF THE LARGER ALTERNATIVE BEING ON THE LEFT SIDE ON THE PROBABILITY OF EACH ELEPHANT CHOOSING THE LARGER ALTERNATIVE, ESTIMATED FROM THE BHM _{RD} IN THE “BOSKOS EXPERIMENT”. THE DASHED RED LINE REPRESENTS A 0 EFFECT OF THE SIDE WHERE THE LARGER ALTERNATIVE IS LOCATED.	109
FIGURE 3.9: THE PROBABILITY THAT THE POSTERIOR DISTRIBUTION OF THE RATIO AND ABSOLUTE DIFFERENCE BETWEEN THE ALTERNATIVES LIE INSIDE THE ± 25 PERCENTAGE POINT CHANGES FROM NOT AFFECTING THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE, CALCULATED AT THE EASIEST PROSPECT (A, RATIO=0.17, ABS.DIFF.=5), THE PROSPECT IN BETWEEN (B, RATIO=0.5, ABS.DIFF.=3), AND THE	

MOST DIFFICULT PROSPECT (C, RATIO=0.83, ABS.DIFF.=1), ESTIMATED FROM THE BHM _{RD} IN THE “BOSKOS EXPERIMENT”	111
FIGURE 3.10: THE PERCENTAGE OF CHOICES OF THE LARGER ALTERNATIVE WHEN THE MAGNITUDE IS SMALL (3 OR 6 PIECES OF BOSKOS) OR LARGE (9, 12, OR 15 PIECES OF BOSKOS) AT CHOICES HAVING RATIO 0.5 (1vs2, 2vs4, 3vs6, 4vs8, AND 5vs10) IN THE SMELL-ONLY CONDITION OF THE “BOSKOS EXPERIMENT”. A CHI-SQUARE HAVING A $P<0.05$ INDICATES THAT THE NUMBER OF CHOICES OF THE LARGER AND SMALLER ALTERNATIVES SIGNIFICANTLY DIFFERS BETWEEN PROSPECTS HAVING SMALL AND LARGE MAGNITUDE.....	112
FIGURE 3.11: THE PERCENTAGE OF CHOICES OF THE LARGER ALTERNATIVE WHEN THE MAGNITUDE IS SMALL (3 OR 6 PIECES OF BOSKOS) OR LARGE (9, 12, OR 15 PIECES OF BOSKOS) AT CHOICES HAVING RATIO 0.5 (1vs2, 2vs4, 3vs6, 4vs8, AND 5vs10) IN THE SMELL-PLUS-SOUND CONDITION OF THE “BOSKOS EXPERIMENT”. A CHI-SQUARE HAVING A $P<0.05$ INDICATES THAT THE NUMBER OF CHOICES OF THE LARGER AND SMALLER ALTERNATIVES SIGNIFICANTLY DIFFERS BETWEEN PROSPECTS HAVING SMALL AND LARGE MAGNITUDE.....	113
FIGURE 3.12: THE AME OF THE MAGNITUDE OF THE ALTERNATIVES ON THE PROBABILITY OF EACH ELEPHANT CHOOSING THE LARGER ALTERNATIVE IN CHOICES HAVING A RATIO OF 0.5, ESTIMATED FROM THE BHM _{RM} IN THE “BOSKOS EXPERIMENT”. THE DASHED RED LINE, BEING THE REFERENCE, REPRESENTS THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE WHEN THE CUMULATIVE MAGNITUDE OF THE ALTERNATIVES IS 3.....	114
FIGURE 3.13: THE PREDICTED POSTERIOR PROBABILITY OF EACH ELEPHANT CHOOSING THE LARGER ALTERNATIVE IN THE SMELL-ONLY CONDITION IN THE FIRST TRIAL (GREEN) AND IN THE LAST TRIAL (BLUE) OF THE CONDITION, ESTIMATED FROM THE BHM _T IN THE “BOSKOS EXPERIMENT”. THE RED DASHED LINE REPRESENTS THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE BY CHANCE.....	115
FIGURE 3.14: THE PREDICTED POSTERIOR PROBABILITY OF EACH ELEPHANT CHOOSING THE LARGER ALTERNATIVE SMELL-PLUS-SOUND CONDITION IN THE FIRST TRIAL (GREEN) AND IN THE LAST TRIAL (BLUE) OF THE CONDITION, ESTIMATED FROM THE BHM _T IN	

THE “BOSKOS EXPERIMENT”. THE RED DASHED LINE REPRESENTS THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE BY CHANCE.....	116
FIGURE 4.1: ONE OF THE TWO PERFORATED BUCKETS CONTAINING ORANGES USED IN THE “APPLE-ORANGE DISCRIMINATION EXPERIMENT”.....	127
FIGURE 4.2: A VIEW OF THE SETUP OF THE CONTACT CONDITION OF THE “APPLE-ORANGE DISCRIMINATION EXPERIMENT”.....	129
FIGURE 4.3: AN OVERVIEW OF THE CHOOSING PHASE OF THE “APPLE-ORANGE DISCRIMINATION EXPERIMENT”. A) THE HANDLERS KEEP THE BUCKETS CONTAINING THE ALTERNATIVES IN PLACE WITH A FOOT WHILE THE ELEPHANT APPROACHES THEM; B) THE ELEPHANT SMELLS THE TOP OF THE BUCKETS TO ACQUIRE INFORMATION ABOUT THE NUMBER OF ORANGES OR APPLES THEY CONTAIN; C) THE ELEPHANT CHOOSES ONE OF THE BUCKETS. USUALLY, THE ELEPHANT EXPRESSES THE CHOICE BY TOUCHING THE CHOSEN BUCKET, HOWEVER SHAN (THE ELEPHANT IN THE PICTURE) BEHAVES DIFFERENTLY, ALWAYS EXPRESSING HER CHOICE BY PUSHING ON THE HANDLER’S LEG.....	130
FIGURE 4.4: THE POSTERIOR DISTRIBUTION OF THE ELEPHANT PROBABILITIES OF CHOOSING THE LARGER ALTERNATIVE ESTIMATED FROM THE BHM _S WITHOUT COVARIATES, BHM _{APPLE} (TOP PANEL) AND BHM _{ORANGE} (BOTTOM PANEL), IN THE “APPLE-ORANGE DISCRIMINATION EXPERIMENT”. THE DASHED RED LINE REPRESENTS THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE BY CHANCE.	134
FIGURE 4.5: THE PREDICTIVE POSTERIOR PROBABILITY OF EACH ELEPHANT CHOOSING THE LARGER ALTERNATIVE IN THE CONTACT CONDITION IN THE FIRST TRIAL (GREEN) AND THE LAST TRIAL (BLUE) OF THE CONDITION WHEN CHOOSING BETWEEN DIFFERENT QUANTITIES OF APPLES, ESTIMATED FROM THE BHM _{TA} IN THE “APPLE-ORANGE DISCRIMINATION EXPERIMENT”. THE DASHED RED LINE REPRESENTS THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE BY CHANCE. THE BLUE CURVE LYING TO THE RIGHT SIDE OF THE GREEN LINE SUGGESTS LEARNING TOOK PLACE THROUGHOUT THE CONDITION.....	138
FIGURE 4.6: THE PREDICTIVE POSTERIOR PROBABILITY OF EACH ELEPHANT CHOOSING THE LARGER ALTERNATIVE IN THE NO-CONTACT CONDITION IN THE FIRST TRIAL (GREEN) AND THE LAST TRIAL (BLUE) OF THE CONDITION WHEN CHOOSING BETWEEN	

DIFFERENT QUANTITIES OF APPLES, ESTIMATED FROM THE BHM _{TA} IN THE “APPLE-ORANGE DISCRIMINATION EXPERIMENT”. THE DASHED RED LINE REPRESENTS THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE BY CHANCE. THE BLUE CURVE LYING TO THE RIGHT SIDE OF THE GREEN LINE SUGGESTS LEARNING TOOK PLACE THROUGHOUT THE CONDITION.	139
FIGURE 4.7: THE PREDICTIVE POSTERIOR PROBABILITY OF EACH ELEPHANT CHOOSING THE LARGER ALTERNATIVE IN THE CONTACT CONDITION IN THE FIRST TRIAL (GREEN) AND THE LAST TRIAL (BLUE) OF THE CONDITION WHEN CHOOSING BETWEEN DIFFERENT QUANTITIES OF ORANGES, ESTIMATED FROM THE BHM _{TO} IN THE “APPLE-ORANGE DISCRIMINATION EXPERIMENT”. THE DASHED RED LINE REPRESENTS THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE BY CHANCE. THE BLUE CURVE LYING TO THE <i>LEFT</i> SIDE OF THE GREEN LINE SUGGESTS <i>NO</i> LEARNING TOOK PLACE THROUGHOUT THE CONDITION.	140
FIGURE 4.8: THE PREDICTIVE POSTERIOR PROBABILITY OF EACH ELEPHANT CHOOSING THE LARGER ALTERNATIVE IN THE NO-CONTACT CONDITION IN THE FIRST TRIAL (GREEN) AND THE LAST TRIAL (BLUE) OF THE CONDITION WHEN CHOOSING BETWEEN DIFFERENT QUANTITIES OF ORANGES, ESTIMATED FROM THE BHM _{TO} IN THE “APPLE-ORANGE DISCRIMINATION EXPERIMENT”. THE DASHED RED LINE REPRESENTS THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE BY CHANCE. THE BLUE CURVE LYING TO THE <i>LEFT</i> SIDE OF THE GREEN LINE SUGGESTS <i>NO</i> LEARNING TOOK PLACE THROUGHOUT THE CONDITION.	141
FIGURE 4.9: THE POSTERIOR DISTRIBUTION OF THE EFFECT OF THE RATIO BETWEEN THE ALTERNATIVES (LEFT SECTION) AND THE ABSOLUTE DIFFERENCE OF THE ALTERNATIVES (RIGHT SECTION) ON THE ELEPHANT PROBABILITIES OF CHOOSING THE LARGER ALTERNATIVE WHEN DISCRIMINATING BETWEEN APPLES, ESTIMATED FROM THE BHM _{MrDA} (TOP PANEL), OR WHEN DISCRIMINATING BETWEEN ORANGES, ESTIMATED FROM THE BHM _{MrDO} (BOTTOM PANEL) IN THE “APPLE-ORANGE DISCRIMINATION EXPERIMENT”. THE DASHED RED LINE REPRESENTS THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE BY CHANCE.	142
FIGURE 4.10: THE AME OF THE LARGER ALTERNATIVE BEING TO THE LEFT SIDE ON THE PROBABILITY OF EACH ELEPHANT CHOOSING THE LARGER ALTERNATIVE WHEN	

DISCRIMINATING BETWEEN APPLES, ESTIMATED FROM THE BHM _{MRDA} (LEFT PANEL) AND WHEN DISCRIMINATING BETWEEN ORANGES, ESTIMATED FROM THE BHM _{MRDO} (RIGHT PANEL) IN THE “APPLE-ORANGE DISCRIMINATION EXPERIMENT”. THE DASHED RED LINE REPRESENTS A 0 AME.	144
FIGURE 4.11: THE AME OF THE CONDITION BEING NO-CONTACT ON THE PROBABILITY OF EACH ELEPHANT CHOOSING THE LARGER ALTERNATIVE WHEN DISCRIMINATING BETWEEN APPLES, ESTIMATED FROM THE BHM _{MRDA} (LEFT PANEL) AND WHEN DISCRIMINATING BETWEEN ORANGES, ESTIMATED FROM THE BHM _{MRDO} (RIGHT PANEL) IN THE “APPLE-ORANGE DISCRIMINATION EXPERIMENT”. THE DASHED RED LINE REPRESENTS A 0 AME.	146
FIGURE 4.12: THE PROBABILITY THAT THE POSTERIOR DISTRIBUTION OF THE RATIO AND THE ABSOLUTE DIFFERENCE BETWEEN THE ALTERNATIVES LIE INSIDE THE ± 25 PERCENTAGE POINTS CHANGE FROM NOT AFFECTING THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE WHEN DISCRIMINATING BETWEEN APPLES, CALCULATED AT THE EASIEST PROSPECT (A, RATIO=0.17, ABS.DIFF.=5), THE PROSPECT IN BETWEEN (B, RATIO=0.5, ABS.DIFF.=3), AND THE MOST DIFFICULT PROSPECT (C, RATIO=0.80, ABS.DIFF.=1), ESTIMATED FROM THE BHM _{MRDA} IN THE “APPLE-ORANGE DISCRIMINATION EXPERIMENT”.....	149
FIGURE 4.13: THE PROBABILITY THAT THE POSTERIOR DISTRIBUTION OF THE RATIO AND THE ABSOLUTE DIFFERENCE BETWEEN THE ALTERNATIVES LIE INSIDE THE ± 25 PERCENTAGE POINT CHANGE FROM NOT AFFECTING THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE WHEN DISCRIMINATING BETWEEN ORANGES, CALCULATED AT THE EASIEST PROSPECT (A, RATIO=0.17, ABS.DIFF.=5), THE PROSPECT IN BETWEEN (B, RATIO=0.5, ABS.DIFF.=3), AND THE MOST DIFFICULT PROSPECT (C, RATIO=0.80, ABS.DIFF.=1), ESTIMATED FROM THE BHM _{MRDO} IN THE “APPLE-ORANGE DISCRIMINATION EXPERIMENT”.....	150
FIGURE 5.1: THE UTILITIES OF CHOVA (TOP) AND MUSSINA (BOTTOM) FOR DIFFERENT QUANTITIES OF BOSKOS, ESTIMATED FROM A CONDITIONAL LOGIT BHM WITHOUT COVARIATES IN THE “BOSKOS EXPERIMENT”. THE BLACK VERTICAL LINE REPRESENTS THE UTILITY ZERO ASSIGNED TO THE UTILITY OF 1 BOSKOS.....	166

FIGURE 5.2: THE INFERRED PROBABILITY OF THE UTILITY OF THE LARGER QUANTITY OF BOSKOS BEING GREATER THAN THE UTILITY OF THE SMALLER QUANTITY OF BOSKOS.	169
FIGURE 5.3: THE INFERRED PROBABILITY OF THE UTILITY OF THE LARGER QUANTITY OF APPLES BEING GREATER THAN THE UTILITY OF THE SMALLER QUANTITY OF APPLES.	170
FIGURE 5.4: THE INFERRED PROBABILITY OF THE UTILITY OF THE LARGER QUANTITY OF ORANGES BEING GREATER THAN THE UTILITY OF THE SMALLER QUANTITY OF ORANGES.	171

LIST OF TABLES

TABLE 2.1: THE 21 COMBINATIONS OF FRUITS OFFERED TO EACH ELEPHANT IN THE “FRUIT PREFERENCE EXPERIMENT”. EACH PROSPECT WAS PROPOSED TO EACH ELEPHANT FOUR TIMES WITH EACH FRUIT BEING THE LEFT AND THE RIGHT ALTERNATIVE TWICE.	68
TABLE 2.2: THE NUMBER OF TIMES EACH FRUIT WAS CHOSEN BY THE INDIVIDUAL ELEPHANTS IN THE “FRUIT PREFERENCE EXPERIMENT”, AND THE PERCENTAGE ACCEPTANCE AVERAGED OVER ALL THE ELEPHANTS OF EACH FRUIT AS THE NUMBER OF TIMES THE FRUIT WAS CHOSEN DIVIDED BY THE NUMBER OF TIMES EACH FRUIT WAS PRESENT IN A TRIAL.	79
TABLE 2.3: THE POSTERIOR ESTIMATES OF THE PROBABILITY OF CHOOSING THE APPLE OVER THE ORANGE FOR EACH ELEPHANT ESTIMATED FROM THE BHM HEAD-TO-HEAD TEST OF THE “FRUIT PREFERENCE EXPERIMENT”. MEAN AND SD REPRESENT THE MEAN AND STANDARD DEVIATION OF THE POSTERIOR DISTRIBUTION, 50% HPD LOW AND 50% HIGH REPRESENT THE THRESHOLDS OF THE 50% HIGHEST PROBABILITY DENSITY OF THE POSTERIOR. THE LAST COLUMN REPRESENTS THE PROBABILITY OF THE POSTERIOR PROBABILITY DISTRIBUTION BEING GREATER THAN 0.50.....	83
TABLE 3.1: BOSKOS NUTRIENTS CONTENT SPECIFICATION BY ALZU BRAND.....	94
TABLE 3.2: THE POSTERIOR ESTIMATES OF THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE FOR EACH ELEPHANT ESTIMATED FROM THE BHM WITHOUT COVARIATES IN THE “BOSKOS EXPERIMENT”. MEAN AND SD REPRESENT THE MEAN AND STANDARD DEVIATION OF THE POSTERIOR DISTRIBUTION, 50% HPD LOW AND 50% HPD HIGH REPRESENT THE THRESHOLDS OF THE 50% HIGHEST PROBABILITY DENSITY OF THE POSTERIOR. THE LAST COLUMN REPRESENTS THE PROBABILITY OF THE POSTERIOR PROBABILITY BEING GREATER THAN 0.50.....	104
TABLE 3.3: THE AME OF THE CONDITION OF THE EXPERIMENT BEING SMELL-PLUS-SOUND AND OF THE LARGER ALTERNATIVE BEING ON THE LEFT SIDE ON THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE FOR EACH ELEPHANT, ESTIMATED FROM THE BHM _{RD} IN THE “BOSKOS EXPERIMENT”. THE LAST COLUMN REPRESENTS THE PROBABILITY OF THE POSTERIOR DISTRIBUTION BEING POSITIVE.	108

TABLE 3.4: THE PREDICTIVE POSTERIOR PROBABILITY OF EACH ELEPHANT CHOOSING THE LARGER ALTERNATIVE IN THE SMELL-ONLY AND THE SMELL-PLUS-SOUND CONDITION IN THE FIRST AND LAST CHOICE OF THE CONDITIONS, ESTIMATED FROM THE BHMt IN THE “BOSKOS EXPERIMENT”. MEAN IS THE MEAN OF THE POSTERIOR DISTRIBUTION, “PROB > 0.50” REPRESENTS THE PROBABILITY OF THE PREDICTIVE POSTERIOR DISTRIBUTION BEING GREATER THAN 0.50.	117
TABLE 4.1: THE POSTERIOR ESTIMATES OF THE PROBABILITY OF CHOOSING THE LARGER ALTERNATIVE FOR EACH ELEPHANT ESTIMATED FROM THE BHMs WITHOUT COVARIATES, BHMAPPLE AND BHMORANGE, PER CONDITION, IN THE “APPLE-ORANGE DISCRIMINATION EXPERIMENT”. MEAN AND SD REPRESENT THE MEAN AND STANDARD DEVIATION OF THE POSTERIOR DISTRIBUTION, 50% HPD LOW AND 50% HPD HIGH REPRESENT THE THRESHOLDS OF THE 50% HIGHEST PROBABILITY DENSITY OF THE POSTERIOR. THE LAST COLUMN REPRESENTS THE PROBABILITY OF THE POSTERIOR PROBABILITY BEING GREATER THAN 0.50.....	135
TABLE 4.2: THE PREDICTIVE POSTERIOR PROBABILITY OF EACH ELEPHANT CHOOSING THE LARGER ALTERNATIVE IN THE FIRST AND LAST TRIALS OF THE CONTACT CONDITION WITH APPLES (A) AND ORANGES (B) AND OF THE NO-CONTACT CONDITION WITH APPLES (C) AND ORANGES (D). MEAN IS THE MEAN OF THE PREDICTED POSTERIOR DISTRIBUTION, “P > 0.50” REPRESENTS THE PROBABILITY OF THE PREDICTIVE POSTERIOR DISTRIBUTION BEING GREATER THAN 0.50. THE TABLE BELOW IS COLOURED TO HELP VISUALISE THE FOUR DIFFERENT COMBINATIONS OF CONDITIONS AND FRUITS PER ELEPHANT.	137
TABLE A1: A SUMMARY OF SOME OF THE RELEVANT LITERATURE ON ANIMAL QUANTITY DISCRIMINATION. WHEN THE EFFECT OF ONE VARIABLE WAS NOT TESTED, IT APPEARS AS A DASH. ASTERISKS INDICATE THAT THE EFFECT OF THE VARIABLE WAS NOT FORMALLY TESTED OR IT WAS NOT STATISTICALLY SIGNIFICANT (BUT CLOSE TO) FOR ALL OR SOME OF THE INDIVIDUALS.	183
TABLE A2: A DESCRIPTION OF THE BINARY COMPARISONS PRESENTED TO THE ELEPHANTS IN THIS STUDY, WITH THEIR RATIO, ABSOLUTE DIFFERENCE, AND CUMULATIVE MAGNITUDE. IN CHAPTER 3 THE ELEPHANTS DISCRIMINATED BETWEEN ALL THE	

COMPARISONS, IN CHAPTER 4 THE ELEPHANTS WERE PRESENTED ONLY WITH THE COMPARISONS IN THE WHITE CELLS.....	190
TABLE A3: A LIST OF THE AVAILABLE STUDIES ON QUANTITY DISCRIMINATION IN ELEPHANTS, INDICATING THE SPECIES, THE NUMBER OF TESTED INDIVIDUALS, THE MODE OF PRESENTATION OF THE STIMULI, THE SENSE INVOLVED IN THE CHOICE, AND THE EFFECT OF RATIO, ABSOLUTE DIFFERENCE, AND CUMULATIVE MAGNITUDE OF THE ALTERNATIVES ON DISCRIMINATION, THE STATISTICAL ANALYSIS USED, AND SOME NOTES. WHEN THE EFFECT OF ONE VARIABLE WAS NOT TESTED, IT APPEARS AS A DASH.....	
	191

CHAPTER 1: General Introduction

Motivation for the study

All animals are required to perform a series of activities to stay alive and produce offspring, such as feeding, drinking, sleeping, avoiding predation, mating, and many more. Since not all activities can be performed at the same time, individuals must choose what to do at any given time, by assigning some priority to the possible available actions (McFarland, 1977). The type of choices an animal faces can be divided into: choices about what to do between continuing to perform the current activity or switching to a new activity; and choices about what to try to obtain, between different alternatives available at the same time (McFarland, 1977). This thesis focuses on the second type of choice, specifically on binary choices between different objects or different quantities of the same object.

A large literature exists on animals' quantity discrimination abilities, demonstrating that every class of vertebrates and also some insects can distinguish different quantities, and, sometimes, have even sophisticated numerical abilities. A few studies have focused on the quantity discrimination ability of Asian elephants (*Elephas maximus*) (Irie-Sugimoto et al., 2009; Irie and Hasegawa, 2012; Irie et al., 2019; Plotnik et al., 2019; Snyder et al., 2021) and only one study to date has involved African elephants (*Loxodonta africana*) (Perdue et al., 2012). These studies found that elephants were able to discriminate between different quantities of food or shapes on a screen presented to them. In some studies, the discrimination of elephants was more accurate when the rewards differed by many units rather than one unit (Perdue et al., 2012;

Plotnik et al., 2019; Snyder et al., 2021), and in other studies, differences in the size of the rewards did not affect the choices of the elephants (e.g. Irie-Sugimoto et al., 2009; Irie and Hasegawa, 2012; Irie et al., 2019). Therefore, there is debate in the elephant literature over whether the quantities of the alternatives at stake affect the elephants' quantity discrimination ability.

The only study of quantity discrimination so far conducted with African elephants tested individuals by offering them different quantities of a vegetable presented item-by-item (Perdue et al., 2012). Both a visual condition, where the elephants could see the final size of the rewards, and a non-visual condition, where the elephants saw and heard each piece of the rewards falling into two barrels but could not see the final size of the rewards, were conducted. No one has ever investigated the ability of African elephants to discriminate using their sense of smell only, as has been done with Asian elephants (Plotnik et al., 2019), or the effect of a different source of food on their discrimination, or the effect of experience through a task on their performance.

This study represents the first step of a larger project aiming to elicit African elephant risk preferences through the use of lotteries, where the rewards vary in both quantity and probability. Among the prerequisites to participate in a lottery is the ability to discriminate quantities and probabilities, and the ability to see quantities as ordered numbers. Therefore, this study aims to investigate African elephants' ability to work with numerosities, in the sense of assigning different increasing utility to single increasing numerosities, assessed through a series of binary discrimination experiments over food. This study also considered what factors drive the choices of individual

elephants between two alternatives offering edible items, in particular focusing on how using different sensory modalities, modes of presentation of the rewards, and kinds of rewards affect the discrimination of elephants, and estimating whether elephants learn through a task.

In addition to being the first study assessing the ability of an animal to do simple arithmetic by using binary quantity discrimination experiments, this thesis represents the first attempt to provide a fully quantitative (that is, structural and parameterised) model of binary spontaneous choice in non-human animals. To do so, I used Bayesian Hierarchical Models (BHM), for the first time in the animal quantity discrimination literature, to analyse a large dataset (4,266 observations), estimating parameters at the levels of both the herd and the single individual.

The information provided by this study will also be useful for guiding and designing interventions to control the human-elephant conflict by expanding our knowledge of the acuity of African elephant senses and the relationship between these and their behaviour. Of course, the extent of this knowledge is limited by the fact that the subject of the study is a group composed of six semi-tame elephants. Though this represents a small sample, which cannot be representative of the species, it would be extremely challenging to gather the same foundational knowledge on African elephant choice behaviour by studying wild animals. However, the value of structural estimation is enhanced by its prospects for contrasting models of future data that are obtained using less controlled behavioural contingencies.

Literature review

Decision theory, maximisation criterion and optimality

Choosing between two readily available objects involves identifying the preferred alternative (Budaev et al., 2019) as well as rejecting the other alternative (Botti and Iyengar, 2006). Since all the alternatives might bring some benefit and are chosen at some cost, some cognitive mechanism is required to compare the pros and cons of all the available alternatives (McFarland, 1977). Cognition is the ability to use perception through the five senses to gain new information about the world, learn by processing such new information, store the information in memory for future use, and make a decision based on the previous steps (Shettleworth and Hampton, 1998). Each of these steps affects the final decision.

The choice of one alternative among many is based on two separate variables: the utility of the alternatives, which is the individual perception of the relative attractiveness of the alternatives, and the individual's evaluation of what will be the consequences of choosing each alternative (McFarland, 1977). Utility has two important aspects: the total utility and the marginal utility of a good, as shown in Figure 1.1. The total utility of an edible good represents the total value attributed to a quantity of food (McFarland, 1977) and it is assumed to be positively correlated with the quantity of food until satiation is reached. The marginal utility represents the value attributed to one additional unit of food and its value changes based on how much food has already been consumed.

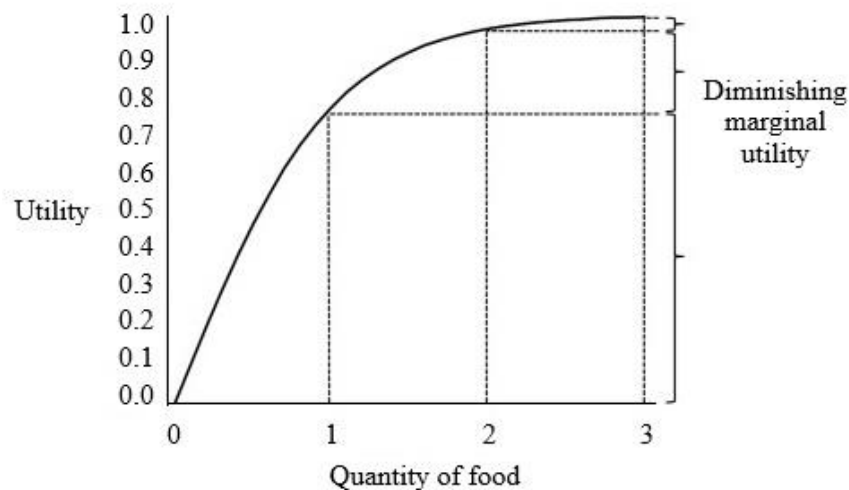


Figure 1.1: The utility curve of food rewards. The more food is obtained, the higher its total utility, and the smaller the marginal utility of each extra unit of food obtained. Figure adapted from Hirt et al. (2016).

Diminishing marginal utility is a principle of economics stating that the more of one item an individual consumes, the less value is attributed to each one-unit increment of the item (Ross, 2014). This implies that when an animal does not show a preference between two quantities of food, the animal might be indifferent between the utilities of the alternatives, rather than not being cognitively able to discriminate between the two quantities. It also implies that when the utilities of two quantities of a good differ, the animal values one quantity of the good more than the other, which implies that the animal recognises the quantities as different.

Decision-making is usually modelled using some optimising principle which reflects marginal trade-offs between attributes of prospects (McFarland, 1977).

Traditional decision theory, developed by psychologists and ethologists, states that animals evaluate all the alternatives available at any time and behave optimally by

choosing the alternative that maximises their fitness (McFarland, 1977). When applied to foraging decisions, Optimal Foraging Theory (OFT) states that to maximise their fitness, animals should maximise their net rate of energy intake (Pyke, 1984). According to the traditional decision theory and OFT, when discriminating between two quantities of the same food, assuming that the animal is not satiated, the optimal choice should be to select the larger quantity of food. This expectation might apply well to experimental designs where many variables influencing the state of the animal are controlled for, but it is too simple to robustly predict animal behaviour in a natural environment.

A major source of complication is that the criterion of optimality might change with the state of the animal, the currency used by the animal, and the environment (McFarland, 1977). Risk-sensitive foraging theory (RSFT) is an extension of OFT assuming that animals choose between variable alternatives in a way that maximises their daily energy income (Caraco et al., 1980). An alternative is variable when the response to a cue, for example the pressing of a lever (Battalio et al., 1985), can deliver different rewards, such as 3 or 7 seeds with a 0.5 probability of occurrence each (Caraco, 1982). Tests of RSFT are usually conducted by offering the animal a choice between a variable reward and a fixed reward, both having the same mean (e.g. Caraco, 1981).

RSFT predicts that an animal on a positive energy budget, meaning an animal that by eating obtains more energy than that required to perform necessary daily activities, would be risk-averse by preferring the less variable or fixed alternative (Pyke, 1984). In contrast, when an animal experiences a negative energy budget, meaning that it is at risk of starvation, it behaves as a risk-lover, preferring the most variable option,

not the larger alternative (Caraco et al., 1980; Bateson, 2002). Studies on small birds and common shrews (*Sorex anareus*), where the animals' energy budgets and the variability of the alternatives were manipulated, demonstrated that the states of the animal can switch between risk-averse and risk-loving (Barnard et al., 1985; Caraco et al., 1990).

Quantity discrimination

Quantity discrimination represents a well-studied field of decision-making in animals. The ability to discriminate between two quantities is widespread in the animal kingdom. The majority of studies have focused on understanding the mechanism regulating discrimination, often comparing different species to investigate how systems of numerical cognition may have evolved. Quantity discrimination tasks usually consist of a single subject choosing between two different quantities of an item. The aim often is to estimate if there is a specific numerical limit at which the animal's discrimination ability fails, and to evaluate what variables affect discrimination (Garland et al., 2012). Such aims are achieved by varying sizes of the binary combinations of the alternatives, also referred to as prospects in the choice theory field of economics, offered to the animal (Hunt et al., 2008). The proportion of times the animal chooses the alternative associated with the larger reward is then comparatively modelled across different sets (often pairs) of prospects (see Agrillo and Bisazza (2014) for a comprehensive review).

There is no universal standard on how to perform a quantity discrimination task. Many different techniques have been used, some of which affected the final result of the

study. For example, the most commonly used reward in quantity discrimination tasks is food, while stimuli involved as choice alternatives have varied. Food has been used as both the stimuli and the reward (Aïn et al., 2009; Baker et al., 2011; Gazzola et al., 2018). Other choice alternatives included 3D or 2D objects (Bogale et al., 2011; Bisazza et al., 2014a) which can be the same in both alternatives or can vary in shape, colour, size, and many more aspects (Gross et al., 2009), and dots on a screen (Cantlon and Brannon, 2007; Tomonaga, 2008). Other important differences across studies involve the senses used by subjects to investigate the alternatives (Bánszegi et al., 2016), by how the alternatives are presented, which can be simultaneously (Emmerton, 1998; Baker et al., 2011), consecutively (Gross et al., 2009; Tornick et al., 2015), or item-by-item (Utrata et al., 2012; Range et al., 2014), which also affects the possibility of sensing the alternatives at the time of the choice (Agrillo and Bisazza, 2014). In addition, quantity discrimination tasks can be conducted in a laboratory (Davis, 1984), with domestic (Ward and Smuts, 2007; Bánszegi et al., 2016) or farm animals (Uller and Lewis, 2009; Rugani et al., 2013), or in the wild (Hauser et al., 2000; Farnsworth and Smolinski, 2006; Hunt et al., 2008).

Quantity discrimination, how it works

The ability to discriminate between different numbers of objects may simply amount to the ability to recognise many versus few (Davis and Memmott, 1982). Therefore, it has been described as an imprecise and more basic ability than the ability to count and perform operations on numbers (Davis and Memmott, 1982). To

quantitatively discriminate between two options animals must be able to both perceive the alternatives as different and to recognise what option would best fulfil a goal.

One of the first modelling concepts for application to animal quantity discrimination is subitizing (Mandler and Shebo, 1982), defined as the intuitive, unconscious, rapid, nonverbal estimation of quantity that is at the base of human nonverbal representation of numerosities (Gallistel and Gelman, 1992). Subitizing is a quick process that is virtually always correct and not affected by the disparity of the alternatives, i.e. it is as easy for people to discriminate 1vs4 as 2vs3 (Butterworth, 2022: Chapter 8), when applied to quantities smaller than 4. However, due to its speed, human subitizing is imprecise with quantities larger than 4 or 5 (Mandler and Shebo, 1982; Gallistel and Gelman, 1992). In addition, it can only be used to discriminate between two quantities that are simultaneously “visible” (not sequentially presented item-by-item) since the comparison is intuitive and does not involve the use of memory (Butterworth, 2022: Chapter 2). Though it was constructed to model the behaviour of adult humans, due to its simplicity and the fact that it does not require the ability to verbally describe numbers, the concept of subitizing has been called upon to model the counting behaviour of non-verbal children, and subsequently of animals (Davis and Memmott, 1982).

Examples of animals that might suggest the use of subitizing is given by studies of semi-free-ranging rhesus monkeys (*Macaca mulatta*) discriminating between two quantities of apple slices (Hauser et al., 2000). Monkeys were successful in discriminating 1vs2, 2vs3, 3vs4, and 3vs5, but they failed to discriminate when both the alternatives were larger than 3 (4vs5, 4vs6, and 4vs8). Honeybees (*Apis mellifera*) could

also be trained to choose 2 rather than 3, and 3 rather than 2 or 4, but they failed to choose 4, 5, or 6 compared to other options, suggesting that their ability to represent quantities stops at 3 (Gross et al., 2009).

The majority of the literature on quantity discrimination has however found that animals are capable of discriminating between arrays larger than 4 objects and presented item-by-item rather than just simultaneously (see Table A1 in Appendix 1). For example, a study compared the discrimination ability of guppies (*Poecilia reticulata*) and undergraduate students presented with small numerical contrast (1vs4, 1vs3, 1vs2, 2vs3, and 3vs4) and large numerical contrast (4vs16, 4vs12, 4vs8, 4vs6, and 6vs8) classes (Agrillo et al., 2012). Both discriminated between all the prospects in the small contrast class, possibly by subitizing. For prospects in the large class, the accuracy of both fish and humans was negatively correlated to the ratio of the alternatives. In particular, guppies could only discriminate between large quantities having a ratio smaller than 0.5 (Agrillo et al., 2012). Therefore, subitizing cannot be the only possible mechanism involved in quantity discrimination. It has been suggested that subitizing is used only when it is advantageous, with respect to speed, accuracy, effort, or utility that captures trade-offs among these attributes. Otherwise, different strategies are chosen, such as verbal counting in humans (Gallistel and Gelman, 1992).

Accumulator model

The majority of the literature on animal quantity discrimination agrees that animals use what has been called an “accumulator model” to deal with quantities. Meck

and Church (1983) suggested that animals possess an internal mechanism functioning like a click counter. It would be composed of a pacemaker sending a pulse every time an event is experienced, plus a mode switch that allows only the pulse signals that are triggered by an event relevant to the count to go to an accumulator which stores the count of pulses. When choosing between two quantities, the last value in the accumulator, representing the quantity of the first alternative, is stored in working memory and compared to the last value in the accumulator representing the quantity of the second alternative (Meck and Church, 1983). A response rule is then applied to make a choice.

The efficient use of an accumulator system requires animals to be able to categorise objects that are relevant for counting from those that are not (Davis and Memmott, 1982). The component responsible for this is known as the “selector” and it is supposed to be the most neurally expensive part of the process (Butterworth, 2022: Chapter 1). To be able to count any object, animals need to adhere to the “abstraction principle”, i.e. numerosity has to be represented as a distinct property of a set, separable from the properties of the items composing the set (Gallistel, 1989). So animals should see “threeness” as a property shared by three green trees and three grey rocks.

Animals must not only select the objects to count, but also remember which objects have already been counted and which still need to be counted, and apply a chain of ordinals in one-to-one correspondence to the objects that are counted (Davis and Memmott, 1982). It is necessary to tag each object only once, in stable order. However, it is not important to store all the numbers used to obtain the final count; only the last quantity in the accumulator is essential to be retained (Davis and Memmott, 1982).

Since the size of the alternatives is stored in memory, the accumulator model supports discrimination between different quantities presented either sequentially or item-by-item (Gallistel, 1989). The fact that memory demand is therefore modest makes the accumulator model plausible for small brains.

Accuracy when using an accumulator model is a function of the magnitude of the quantity (Gallistel, 1989) following what is known as Weber's law (Gallistel and Gelman, 1992). The discriminability of two quantities decreases with magnitude because the noise involved in mentally mapping the quantities is scalar (Gallistel and Gelman, 1992; Butterworth, 2022: Chapter 1). This implies that as the cumulative magnitude of the alternatives increases, a larger disparity between the alternatives is needed to observe the same discrimination accuracy (Agrillo et al., 2010). Mechner (1958) developed a paradigm where a rat (genus *Rattus*) had to press a lever a specific number of times to activate a second lever which would release a reward. If the rat left the first lever too soon, it would receive a penalty. The results showed that rats were not only able to count how many times they pressed the first lever and to compare this number with the minimum required number of presses determined by the experimenter, but the higher the required number of lever presses, the more imprecise the rats became (Mechner, 1958). This suggests that rats adhere to an accumulator model characterised by Weber's law.

The magnitudes of alternatives are spaced linearly with scalar variability, allowing the approximate quantification of large numbers (Sulkowski and Hauser, 2001) and making the ratio between the alternatives, seen as the smaller divided by the larger alternative, the primary limiting factor on the ability of an animal to discriminate

quantitatively (Barnard et al., 2013; Butterworth, 2022: Chapter 1). Two quantities with a small ratio, and therefore differing by many units (i.e. having a large absolute difference), are easier to discriminate than alternatives that differ by only 1 or a few units (Gallistel and Gelman, 1992; Aïn et al., 2009). In addition, there is no upper limit to the magnitude of the alternatives (the sum of the objects composing both alternatives) that one can discriminate (Barnard et al., 2013), contrary to what happens with subitizing. Among the studies that have shown support for the accumulator model, Aïn et al. (2009) gave three African grey parrots (*Psittacus erithacus*) binary choices between different quantities of seeds, with ratios spanning from 0.2 to 0.8 and magnitudes between 3 and 9 seeds. The performance of each parrot was better the lower the ratio of the alternatives and the higher the absolute difference of the alternatives, while the cumulative magnitude did not have an effect on the discrimination accuracy (Aïn et al., 2009).

When using an accumulator model governed by Weber's law, the cumulative magnitude of the alternatives could only affect discrimination when comparing accuracy between prospects having the same ratio but different magnitudes, e.g. 1vs2 and 5vs10. Indeed the accumulator model predicts that the larger the alternatives, the harder it is to discriminate (Gallistel and Gelman, 1992). However, such an effect of magnitude would be observed only if the representations of the alternatives were so noisy that their count distributions tended to overlap. Therefore, according to the accumulator model, it should be easier to discriminate 1vs6 (ratio 0.17) than 5vs6 (ratio 0.83), and discriminating 2vs3 (ratio 0.67) could be easier than 4vs6 (ratio 0.67). Magnitude at a fixed ratio has been found to have a negative effect on the discrimination of horses

(*Equus caballus*), which succeeded in discriminating 2vs3 but failed with 4vs6 artificial apples (Uller and Lewis, 2009). On the other hand, mosquitofish (*Gambusia holbrooki*) discrimination was affected by the ratio of the alternatives: they succeeded with ratio 0.5 while failing with ratio 0.75, but their performance did not depend on the magnitude of the alternatives in any way, they were as good with 4vs8 as with 100vs200 (Agrillo et al., 2010).

A few studies have not found negative effects of the ratios of the alternatives on the discrimination abilities of animals. Abramson et al. (2013) tested a beluga whale (*Delphinapterus leucas*) and three bottlenose dolphins (*Tursiops truncatus*) in several quantity discrimination tasks involving different senses and presentation modalities and found that ratio was never a good predictor. Honeybees were studied in a trained quantity discrimination task where their discrimination ability was not affected by the ratio but rather by the magnitude of the alternatives (Gross et al., 2009). Asian elephant discrimination ability has been described as not affected by ratio, absolute difference or magnitude of the alternatives in three different studies (Irie-Sugimoto et al., 2009; Irie and Hasegawa, 2012; Irie et al., 2019). Only one of them reported that the single elephant tested in a trained task took longer to make a decision when the prospects had a large ratio and a small absolute difference, but this did not affect her accuracy (Irie et al., 2019).

Trained vs untrained discrimination tests

The ability to discriminate between two finite non-variable sets that contain a different amount of the same, or similar, items has been mainly tested in either a *trained* or *untrained* setting. In the animal cognition literature, untrained discrimination tests are more commonly known as *spontaneous* choice tests (Agrillo and Bisazza, 2014). The use of the word “spontaneous” could be confusing to scholars from other fields, such as economics, who might think that it implies the absence of cognition or deliberation. In the field of animal cognition, “spontaneous” refers to an aspect of behaviour indicating the autonomous determination of a choice, in the absence of training (Hauser et al., 2000). Trained and untrained paradigms are each useful for addressing different kinds of questions.

When the trained discrimination ability is tested, the animal undergoes a phase of training, during which it needs to learn a numerical rule to make the correct choice. The subject receives two neutral stimuli as alternatives, one of which, defined by the researchers, will lead to getting a reward (Gatto et al., 2017). By using this methodology, one alternative, the one the animal is conditioned to choose, can be specified as the correct one, while the choice of the other alternative, specified as the wrong one, leads to no reward or a timeout from the experiment. The definition of “the correct choice” is arbitrary and is defined by the researchers, not the animals. For example, Davis (1984) studied the trained discrimination ability of a racoon (*Procyon lotor*) after conditioning him to choose 3 objects over any other quantity presented as the alternative. In other studies, some of the subjects have been trained to choose the larger and some to choose the smaller alternative, as has been done with blind cavefish

(*Phrearichthys andruzzii*) (Bisazza et al., 2014b) or with domestic cats (*Felis silvestris catus*) (Pisa and Agrillo, 2009). A subject is usually considered successful in discriminating between the alternatives when it chooses the correct one more than by chance.

The contrast setting is untrained discrimination. In such tests, the animal is offered binary choices between two alternatives, where there is no correct or wrong choice. It is the animal that freely chooses the alternative it prefers and is rewarded with it (Bánszegi et al., 2016). When testing untrained discrimination, it is common to use food as both the stimulus and the reward. In this case, the animal is considered successful in discriminating between two quantities when it chooses the larger alternative, or the alternative delivering the higher utility, more than by chance.

A different untrained task paradigm, often used for fish, amphibians, and insects, employs the size of groups of conspecifics as the stimulus, and a larger proportion of time spent in proximity of the larger group as a successful discrimination choice (Agrillo et al., 2007; Carazo et al., 2009; Agrillo et al., 2012; Balestrieri et al., 2019). In a less common procedure, the stimuli used are obstacles in front of food, in which case choosing the smaller alternative increases the energy intake. For example, if the choice is between different numbers of bamboo sticks that must be removed to obtain food, Northern Mockingbirds (*Mimus polyglottos*) could spontaneously choose fewer sticks to maximise their energy intake (Farnsworth and Smolinski, 2006). Similarly, striped field mice (*Apodemus agrarius*) were able to minimise the risk of their hunt by voluntarily choosing the smaller of the two groups of aggressive ants presented to them (Panteleeva et al., 2013).

Untrained settings require biologically relevant stimuli while trained settings can make use of neutral stimuli. This difference itself can affect estimations of cognitive ability, as demonstrated in olive baboons (*Papio anubis*) and long-tailed macaques (*Macaca fascicularis*) which were better at discriminating between different quantities of rocks than between the same different quantities of food (Schmitt and Fischer, 2011).

Continuous features of alternatives that vary with quantity, such as volume, area, shape, and density might be used by an animal to discriminate, confounding the ability to discriminate based on numerosity only (Agrillo and Bisazza, 2014). For example, in experiments using dots on a screen as stimuli, domestic cats based their discrimination on the area occupied by the dots (Pisa and Agrillo, 2009) and the discrimination of chimpanzees (*Pan troglodytes*) was affected by the density of the dots (Tomonaga, 2008). Using trained tasks where the stimuli are neutral makes it easier to control for such continuous variables.

On the other hand, the use of biologically relevant stimuli in untrained tasks implies the risk that animals choose based on non-numerical cues (Agrillo and Bisazza, 2014). However, there are some precautions a researcher can take in an untrained task to control for continuous variables. For example, in studies on rhesus monkeys, New Zealand robins (*Petroica australis*), and horses, researchers loaded the alternatives item-by-item, never showing the total size of the alternatives to the subjects, and controlled for the volume of the alternatives, finding that the subjects used numerosity rather than volume when discriminating (Hauser et al., 2000; Hunt et al., 2008; Uller and Lewis, 2009).

When presenting the alternatives item-by-item, the time spent by the researcher at each alternative becomes an additional continuous variable to control for. For example, domestic dogs (*Canis familiaris*) seemed to base their discrimination on the time needed by the researcher to fill in both alternatives (Range et al., 2014). This variable can be controlled for by adding fake drops (Perdue et al., 2012) or neutral objects (Sulkowski and Hauser, 2001) to the smaller alternative to make the time needed to fill the alternatives equal.

The use of food both as a stimulus and reward in untrained tasks has further implications. Since the animal needs to be motivated to make an untrained choice, the stimuli cannot be too small or the animal will not be interested in the task, and cannot be too large or the animal will be satiated quickly and lose interest in more food. Consequently, in the majority of cases, only a few trials can be run per animal per day, making it necessary to test a lot of animals or to allow a long experimental frame to obtain robust results (Agrillo and Bisazza, 2014; Balestrieri et al., 2019). In trained discrimination, where the choice is between neutral stimuli leading to receiving a reward or nothing, an animal would lose motivation to the task only when the reward at stake is considered not worth the action of selecting one of the alternatives. The choice of a reward of the correct size to keep the animal interested in it for many trials without satiating it allows individuals to perform many more trials in trained experiments compared to untrained ones, in the range of thousands of trials (Brannon et al., 2001).

In addition, since the stimuli used in the discrimination test need to be relevant to the tested species or even to the specific animal, results obtained through untrained procedures might be more difficult to compare between different species. Instead, the

same training procedures can be replicated with different species, which might lead to results that can be directly comparable across species or individuals. On the other hand, in untrained tasks, animals exhibit their natural behaviour (Bánszegi et al., 2016), while in trained tasks the results might reflect a specific behaviour elicited by the specifics of the training. Indeed, results might depend on different learning abilities of the species for a specific task rather than different numerical abilities (Agrillo and Bisazza, 2014). Therefore, even though the results obtained from untrained discrimination tasks are more difficult to compare with those of other species, they might give a better understanding of the natural discrimination ability of a species than trained tasks.

One disadvantage of trained tasks is that both the length and modality of the training session itself can influence the results. Guppies' trained discrimination ability was found to improve after extensive training (Bisazza et al., 2014a). In a quantity discrimination experiment with mosquitofish, if the animals were trained without controlling for the cumulative surface area of the geometric figures used as stimuli, the fish were not able to discriminate between the alternatives once this variable was controlled for in the experimental phase. However, if the fish were strictly trained to discriminate numerosity by controlling all the relevant continuous variables that vary with quantity, they could discriminate based on number only in the experimental phase (Agrillo et al., 2010).

An additional factor that can affect animals' choices is the involvement of humans in the task. Humans observing an experiment and knowing the correct answer might, deliberately or accidentally, give cues that lead the animal to the correct choice, producing what is called the Clever Hans effect. Clever Hans was a horse who was

believed to be extremely accurate at counting several classes of objects by stomping his foreleg the correct number of times (Davis and Memmott, 1982). After a thorough investigation, it was discovered that Hans was very sensitive to the small movements of his trainer who was unconsciously suggesting the answers. Possible influences from humans can be minimised in discrimination experiments by running blind or double-blind trials (e.g. Barnard et al., 2013), and can be checked for in the data analysis.

The participation of humans in untrained tasks, for example when the protagonist of the study is a captive or semi-captive animal, involves an additional potential confound to the inference. Human-dependent animals might frame their problem not as identifying the best reward by their own lights, but rather as identifying which option the experimenter prefers them to select. Awareness of this concern motivates designing simple tasks that are as similar as possible to the problems faced by the animal under conditions when the animal is acting freely.

The effect of the sense and mode of presentation of the alternatives

The sensory modality used to investigate the alternatives (e.g. visual, olfactory, or auditory cue), might affect the performance of an animal. For example, the discrimination ability of a beluga whale was not affected by either ratio, absolute difference, or magnitude of the alternatives when using sight, but when the alternatives were echolocated, the discrimination was negatively correlated with their magnitude. Similarly, coyotes (*Canis latrans*) were able to discriminate between piles of food of different sizes up to a ratio of 0.50 when they could see the alternatives, but they failed

to discriminate 1vs6 (ratio of 0.17) when they could only smell them (Baker et al., 2011).

In discrimination tests, quantities can be presented simultaneously, consecutively, or item-by-item (Agrillo and Bisazza, 2014). Usually, when the alternatives are presented simultaneously, they are also available at the time of the choice. When the alternatives are presented consecutively or item-by-item, the information about the total size of both alternatives or the single alternatives, is never accessible (e.g. Range et al., 2014). In such cases, the animal needs to count and remember the size of the alternatives to choose the larger reward. A study with one beluga and two bottlenose dolphins tested all three modalities of presentation, finding that the discrimination ability of these mammals with respect to magnitude, absolute difference, or ratio varied across presentation modalities (Abramson et al., 2013). Similarly, in a study with four different species of great apes, discrimination was affected only by the ratio when the alternatives were presented item-by-item and was affected by the ratio and absolute difference of the alternatives if they were presented simultaneously or consecutively (Hanus and Call, 2007).

The effect of side preference

Another characteristic of binary choices that can affect the choice of the animals is the fact that the prospects are commonly presented to each side of the animal. The animal might prefer one side to the other, with the consequence of choosing prospects on that side of its body more than prospects on the other side, independently of the alternatives at stake (Plotnik et al., 2014). A side preference has been found, for

example, in studies with African grey parrots (Ain et al., 2009), domestic cats (Bánszegi et al., 2016), and domestic dogs (Ward and Smuts, 2007). The preference for one side can be innate or learned. Thus researchers plan experiments so to avoid the development of a side preference, usually by not placing the larger/correct alternative on the same side more than a few (generally three) consecutive times (Hunt et al., 2008; Range et al., 2014). Commonly, individuals showing a strong side preference have been excluded from the experiment (Ward and Smuts, 2007; Bánszegi et al., 2016), with the consequence of losing variation within the studied group and reducing the amount of informative data.

Learning in quantity discrimination tasks

Learning is the process through which an animal changes its behaviour based on its previous experience and its current environment (Rescorla, 1988). The vast majority of the literature assumes that animals learn according to one or another model of reinforcement learning (Sutton and Barto, 2020). Reinforcement learning is based on Thorndike's (1911) *law of effect*. The law of effect states that if the behaviour of an animal is followed by a satisfying consequence, such as rewards, such behaviour is more likely to be repeated in the future, while behaviours followed by negative consequences, such as punishments, are less likely to be repeated (Castro and Wasserman, 2010).

Bayesian learning is more powerful and appears to more accurately model learning in animals with relatively dense cortical networks. For example, it has been

found to apply to the foraging behaviour of several species of free-ranging mammals and birds (Valone and Brown, 1989; Van Gils et al., 2003). It is based on the idea that information about the world constitutes a prior which gets updated as new information arrives. Priors can be expected to represent combinations of the adaptive behaviours evolved through an evolutionary lineage and an individual's past idiosyncratic experiences (McNamara et al., 2006). Bayes' theorem is a mathematical formula that combines the prior knowledge of probability distributions with current information about the environment to formulate an estimated posterior distribution of a parameter (Valone, 2006). Such posterior distributions are stored in memory to be used as an updated prior for subsequent learning episodes (McNamara et al., 2006).

The Bayesian learning framework has uncertainty at its base. The more uncertain an animal is about a current belief, the more weight it will place on newly acquired information, with the consequence of learning faster (Foley and Marjoram, 2017). According to a Bayesian model, an animal would choose the larger alternative more often at the end of a sequence of highly regular tasks than at its beginning (Foley and Marjoram, 2017). Residual estimation of uncertainty depends on the fact that the world is not static, but constantly changes, and that the information gathered from the world is always imprecise to some degree (McFarland, 1977).

Since the actions involved in foraging, i.e. searching for food and choosing what to eat, are recurrent in the life of an animal and have a high impact on its fitness, learning is expected to be operative in foraging behaviour. Therefore, by comparing many experiences of discrimination, learning should be observable (Shettleworth, 2001). Several studies have tested learning, seen as an increase in the number of correct

choices made over time, or as an improvement of the performance of the animal over time (Ward and Smuts, 2007; Pisa and Agrillo, 2009). One way to test learning is to compare the performance of the animal in the first few and last number of trials, or in the first and second halves of the task, to see if the animal was more accurate at the end than at the beginning of the study (Ward and Smuts, 2007; Aïn et al., 2009; Pisa and Agrillo, 2009; Bisazza et al., 2014b; Plotnik et al., 2014). Otherwise, learning has been evaluated by looking for a correlation between the performance of the animal with respect to each set of prospects and the order of the trials (Bánszegi et al., 2016), or by assigning half of the subjects to discriminate between alternatives having a small ratio and the other half to alternatives having a large ratio first, and comparing the performance of the two groups (Ward and Smuts, 2007).

Quantity discrimination in elephants

Several studies have focused on the ability of elephants (Asian and African) to discriminate between different quantities of the same item. These studies focused on how measures of differences between alternatives such as ratio, magnitude, and absolute difference of the alternatives affect the ability of elephants to choose higher-valued prospects. Three studies found that Asian elephant discrimination was not affected by the ratio, magnitude, or absolute difference between alternative food rewards (Irie-Sugimoto et al., 2009; Irie and Hasegawa, 2012) or different numbers of shapes on a screen (Irie et al., 2019). Two additional studies on Asian elephants described a negative correlation between discrimination and the ratios of the alternatives (Plotnik et al., 2019; Snyder et al., 2021), similar to what was observed in the only study conducted on

African elephants to date (Perdue et al., 2012). Finally, no effect of magnitude was found on the discrimination ability of African and Asian elephants at a fixed 1:2 ratio (Perdue et al., 2012; Plotnik et al., 2019; Snyder et al., 2021) and of Asian elephants also at a fixed 1:3 ratio (Plotnik et al., 2019).

These studies altogether found that elephants can discriminate between different quantities of the same food when they are visually presented simultaneously (Irie-Sugimoto et al., 2009), or presented item-by-item both visually or by hearing the sound of each piece of food being dropped (Irie-Sugimoto et al., 2009; Irie and Hasegawa, 2012; Perdue et al., 2012; Snyder et al., 2021), or sequentially investigated via smell only (Plotnik et al., 2019).

The current study is the first to test African elephants in untrained tasks involving smell as the only sense used to investigate the alternatives (Plotnik et al. (2019) did this with Asian elephants), either by allowing trunk contact with the vessels containing the rewards or by smelling the enclosed rewards from a distance. It is also the first study, to our knowledge, testing the preference of African elephants for different fruits. In addition to considering the effect of ratio, absolute difference, magnitude of the alternatives, and the sense involved (smell-only or smell-plus-sound), this study also assesses whether elephants learn throughout a task. Different foods are used both as stimuli and rewards throughout the study (two fruits and commercially available game feed) allowing for comparisons of the quantity discrimination of elephants between different foods. Finally, this is the first study of quantity discrimination using Bayesian methods, allowing for the estimation and the comparison of the utility parameters both at the herd and the individual level, for each quantity of

each presented food source. The utility curves estimated in each experiment will be compared in the final chapter to answer the question: can elephants do simple arithmetic?

Aim and objectives

This thesis represents the first step in a larger project aiming to elicit African elephant risk preferences through the use of lotteries, as is commonly done with humans. For that project to be successful, we need to know if elephants treat numerosities ordinally, as humans do. Therefore, this thesis aims to determine whether African elephants are sensitive in their behaviour to the arithmetic of small integers. To reach this aim, I compared the utility functions each elephant attributes to a specific numerosity derived from a series of binary choices involving different quantities of various foods. Each chapter of the thesis fulfils a specific goal.

- Objective 1: To investigate African elephant fruit preferences and apply BHM to a simple case study.
- Objective 2: To assess factors affecting the choices of African elephants when choosing between different quantities of the same edible item in binary choices, and the role of experience on their performance. In particular, to test the difference between a smell-only simultaneous presented condition and a smell-plus-sound item-by-item presented condition.
- Objective 3: To evaluate how the use of different fruits as the stimulus and the use of different conditions (contact vs no-contact) affect the choices of African

elephants for different quantities of the same edible item, and if their performance improves with experience, in binary choices involving smell only.

- Objective 4: To investigate whether elephants assess prospects by counting available items through the estimation of individual utilities for each prospect.

General Methodology

Study species

The African elephant is the largest living land animal. It is found in several sub-Saharan countries and it is listed as “Vulnerable” by the IUCN Red List (IUCN, 2023). The average weight for African elephants is between 1.8 and 6 tons which is maintained by ingesting every day about 1 to 1.5% of body weight in the form of daily dry matter intake (Ullrey et al., 1997). In the wild, elephants live in fission-fusion herds formed by females and calves they are related to and led by the matriarch, and bachelor herds of males.

African elephants possess the largest brains among terrestrial mammals, having an average weight of 5 kg (Herculano-Houzel, 2016: Chapter 8). Their cognitive performance in visual discrimination learning is poor in comparison to some other mammals such as chimpanzees, but they do excel in long-term and spatial-temporal memory (Hart et al., 2008). African elephants’ spatial-temporal memory is demonstrated by the fact that they travel long distances to reach locations they previously have visited that offered resources such as food or water (Hart et al., 2008). For example, during a 3-year drought in the Tarangire National Park in Tanzania, matriarchs old enough to have experienced a previous comparably severe drought led their families outside the park,

possibly to locations visited in the past and known to carry resources (Foley, 2002).

Younger matriarchs who had not experienced a previous drought did not leave the park, leading to high infant mortality (Foley, 2002).

The African elephant brain has three times the number of neurons of humans, 98% of which are located in the cerebellum (Herculano-Houzel, 2016: Chapter 6). This part of the brain is involved in several aspects of the life of an animal, for example, it coordinates movements of different body parts allowing for fine and precise movement, and participates in spatial and movement learning (Snow et al., 2014). The trunk, being a large muscular organ capable of extremely fine movements, has been proposed as the most probable source of selective pressure for such an uncommonly large number of highly packed neurons in the cerebellum of African elephants (Herculano-Houzel, 2016: Chapter 6). Such an abundance of neurons makes the African elephant brain extremely metabolically expensive (Herculano-Houzel, 2016: Chapter 9).

The knowledge we have about the acuity of African elephants' senses is limited. We know that they possess more than 2000 genes encoding for functional olfactory receptors (Niimura et al., 2014). In comparison, humans have roughly 400 and dogs have about 800 of these genes (Niimura and Nei, 2003; Niimura et al., 2014). Elephants have overperformed dogs in detecting the presence of TNT through smell (Miller et al., 2015) and they are known to make optimal foraging choices based on their olfaction (Schmitt et al., 2018). In addition, they use their trunk and vomeronasal organ to acquire information about their conspecifics, such as sexual state, identity, and health status (Jacobson and Plotnik, 2020). They were also able to choose their favourite food when it was confounded by a stronger smell of another food (McArthur et al., 2019), and

could correctly match a human scent sample from several others (von Dürckheim et al., 2018). Olfaction might indeed be their most important sense when making foraging choices (Plotnik et al., 2014; Schmitt et al., 2018).

African elephants' sight is known for being poor, though only a few studies have tested it. In one study a single elephant was able to discriminate a full circle from a circle having a 2.75 cm gap from a distance of almost 2 m (Shyan-Norwalt et al., 2010). African elephants could visually recognise clothes of different colours, red or white, from a distance of approximately 6.5 m (Bates et al., 2007), and they were able to find a reward by following visual cues (human pointing) only (Smet and Byrne, 2013). African elephants see colours like colour-blind deuteranopic humans during the day and they possibly have better vision at night time (Yokoyama et al., 2005). Elephants almost certainly have less acute visual resolution than primates (Hart et al., 2008) and even the anatomy of their brain, where the olfactory and temporal lobes are more developed than the occipital lobe, suggests that vision is not their strongest sense (Jacobson and Plotnik, 2020).

If their sight is poor, their hearing is highly developed. One study on Asian elephants found that they can hear sounds between 17 and 12000 Hz (Heffner and Heffner, 1982). A recent study confirmed that the hearing of African elephants spans a range larger at both ends than Asian elephants' (Scheifele et al., in press). African elephants can hear and recognise the individual calls of up to 100 conspecifics (McComb et al., 2000) at distances up to 1.5 km (McComb et al., 2003), demonstrating highly developed social memory in addition to fine hearing.

Study subjects

The subjects of the study were six semi-tame African elephants hosted at Adventures with Elephants (AwE), in Limpopo, South Africa (Figure 1.2). Four elephants are adults: Mussina, Nuanedi, and Shan are females, aged 18, 18, and 19 years respectively at the beginning of the study, and Chova, a male, was 28-year-old at the beginning of the study. These elephants have been in the care of humans for about 15 years. The additional two elephants are Bela Bela, a female aged 5 years, and Zambezi, a male aged 6 years at the beginning of the study. They were both born at AwE and they share Chova as a father. Bela Bela's mother is Mussina, and Zambezi's mother is Shan. The two youngsters took part in only one of the experiments described in this thesis, due to their inability to respond to some commands required to perform the other two experiments.

Chova's trunk tip was sheared as the result of an accident that happened about 10 years before the beginning of the study. Though the injury was severe, handlers gave Chova food and water directly in his mouth, allowing his trunk to heal. Chova is now able to drink and forage by himself, and, since he lost the prehensile part of his trunk, he has developed strategic techniques to pick up food, such as using suction pressure. It is not clear whether his ability to smell has been affected by this injury.

These elephants are part of a herd of seven living in the 300 ha AwE reserve. During the day the herd spends most of its time freely foraging in the savanna environment. In addition, the elephants take part in daily educational interactions with the public. They are trained to follow several commands given by the handlers that always accompany them, such as "Come", "Back up", and "Mat". As an addition to

their diet they receive bana grass (*Pennisetum purpureum x P. americanum*) and, every time they respond to a command, they are rewarded with some pieces of boskos (brand ALZU), commonly known as game pellets. The elephants spend each night in individual stables, next to the houses of two handlers who feed them overnight and can intervene in case of an emergency.

The herd is accustomed to being part of experimental research activities, having participated in several studies on elephant body features, sound emission, and smell detection (Miller et al., 2015; Panagiotopoulou et al., 2016; Lamb et al., 2020; Wood et al., 2022; Bester et al., 2023). Previous studies conducted with the same group of elephants used in this study found that, based on smell cues only, elephants can distinguish their preferred plants from their less preferred ones at different spatial scales (Schmitt et al., 2018), that they choose between marula fruits at different stages of maturation based on their sugar content (Nevo et al., 2020), and were able to locate the presence of water at a small spatial scale (Wood et al., 2022). In addition, Miller et al. (2015) found that Mussina and Shan reliably detected the presence of TNT via smell only, with a higher sensitivity than dogs, even in the presence of distractive odours.

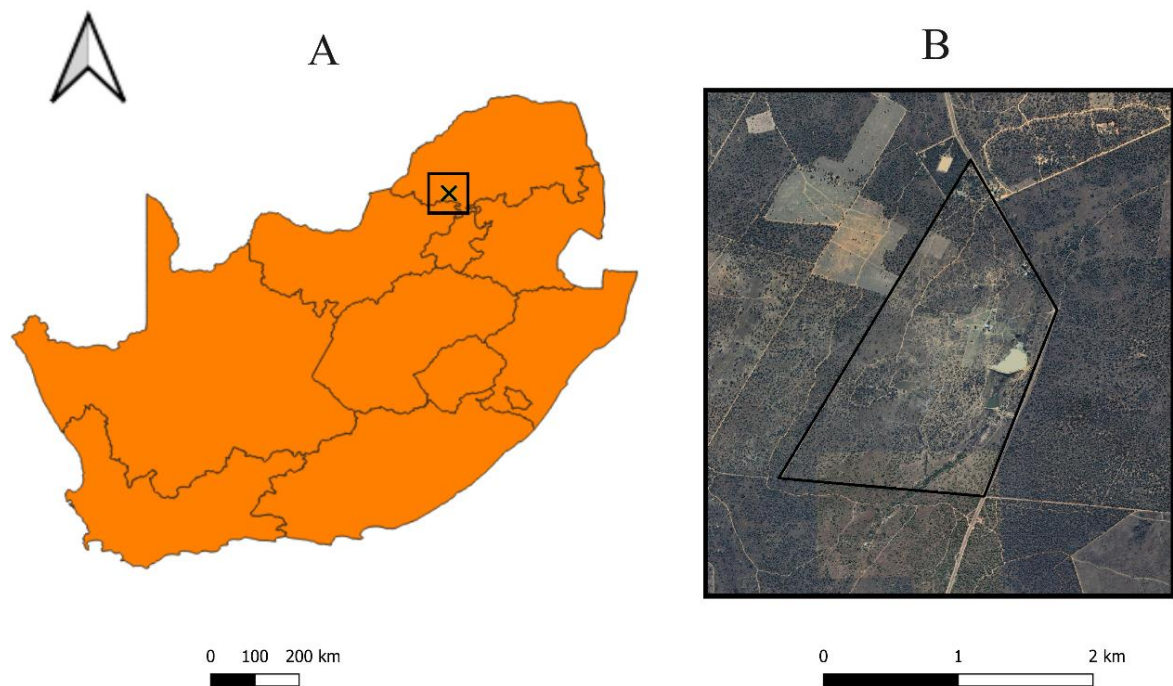


Figure 1.2: The location of Adventures with Elephants in Limpopo province, South Africa (A), and an aerial view of the reserve (B).

Study design

The data collected to produce this thesis span 25 consecutive months between 2021 and 2023, as shown in Figure 1.3. The data were collected at different locations inside the AwE reserve, based on the elephants' location at the time designated for the experiment. The data collection was similar for each experiment presented in the thesis, therefore I here describe the general methods. Each chapter contains a section offering a detailed description of how the data relevant to that chapter were collected.

Every experiment presented in this thesis involves balanced binary choices made by an individual elephant between different types of fruits or different quantities of the same edible item, either boskos or a fruit. The elephants were always tested individually, and each experiment started with a handler asking the elephant to “Mat”.

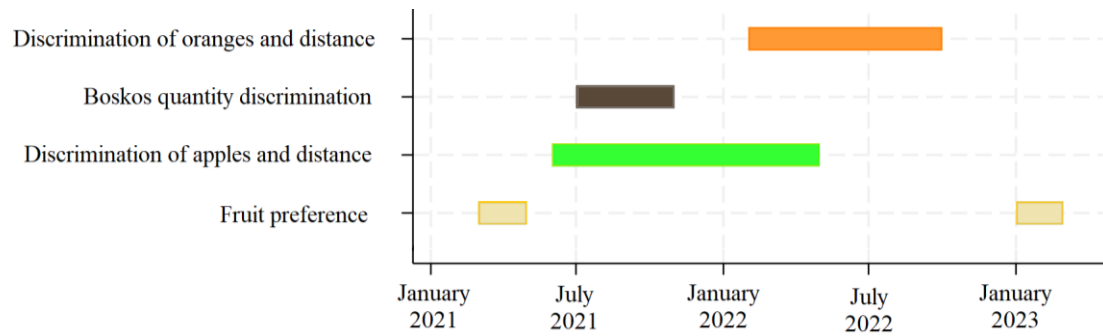


Figure 1.3: A Gantt chart showing the timeline of the data collected for this thesis, from March 2021 to March 2023.

The elephants know that the command “Mat” means to place both their front feet on a canvas mat and to wait for further instructions. The mat was used to define the starting position of each experiment, placed so that the mat and the alternatives to choose between formed the shape of a V, always being equidistant to each other. Once on the mat, the elephant was asked by the handler to either smell the alternatives and choose, or directly choose one of the alternatives depending on the task.

The alternatives were always presented underneath white plastic buckets of different sizes in which holes had been drilled to allow the elephants to smell the hidden content. The elephant indicated his or her choice by pointing at or approaching the preferred alternative, usually after smelling the top of the buckets containing each alternative. In every trial of each experiment, the elephant consumed the chosen reward while the unchosen option was removed. To avoid Clever Hans effects, different handlers participated in the experiments every day. When possible, the handlers did not know the content of the alternatives and the researcher gave her back to the experiment. In any case, no people involved in the experiments indicated any side to the elephant.

A description of the prospects offered to the elephants throughout the thesis is presented in Table A2, in Appendix 1. No trials in Chapter 2 offered a choice between the same fruit, and no trials in Chapters 3 and 4 included a choice between the same number of items. The side of presentation of the rewards was pseudo-randomised so that a specific fruit (Chapter 2) or the larger reward (Chapters 3 and 4) was not presented on the same side for more than 3 consecutive trials. In addition, each fruit and each specific quantity of food was presented to the right and left side of each elephant in a balanced, random manner.

Statistical analysis

The data analysis in this thesis has been conducted using Bayesian methods in Stata 18, documented by StataCorp (2023). Bayesian analysis differs from frequentist analysis in many ways (Kruschke and Liddell, 2018a). For example, Bayesian analysis calculates the probability that a hypothesis is true rather than calculating how probable it is to observe the distribution of the collected data set assuming that the null hypothesis is true (Fornacon-Wood et al., 2022). Bayesian statistical methods are used because they are the most appropriate for the inferences about individual elephant behaviour that are required. No attempt is made to show that Bayesian methods generate different conclusions than Classical statistical methods or to contrast the two methods.

In Bayesian analysis, when a planned data set can be explained in more than one way, one typically assigns different credibility to each possible explanation, based on previous literature or experience, before actually looking at the data. Such beliefs

constitute the analyst's *priors*. After looking at the data, one reallocates credibility among the possible explanations, assigning higher credibility to the explanations that better account for the data, in the form of what is known as a *posterior* belief. If new data are collected, the posterior can then become a prior used to estimate a new posterior credibility, in a potentially endless updating loop. In short, Bayesian analysis combines the probability distributions of the priors and the probability distributions of the likelihood of the observed data to estimate posterior probability distributions. Consequently, the posterior probability distribution always “sits” in between the prior and the likelihood distribution, as in Figure 1.4. For an easy-to-follow explanation of Bayesian analysis and how it differs from frequentist analysis see Kruschke and Liddell (2018a, 2018b).

The statistical analysis across all chapters of this thesis considers binary dependent variables (1 for yes, or 0 for no). In Chapter 2 the 0/1 binary variable indicates if a specific reward, different types of fruit, in this case, was chosen or not. In Chapters 3 and 4, the 0/1 binary variable indicates if a “correct” choice was made by an elephant when choosing between different quantities of boskos, apples, or oranges. In this instance “correct” was defined as the choice of the larger number of boskos, apples, or oranges, deriving from the assumption that, to maximise their net energy intake, elephants would prefer more food to less (Pyke, 1984).

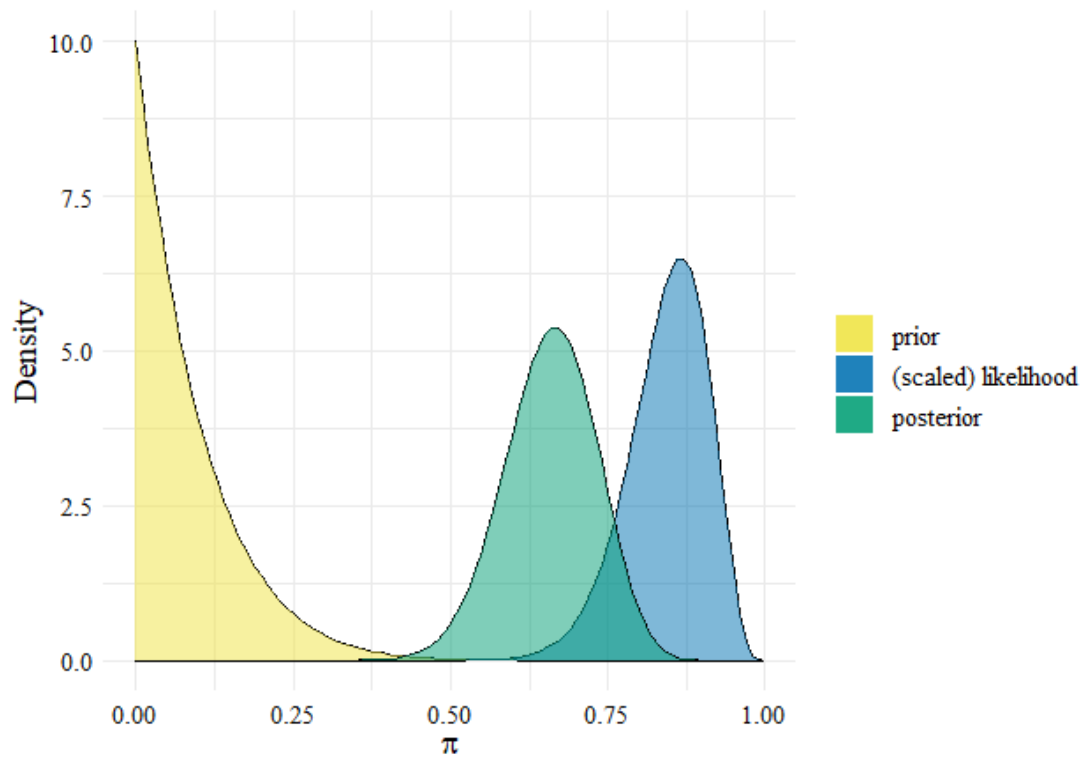


Figure 1.4: A Beta probability density function (yellow) represents the prior, the scaled Binomial likelihood function (light blue) represents the likelihood distribution of the observed data, and the Beta probability density function (green) obtained by combining the prior and the likelihood represents the posterior.

Since the dependent variable y was always binary, a probit distribution was used in what is called the “head-to-head” comparison in Chapter 2, and in the analyses of Chapters 3 and 4, to characterise the data-generating process. A probit model evaluates a latent linear index, using a cumulative distribution function of the standard normal distribution to transform the linear index into a probability of observing y . A probit function can take any number from $\pm\infty$ from the estimated latent index and transform it into a number between 0 and 1. A logit model behaves similarly, with the difference of using a cumulative standard logistic distribution. The probit and the logit models provide similar results (Greene, 1990), and both could be used for the analysis presented

in this thesis. Since this analysis is commonly applied in econometrics using a probit model, I also preferred a probit to a logit model when performing BHM.

Formally, a probit model has a latent index that has the form: $y^* = \alpha + \beta x_1 + \gamma x_2 + \dots + \varepsilon$, where y^* is the latent preference for one alternative over the other; $x_1, x_2, \dots, x_k$ are observable covariates (e.g. the absolute difference between the alternatives), α is the intercept, β and γ are the coefficients of the covariates x_1 and x_2 that need to be estimated, and ε is an error parameter to be estimated and is assumed to be distributed according to the standard normal distribution $N(0,1)$. There can be multiple covariates, each having a coefficient to be estimated. For example, covariates considered in this thesis focus on the difference in the size of the alternatives, the different conditions used in the specific chapter, or the side of the chosen alternative, depending on the context.

Let y be the observed choice of the elephant between a larger and a smaller alternative, as in Chapters 3 and 4. In a Bayesian analysis, all coefficients to be estimated are treated as random variables. To allow each elephant to have a different intercept we assume the intercept to be $\alpha_j \sim N(\mu_j^\alpha, \sigma_j^\alpha)$, where α_j is the intercept α of elephant j , “ $\sim$ ” means “is assumed to be distributed as”, and $N(\mu_j^\alpha, \sigma_j^\alpha)$ refers to a normal distribution with mean μ_j^α and standard deviation σ_j^α . Similarly, to allow each elephant to have a different slope for the linear relationship between y^* and each covariate, we assume each covariate, such as β and γ , to be $\beta_j \sim N(\mu_j^\beta, \sigma_j^\beta)$, $\gamma_j \sim N(\mu_j^\gamma, \sigma_j^\gamma)$, and so on.

Bayesian analysis requires a prior for each of the estimated parameters. As a prior for the intercept of the latent index for each elephant α_j , a modestly informative

prior, a normal distribution $N(0,5)$, was always used. This prior was chosen because it represents diffuse expectations about how probable it is for each individual elephant to choose one alternative or the other. Specifically, a prior $N(0,5)$ has a mean of $\mu = 0$, corresponding to the expectation that the elephant has a high probability of choosing both alternatives an equal number of times (50% each) since the probit model converts a value of 0 for the latent index to a modal probability 0.5, a lower probability of choosing one alternative more than the other, and the lowest probability of choosing exclusively one alternative. The normal distribution $N(0,5)$ prior was also used for any covariate in the latent index (e.g. β and γ), also representing a vague belief that no particular variable would especially affect the probability of the elephants choosing the larger alternative.

Figure 1.5 offers four examples of normal cumulative density functions showing the probability that four theoretical individual elephants choose the alternative on the right as the quantitative difference in size between the alternatives varies. This illustrates how a covariate, in this case the absolute difference in rewards, can affect the probability of making the “correct” choice. The x-axis spans between -5 (a choice between 6 items on the left vs. 1 item on the right), and 5 (a choice between 1 item on the left vs. 6 items on the right). A difference of 0 represents a choice between two alternatives that are identical in size (this actual choice was not offered to the elephants). The plot for individual 1 is what we would expect if an individual always chooses the larger alternative. The plot for individual 2 represents an individual who prefers the larger alternative most of the time but sometimes chooses the smaller alternative when the alternatives differ by 1 unit.

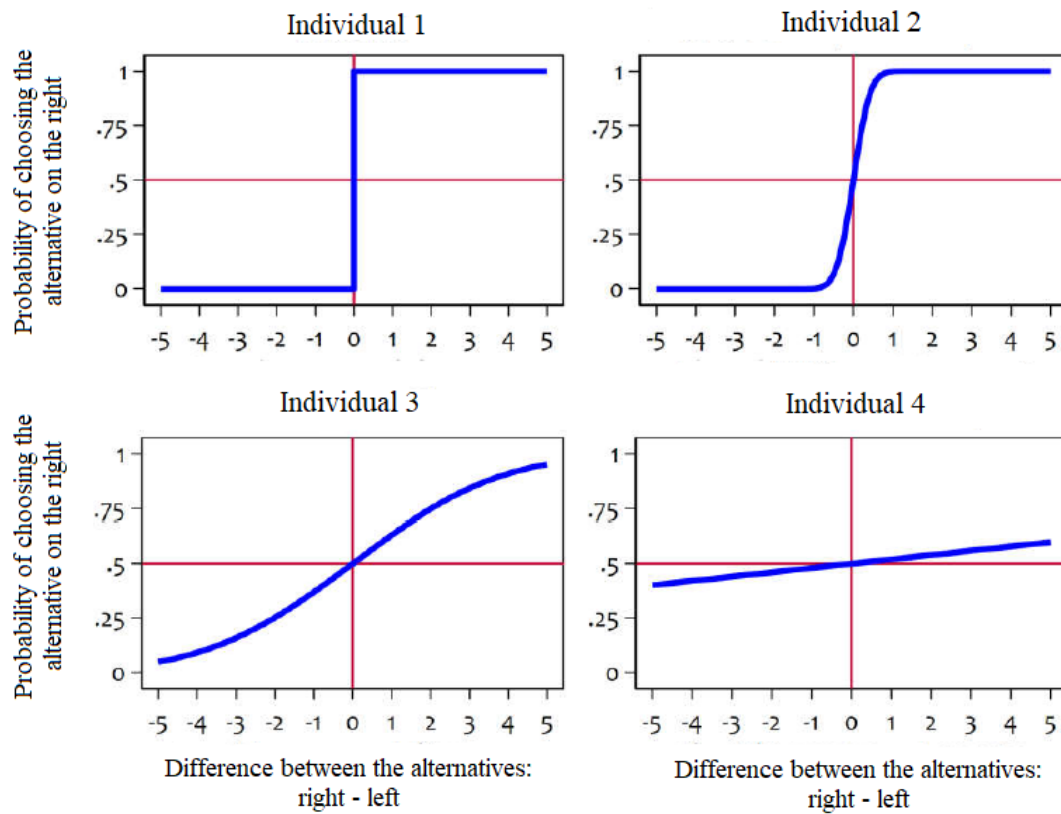


Figure 1.5: Normal cumulative density functions used in a probit model. The four individuals represent hypothetical individuals having different strengths of preference for the larger alternative.

The plot for individual 3 represents an individual who is less likely than individual 2 to choose the larger alternative when both have the same difference between right and left rewards. Individual 4 is close to being indifferent to the alternatives, and never exclusively chooses the larger one for the reward differences shown in the plot. In all four plots, the individuals would be indifferent to the alternatives if they were identical in size.

Finally, the estimation was conducted using a Bayesian Hierarchical Model (BHM) with a probit distribution. The power of using a BHM in this setting lies in how

it accounts for grouped data, meaning data where there are repeated observations over a group, in this case over individual elephants in a herd, to generate an informative prior to estimating parameters for each individual elephant. The use of BHM is spreading in the field of ecology, where BHM analysis is applied to field studies (Wikle, 2003; Royle et al., 2009; Webb et al., 2010; Schofield and Barker, 2014) and there are many books explaining its use (e.g. Clark and Gelfand, 2006; Royle and Dorazio, 2008; Hobbs and Hooten, 2015).

A BHM uses all the data, here observations from all the elephants, to calculate a global posterior distribution for each observation, then uses this posterior distribution for the group as the prior for estimating the posterior distributions of *each elephant in the group*. This is often referred to as *partial pooling*, and its main advantage is to allow the behaviour of each individual in the group to influence the posterior distribution of every other individual in the group, permitting robust inferences at the level of the individual elephant. The result of partial pooling is referred to as shrinkage, in which the posterior distributions of the individuals inside a group are, to some extent, pulled toward the global posterior distribution, reflecting the fact that the individuals are members of the group and share many of its characteristics. The extent of the shrinkage varies between individuals (Johnson et al., 2022: Chapter 16).

BHM was selected to analyse the data because of its use of hierarchical priors which allows making robust inferences about individual elephants, as well as for the herd, even with a small sample of elephants. Assume that the probit model is defined over the *parameters* α_i and β_i . We then posit two *hyper-parameters* that describe the distribution that characterizes *each* of

- α_i , the intercept for elephant i ; and
- β_i , a coefficient of some attribute of the specific choice by elephant i (e.g., the ratio of the two rewards in that specific choice).

Hence we estimate 4 hyper-parameters in all, based on the pooled data across all N elephants. In addition, we estimate α_i , and β_i for each elephant $i = 1, \dots, N$. In all, therefore, we jointly estimate $4 + (2 \times N)$ parameters for the full hierarchical model. Since $N = 4$ or 6 in our data, we jointly estimate 12 or 16 parameters, respectively. In many of the BHM models we have more than one covariate.

For each hyper-parameter we must specify a hyper-prior. The estimated hyper-*posterior* for each hyper-parameter then becomes the informative *prior* for each parameter, at the level of the individual elephant. Although the distinction between parameters for each elephant and hyper-parameters for the pooled herd might seem confusing at first, it is fundamental to the specification of a BHM. In principle, a BHM can have two or more levels of hyper-parameters, but in our case we only have one hierarchical level: the herd of N elephants.

Formally, we assume that α_i is characterized by a Normal *prior*:

$$\alpha_i \sim N(m_\alpha, \sigma_\alpha^2), \quad (1)$$

where there is a diffuse Normal *hyper-prior* for m_α given by

$$m_\alpha \sim N(0, 5), \quad (2)$$

and there is a diffuse Inverse Gamma *hyper-prior* for σ_α^2 given by

$$\sigma_\alpha^2 \sim \text{IG}(0.1, 0.1). \quad (3)$$

The idea is that there is an informative, non-diffuse prior specified in (1) for each elephant i , where the values for m_α and σ_α^2 come from the posterior distributions generated by the data for all N elephants *and* the diffuse hyper-priors in (2) and (3). We can restate (1) in conditional form as

$$\alpha_i \mid m_\alpha, \sigma_\alpha^2 \sim N(m_\alpha, \sigma_\alpha^2), \quad (1')$$

to remind us that if we knew the mean and the variance of the prior we would have much more information about the individual α_i parameter values than if we had assumed a diffuse prior for these individual parameter values.

The remaining prior distribution assumptions are similar. We assume that β_i is also characterized by a Normal *prior*:

$$\beta_i \sim N(m_\beta, \sigma_\beta^2), \quad (4)$$

where there is a diffuse Normal *hyper-prior* for m_β given by

$$m_\beta \sim N(0, 5), \quad (5)$$

and there is a diffuse Inverse Gamma *hyper-prior* for σ_β^2 given by

$$\sigma_\beta^2 \sim \text{IG}(0.1, 0.1). \quad (6)$$

Every time a BHM was evaluated in this thesis, the posterior distributions were obtained through a Markov Chain Monte Carlo (MCMC) simulation with Metropolis-Hastings sampling, as well as Gibbs sampling when possible (see Kruschke, 2015: Chapter 7; Johnson et al., 2022: Chapter 7).

An MCMC simulation is a random process that allows the simulation of the posterior distribution based on the fact that the posterior distribution is proportional to the product of the prior distribution and the likelihood function, which are both known. The MCMC simulation can be seen as a tour of all the posterior plausible values, where the most visited values are also the most probable posterior values. The first visit of an MCMC is a random or predetermined probability value between 0 and 1, which has a specific credibility in the posterior distribution, based on the prior and the likelihood function. The MCMC simulation proposes the next random location, being another probability value between 0 and 1 with its own credibility in the posterior distribution. If the credibility of the new location is higher than the credibility of the current location, the simulation moves to the next point. If the credibility of the next location is lower than the current location, the simulation moves to the next location with probability α or stays and the current location for another iteration with probability $\alpha-1$. This mechanism implies that each step is correlated to the previously visited location and that the tour will stop more often on the posterior values that are the most credible. The first steps of the simulation are correlated to the chosen initial value and do not span all the possible values of the posterior distribution. Consequently, the first steps of the MCMC are not representative of the posterior distribution, especially when, as in this thesis, the priors used are modestly informative. These steps are known as the *burn-in* period and are excluded from the sample. Commonly burn-in periods are made of hundreds or even thousands of steps (Kruschke, 2015: Chapter 7), depending on the model and the priors used.

To ensure that the MCMC simulations reached full convergence, and therefore simulated a reliable posterior distribution, four standard convergence diagnostics plots were assessed, as shown in Figure 1.6. The *trace* plot, which represents the values of the posterior distribution visited by the MCMC simulation over time, should not show any upward, downward, or cycling trend, indicating that the simulation settled on all the possible values of the posterior distribution without becoming “stuck” on some specific parameter values. The *autocorrelation* plot shows how much each consecutive value reached by the MCMC simulation depends on the previous value. It should initially show a high level of autocorrelation when the previously simulated value was literally the previous value, and then it should steadily decline towards 0 as the previously simulated value was many values prior, indicated as a high “lag”. The *histogram* of the posterior distribution should be unimodal, and the *kernel density* of each chain and the first and second halves of the chain need to be similar to each other, to ensure that the MCMC simulation is stable. Unless otherwise stated, all estimated models in the thesis exhibited satisfactory convergence by these criteria.

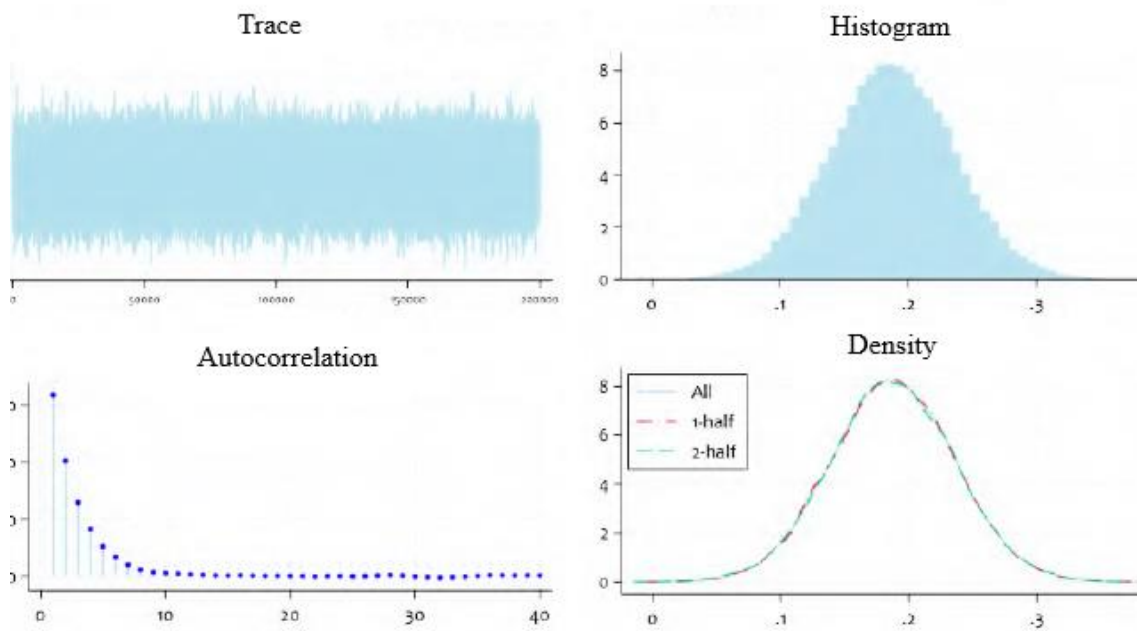


Figure 1.6: Four standard graphical diagnostic plots (Trace, Autocorrelation, Histogram, and Kernel Density) for the convergence of the MCMC simulation used in BHMs.

Chapters 3 and 4 of this thesis display the density of the posterior distribution of the BHM without covariates, to show how probable it was for each elephant to prefer the larger alternative. The effect of the covariates added to each model is often presented in the form of the Average Marginal Effect (AME). AMEs show how much one individual elephant's probability of choosing the larger alternative changes when one of the variables increases by one unit, everything else being constant (Williams, 2018). We focus here on binary covariates since they are the most common covariate used in these analyses. In this case, the increase by 1 unit is literally an increase of 1 unit; when there is a continuous variable the unit is usually infinitesimally small (Cameron and Trivedi, 2005: Chapter 3).

When calculating the AME, the probability of choosing the larger alternative is predicted for each elephant by running MCMC simulations where all the variables contained in the model, other than the variable of interest for the AME, are set to be equal to their actual, observed values. An alternative way of calculating the marginal effect is to set the variables other than the variable of interest equal to their average. The AME is generally preferred in the literature (Williams, 2018).

In the case of a binary covariate, the AME is calculated as the *difference* between the predicted probability of choosing the correct alternative when the binary variable takes on the value 1 instead of 0. When the covariate of interest is continuous or has many discrete variables, it is possible to use the same method of calculating an AME for selected discrete values of the variable of interest, evaluating each possible discrete value that the variable of interest for the AME can take. For example, consider the absolute difference in rewards between the alternatives, which in this thesis typically ranges from 1 to 5. In this case, if the predicted probability when the difference is 4 is compared to the predicted probability when the difference is 3, then we are using the same method of calculating the AME for a binary value. This applies as well to the unit difference between any two numbers.

Among the variables whose results are shown as AME, there is side preference. There are two ways to make inferences about an elephant's side preference by estimating how the probability of choosing the larger reward varies based on the side where it is located.

The first way focuses on the *unconditional* probability, that is, considers all the choices given to the elephant, and estimates his/her probability of choosing the larger alternative more often on one side than on the other. When an elephant has a higher probability of choosing the larger reward when choosing one side, this indicates that the elephant has a preference for the opposite side. A higher probability of choosing the larger alternative, for example, on the left side indicates that the elephant, for specific causes that are not necessarily known, assigns higher utility to the right side than to the left side. Therefore, such an elephant would choose the reward on the left side only when its utility overcomes the utility of the reward on the right side *plus* the utility of choosing the right side itself. A numerical example using hypothetical data might help. Assume that Mussina is offered 100 choices between different quantities of apples. Suppose she chooses the larger alternative 39 times out of the 42 choices she makes to the left, and 42 times out of the 58 choices she makes to the right side. Mussina has a higher probability of choosing the larger reward when she chooses the left side ($39/42 = 93\% > 42/58 = 72\%$) and therefore, she has a right-side preference (58 choices to the right $>$ 42 choices to the left).

The second way to make inferences about an animal's side preference is to consider the *conditional* probability of choosing the larger reward, conditional on the side where the larger reward is located. This means that the probability of choosing the larger reward is estimated by considering *only* the choices made when the larger reward was on the left side or *only* choices made when the larger reward was on the right side and then comparing them.

In estimating the conditional probability of choosing the larger alternative, it is advantageous if the binary choices offered to the animal are balanced so that the larger reward is presented on each side of the animal the same amount of times. If the rewards are not presented in such a balanced way, an identification problem would arise with this method of inference: one would not be able to assess if a higher probability of choosing the larger reward depends on the animal's side preference or if it is due to the larger alternative appearing more often on one side than the other. This identification problem could be solved by performing an independent estimation of the effect size of the side preference as determined based on the unconditional probabilities. This additional estimation step would add an estimation error, which would be multiplied by the error on the conditional estimate used to calculate the AME. This would reduce the precision of results. By offering choices balanced in regards to the side location of the larger reward, as has always been done in the studies presented in this thesis, we obtain more precise quantitative estimates of side preferences than would otherwise be possible.

When considering the probability of an elephant choosing the larger reward conditional on its side of presentation, an elephant having a higher probability of choosing the larger reward when the larger reward is on one side, has a preference for that side. Consider the previous example where Mussina made 100 binary choices between varying numbers of apples. Let us assume she made the same choices as before (42 to the left, 58 to the right), but now we focus on her conditional probability of choosing the larger reward. Out of the 50 choices she made where the larger alternative was located on the left side, Mussina chose it 33 times, and out of the 50 choices she

made where the larger alternative was on the right side (notice the balance), Mussina chose it 48 times. Mussina had a higher conditional probability of choosing the larger reward when it was located on her right side ($48/50 = 96\% > 33/50 = 66\%$), and thus Mussina had a right-side preference.

In Chapter 2 the preference for different fruit types by the elephants was evaluated through a BHM using a Conditional Logistic (CL) specification of the likelihood of the observation. The CL model was developed by McFadden (1974), who won a Nobel Prize in Economics for this work and has been previously used in ecology, though in a frequentist rather than a Bayesian environment, by Duchesne et al. (2010). This model evaluates the likelihood of the choices of the pairwise combinations of fruits, estimating the utility of each fruit, from which the probability that each fruit would be chosen by each elephant is calculated. The same Bayesian CL model has been used in Chapter 5 to estimate the utilities of each elephant for each quantity of boskos, apples, and oranges tested in Chapters 3 and 4.

Frequentist analysis usually aims at testing the significance of the null hypothesis. This involves computing a p -value that is compared to a threshold value, commonly 0.05, and if the p -value is smaller than the threshold, then the null hypothesis is rejected (Kruschke and Liddell, 2018a). The null hypothesis almost always states that the effect of an independent variable on the response variable is equal to 0, allowing for the effect to only be equal to a single value. A Bayesian analysis, on the other hand, requires the use of interval hypothesis tests, where the posterior distribution of a variable is compared to an interval of values rather than to a specific value (Kruschke

and Liddell, 2018a). This method is based on the Region of Practical Equivalence (ROPE).

Assume that the normal distributions presented in panel A of Figure 1.7 are the posterior distributions of the ratio and absolute difference of the alternatives on the probability of an elephant choosing the larger reward in binary choices. The posterior distribution of the ratio is centred on 0, suggesting there is high credibility of this variable *not* affecting the final choice. Instead, the posterior distribution of the absolute difference is centred on 2, suggesting there is high credibility of this variable having a positive effect on the larger reward being chosen. The posterior distribution of the absolute difference crosses the dashed line indicating 0, meaning that there is a certain credibility, though small, that this variable does not affect the final choice. A ROPE can be used to assess how probable it is that one variable has a 0 effect on the response variable, or to directly compare the probability of more variables not affecting the response variable.

A ROPE represents an interval of values that can be considered equivalent to a value of interest, such as 0. The amount of the posterior distribution of a variable falling inside the ROPE interval represents the probability that such a variable does not affect the response variable in terms of the range of possible values around 0 included in the ROPE. For example, in panel A of Figure 1.7, the portions of the normal distributions included in a ROPE of ± 1 and ± 2 in the top and bottom panels respectively, are represented as 4 shaded areas. By using the same ROPE intervals and calculating the size of the shaded areas under the curves, it is possible to compare the effects of different variables. Indeed, as shown in panel A of Figure 1.7, there is a 69% probability

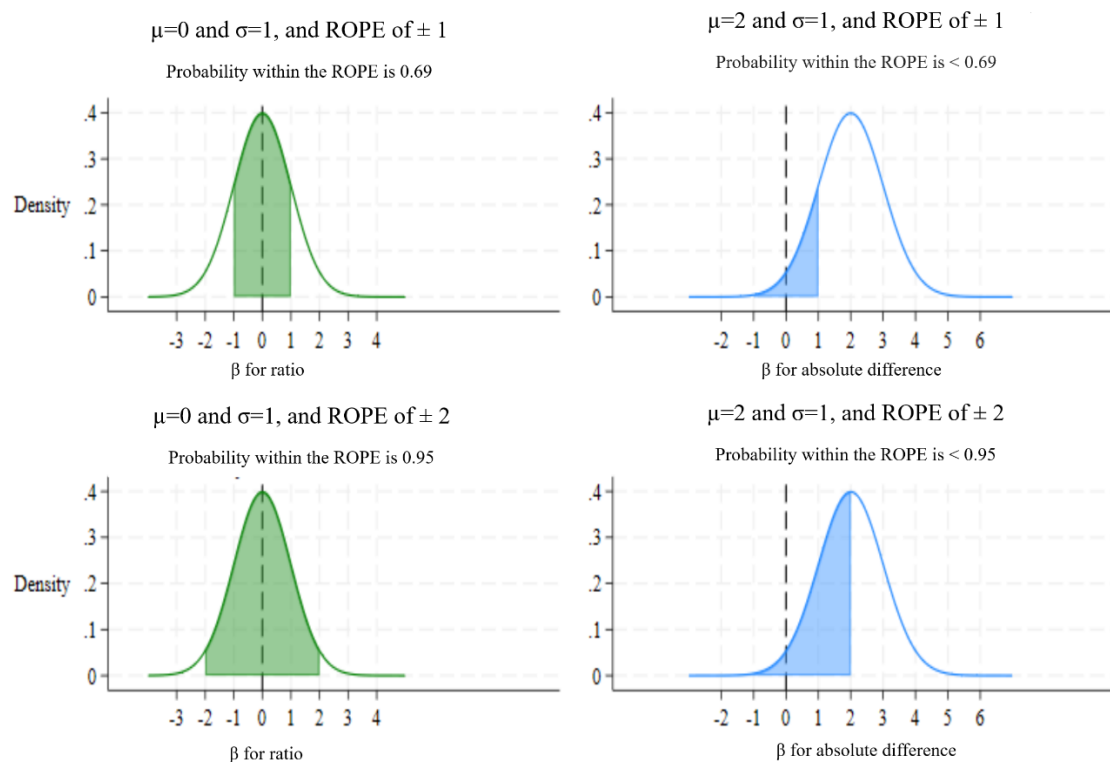
that the effect of the ratio of the alternatives is practically equivalent to the null value. The probability of the posterior distribution of the absolute difference between the alternatives being practically equivalent to the null value is <69%, therefore, in this example, the absolute difference has a stronger effect on the choice of the larger reward than the ratio.

The ROPE limits must be chosen wisely, and they mainly depend on the question one wants to answer (Kruschke, 2018). To avoid choosing a specific limit for the ROPE, the visual representation shown in panel B of Figure 1.7 can be used. Panels A and B of Figure 1.7 convey the same information, but as panel A shows the probability of the variables being practically equivalent to a single ROPE interval, panel B does the same on a continuous scale of ROPE intervals.

As will be the case, by experimental design in this thesis, assume that the ratio of the alternatives goes from 0.17 to 0.83, and the absolute difference between the alternatives goes from 1 to 5. To make the effects of these variables comparable in panel

A

ROPE Illustration Using Normal Distributions

**B**

ROPE Illustration of Both Variables in Percentage Point Scale

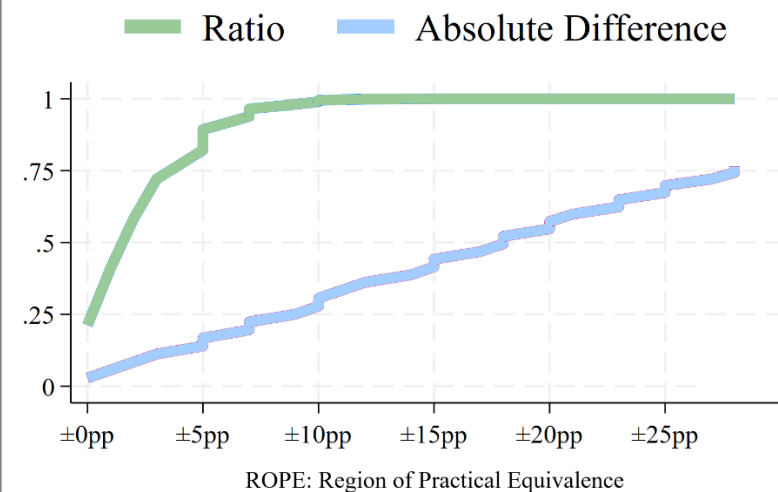


Figure 1.7: Two ways of visualising a ROPE. In panel A, the probabilities that the ratio (green) and absolute difference (light blue) of the alternatives are included in ± 1 (top) or ± 2 (bottom) ROPEs are indicated by the shaded areas under the curves. In panel B, the same probabilities are shown on the y-axis, and each $\pm 5pp$ indicates an area of 10 percentage point change, 5 being on the left and 5 on the right of the $\beta = 0$ used as the reference.

B of Figure 1.7, the ROPE has been converted to percentage point (pp) changes, with the consequence that the x-axis starts from the null value and increases by intervals of 10 pp, 5 pp being smaller than 0 and 5 being larger than 0. The plot (panel B) shows that the ratio, in green, has a high probability of being practically equivalent to the null value from a ROPE of ± 5 pp. On the other hand, the absolute difference between the alternatives, in light blue, has a probability $< 25\%$ of being practically equivalent to 0 in a ROPE of ± 5 pp, and it is not completely equivalent to 0 even when using a ROPE of ± 30 pp.

An easy way to interpret panel B of Figure 1.7 is to think that the slower the curve reaches the 100% probability on the y-axis, the larger its effect on the response variable. Chapters 3 and 4 of this thesis show ROPE comparing the effect of ratio and absolute difference on the probability of each elephant choosing the larger reward at specific prospects as shown in panel B of Figure 1.7.

Many of the displays of results in later chapters reflect this type of calculation, where the posterior distribution for the entire sample is evaluated. Inferences about the effect of intra-task experience on the choices of the elephants require, however, that we evaluate a closely related distribution, known as the posterior *predictive* distribution. This distribution is based on the *posterior* beliefs after sampling is completed. The most common application is to predict what would happen if we then present the elephants with some new choices. In effect, this distribution predicts what the elephants will do next, in some as-yet-unobserved choices, whereas the posterior distribution can be used to predict what the elephants did in the observed choices. Excellent textbook

expositions of these differences are provided by Winkler (2003: p. 102) and Johnson et al. (2022: p. 192).

In this thesis, the primary application of the posterior predictive distribution is to characterize the effect of the experience that the elephants have gained from participating in the task. One could ask if the *first or last* choice that an elephant made had a better than 50% chance of being the larger alternative, relying solely on the *posterior* distribution and some covariate for task order that allows conditioning on the first or final task. Or one could ask if the *first or next* choices that the elephant will make in some new, simulated choices have a better than 50% chance of being the larger reward, relying on the *posterior predictive* distribution and the selected characteristics of these simulated choices.

The latter calculation is more attractive for our purposes because we can control the characteristics of the simulated choices (e.g. only looking at choices with reward differences of 3 or more, or ensuring balance with respect to whether the larger reward was on one side or the other). The “problem” with using the posterior distribution for these inferences is that the actual choices at the beginning and end of the observed data may not be the ones we are interested in, or might not be balanced in terms of some criteria. Since the posterior predictive distribution is evaluated by simulating the choice behaviour on a new set of choices (as small or large as we want), we can select those simulated choices to be comparable and hence get a controlled comparison of learning behaviour throughout the task. In later chapters, simulated choices were usually balanced with respect to the absolute difference in the rewards in each choice, and whether the maximum reward was on the left or the right. This involves between 40 and

70 simulated choices, varying from chapter to chapter based on the experimental design used.

Ethical approval

This study was approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (AESC 2020/10/03/B) and by the Animal Care and Use Committee of Georgia State University (Protocol #A21022).

Thesis outline

Chapter 1 of this thesis is meant to be the general introduction to the thesis with a review of the relevant literature and an in-depth introduction to the Bayesian approach used in the subsequent data chapters. Chapters 2-4 are written as individual data chapters, each with an introduction, methods, results, discussion, and references. Therefore, there is a certain amount of inevitable repetition which has however been kept to the minimum. Chapter 2 investigates fruit preferences, Chapter 3 presents the ability of elephants to discriminate between different quantities of boskos in two different sensorial conditions. Chapter 4 presents the ability of elephants to discriminate between different quantities of fruit at different ranges of smell and with different fruits. Chapter 5 investigates the ability of elephants to do simple arithmetic, based on the data from the previous chapters. The overall synthesis and recommendations are in Chapter 6. Tables that are relevant to the understanding of the results but not essential have been placed in the appendix located at the end of the thesis.

Outputs

The “boskos experiment” exposed in Chapter 3 was presented at the 17th International Elephant Conservation & Research Symposium on the 15th of November 2021, with the title “Discrimination ability of African elephants when using olfactory cues”. In addition, a paper entitled “Fruit Preferences of African Elephants: A Bayesian Analysis” has been submitted to the *Journal of Animal Ecology*.

References

- Abramson, J.Z., Hernández-Lloreda, V., Call, J., Colmenares, F., 2013. Relative quantity judgments in the beluga whale (*Delphinapterus leucas*) and the bottlenose dolphin (*Tursiops truncatus*). *Behavioural Processes* 96, 11–19.
- Agrillo, C., Bisazza, A., 2014. Spontaneous versus trained numerical abilities. A comparison between the two main tools to study numerical competence in non-human animals. *Journal of Neuroscience Methods* 234, 82–91.
- Agrillo, C., Dadda, M., Bisazza, A., 2007. Quantity discrimination in female mosquitofish. *Animal Cognition* 10, 63–70.
- Agrillo, C., Piffer, L., Bisazza, A., 2010. Large Number Discrimination by Mosquitofish. *PLoS One* 5(12), e15232.
- Agrillo, C., Piffer, L., Bisazza, A., Butterworth, B., 2012. Evidence for Two Numerical Systems That Are Similar in Humans and Guppies. *PLoS One* 7(2), e31923.
- Aïn, S.A., Giret, N., Grand, M., Kreutzer, M., Bovet, D., 2009. The discrimination of discrete and continuous amounts in African grey parrots (*Psittacus erithacus*). *Animal Cognition* 12, 145–154.
- Baker, J.M., Shivik, J., Jordan, K.E., 2011. Tracking of food quantity by coyotes (*Canis latrans*). *Behavioural Processes* 88(2), 72–75.
- Balestrieri, A., Gazzola, A., Pellitteri-Rosa, D., Vallortigara, G., 2019. Discrimination of group numerosness under predation risk in anuran tadpoles. *Animal Cognition* 22(2), 223–230.
- Bánszegi, O., Urrutia, A., Szenczi, P., Hudson, R., 2016. More or less: spontaneous quantity discrimination in the domestic cat. *Animal Cognition* 19, 879–888.
- Barnard, A.M., Hughes, K.D., Gerhardt, R.R., DiVincenti, L., Bovee, J.M., Cantlon, J.F., 2013. Inherently Analog Quantity Representations in Olive Baboons (*Papio anubis*). *Frontiers in Psychology* 4, 253.
- Barnard, C.J., Brown, C.A.J., Houston, A.I., McNamara, J.M., 1985. Risk-Sensitive Foraging in Common Shrews: An Interruption Model and the Effects of Mean and Variance in Reward Rate. *Behavioral Ecology and Sociobiology*, 139–146.

- Bates, L.A., Sayialel, K.N., Njiraini, N.W., Moss, C.J., Poole, J.H., Byrne, R.W., 2007. Elephants Classify Human Ethnic Groups by Odor and Garment Color. *Current Biology* 17(22), 1938–1942.
- Bateson, M., 2002. Recent advances in our understanding of risk-sensitive foraging preferences. *Proceedings of the Nutrition Society* 61(4), 509–516.
- Battalio, R.C., Kagel, J.H., MacDonald, D.N., 1985. Animals' choices over uncertain outcomes: Some initial experimental results. *The American Economic Review* 75(4), 597–613.
- Bester, T., Schmitt, M.H., Shrader, A.M., 2023. The deterrent effects of individual monoterpene odours on the dietary decisions of African elephants. *Animal Cognition* 26(3), 1049–1063.
- Bisazza, A., Agrillo, C., Lucon-Xiccato, T., 2014a. Extensive training extends numerical abilities of guppies. *Animal Cognition* 17, 1413–1419.
- Bisazza, A., Tagliapietra, C., Bertolucci, C., Foà, A., Agrillo, C., 2014b. Non-visual numerical discrimination in a blind cavefish (*Phreatichthys andruzzii*). *Journal of Experimental Biology* 217(11), 1902–1909.
- Bogale, B.A., Kamata, N., Mioko, K., Sugita, S., 2011. Quantity discrimination in jungle crows, *Corvus macrorhynchos*. *Animal Behaviour* 82(4), 635–641.
- Botti, S., Iyengar, S.S., 2006. The Dark Side of Choice: When Choice Impairs Social Welfare. *Journal of Public Policy & Marketing* 25(1), 24–38.
- Brannon, E.M., Wusthoff, C.J., Gallistel, C.R., Gibbon, J., 2001. Numerical Subtraction in the Pigeon: Evidence for a Linear Subjective Number Scale. *Psychological Science* 12(3), 238–243.
- Budaev, S., Jørgensen, C., Mangel, M., Eliassen, S., Giske, J., 2019. Decision-Making From the Animal Perspective: Bridging Ecology and Subjective Cognition. *Frontiers in Ecology and Evolution* 7, 164.
- Butterworth, B., 2022. *Can Fish Count?: What Animals Reveal about Our Uniquely Mathematical Mind*. Hachette UK.
- Cameron, A.C., Trivedi, P.K., 2005. *Microeconometrics: methods and applications*. Cambridge university press.
- Cantlon, J.F., Brannon, E.M., 2007. Basic Math in Monkeys and College Students. *PLoS Biology* 5(12), e328.
- Caraco, T., 1981. Energy budgets, risk and foraging preferences in dark-eyed juncos (*Junco hyemalis*). *Behavioral Ecology Sociobiology* 8, 213–217.
- Caraco, T., 1982. Aspects of risk-aversion in foraging white-crowned sparrows. *Animal Behaviour* 30(3), 719–727.
- Caraco, T., Blanckenhorn, W.U., Gregory, G.M., Newman, J.A., Recer, G.M., Zwicker, S.M., 1990. Risk-sensitivity: ambient temperature affects foraging choice. *Animal Behaviour* 39(2), 338–345.
- Caraco, T., Martindale, S., Whittam, T.S., 1980. An empirical demonstration of risk-sensitive foraging preferences. *Animal Behaviour* 28(3), 820–830.
- Carazo, P., Font, E., Forteza-Behrendt, E., Desfilis, E., 2009. Quantity discrimination in *Tenebrio molitor*: evidence of numerosity discrimination in an invertebrate? *Animal Cognition* 12, 463–470.
- Castro, L., Wasserman, E.A., 2010. Animal learning. *Wiley Interdisciplinary Reviews: Cognitive Science* 1(1), 89–98.

- Clark, J.S. Gelfand, A.E., 2006. Hierarchical modelling for the environmental sciences: statistical methods and applications. Oxford University Press.
- Davis, H., 1984. Discrimination of the number three by a raccoon (*Procyon lotor*). *Animal Learning & Behavior* 12(4), 409–413.
- Davis, H., Memmott, J., 1982. Counting Behavior in Animals: A Critical Evaluation. *Psychological Bulletin* 92(3), 547–570.
- Duchesne, T., Fortin, D., Courbin, N., 2010. Mixed conditional logistic regression for habitat selection studies. *Journal of Animal Ecology* 79(3), 548–555.
- Emmerton, J., 1998. Numerosity differences and effects of stimulus density on pigeons' discrimination performance. *Animal Learning & Behavior* 26, 243–256.
- Farnsworth, G.L., Smolinski, J.L., 2006. Numerical discrimination by wild Northern Mockingbirds. *The Condor* 108(4), 953–957.
- Foley, B.R., Marjoram, P., 2017. Sure enough: efficient Bayesian learning and choice. *Animal Cognition* 20(5), 867–880.
- Foley, C.A., 2002. The effects of poaching on elephant social systems. Princeton University.
- Fornacon-Wood, I., Mistry, H., Johnson-Hart, C., Faivre-Finn, C., O'Connor, J.P.B., Price, G.J., 2022. Understanding the Differences Between Bayesian and Frequentist Statistics. *International Journal of Radiation Oncology, Biology, Physics* 112(5), 1076–1082.
- Gallistel, C.R., 1989. Animal Cognition: The Representation of Space, Time and Number. *Annual Review of Psychology* 40(1), 155–189.
- Gallistel, C.R., Gelman, R., 1992. Preverbal and verbal counting and computation. *Cognition* 44(1-2), 43–74.
- Garland, A., Low, J., Burns, K.C., 2012. Large quantity discrimination by North Island robins (*Petroica longipes*). *Animal Cognition* 15, 1129–1140.
- Gatto, E., Lucon-Xiccato, T., Savaşçıl, B.B., Dadda, M., Bisazza, A., 2017. Experimental setting affects the performance of guppies in a numerical discrimination task. *Animal Cognition* 20, 187–198.
- Gazzola, A., Vallortigara, G., Pellitteri-Rosa, D., 2018. Continuous and discrete quantity discrimination in tortoises. *Biology Letters* 14(12), 20180649.
- Greene, W.H., 1990. *Econometric Analysis*. MacMillan Publishing Company, New York.
- Gross, H.J., Pahl, M., Si, A., Zhu, H., Tautz, J., Zhang, S., 2009. Number-Based Visual Generalisation in the Honeybee. *PLoS One* 4(1), e4263.
- Hanus, D., Call, J., 2007. Discrete quantity judgments in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*): The effect of presenting whole sets versus item-by-item. *Journal of Comparative Psychology* 121(3), 241–249.
- Hart, B.L., Hart, L.A., Pinter-Wollman, N., 2008. Large brains and cognition: Where do elephants fit in? *Neuroscience & Biobehavioral Reviews* 32(1), 86–98.
- Hauser, M.D., Carey, S., Hauser, L.B., 2000. Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267(1445), 829–833.

- Heffner, R.S., Heffner, H.E., 1982. Hearing in the elephant (*Elephas maximus*): absolute sensitivity, frequency discrimination, and sound localization. *Journal of comparative and physiological psychology* 96(6), 926.
- Herculano-Houzel, S., 2016. The human advantage: a new understanding of how our brain became remarkable. MIT Press.
- Hirt, E.R., Clarkson, J.J., Jia, L., 2016. Self-regulation and ego control. Academic Press.
- Hobbs, N.T., Hooten, M., 2015. Bayesian Models: A Statistical Primer for Ecologists. Princeton University Press.
- Hunt, S., Low, J., Burns, K.C., 2008. Adaptive numerical competency in a food-hoarding songbird. *Proceedings of the Royal Society B: Biological Sciences* 275(1649), 2373–2379.
- Irie, N., Hasegawa, T., 2012. Summation by Asian Elephants (*Elephas maximus*). *Behavioral Sciences* 2(2), 50–56.
- Irie, N., Hiraiwa-Hasegawa, M., Kutsukake, N., 2019. Unique numerical competence of Asian elephants on the relative numerosity judgment task. *Journal of Ethology* 37, 111–115.
- Irie-Sugimoto, N., Kobayashi, T., Sato, T., Hasegawa, T., 2009. Relative quantity judgment by Asian elephants (*Elephas maximus*). *Animal Cognition* 12, 193–199.
- IUCN, 2023. The IUCN Red List of Threatened Species. Version 2023-1. <https://www.iucnredlist.org>.
- Jacobson, S.L., Plotnik, J.M., 2020. The importance of sensory perception in an elephant's cognitive world. *Comparative Cognition & Behavior Reviews* 15, 131–148.
- Johnson, A.A., Ott, M.Q., Dogucu, M., 2022. Bayes Rules! An Introduction to Applied Bayesian Modeling. Chapman and Hall/CRC, New York.
- Kruschke, J.K., 2015. Doing Bayesian data analysis: A tutorial with R, JAGS, and Stan. Academic Press, Second Edition.
- Kruschke, J.K., 2018. Rejecting or Accepting Parameter Values in Bayesian Estimation. *Advances in Methods and Practices in Psychological Science* 1(2), 270–280.
- Kruschke, J.K., Liddell, T.M., 2018a. Bayesian data analysis for newcomers. *Psychonomic bulletin & review* 25(1), 155–177.
- Kruschke, J.K., Liddell, T.M., 2018b. The Bayesian New Statistics: Hypothesis testing, estimation, meta-analysis, and power analysis from a Bayesian perspective. *Psychonomic bulletin & review* 25, 178–206.
- Lamb, O., Shore, M., Lees, J., Lee, S., 2020. Monitoring African Bush Elephants with the OSOP Raspberry Shake and Boom, EGU General Assembly 2020, Online, 4–8 May 2020, EGU2020-1503.
- Mandler, G., Shebo, B.J., 1982. Subitizing: An Analysis of Its Component Processes. *Journal of Experimental Psychology: General* 111(1), 1.
- McArthur, C., Finnerty, P.B., Schmitt, M.H., Shuttleworth, A., Shrader, A.M., 2019. Plant volatiles are a salient cue for foraging mammals: elephants target preferred plants despite background plant odour. *Animal Behaviour* 155, 199–216.
- McComb, K., Moss, C., Sayialel, S., Baker, L., 2000. Unusually extensive networks of vocal recognition in African elephants. *Animal Behaviour* 59(6), 1103–1109.

- McComb, K., Reby, D., Baker, L., Moss, C., Sayialel, S., 2003. Long-distance communication of acoustic cues to social identity in African elephants. *Animal Behaviour* 65(2), 317–329.
- McFadden, D.L., 1974. Conditional logit analysis of qualitative choice behavior. In: *Frontiers in Econometrics*, ed. P. Zarembka. New York: Academic Press, 105–142.
- McFarland, D.J., 1977. Decision making in animals. *Nature* 269(5623), 15–21.
- McNamara, J.M., Green, R.F., Olsson, O., 2006. Bayes' theorem and its applications in animal behaviour. *Oikos* 112(2), 243–251.
- Mechner, F., 1958. Probability relations within response sequences under ratio reinforcement. *Journal of the Experimental Analysis of Behavior* 1(2), 109.
- Meck, W.H., Church, R.M., 1983. A mode control model of counting and timing processes. *Journal of experimental psychology: animal behavior processes* 9(3), 320.
- Miller, A.K., Hensman, M.C., Hensman, S., Schultz, K., Reid, P., Shore, M., Brown, J., Furton, K.G., Lee, S., 2015. African elephants (*Loxodonta africana*) can detect TNT using olfaction: Implications for biosensor application. *Applied Animal Behaviour Science* 171, 177–183.
- Nevo, O., Schmitt, M.H., Ayasse, M., Valenta, K., 2020. Sweet tooth: Elephants detect fruit sugar levels based on scent alone. *Ecology and Evolution* 10(20), 11399–11407.
- Niimura, Y., Matsui, A., Touhara, K., 2014. Extreme expansion of the olfactory receptor gene repertoire in African elephants and evolutionary dynamics of orthologous gene groups in 13 placental mammals. *Genome Research* 24(9), 1485–1496.
- Niimura, Y., Nei, M., 2003. Evolution of olfactory receptor genes in the human genome. *Proceedings of the National Academy of Sciences* 100(21), 12235–12240.
- Panagiotopoulou, O., Pataky, T.C., Day, M., Hensman, M.C., Hensman, S., Hutchinson, J.R., Clemente, C.J., 2016. Foot pressure distributions during walking in African elephants (*Loxodonta africana*). *Royal Society Open Science* 3(10), 160203.
- Panteleeva, S., Reznikova, Z., Vygonyailova, O., 2013. Quantity judgments in the context of risk/reward decision making in striped field mice: first “count,” then hunt. *Frontiers in Psychology* 4, 53.
- Perdue, B.M., Talbot, C.F., Stone, A.M., Beran, M.J., 2012. Putting the elephant back in the herd: elephant relative quantity judgments match those of other species. *Animal Cognition* 15, 955–961.
- Pisa, P.E., Agrillo, C., 2009. Quantity discrimination in felines: a preliminary investigation of the domestic cat (*Felis silvestris catus*). *Journal of Ethology* 27, 289–293.
- Plotnik, J.M., Brubaker, D.L., Dale, R., Tiller, L.N., Mumby, H.S., Clayton, N.S., 2019. Elephants have a nose for quantity. *Proceedings of the National Academy of Sciences* 116(25), 12566–12571.
- Plotnik, J.M., Shaw, R.C., Brubaker, D.L., Tiller, L.N., Clayton, N.S., 2014. Thinking with their trunks: elephants use smell but not sound to locate food and exclude nonrewarding alternatives. *Animal Behaviour* 88, 91–98.

- Pyke, G., 1984. Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology, Evolution and Systematic* 15(1), 523–575.
- Range, F., Jenikejew, J., Schröder, I., Virányi, Z., 2014. Difference in quantity discrimination in dogs and wolves. *Frontiers in Psychology* 5, 1299.
- Rescorla, R.A., 1988. Behavioral Studies of Pavlovian Conditioning. *Annual Review of Neuroscience* 11(1), 329–352.
- Ross, D., 2014. *Philosophy of economics*. Palgrave Philosophy Today. Palgrave Macmillan, London.
- Royle, J.A., Dorazio, R.M., 2008. *Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations, Metapopulations and Communities*. Elsevier.
- Royle, J.A., Nichols, J.D., Karanth, K.U., Gopalaswamy, A.M., 2009. A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology* 46(1), 118–127.
- Rugani, R., Vallortigara, G., Regolin, L., 2013. Numerical Abstraction in Young Domestic Chicks (*Gallus gallus*). *PLoS One* 8(6), e65262.
- Schmitt, M.H., Shuttleworth, A., Ward, D., Shrader, A.M., 2018. African elephants use plant odours to make foraging decisions across multiple spatial scales. *Animal Behaviour* 141, 17–27.
- Schmitt, V., Fischer, J., 2011. Representational format determines numerical competence in monkeys. *Nature Communications* 2(1), 257.
- Schofield, M.R., Barker, R.J., 2014. Hierarchical Modeling of Abundance in Closed Population Capture–Recapture Models Under Heterogeneity. *Environmental and Ecological Statistics* 21, 435–451.
- Shettleworth, S.J., 2001. Animal cognition and animal behaviour. *Animal Behaviour* 61(2), 277–286.
- Shettleworth, S.J., Hampton, R.R., 1998. Adaptive specializations of spatial cognition in food-storing birds? Approaches to testing a comparative hypothesis. In: *Animal Cognition in Nature*. Academic Press, 65–98.
- Shyan-Norwalt, M.R., Peterson, J., Milankow King, B., Staggs, T.E., Dale, R.H.I., 2010. Initial findings on visual acuity thresholds in an African elephant (*Loxodonta africana*). *Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association* 29(1), 30–35.
- Smet, A.F., Byrne, R.W., 2013. African Elephants Can Use Human Pointing Cues to Find Hidden Food. *Current Biology* 23(20), 2033–2037.
- Snow, W.M., Stoesz, B.M., Anderson, J.E., 2014. The cerebellum in emotional processing: evidence from human and non-human animals. *AIMS Neuroscience* 1(1), 96–119.
- Snyder, R.J., Barrett, L.P., Emory, R.A., Perdue, B.M., 2021. Performance of Asian elephants (*Elephas maximus*) on a quantity discrimination task is similar to that of African savanna elephants (*Loxodonta africana*). *Animal Cognition* 24(5), 1121–1131.
- StataCorp, 2023. *Stata 18 Bayesian Analysis Reference Manual*. College Station, TX: Stata Press.
- Sulkowski, G., Hauser, M.D., 2001. Can rhesus monkeys spontaneously subtract? *Cognition* 79(3), 239–262.

- Sutton, R.S., Barto, A., 2020. Reinforcement learning: an introduction, Second edition. ed, Adaptive computation and machine learning. The MIT Press, Cambridge, Massachusetts London, England.
- Thorndike, E.L., 1911. Mental fatigue. *Journal of Educational Psychology* 2(2), 61.
- Tomonaga, M., 2008. Relative numerosity discrimination by chimpanzees (*Pan troglodytes*): evidence for approximate numerical representations. *Animal Cognition* 11, 43–57.
- Tornick, J.K., Callahan, E.S., Gibson, B.M., 2015. An investigation of quantity discrimination in Clark's nutcrackers (*Nucifraga columbiana*). *Journal of Comparative Psychology* 129(1), 17–25.
- Uller, C., Lewis, J., 2009. Horses (*Equus caballus*) select the greater of two quantities in small numerical contrasts. *Animal Cognition* 12, 733–738.
- Ullrey, D.E., Crissey, S.D., Hintz, H.F., 1997. Elephants: nutrition and dietary husbandry. In: Allen M, Edwards M, Roocroft A, eds. Nutrition Advisory Group. Silver Spring: Association of Zoos and Aquariums (AZA), 1–20.
- Utrata, E., Virányi, Z., Range, F., 2012. Quantity Discrimination in Wolves (*Canis lupus*). *Frontiers in Psychology* 3, 505.
- Valone, T.J., 2006. Are animals capable of Bayesian updating? An empirical review. *Oikos* 112(2), 252–259.
- Valone, T.J., Brown, J.S., 1989. Measuring Patch Assessment Abilities of Desert Granivores. *Ecology* 70(6), 1800–1810.
- Van Gils, J.A., Schenk, I.W., Bos, O., Piersma, T., 2003. Incompletely Informed Shorebirds That Face a Digestive Constraint Maximize Net Energy Gain When Exploiting Patches. *The American Naturalist* 161(5), 777–793.
- von Dürckheim, K.E.M., Hoffman, L.C., Leslie, A., Hensman, M.C., Hensman, S., Schultz, K., Lee, S., 2018. African elephants (*Loxodonta africana*) display remarkable olfactory acuity in human scent matching to sample performance. *Applied Animal Behaviour Science* 200, 123–129.
- Ward, C., Smuts, B.B., 2007. Quantity-based judgments in the domestic dog (*Canis lupus familiaris*). *Animal Cognition* 10, 71–80.
- Webb, J.A., Stewardson, M.J., Koster, W.M., 2010. Detecting Ecological Responses to Flow Variation Using Bayesian Hierarchical Models. *Freshwater Biology* 55(1), 108–126.
- Wikle, C.K., 2003. Hierarchical Bayesian Models for Predicting the Spread of Ecological Processes. *Ecology* 84(6), 1382–1394.
- Williams, R., 2018. Marginal Effects for Continuous Variables. University of Notre Dame.
- Winkler, R.L., 2003. An Introduction to Bayesian Inference and Decision, Second Edition. ed. Probabilistic Publishing: Gainesville, FL.
- Wood, M., Chamaillé-Jammes, S., Hammerbacher, A., Shrader, A.M., 2022. African elephants can detect water from natural and artificial sources via olfactory cues. *Animal Cognition* 25(1), 53–61.
- Yokoyama, S., Takenaka, N., Agnew, D.W., Shoshani, J., 2005. Elephants and Human Color-Blind Deuteranopes Have Identical Sets of Visual Pigments. *Genetics* 170(1), 335–344.

CHAPTER 2: Fruit Preference of Six Semi-Tame African Elephants

Introduction

Understanding animal cognition and choice behaviour is a fundamental goal in many fields of biology and ecology. Because many of the concepts underlying behaviour and cognition are not directly observable, formal theoretical modelling and consistent statistical modelling are required.

In ecology, data are often collected at the level of the individual to estimate the effect of variables that act at the population level (e.g. Mariotti et al., 2020). Reliable inferences at the level of the individual are equally important in modelling processes thought to be regulating populations at broader spatial and temporal scales. In ecology, the discussion of this issue has focussed on the potential importance of more reliable ways of modelling the sources of idiosyncratic variability (Clark, 2003). Accounting for individual variability, whether through observable covariates or statistical residuals, is vital for accurate inference, prediction, and normative evaluation.

The need for reliable and robust inference at both the individual and the population level can be fulfilled by Bayesian Hierarchical Models (BHM). BHM use hierarchical priors based on pooled behaviour over all the observations collected from many individuals to make informed inferences about the cognitive processes generating the observed behaviour of *individual* animals. As an additional advantage, these models allow us to make robust inferences about individual animals without the need for extensive individual observations.

It is intuitive to think of data from sampled individuals changing beliefs about (the parameters of) statistically latent processes regulating variables affecting the

population, such as abundance, fecundity, mortality, and between-species competition. In microeconomics the opposite happens: theoretical models of processes operate at the scale of the individual, reflecting the interactions of that individual's inferentially constructed preferences and beliefs, leading to an observed choice by that individual. Hence, most of the hierarchical models in economics have focused on using information from groups of individuals to inform inferences about specific individuals, crucial for the identification and estimation of individual-level parameters of models of choice patterns.

Most of the applications of hierarchical models in ecology have used Bayesian approaches (Wikle, 2003; Royle et al, 2009; Webb et al., 2010; Schofield and Barker, 2014). Bayesian statistical methods have also been applied across a variety of different fields, such as marketing (Rossi et al., 2005), cognitive psychology (Lee and Wagenmakers, 2013), economics (Gao et al., 2023), cognitive science (Ma et al., 2023), and in the design of clinical trials (Berry et al., 2010).

A key feature of many hierarchical models in ecology is a clear distinction between two phases of data collection, leading to an observation model that accounts for possible measurement errors, and a sampling model that accounts for possible effects of the procedures used to observe the data (Hobbs and Hooten, 2015; Kéry and Royle, 2016, 2021). On top of these models, hierarchical models add a latent ecological process model.

This chapter illustrates the use of the BHM in a case study of six semi-tame African elephants (*Loxodonta africana*), evaluating their individual preferences for various fruits that we considered as potential rewards for a broader project that aims to elicitate the elephant risk preferences over reward lotteries that are not stochastically-

dominated. Inferences about risk preferences in the final phase will be conditional on our beliefs about the ability of each elephant to discriminate reward quantities *and* probability levels.

In determining what would be a good reward to motivate our elephants in the quantity discrimination tasks necessary to elicit the risk preferences of elephants, it was decided to use fruit. Previous studies of quantity discrimination, food location ability, and food preference of elephants used different types of food as rewards. For example, for Asian elephants (*Elephas maximus*), past studies have used different numbers of pieces of each elephant's previously determined favourite fruit (i.e. orange, apple, and cucumber respectively) (Irie and Hasegawa, 2012), or pieces of fruit not usually present in the diet of the elephants (i.e. melons, watermelons, bananas, and apples) (Irie-Sugimoto et al., 2009), parts of plants such as sugar cane (Irie-Sugimoto et al., 2009), sunflower seeds alone or in combination with pineapple (Plotnik et al., 2013, 2014, 2019), and even commercial biscuits for mammalian herbivores (Snyder et al., 2021). For African elephants, past experiments have used marula fruits at varying stages of ripeness (Nevo et al., 2020), different numbers of pieces of vegetables (i.e. carrots and rutabaga) (Perdue et al., 2012), or branches from different species of tree (Schmitt et al., 2018).

Fruits have the advantages of being a font of micro and macronutrients that are known to be liked by elephants (Nevo et al., 2020), have been used in similar studies, are not difficult to purchase, transport, or store, and are easy to cut into small pieces of comparable size. Finally, lots and lots of pieces of fruit would be needed to satiate an elephant.

Although many studies have focused on elephant diet selection (Owen-Smith and Chafota, 2012; Pretorius et al., 2012; Berliani et al., 2018), seed dispersion of different species of plants (Dudley, 1999; Gonthier, 2009), the distance at which elephants can disperse a seed (Sekar and Sukumar, 2015), and the necessity of elephant dispersion for some plants to survive (Babweteera et al., 2007), no study has investigated which fruits African elephants might prefer in a comparative study. It was known from previous studies that these elephants liked marulas, used in a previous experiment (Nevo et al., 2020), and oranges, which they had often received as a reward in training (S. Hensman pers. comm.).

Elephants are known to base foraging choices on their olfaction (Plotnik et al., 2014; Schmitt et al., 2018). Two studies conducted with our study elephants showed that they were able, by using smell cues only, to distinguish their preferred plants from their less preferred ones at different spatial scales (Schmitt et al., 2018) and to discriminate between marula fruits at different stages of maturation (Nevo et al., 2020). Therefore, the test fruits here used were presented as binary options in such a way that the elephant could smell but not see them, under two perforated buckets. A similar procedure has been used by Plotnik et al. (2019) in a quantity discrimination test with Asian elephants. This methodology had the advantage of placing a physical barrier between the alternatives and the choosing elephant, which prevented them from seeing as well as stealing unchosen fruits.

As a case study, our application introduces several essential features of our overall project. First, we must be able to generate inferences at the level of the choices of each individual elephant. These inferences take the form of our posterior beliefs, which can then be used as (predictive) priors for later stages of the overall project.

Second, those inferences must be about unobserved parameters of a theoretical model of the cognitive process. In our case, the unobserved parameters are the inferentially constructed preferences of each elephant for each fruit, from a model that assumes that the elephant maximizes the utility to the elephant of each fruit on offer when making a choice. Third, the inferences for each individual elephant must be conceptually and statistically consistent with any inferences drawn about the herd as a whole. The use of hierarchical priors for each individual elephant, based on pooled behaviour over all elephants, does all of this naturally when applied in a BHM.

This case study demonstrates that the use of Bayesian Hierarchical Models coupled with controlled experimental choice data, can provide rich insights into animal cognition processes and behaviour, particularly when focusing on the level of the individual animal.

Methods

Data collection

All six elephants presented in the General Methodology section of Chapter 1 took part in this experiment. To assess the rank preference of each elephant for different fruit types, a series of balanced binary choices between each possible combination of pairs of six different fruit types was presented to each individual. The two young elephants, born in the reserve, had never tasted these fruit types before, and the adults had rarely consumed them during the 15 years they had been under the care of humans (S. Hensman pers. comm.). The selected fruits were mango (family Anacardiaceae), banana (family Musaceae), melon (family Cucurbitaceae), apple, nectarine, and pear (family Rosacea).

First, for 6 days, each elephant was fed some pieces of each fruit, one type per day, to make them accustomed to taste and palatability. In order, they were fed pear, banana, nectarine, melon, apple, and mango. After these six days, each elephant was presented with binary choices between 50 g of each fruit, which included all possible binary combinations of fruits, and the option of each fruit vs nothing to verify that they could smell the presence of the fruit. In total, each elephant was presented with 21 different combinations of the alternatives, also known, following choice theory in economics, as prospects. A list of the prospects used is given in Table 2.1.

Table 2.1: The 21 combinations of fruits offered to each elephant in the “fruit preference experiment”. Each prospect was proposed to each elephant four times with each fruit being the left and the right alternative twice.

Prospects		
apple-banana	apple-mango	apple-melon
apple-nectarine	apple-none	apple-pear
banana-none	banana-mango	banana-melon
banana-nectarine	banana-pear	mango-melon
mango-nectarine	mango-none	mango-pear
melon-nectarine	melon-none	melon-pear
nectarine-none	nectarine-pear	pear-none

The materials used in this experiment were a canvas mat, two small white plastic buckets in which 60 holes with a 1 cm diameter had been drilled, both on the side and the bottom, and two plastic lids on top of which the inverted buckets were located. The two buckets were located at a distance of four metres from the mat, and 50 cm from

each other. The perforated buckets were hand-washed with dish soap before each daily session to remove the smell of the fruits used in the previous session.

The researcher and one handler each kept one foot on the top of one of the buckets to prevent the elephants from obtaining the reward before they smelled both alternatives and chose one (Figure 2.1). The elephant started the exercise by standing stationary on the mat. When the elephant was released with the command “Walk up and smell”, he or she approached the alternatives, smelled both of them by placing the trunk on the buckets alternatively, and indicated a choice by touching the preferred bucket with the trunk. The elephant received and consumed the content of the chosen bucket whilst the other bucket and its content were removed. One trial per elephant per day was conducted between March and May 2021 and between January and March 2023.

In 2022 it was decided to add a head-to-head comparison between preferences over oranges and apples. The elephants had been accustomed to oranges for a long time, and oranges were going to be used as a reward in future experiments with these elephants. Apple was the fruit type that was the most favoured in the fruit comparison experiment at that time, based on inspection of the raw data. The aim was to evaluate if oranges would be better, in terms of being even more popular, than the most favoured fruit from the fruit comparison experiment at that point. This additional comparison also makes the results of more general use to other researchers contemplating fruits that might be used as rewards. The methodology used was the same as that described above, except that only the adult elephants participated and half a fruit was used as the reward instead of 50 g. The data for the head-to-head experiment were collected between February and April 2022.



Figure 2.1: An overview of the “fruit preference experiment”. a) The elephant (Chova) faces the two alternatives from the starting position, before approaching them; b) A view of one of the alternatives from the top; c) A view of the alternative when Chova smells it and the researcher keeps a foot on top of it.

Data analysis

To determine how each fruit was ranked, both individually by each elephant and jointly by all the elephants, the McFadden (1974) Conditional Logit (CL) model was estimated in the form of a BHM. This model evaluates the likelihood of the observed choices of pairwise combinations of some categorical dependent variable with more than two categories, here six different types of fruit. The model estimates the choice probabilities that best explain the observed choices. Applications of the CL model to

choices by animals include mammal habitat selection changes as the availability of resources varies (Duchesne et al., 2010).

The CL model was selected because it estimates what economists refer to as the “random utility” values of each choice alternative. “Utility” here is simply a modelling concept that is consistent with observed choices. These random utilities are used to determine the probabilities of choice of one fruit or another, in a manner explained below. These utilities are referred to as “random” because they reflect the imprecision of the observer’s inferences about the value of the fruit to each elephant, not because the elephant is assumed to choose the fruits randomly.

Once these random utilities are estimated, the model predicts the probability of choice from a specific reward pairing. The likelihood of the model takes into account the stratification of the data by evaluating the conditional likelihood, specifically conditioning on the number of cases in each stratum, to return the probability of each fruit to be chosen. In this experiment, the strata were represented by the 21 binary combinations of fruits offered to the elephants.

Bayesian analysis combines probability distributions of the priors over CL model parameters, and the probability distributions of the likelihood of the observed data for different values of those parameters, to estimate posterior probability distributions over the parameters. The BHM accounts for data containing repeated observations over a group, in our case the six elephants.

The BHM uses a diffuse prior to calculate a pooled posterior distribution for the joint choices of all elephants. The expression “joint choices” here refers simply to the combination of all choices across the individual elephants and does not imply a herd

choice, which would be the case if the herd had made choices together. The use of a diffuse prior indicates that there is no particular expectation about how the elephants as a group will choose. The model then uses the *pooled posterior* distribution for the group as the *informative prior* for the CL coefficients for the preference of *each individual elephant in the group*.

When compared to inferences for an individual elephant that only use the data from that elephant and diffuse priors, this hierarchical prior allows more informed and robust inferences about fruit choice probabilities at the level of the individual. It relies on the prior that the elephants are somewhat similar to each other when it comes to fruit preferences, even if there is individual variation. Thus, while we only have 4 observations on each of the 21 binary combinations for each elephant, at the group level we have 24 observations. Allowing this larger sample to influence the choice probabilities of the smaller individual samples provides more precise and reliable estimates for each individual elephant.

The data were analysed using Stata 18, documented in StataCorp (2023). The simulations to approximate the posterior distribution of the BHM consisted of 500,000 Markov Chain Monte Carlo (MCMC) samples, in addition to 250,000 burn-in samples, over 5 chains. The response variable was the event of a specific fruit being chosen by the elephant in any given trial: 0 for the specific fruit not chosen, or 1 for the specific fruit chosen.

More formally, each elephant was assumed to make choices based on the relative utility of each food type on offer. All estimates are for the full data set, spanning all elephants and all fruit choice combinations. The general utility function, defined over

all of the elephants and all of the fruits, and capturing the utility for each elephant from each possible fruit choice, can be written as:

$$U_{i,j} = V_{i,j} + \varepsilon_{i,j} \quad (1)$$

where $i = 1, \dots, 6$ is the subscript for each elephant and $j = 1, \dots, 7$ is the subscript for each fruit, including the option of None. In this random utility specification, V is the part of the utility function we estimate, and ε is an error term. The error term is an independent type I (Gumbel-type) extreme-value random variable (Gumbel, 1958).

When $i=\text{Chova}$ and $j=\text{Apples}$, we have the following random utility function for Chova:

$$U_{\text{Chova},\text{Apples}} = V_{\text{Chova},\text{Apples}} + \varepsilon_{\text{Chova},\text{Apples}} \quad (1b)$$

The estimated part of the utility is then specified as this linear function,

$$V_{i,j} = \alpha_j + \beta_j E_i + \gamma_{i,j} E_i F_j \quad (2)$$

where E_i is a dummy variable that takes the value 1 for each elephant when the choice data comes from that elephant, and F_j is a dummy variable that takes the value 1 for each fruit when the choice data involves that fruit. For example, when we are estimating data from Chova and his apple choices we have $E_{\text{Chova}} = 1$, while all the other $E_{i \neq \text{Chova}} = 0$ and $F_{\text{Apples}} = 1$, while all the other $F_{j \neq \text{Apples}} = 0$. In this case, the estimated part of the utility for Chova and apples would be specified as:

$$V_{\text{Chova},\text{Apples}} = \alpha_{\text{Apples}} + \beta_{\text{Apples}} \times (E_{\text{Chova}}=1) + \gamma_{\text{Apples},\text{Chova}} \times (E_{\text{Chova}}=1) \times (F_{\text{Apples}}=1) \quad (2b)$$

where α , β and γ are coefficients to be estimated from the observed choice data of Chova. In the language of these CL models, the “attribute” is the *kind* of fruit that was offered for choice. The coefficient α is a constant term for apples, the coefficient β is a parameter that varies with the fruit, and γ is a parameter that varies with the interaction

of the elephant and the fruit. The parameter β has the Chova dummy as a covariate, but refers to the fruit, which is apple in this case.

For this model, it is only relative utility that matters when an elephant is evaluating two fruits on offer. So the utility of one fruit must be normalised to be some constant, normally 0 or 1, to identify the utility values of all other fruits. The option None, representing an alternative containing no fruits, was naturally normalised to have utility set to 0. This normalisation choice affects the level of the utility values estimated, but it does not affect the inferred probabilities of choice. By normalising the option with the smallest utility to have utility 0, the utility values of the other fruits will all be positive and easy to visualise in a display.

Once the utility U is estimated for each elephant and fruit attribute, the probability of each fruit being chosen can be evaluated. For example, the probability of Chova picking apples over mangos is

$$\Pr_{\text{Chova, Apples} > \text{Mangos}} = \Pr(U_{\text{Chova, Apples}} > U_{\text{Chova, Mangos}}) \quad (3)$$

where $>$ in the subscript of the left-hand expression indicates a preference for apples over mangos, while $>$ in the right-hand expression indicates a higher utility value for apples than for mangos. To obtain an estimate of Chova's probability of choosing apples over other fruits, equation (3) can be expanded to consider the choices by Chova of all of the combinations of apples and other fruits.

Results

Illustrative Results

To interpret the estimated model we first illustrate by discussing the results for Chova. The estimated distributions of utilities for Chova for the six fruits are shown in Figure 2.2. They are distributions because utilities are random, and we are using Bayesian methods.

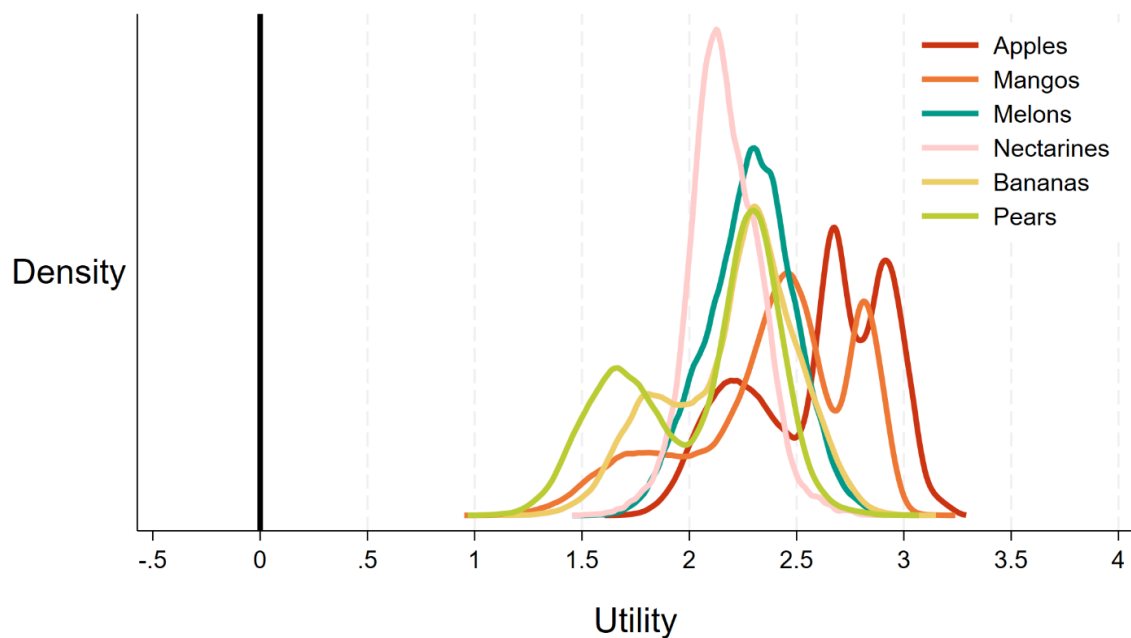


Figure 2.2: The utilities of Chova for different fruits, estimated from a Conditional Logit BHM from choices in the experiment. The black vertical line represents the utility zero assigned to the utility of option None.

Some utility distributions are narrower, showing less estimation uncertainty than others, such as nectarines and melons. Others are wider, showing greater estimation uncertainty, such as mangos. The plot shows that each of the fruits had a higher utility than option None, which is normalised to utility 0. This shows that Chova was indeed able to smell the presence of some desirable fruit in our bucket setup. Apples appear to have the highest utility, closely followed by mangos, and pears and bananas appear to

have the lowest utilities. There is a great deal of overlap in the utility distributions for all fruits.

To better visualise the relationship between the utility of a pair of fruits it is possible to show separate graphs, as in Figure 2.3 for apples and bananas. In the BHM implementation of the CL model, the utility values for each fruit are not independent. When the 500,000 simulations from the BHM are compared, one simulation at a time, the lower utility values for bananas tend to be compared to the lower utility values for apples, and similarly for the higher utility values. As a result, the probability of the utility for apples being greater than the utility for bananas is often larger than the overlap of utility distributions might suggest if one had assumed that the two distributions were statistically independent. Despite the considerable overlap in the two distributions in Figure 2.3, there is a probability of 0.63 that Chova prefers apples to bananas.

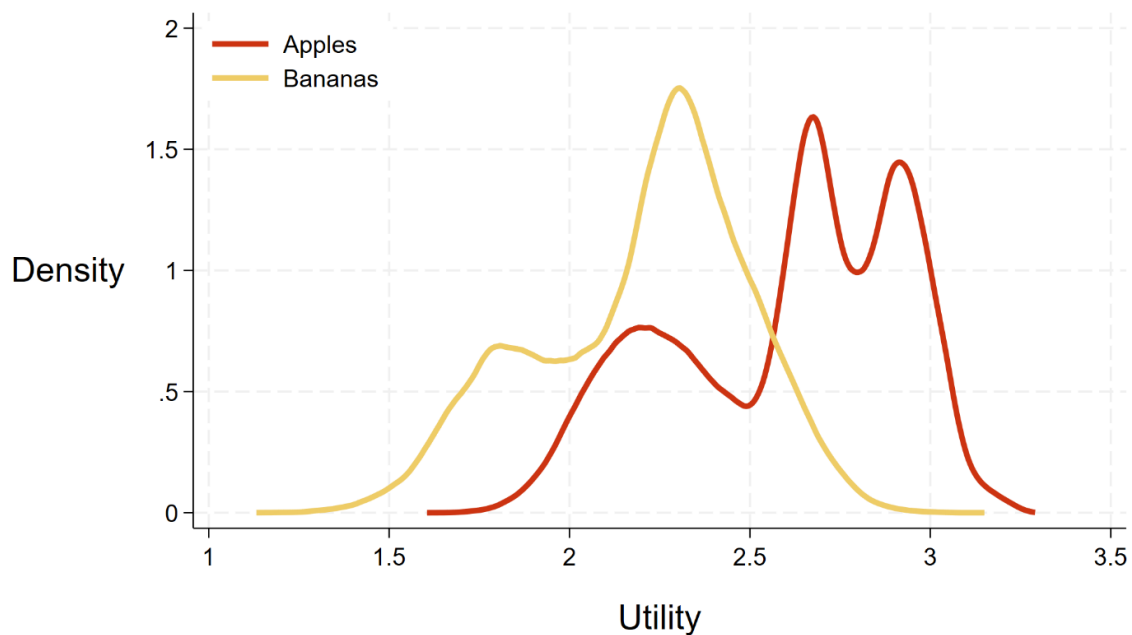


Figure 2.3: The utilities of Chova for Apples and Bananas estimated from a Conditional Logit BHM from choices in the experiment.

One of the most remarkable features of the BHM is that we are able, as just illustrated for Chova and a specific pair of fruits, to draw inferences at a granular scale without needing a large number of observations at that granularity. This is because we are using inferences from the group level data to inform inferences about the individual level data. Of course, more observations at each level will generally improve statistical inference, whether it is Bayesian or not.

We now focus on the results for choice probabilities and do so for all the elephants. These are reported as plots of the estimated average posterior probability of each fruit type being chosen by each elephant along with the 50% Highest Density Interval (HDI). The choice probabilities are inferred by the CL model from the estimated posterior distributions for random utilities. The 50% HDI represents the range of values of the probability that are more credible than not in the posterior, in the sense that the interval contains 50% of the posterior distribution and that the interval has a higher posterior density than all values outside of the interval.

When the 50% HDI of a fruit is completely above the 0.5 probability of the fruit being chosen, we infer that the weight of the evidence (“better than a 50:50 chance”) suggests that the fruit was preferred by the elephant in comparison to the alternative. Of course, symmetric inferences follow when the 50% HDI of a fruit is completely below the 0.5 probability.

To determine the probability of each elephant choosing oranges or apples in the separate, head-to-head task, a BHM with a probit likelihood was estimated, instead of the CL. The posterior distributions for this model were also obtained with 500,000 MCMC samples, with an additional 250,000 burn-in samples, all over 5 chains. The

choice of the apple in any trial was used as the response variable for the model, and the other explanatory variables used were the side where the apple was located and a binary variable to indicate the elephant making the choice.

The BHM model with the six fruits using the CL specification and the BHM model with two fruits using the probit specification reached a satisfactory degree of convergence by the usual criteria (Gao et al., 2023, Appendix B; StataCorp, 2023, p. 15-19).

Detailed Results

Choice Over Multiple Fruits

Our sample consisted of 504 observations, based on 84 choices made by each elephant, 4 of each of the 21 combinations. Rates of acceptance of each fruit, calculated as the number of times a fruit was selected over the number of times it was offered, are reported in the top part of Table 2.2. On average, apple was the most favoured fruit, with a rate of acceptance of 68%. Mango is a close second with a rate of acceptance of 65%.

Inferred choice probabilities from the BHM are shown in Figures 2.4 and 2.5. Figure 2.4 confirms that on average apples and mangos were favoured by all the elephants over the alternatives offered in the binary choice tasks, where “favoured” just means that the lower end of the HDI of the inferred choice probability is greater than 0.5. Note that even if apples are preferred to mangos on a pairwise basis, mangos may be preferred to all other fruits.

Table 2.2: The number of times each fruit was chosen by the individual elephants in the “fruit preference experiment”, and the percentage acceptance averaged over all the elephants of each fruit as the number of times the fruit was chosen divided by the number of times each fruit was present in a trial.

Chosen	Bela	Chova	Mussina	Nuanedi	Shan	Zambezi	Total	% chosen by all elephants
Apple	16	16	19	15	14	18	98	68%
Mango	15	15	17	19	16	12	94	65%
Melon	15	14	9	16	14	13	81	56%
Nectarine	13	12	14	11	12	13	75	52%
Banana	13	13	14	8	13	11	72	50%
Pear	8	12	7	9	14	14	64	44%
None	4	2	4	6	1	3	20	14%
Total	24	24	24	24	24	24	144	
Apple	-	19	15	20	12	-	66	47%
Orange	-	16	20	15	23	-	74	53%
Total	-	35	35	35	35	-	140	

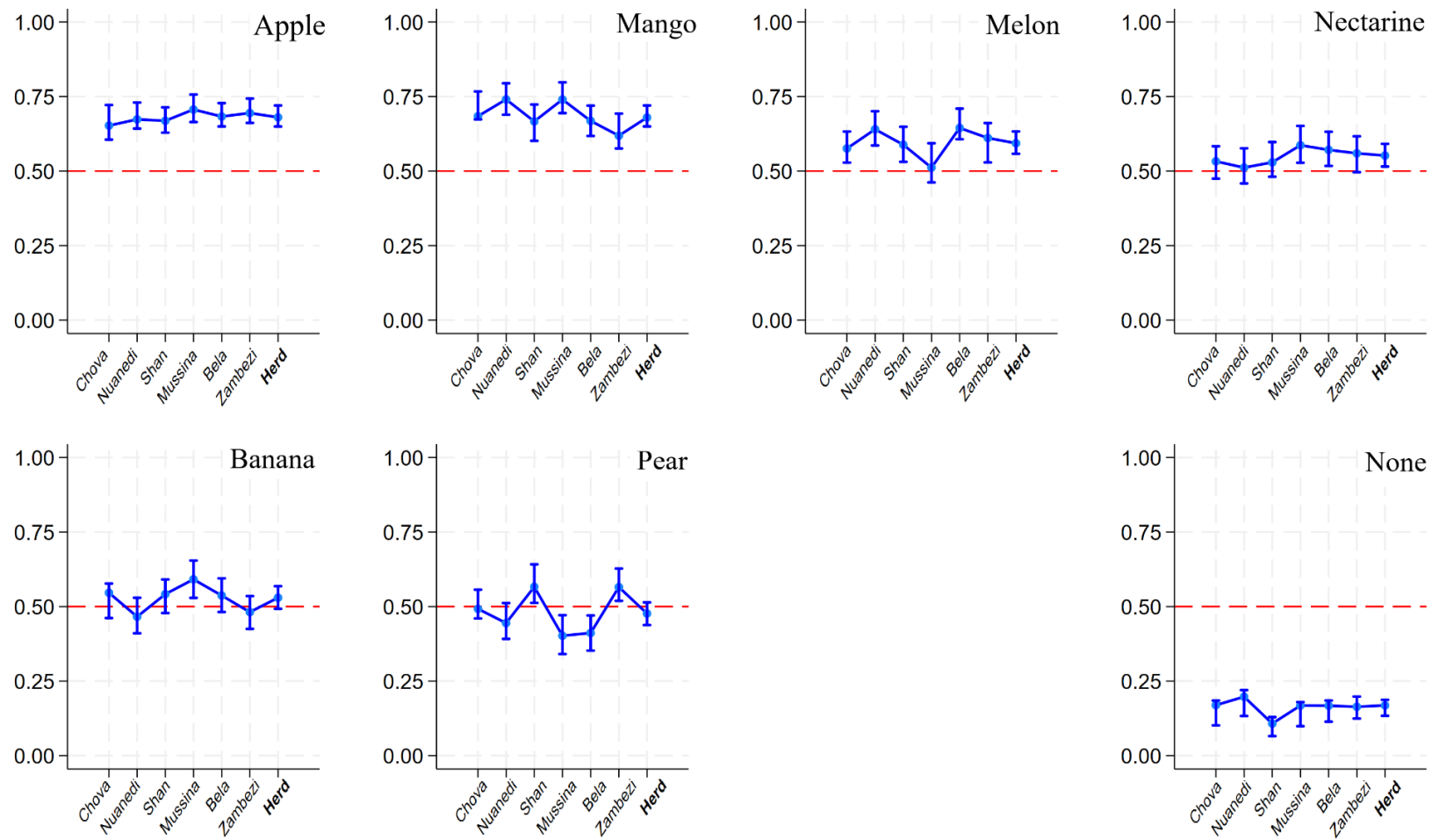


Figure 2.4: The probability of each fruit being chosen by each elephant in a binary choice task estimated from the BHM in the “fruit preference experiment”. The dashed red line shows the 50% probability for that fruit to be chosen compared to the alternatives. The vertical blue lines represent the 50% HDI.

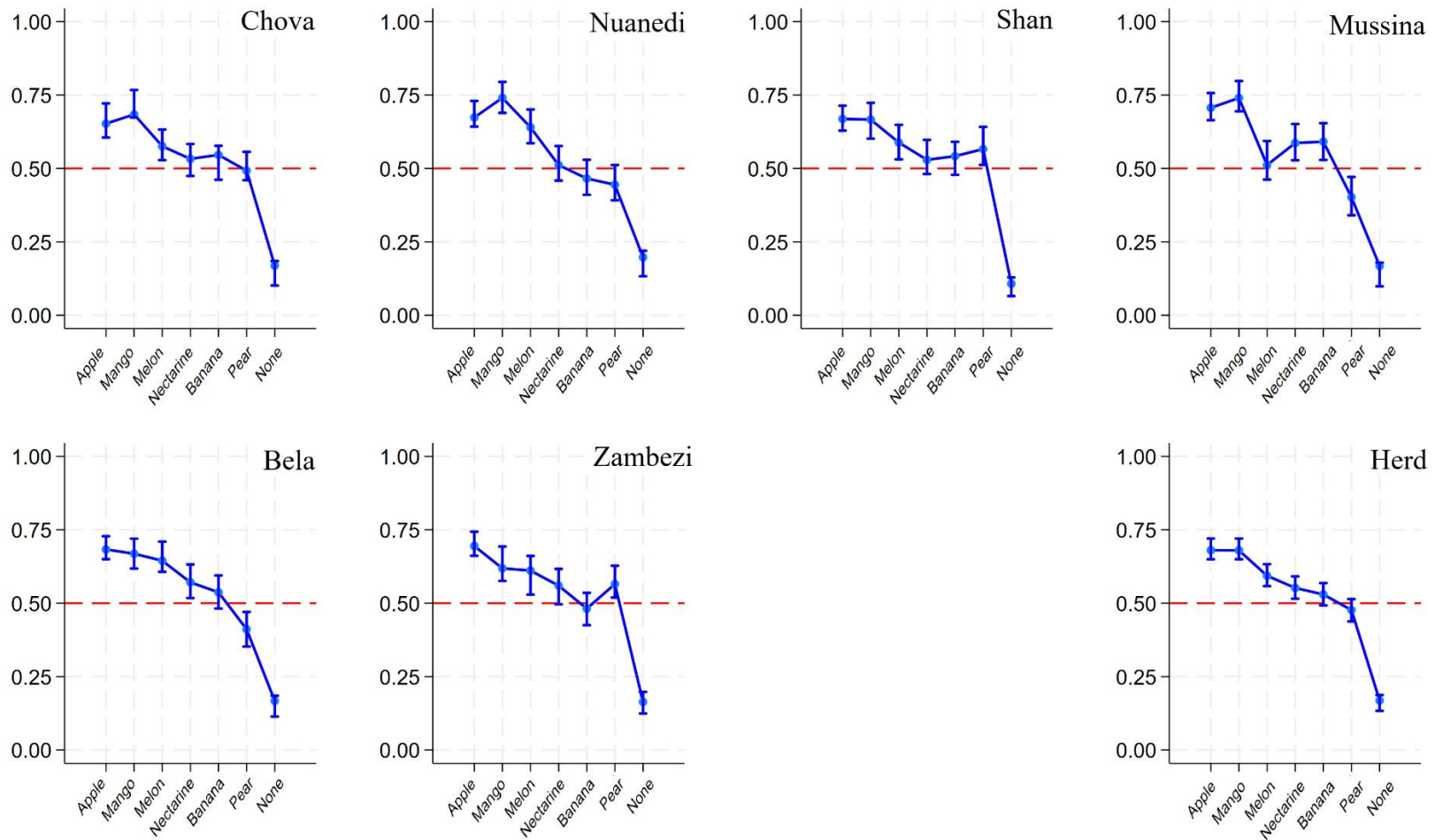


Figure 2.5: The probability of each elephant and all of the elephants choosing each fruit in a binary choice task estimated from the BHM in the “fruit preference experiment”. The dashed red line shows the 50% probability for that fruit to be chosen compared to the alternatives. The vertical blue lines represent the 50% HDI.

Melons appear also to be a popular alternative, except for Mussina. Nectarines were favoured only by Mussina and Bela, bananas were favoured only by Mussina, and pears were favoured only by Shan and Zambezi. Pears are disliked by both Mussina and Bela. Each graph also includes the pooled estimates (labelled “Herd”) that form the priors for inferences about individual elephants, and they show that pears are disliked. Finally, the option None was disliked by each elephant, providing evidence that they could smell the presence of fruits in the buckets.

Compared to each other, the elephants did not show very different patterns of preference over the various fruits, as shown in Figure 2.5. For every elephant, apples and mangos were the most favoured fruits, and None was disliked by all. There are some similarities between mothers and their calves: both Bela and Mussina favoured nectarines and disliked pears, and both Shan and Zambezi favoured pears.

Head-to-head comparison

The head-to-head comparison was conducted between apples and oranges. Each of the four adult elephants made 35 choices, for a total of 140 choices. On average there was a slight preference for oranges over apples, with choice probabilities of 53% and 47%, respectively, shown in the bottom part of Table 2.2. However, there is considerable individual variation.

Figure 2.6 shows the posterior distributions of the choice probability for apples separately for each elephant. The dashed vertical red lines again show the 0.5 probability, the choice by chance. For Chova and Nuanedi the averages of the distributions are above 0.5, indicating a slight preference for apples over oranges: the

model implies that these elephants choose apples 58% and 55% of the time, respectively. There is a 0.78 and 0.70 posterior probability that Chova and Nuanedi, respectively, chose apples more frequently than by chance, as shown in Table 2.3. Mussina and Shan, on the other hand, showed a strong preference for oranges over apples, with an average posterior probability of choosing apples only 32% and 20% of the time, respectively. The posterior probability that Mussina and Shan chose oranges more frequently than by chance is 0.96 and 1.00, respectively.

Table 2.3: The posterior estimates of the probability of choosing the apple over the orange for each elephant estimated from the BHM head-to-head test of the “fruit preference experiment”. Mean and Sd represent the mean and standard deviation of the posterior distribution, 50% HPD low and 50% high represent the thresholds of the 50% Highest Probability Density of the posterior. The last column represents the probability of the posterior probability distribution being greater than 0.50.

Subject	Mean	Sd	50% HPD low	50% HPD high	Prob > 0.50
Chova	0.58	0.10	0.51	0.65	0.78
Nuanedi	0.56	0.10	0.49	0.63	0.70
Shan	0.21	0.09	0.13	0.24	0.00
Mussina	0.32	0.10	0.24	0.37	0.04
Pooled	0.41	0.15	0.29	0.48	0.26

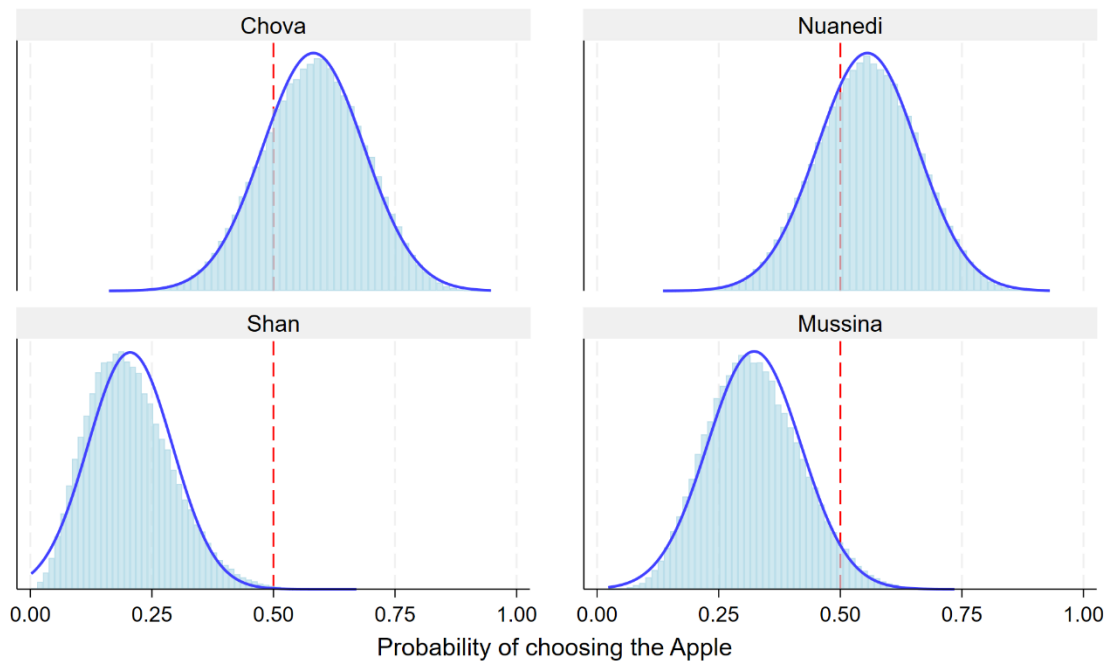


Figure 2.6: The posterior distribution of the elephant probabilities of choosing apple estimated from the BHM in the head-to-head test of the “fruit preference experiment”. The dashed red line represents the probability of choosing apple by chance.

Discussion

The fruits most favoured by the elephants were apples and mangos, and the two least favoured fruits were bananas and pears. Here “favoured” means that the inferred choice probability of each elephant choosing the fruit is greater than 0.5 with a probability greater than 0.5. Both apples and mangos were *generally* preferred over other fruits by all elephants, with melons usually preferred, nectarines generally chosen as if by chance, and bananas and pears generally not preferred. There was some heterogeneity in the strength of the preferences across individual elephants, but the major likes and dislikes were qualitatively consistent across elephants.

It is no surprise that each elephant avoided the None option, choosing it only between 1 (Shan) and 6 times (Nuanedi) out of the 24 times they encountered it.

Nuanedi has a small hole in her trunk from an old injury, which may lead to difficulty detecting the smell of fruit. This result suggests that elephants can localise the presence or absence of food solely based on its smell (or lack of it). This ability has also been shown for Asian elephants who were able to select a bucket containing hidden food via direct olfactory investigation of either a baited or empty bucket (Plotnik et al., 2014).

One specific goal of the tasks analysed here was to select the fruits most favoured on average by all the elephants, to be used as rewards for conducting further cognitive tests, such as quantity discrimination, probability discrimination, and risk preference choices, with this group of six elephants. The results show that apples and mangos represent good, high-reward candidates for each elephant, with apples being particularly suitable for year-round experiments due to their availability, unlike the seasonal mangos.

The additional comparison between apples and oranges showed a preference heterogeneity among the adult elephants, with two showing a slight preference for apples, and the other two having a strong preference for oranges. A preference for oranges might be due to their stronger smell in comparison to apples, made even more detectable by the fact that the fruits were cut in half in the supplementary task.

The results show that Bayesian methods can generate robust estimates of the fruit preferences of individual elephants, defined in terms of a consistent model of preference from economics and estimated from observed choices. What “robust” means here is that the inferences for each elephant rely on informative priors that are generated from the joint behaviour of all elephants in the sample. This approach aligns with a theoretical framework from economics characterizing preferences in terms of random

utilities, that can be displayed and evaluated directly, as illustrated in Figures 2.2 and 2.3. These utilities can then be directly used to consistently infer fruit preferences for each elephant and all possible fruit choices, as illustrated in Figures 2.4 and 2.5.

The crucial methodological insight is that these methods can generate results at the level of each elephant, and each possible fruit considered. Moreover, choice probabilities are estimated jointly for all elephants and fruits, allowing consistent inferences about individual and herd preferences. The flexibility of inferring both individual estimates and aggregate group estimates is crucial for practical applications, such as designing tasks with either elephant-specific or herd-level (simultaneous) fruit choices, while still accounting for individual preference heterogeneity for each elephant. This flexibility is central to our broader research objective of inferring risk preferences of elephants.

The approach presented here can be extended to study why and when elephants prefer some fruits over others. Although the design controlled for the presentation of fruits on the left vs the right through randomization, and it is captured in the models, there may be an interest in the evaluation of side preferences by individual elephants. Similarly, external environmental factors, such as temperature or seasonal changes, might influence preferences and could be included in the analysis. Attributes of the fruits, such as nutrient and water content, could also be evaluated. All of these types of extensions are standard with the economic model of preference used here. For the inferential goals of this Chapter, in terms of the broader research aims of the project, they were not critical. Another immediate extension of our analysis of the choices of individual elephants would be to allow the herd to make collective choices. It would then be possible to see how the herd choice trades off individual preferences,

particularly important when there are pregnant females, or very young elephants (Haynes, 1991).

Implementing these experiments with wild elephants would introduce additional hierarchical layers, to model which elephants make choices for which fruit-choice pairs, and on what days. The methodological point is that we can readily adapt the BHM to include such issues, building on existing BHM specifications from ecology (Clark and Gelfand, 2006; Clark, 2007; Royle and Dorazio, 2008; Hobbs and Hooten, 2015), and yet maintain our goal of making inferences about decision processes operating at the granular level of each elephant.

References

- Babweteera, F., Savill, P., Brown, N., 2007. *Balanites wilsoniana*: Regeneration with and without elephants. *Biological Conservation* 134(1), 40–47.
- Berliani, K., Alikodra, H.S., Masy'Ud, B., Kusriani, M.D., 2018. Food preference of Sumatran elephant (*Elephas maximus sumatranus*) to commodity crops in human-elephant conflict area of Aceh, Indonesia. In: *Journal of Physics: Conference Series* 1116(5), 052015.
- Berry, S.M., Carlin, B.P., Lee, J.J., Muller, P., 2010. *Bayesian Adaptive Methods for Clinical Trials* (New York: Routledge).
- Clark, J.S., 2003. Uncertainty and variability in demography and population growth: A hierarchical approach. *Ecology*, 84, 1370–1381.
- Clark, J.S., 2007. *Models for Ecological Data: An Introduction* (Princeton: Princeton University Press).
- Clark, J.S., Gelfand, A.E., 2006. *Hierarchical Modelling for the Environmental Sciences: Statistical Methods and Applications* (New York: Oxford University Press).
- Duchesne, T., Fortin, D., Courbin, N., 2010. Mixed Conditional Logistic Regression for Habitat Selection Studies. *Journal of Animal Ecology*, 79(3), 548–555.
- Dudley, J.P., 1999. Seed dispersal of *Acacia erioloba* by African bush elephants in Hwange National Park, Zimbabwe: Seed dispersal of *Acacia erioloba* by elephant. *African Journal of Ecology* 37(4), 375–385.
- Gao, X.S., Harrison, G.W., Tchernis, R., 2023. Behavioral Welfare Economics and Risk Preferences: A Bayesian Approach. *Experimental Economics*, 26(2), 273–303.
- Gonthier, D.J., 2009. Notes on seeds deposited in elephant dung at Tarangire National Park, Tanzania. *African Journal of Ecology* 47(2), 252–256.
- Gumbel, E.J., 1958. *Statistics of Extremes* (New York: Columbia University Press).

- Haynes, G., 1991. *Mammoths, Mastodons, and Elephants: Biology, Behavior and the Fossil Record* (New York: Cambridge University Press).
- Hobbs, N.T., Hooten, M., 2015. *Bayesian Models: A Statistical Primer for Ecologists* (Princeton: Princeton University Press).
- Irie, N., Hasegawa, T., 2012. Summation by Asian Elephants (*Elephas maximus*). *Behavioral Sciences* 2(2), 50–56.
- Irie-Sugimoto, N., Kobayashi, T., Sato, T., Hasegawa, T., 2009. Relative quantity judgment by Asian elephants (*Elephas maximus*). *Animal Cognition* 12, 193–199.
- Kéry, M., Royle, J.A., 2016. *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS: Volume 1: Prelude and Static Models* (New York: Elsevier).
- Kéry, M., Royle, J.A., 2021. *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS: Volume 2: Dynamic and Advanced Models* (New York: Elsevier).
- Lee, M.D., Wagenmakers, E.J., 2013. *Bayesian Cognitive Modeling: A Practical Course* (New York: Cambridge University Press).
- Ma, W.J., Kording, K.P., Goldreich, D., 2023. *Bayesian Models of Perception and Action: An Introduction* (Boston: MIT Press).
- Mariotti, E., Parrini, F., Louw, C.J., Marshal, J.P., 2020. Habitat use by a large herbivore guild in a fenced South African protected area. *African Journal of Wildlife Research*, 50(1), 86-101.
- McFadden, D.L., 1974. Conditional logit analysis of qualitative choice behavior. In: *Frontiers in Econometrics*, ed. P. Zarembka. New York: Academic Press, 105–142.
- Nevo, O., Schmitt, M.H., Ayasse, M., Valenta, K., 2020. Sweet tooth: Elephants detect fruit sugar levels based on scent alone. *Ecology and Evolution* 10(20), 11399–11407.
- Owen-Smith, N., Chafota, J., 2012. Selective feeding by a megaherbivore, the African elephant (*Loxodonta africana*). *Journal of Mammalogy* 93(3), 698–705.
- Perdue, B.M., Talbot, C.F., Stone, A.M., Beran, M.J., 2012. Putting the elephant back in the herd: elephant relative quantity judgments match those of other species. *Animal Cognition* 15, 955–961.
- Plotnik, J.M., Brubaker, D.L., Dale, R., Tiller, L.N., Mumby, H.S., Clayton, N.S., 2019. Elephants have a nose for quantity. *Proceedings of the National Academy of Sciences* 116(25), 12566–12571..
- Plotnik, J.M., Pokorny, J.J., Keratimanochaya, T., Webb, C., Beronja, H.F., Hennessy, A., Hill, J., Hill, V.J., Kiss, R., Maguire, C., Melville, B.L., Morrison, V.M.B., Seecoomar, D., Singer, B., Ukehaxhaj, J., Vlahakis, S.K., Ylli, D., Clayton, N.S., Roberts, J., Fure, E.L., Duchatelier, A.P., Getz, D., 2013. Visual Cues Given by Humans Are Not Sufficient for Asian Elephants (*Elephas maximus*) to Find Hidden Food. *PLoS One* 8, e61174.
- Plotnik, J.M., Shaw, R.C., Brubaker, D.L., Tiller, L.N., Clayton, N.S., 2014. Thinking with their trunks: elephants use smell but not sound to locate food and exclude nonrewarding alternatives. *Animal Behaviour* 88, 91–98.
- Pretorius, Y., Stigter, J.D., De Boer, W.F., Van Wieren, S.E., De Jong, C.B., De Knegt, H.J., Grant, C.C., Heitkönig, I., Knox, N., Kohi, E., Mwakiwa, E., Peel, M.J.S., Skidmore, A.K., Slotow, R., Van Der Waal, C., Van Langevelde, F., Prins,

- H.H.T., 2012. Diet selection of African elephant over time shows changing optimization currency. *Oikos* 121(12), 2110–2120.
- Rossi, P.E. Allenby, G.M., McCulloch, R., 2005. *Bayesian Statistics and Marketing* (Chichester, UK: Wiley).
- Royle, J.A., Dorazio, R.M., 2008. *Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations, Metapopulations and Communities* (New York: Elsevier).
- Royle, J.A., Nichols, J.D., Karanth, K.U., Gopalaswamy, A.M., 2009. A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology*, 46(1), 118–127.
- Schmitt, M.H., Shuttleworth, A., Ward, D., Shrader, A.M., 2018. African elephants use plant odours to make foraging decisions across multiple spatial scales. *Animal Behaviour* 141, 17–27.
- Schofield, M.R., Barker, R.J., 2014. Hierarchical Modeling of Abundance in Closed Population Capture–Recapture Models Under Heterogeneity. *Environmental and Ecological Statistics*, 21, 435–451.
- Sekar, N., Sukumar, R., 2015. The Asian elephant is amongst the top three frugivores of two tree species with easily edible fruit. *Journal of Tropical Ecology* 31(5), 385–394.
- Snyder, R.J., Barrett, L.P., Emory, R.A., Perdue, B.M., 2021. Performance of Asian elephants (*Elephas maximus*) on a quantity discrimination task is similar to that of African savanna elephants (*Loxodonta africana*). *Animal Cognition* 24(5), 1121–1131.
- StataCorp, 2023. *Stata 18 Bayesian Analysis Reference Manual*. College Station, TX: Stata Press.
- Webb, J.A., Stewardson, M.J., Koster, W.M., 2010. Detecting Ecological Responses to Flow Variation Using Bayesian Hierarchical Models. *Freshwater Biology*, 55(1), 108–126.
- Wikle, C.K., 2003. Hierarchical Bayesian Models for Predicting the Spread of Ecological Processes. *Ecology*, 84(6), 1382–1394.

CHAPTER 3: African Elephant Non-Visual Reward Quantity Discrimination: A Choice Experiment

Introduction

The ability to discriminate between different numbers of the same entity (e.g. food, individuals of the same or a different species) is an important aspect of the life of animals. It is needed, for example, to make optimal foraging choices between two feeding stations (Caraco et al., 1980), to choose the best refuge to avoid being predated upon (Bisazza and Gatto, 2021), to avoid conflict against groups of conspecifics larger than your own (Benson-Amram et al., 2018), and to select groups of conspecifics having the most favourable sex ratio and thus increasing the probabilities of mating (Agrillo et al., 2008). In all of these situations, being able to discriminate between different quantities of two alternatives and choose the most favourable option can improve the fitness of the animal. Due to its advantages, quantity discrimination ability is shared by many taxa (Vonk and Beran, 2012) and has been tested and demonstrated in a wide variety of animals, from insects to mammals (see Table A1 in Appendix 1).

Quantity discrimination ability has usually been tested by presenting animals with choices over binary outcomes offering rewards differing in numbers, where the choice is made either in a trained or untrained manner. To test the discrimination ability of an animal in a *trained* way means that the animal undergoes a phase of training, where it is conditioned to choose a specific alternative over others, identified by the researcher as the correct one (for example, Davis, 1984). In such a protocol, the animal is rewarded every time it chooses the correct alternative, and receives no reward when it chooses the wrong alternative (Kilian et al., 2003).

Untrained discrimination ability refers to experiments that do not require any training or conditioning, and it is sometimes referred to as “spontaneous” discrimination (for example, Bánszegi et al. (2016)). In this setup, the animal faces binary choices between different alternatives and freely chooses the one it prefers, with which it is rewarded (for example, Hauser et al., 2000). The common expectation in all these experiments is that animals' choices maximise their net energy intake (Pyke, 1984) and, therefore, an animal would choose the larger alternative when it recognises and values the alternatives as different. Agrillo and Bisazza (2014) suggested that testing the discrimination ability in an untrained way, rather than in a trained way, has the possible advantage of mirroring the numerical ability of an animal in the wild.

The most studied drivers of quantity discrimination are measures of the numerosity of the alternatives, such as the ratio (smaller divided by larger), the absolute difference (larger minus smaller), and the cumulative magnitude (smaller plus larger) of the alternatives. These variables can affect both the ability of an animal to perceive the alternatives as different and the individual preference for an alternative over another.

Representations of quantities are typically noisy, and the noise increases with the numerosity of objects represented, a phenomenon called scalar variability (Butterworth, 2022: Chapter 1). Therefore, when comparing two alternatives, the larger the total quantities the more imprecise their representations, and the more similar the quantities, the more probable it is that their representations overlap. If the representations of the alternatives differ less than the *just noticeable difference* proper of the animal, which represents the minimum difference required between two stimuli to be recognised as different by an individual, the animal cannot perceive two quantities as different (Butterworth, 2022: Chapter 1). In addition, the motivation to participate in the

experiment plays a role in determining what an animal would choose (Battalio et al., 1985; Agrillo and Bisazza, 2014; Miletto Petrazzini et al., 2017). If the rewards are not perceived as big or different enough for one of them to be preferred, the animal will be indifferent to the alternatives and might not choose attentively.

The majority of previous studies focused on the cognitive constraints concerning the representation of the alternatives. Most of them have found that discrimination is negatively correlated with the ratio or positively correlated with the absolute difference of the alternatives, while it is not affected by their cumulative magnitude. Only a few studies have found the opposite, with discrimination not being affected by the ratio but being negatively correlated with the cumulative magnitudes.

Elephants are among the animals whose discrimination ability has been tested. Some studies conducted on Asian elephants (*Elephas maximus*) found that their discrimination ability was not affected by the ratio, magnitude, or absolute difference of the alternatives (Irie-Sugimoto et al., 2009; Irie and Hasegawa, 2012; Irie et al., 2019). Other studies described discrimination as negatively correlated with the ratio of the alternatives, positively correlated with the absolute difference of the alternatives, and not affected by the cumulative magnitude (Plotnik et al., 2019; Snyder et al., 2021), similar to what was observed in the only study to date on African elephants (*Loxodonta africana*) (Perdue et al., 2012). A summary of the current literature on elephant quantity discrimination is shown in Table A3, in Appendix 1. Some studies also investigated the choices of elephants when discriminating between alternatives with a fixed ratio and varying magnitude, and found no difference in the probability of the elephants choosing the larger alternative (Perdue et al., 2012; Plotnik et al., 2019; Snyder et al., 2021).

In this study, African elephants were tested in an untrained discrimination task using a series of binary choices between alternatives with the same reward type, differing only in their quantities, to determine the major drivers of their choices. Based on the existing literature, the effects of ratio, absolute difference, and cumulative magnitude of the alternatives on the probability of each elephant choosing the larger reward were tested. In addition, the effect of the cumulative magnitude of the alternatives in choices having fixed ratios was investigated. Given the mixed results found in the Asian elephants literature, the magnitude of the alternative is not expected to affect the choice of the elephants, while the ratio and the absolute difference could either have no effect on the choice, or affect the choice negatively and positively, respectively. The effect of experience on the probability of each elephant choosing the larger alternative and the side preference of each elephant was also investigated.

The elephants were tested in two conditions providing information about the alternatives in two different modalities: through olfaction only, as per Plotnik et al. (2019) with Asian elephants, and through a combination of olfaction and hearing. To date, no studies have tested the choices of African elephants by giving information on the alternatives through these modalities, since the only such African elephant study was based on visual or sound cues only (Perdue et al., 2012). This gap in the literature is particularly interesting to explore since elephants can discriminate different odours with high sensitivity (Rizvanovic et al., 2013; Miller et al., 2015), rely on smell to find food and water (Plotnik et al., 2014; Schmitt et al., 2018; Wood et al., 2022), and use olfaction and auditory exchanges in social interactions (McComb et al., 2003; Bates et al., 2008). The results of this study contribute to filling a gap in the literature and add fresh information to the available knowledge on quantity discrimination in elephants.

Methods

The subjects of the study were four semi-tame adult African elephants hosted at Adventures with Elephants (AwE), in Limpopo, South Africa. Details about each elephant can be found in the General Methodology section of Chapter 1.

Boskos, a common game pellet used for wild herbivores, have been used as the stimulus and the reward. Boskos closely resembles the natural diet of wild herbivores and is never declined by any of the focal elephants. The composition of boskos is reported in Table 3.1. Note that the word “boskos” applies to a single as well as to multiple pellets.

Table 3.1: Boskos nutrients content specification by ALZU brand.

Item	Quantity	Min/Max
Protein	100g/Kg	Min
Moisture	120g/Kg	Max
Fat	15g/Kg	Min
Fibre	120g/Kg	Max
Calcium	10g/Kg	Min
Phosphorus	3g/Kg	Min
Energy	9.5 MJ/Kg	Min

Data collection

The procedures used in this task are similar to those used by Perdue et al. (2012) with African elephants, and by Plotnik et al. (2019) and Snyder et al. (2021) with Asian elephants. To assess what factors affect the untrained tendency of African elephants to

discriminate between different numbers of the same edible item, each elephant was offered a series of binary choices between two different quantities of boskos presented in two perforated buckets. The perforated buckets had 44 drilled holes with a diameter of 1 cm on their sides, and 23 drilled holes on their lids, as can be seen in Figure 3.1.



Figure 3.1: The researcher preparing to place the perforated buckets containing the pieces of boskos in front of the elephant in the “boskos experiment”.

The test was conducted under two different conditions: a smell-only condition and a smell-plus-sound condition. In the first condition, the elephant could investigate the alternatives only by smelling the rewards contained in the buckets immediately before making a choice. In the second condition, the elephant could hear the number of pieces of boskos falling in both buckets while they were loaded, and also smell them afterwards. In both conditions, each session of the experiment involved one elephant, one researcher, three handlers, two perforated buckets, a canvas mat, and a specific number of boskos, as illustrated in Figure 3.2.

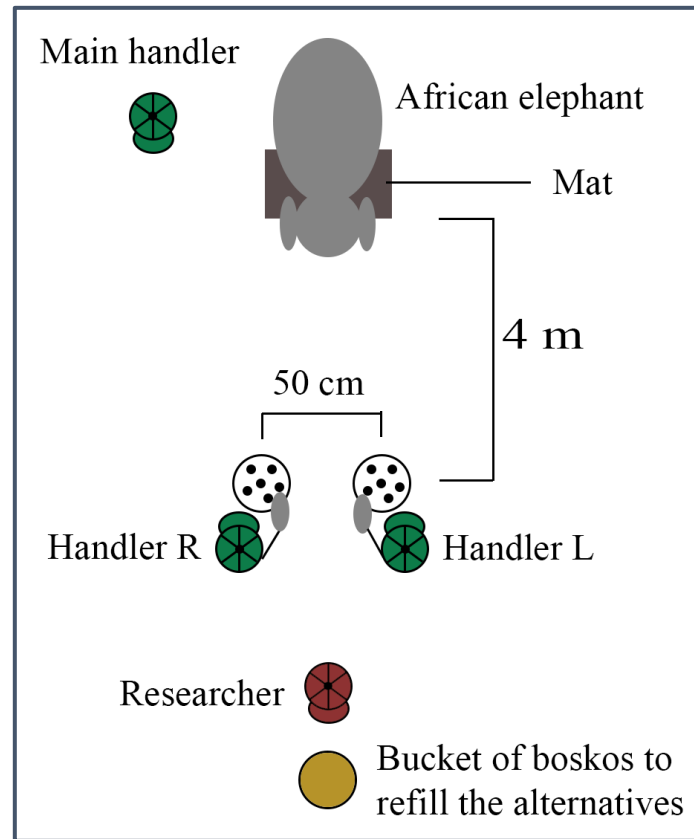


Figure 3.2: The general set-up of the two conditions of the “boskos experiment” showing the location of the researcher, handlers, and buckets in relation to the elephant.

Each session started with the elephant being on the mat. The elephant faced two white buckets placed four meters away and approximately 50 cm from each other. One handler stood next to each bucket, and the researcher stood between the buckets, approximately two metres behind the handlers, giving her back to the handlers and the elephant. In both conditions, the elephant waited on the mat for each bucket to be loaded with a predetermined number of boskos, as shown in Figure 3.3.



Figure 3.3: A view of the beginning of each trial of the “boskos experiment”. The elephant (Chova) is waiting on the mat, the buckets have been loaded with the predetermined quantities of boskos, and the handlers (Edward and Thabo) are ready to place one foot on their bucket and wait for the elephant to walk towards them, smell the buckets, and choose one.

In the smell-only condition, the researcher took both buckets to her initial position and inserted the pieces of boskos in each bucket at the same time without producing a sound. The lids were then put on top of the buckets and the researcher walked backwards to the handlers. The buckets were placed at their final locations and the researcher walked back to her starting position. To avoid Clever Hans effects, the handlers looked away during the loading of the boskos, and the researcher always showed her back to both the handlers and the elephant.

In the smell-plus-sound condition, while the elephant was waiting on the mat, the buckets were placed at their final locations without the lids. The researcher loaded the bucket to the left of the elephant first, dropping one piece of boskos at a time. Since the study was conducted in an outside environment which is never completely silent, to ensure that the elephant would hear the sound made by each piece of boskos inserted in

the buckets, the buckets were hit with a wooden stick every time a piece of boskos was inserted into them.

To keep the amount of time spent at each bucket constant, the researcher performed a number of fake drops when loading the smaller alternative, where she inserted her hand in the bucket without dropping any boskos or producing any sound. In addition, to ensure the elephants would not avoid the alternative where fake drops were performed, one fake drop also took place when loading the larger alternative. For example, in a trial between 1 and 5 pieces of boskos, six drops were performed in each bucket, where only 1 or 5 were real and accompanied by hitting the bucket with the wooden stick.

Once the left bucket had been loaded, it was covered with the perforated lid and the right bucket was loaded following the same procedure. For safety reasons, it was not possible to equip the handlers with earmuffs, so to avoid Clever Hans effects under the smell-plus-sound condition the handlers were told to not pay attention to what the researcher did and to sing a song in their heads.

In both conditions, after loading the buckets, the researcher came back to her initial position, counted to three and said “All right”, at which point the main handler released the elephant with the command “Walk up and smell”. The two handlers then placed a foot on their bucket, to prevent the elephant from opening them deliberately or by mistake. The elephant walked to the buckets, smelled the content of both buckets by placing their trunk sequentially on each perforated lid, and indicated the choice by pointing at the chosen bucket with the trunk. The handler responsible for the chosen bucket gave its content to the elephant and communicated to the researcher that the

elephant had chosen his bucket. The main handler called the elephant back to the mat, and the researcher retrieved both buckets and emptied the unchosen one.

During the experiment, each elephant was presented with 17 combinations of alternatives, listed in Table A2 in Appendix 1. The prospects used were every possible combination between 1 and 6 pieces of boskos (15 combinations), trials between 4vs8 boskos, and trials between 5vs10 pieces of boskos (2 additional combinations). These two additional prospects were added to test whether the elephant's discrimination between alternatives having the same ratio of 0.50 was affected by the cumulative magnitude of the alternatives. Each daily experimental session consisted of 10 trials per elephant and three to five sessions were conducted per week. The elephants were considered to have made the correct choice when they selected the larger alternative.

Data analysis

The statistical analysis has been conducted with Stata 18, documented by StataCorp (2023), using Bayesian Hierarchical Models (BHM) with a probit likelihood. The dependent variable used is the binomial variable "choice of the larger alternative" (1 for yes or 0 for no). The full specification of the probit model is given in Chapter 1.

To assess if each elephant chose the larger alternative more than by chance, a BHM without any covariates was estimated, using 5 MCMC chains of 100,000 samples per chain, and an additional 50,000 burn-in samples per chain.

To assess whether the probability of each elephant choosing the larger alternative *improved over time*, a BHM with a continuous covariate added to measure

experience, interacted with the condition of the experiment, was estimated, which will be referred to as BHMt. The covariate to measure experience was just an ordered count of the choice task. BHMt was estimated using a single-chain MCMC of 500,000 samples, and an additional discarded 250,000 burn-in samples.

To assess what *variables* affected the probability of the elephants choosing the larger reward and how, a BHM was estimated using the relevant explanatory variables (continuous ratio and absolute difference, and categorical condition and chosen side) in interaction with the variable for individual elephants. This model will be referred to as BHMrd. The continuous cumulative magnitude is not included in this model as it is highly correlated to the ratio and absolute difference of the alternatives. The simulation for this BHMrd was done with 5 MCMC chains of 500,000 samples per chain, plus 50,000 burn-in samples per chain.

In addition to showing the effect of single explanatory variables on the response variable, we report the results of evaluating the hypothesis: Does the *ratio* or the *absolute difference* between the alternatives have an effect on the response variable that is different from 0? To evaluate this hypothesis, the probability that the posterior distributions of each of these variables lie in a range of values for the Region of Practical Equivalence (ROPE) in intervals on either side of 0 is reported.

This is one way to compare the relative effect that these two variables have on the choice between specific prospects. In particular, the focus is on what should be the *easiest prospect* to discriminate, i.e. the prospect having the smallest ratio and the highest absolute difference: 1 vs 6 (ratio = 0.17, absolute difference = 5), what should be the *most difficult prospect*, i.e. the prospect with the largest ratio and the smallest

absolute difference, 5vs6 (ratio = 0.83 and absolute difference = 1), and the *prospect in between* having the middle values of ratio and absolute difference, i.e. 3vs6 (ratio = 0.5 and absolute difference = 3). For a more detailed explanation of ROPEs, refer back to Chapter 1 and Figure 1.7.

To test the effect of the *cumulative magnitude* of the alternatives on the probability of the larger alternative being chosen by the elephants a BHM, named BHMrm, was estimated by adding magnitude and eliminating the absolute difference from the model, to avoid a correlation between the alternatives. The simulation for this model was done with 5 MCMC chains of 500,000 samples per chain, plus 50,000 burn-in samples per chain. Each of the mentioned BHMs has passed convergence tests. The numerous displays of convergence are not shown here because of space constraints but are available upon request.

The effect of cumulative magnitude in choices having a fixed 0.5 ratio was estimated in two different ways. In one analysis, the magnitudes of the alternatives were divided into small (magnitudes of 3 and 6) or large (magnitudes of 9, 12, and 15) groups and a Pearson's Chi-square test was estimated, following previous literature (Perdue et al., 2012; Plotnik et al., 2019; Snyder et al., 2021). The null hypothesis for Pearson's Chi-square tests is that there is no difference between choices made with small or large magnitudes. The second way in which data were analysed was by treating magnitude as a continuous variable and estimating its Average Marginal Effect (AME) from model BHMrm. The ratio 0.5 was specifically chosen because it is represented by multiple prospects having different magnitudes.

The effect of each of the single variables reported in this chapter is presented in the form of the AME. Since the AME of a variable represents how much the probability of choosing the larger alternative changes as the variable of interest changes, each AME display contains a dashed red line which represents the reference level of zero marginal effect of the variable of interest. When the variable of interest is binary, as in the condition (being smell-only or smell-plus-sound) or in the side offering the larger alternative (being right or left), the reference level indicates a zero effect of the variable of interest on the probability of choosing the larger alternative. In the AME display of magnitude, a variable that takes 11 possible values, the dashed red line represents the probability of choosing the larger reward when the alternatives have magnitude 3, i.e. 1 vs 2-2 vs 1, which is taken as the reference level.

The AME of side preference has been calculated by looking at the difference in the estimated probability of an elephant choosing the larger reward based on the side where the larger reward was offered. If an elephant makes the same proportion of correct choices on both sides, there is no side preference, regardless if the proportion of correct choices is high or low in general. The AME of side preference refers to the estimated probability of choosing the larger alternative *conditional* on the larger alternative being on one side. This means that it compares the probability of choosing the larger alternative *only* when the larger alternative was on the left side, to the probability of choosing the larger alternative *only* when the larger alternative was on the right side.

Consider for example an experimental design that is balanced so that the larger alternative is on each side in half of the choices. Assume that one elephant, for example Chova, always chooses the left side. When the larger alternative is on the left side, he

has a probability of 1 of choosing it. Consequently, when the larger alternative is on the right side he has a probability of 0 of choosing it. Since the AME of the larger alternative being on the left side is obtained by evaluating the *conditional* probability of Chova choosing the larger alternative when it is on the left *minus* the *conditional* probability of Chova choosing the larger alternative when it is on the right, in this example Chova has an AME of $1 - 0 = 1$. A positive AME indicates that the elephant has a left-side preference. Conversely, an elephant having a right-side preference would have a negative AME.

Results

The study consisted of 2,302 trials, 204 choice trials per elephant in each condition plus a variable number of 1vs6-6vs1 choices per elephant in each condition. The raw data show that Chova chose the larger alternative in 57% of trials, Nuanedi in 68% of trials, Mussina in 70% of trials, and Shan in 72% of trials. The BHM without covariates shows that the elephants overall chose the larger alternative more than by chance, as shown in Figure 3.4. The mean posterior estimate of the probability of each elephant choosing the larger alternative and the probability that this rate was better than by chance, which was almost 1 for each elephant, are reported in Table 3.2.

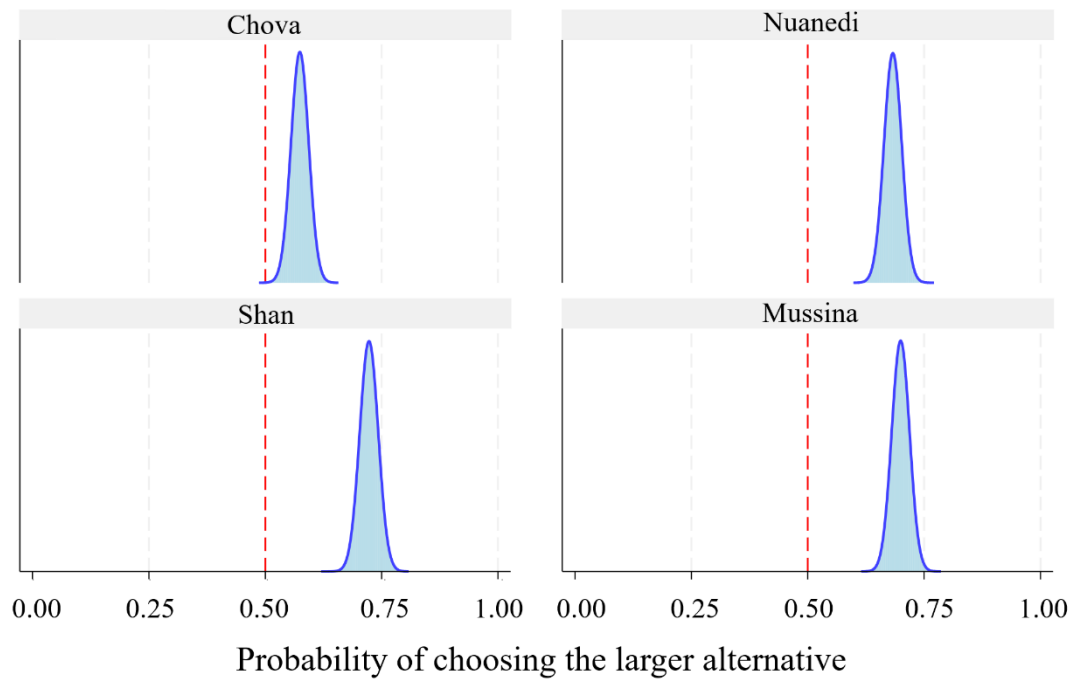


Figure 3.4: The posterior distribution of the elephant probabilities of choosing the larger alternative estimated from the BHM without covariates in the “boskos experiment”. The dashed red line represents the probability of choosing the larger alternative by chance.

Table 3.2: The posterior estimates of the probability of choosing the larger alternative for each elephant estimated from the BHM without covariates in the “boskos experiment”. Mean and Sd represent the mean and standard deviation of the posterior distribution, 50% HPD low and 50% HPD high represent the thresholds of the 50% Highest Probability Density of the posterior. The last column represents the probability of the posterior probability being greater than 0.50.

Subject	Mean	Sd	50% HPD low	50% HPD high	Prob > 0.50
Chova	0.60	0.03	0.59	0.62	1.00
Nuanedi	0.70	0.03	0.68	0.71	1.00
Shan	0.74	0.03	0.72	0.76	1.00
Mussina	0.70	0.03	0.69	0.73	1.00

Effects on choice

The BHMrd results showed that the *ratio* of the alternatives negatively affected the probability of choosing the larger alternative for each elephant. This effect is in the direction expected in case the ratio did affect the choices of the elephants. The estimates also showed that the *absolute difference* between the alternatives had a positive effect on the probability of Nuanedi and Shan choosing the larger alternative, which is again the expected direction of the observable effect, while it did not affect the choices of Chova and Mussina. These results are displayed in Figure 3.5.

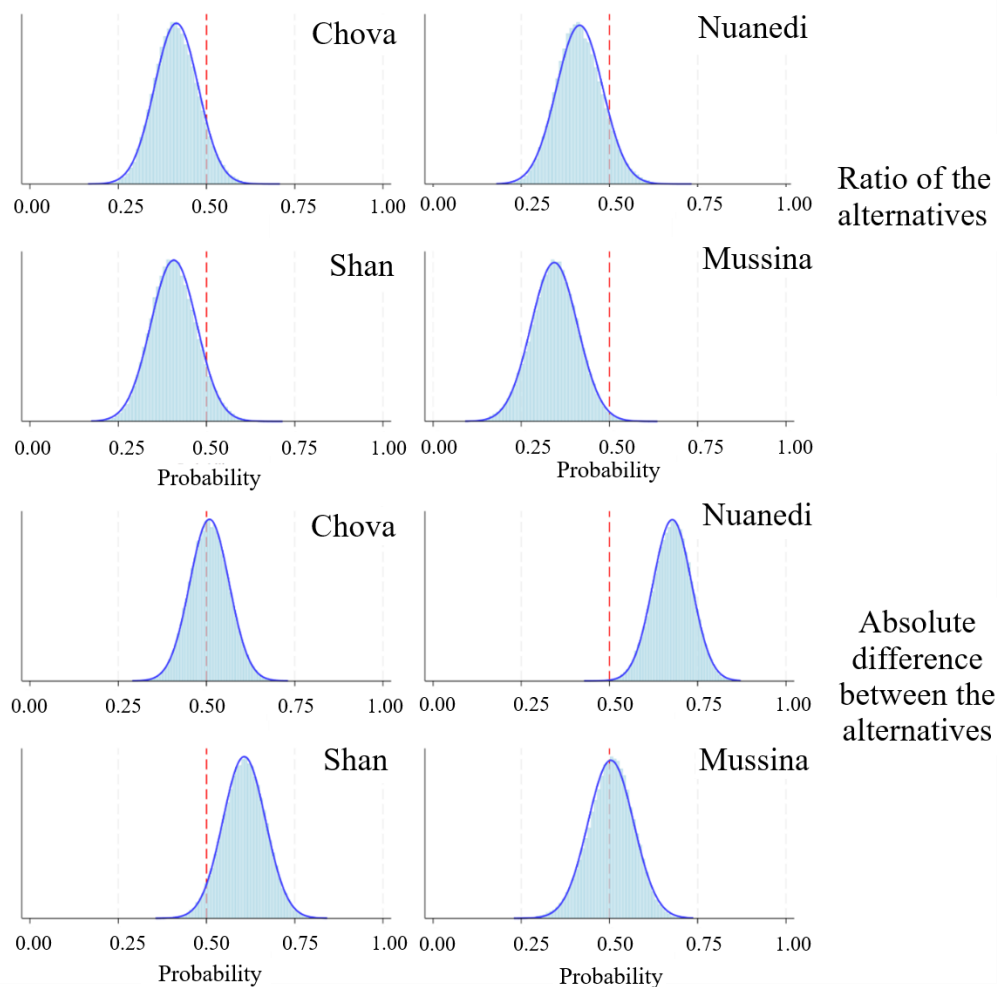


Figure 3.5: The posterior distribution of the effect of the ratio between the alternatives (top panel) or the absolute difference of the alternatives (bottom panel) on the elephant probabilities of choosing the larger alternative estimated from the BHMrd in the “boskos experiment”. The dashed red line represents the probability of choosing the larger alternative by chance.

The results from BHMrm showed that the *cumulative* magnitude of the alternatives did not affect Chova’s choices. On the other hand, it had a slight negative effect on the probability of Mussina, and a strong positive effect on the probability of Nuanedi and Shan, choosing the larger alternative. This effect was unexpected. These results are shown in Figure 3.6.

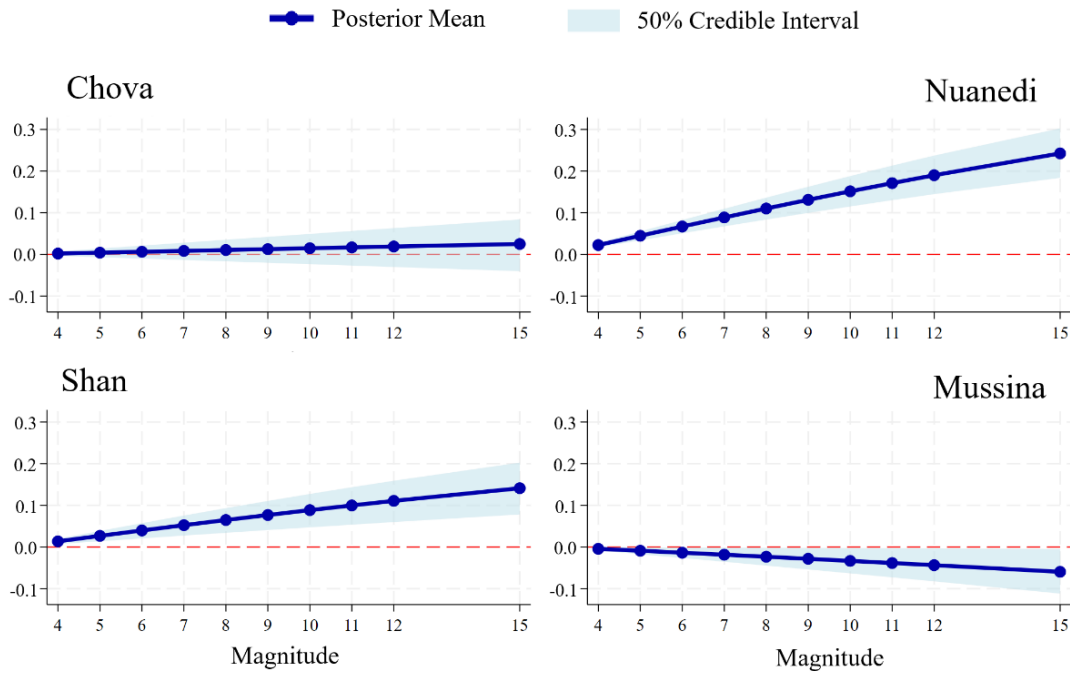


Figure 3.6: The AME of the magnitude of the alternatives on the probability of each elephant choosing the larger alternative, estimated from the BHMrm in the “boskos experiment”. The dashed red line, being the reference, represents the probability of choosing the larger alternative when the cumulative magnitude of the alternatives is 3.

Each elephant chose the larger alternative slightly less when choosing in the smell-plus-sound condition than in the smell-only condition, as can be seen in Figure 3.7. Though this negative effect was more likely than not for each elephant, the change in the probability of each elephant choosing the larger alternative due to the condition of the experiment being smell-plus-sound decreased only by 3 or 4 percentage points on average. Therefore, even though the elephants chose the larger reward less often in the

smell-plus-sound condition, each elephant still chose better than by chance in both conditions. The effect of the condition of the experiment is reported in Table 3.3.

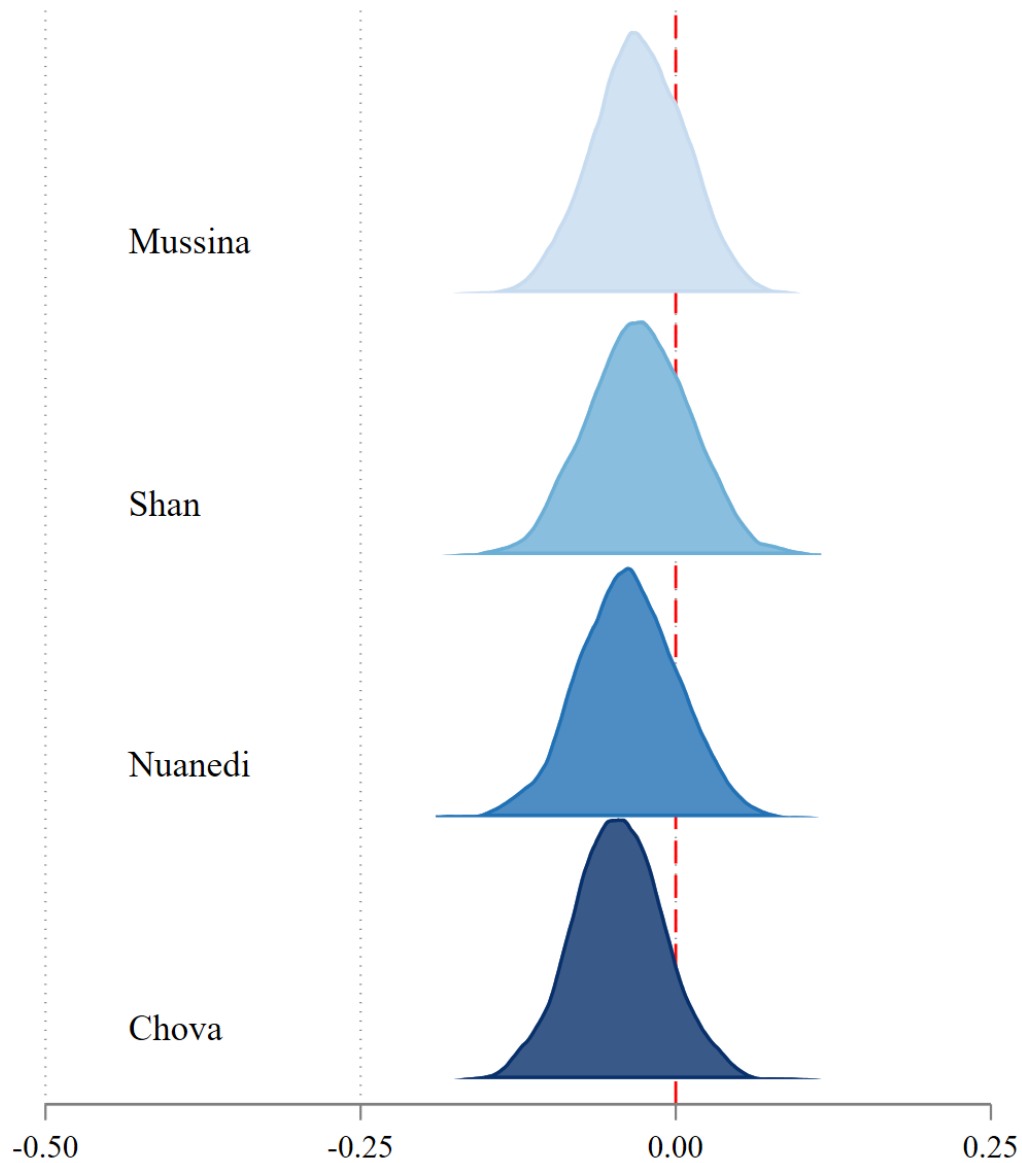


Figure 3.7: The AME of choosing in the smell-plus-sound condition on the probability of each elephant choosing the larger alternative, estimated from the BHMrd in the “boskos experiment”. The dashed red line represents a 0 effect of the condition on the probability of each elephant choosing the larger alternative.

Table 3.3: The AME of the condition of the experiment being smell-plus-sound and of the larger alternative being on the left side on the probability of choosing the larger alternative for each elephant, estimated from the BHMrd in the “boskos experiment”. The last column represents the probability of the posterior distribution being positive.

Subject	AME	Prob > 0
Condition: smell-plus-sound compared to smell-only		
Chova	-0.04	0.11
Nuanedi	-0.03	0.17
Shan	-0.03	0.23
Mussina	-0.02	0.23
Side: larger alternative being on the left side compared to on the right side		
Chova	-0.16	<0.01
Nuanedi	-0.14	<0.01
Shan	-0.06	0.04
Mussina	-0.04	0.11

The AME of the side where the larger alternative was located is shown in Figure 3.8. The fact that all the distributions shown in Figure 3.8 are centred on the left side of the reference line, indicates that the effect of the variable was negative, thus each elephant had a right-side preference. Indeed, the plot shows that, conditional on the larger reward being on the left side, each elephant had a lower probability of choosing it compared to their probability of choosing the larger reward conditional on it being on the right side.

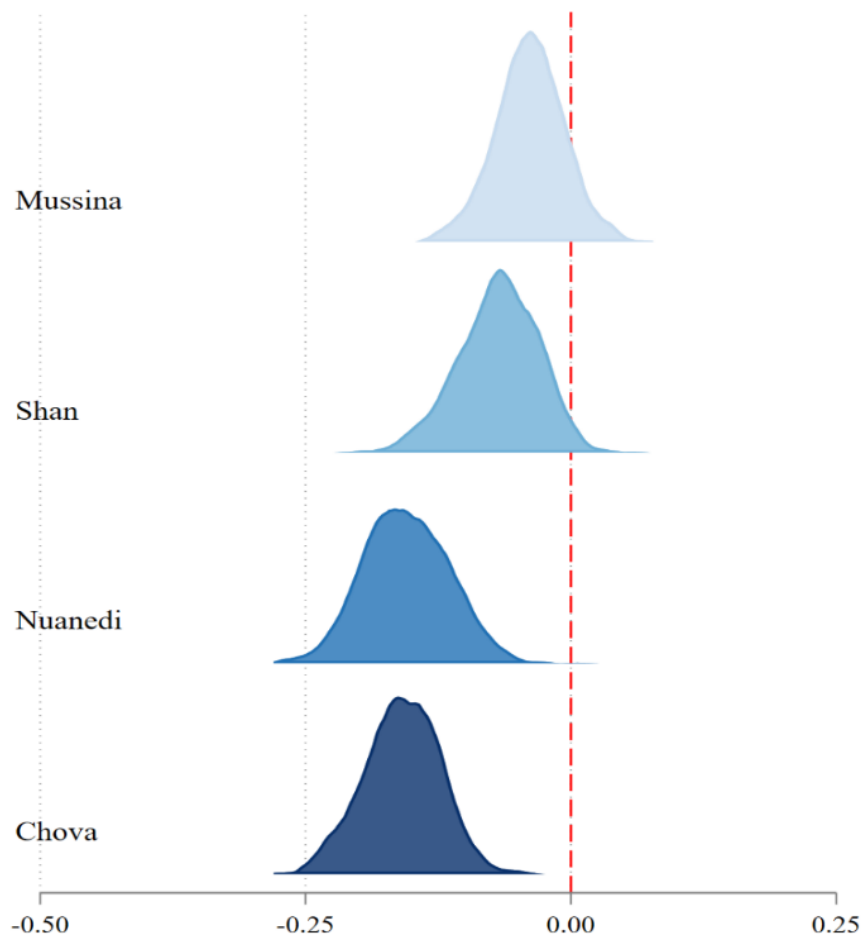


Figure 3.8: The AME of the larger alternative being on the left side on the probability of each elephant choosing the larger alternative, estimated from the BHMrd in the “boskos experiment”. The dashed red line represents a 0 effect of the side where the larger alternative is located.

The ROPE

The ROPE displays show how much of the posterior distributions for the effect of absolute difference and ratio lie in intervals of the probability of choosing the larger alternative, starting from a ROPE ± 0 percentage points (pp) and spanning symmetrically to ± 25 pp. If the curve of a variable quickly reaches 1 on the y-axis, it shows that the variable does not have a strong effect on the probability of choosing the larger alternative, since most of its posterior distribution is found in an area that can practically

be considered equivalent to having no effect. The longer it takes for the curve of the variable to reach 1 on the y-axis, the stronger the effect of that variable on the response variable.

The results of the ROPEs, reported in Figure 3.9, show how differently the variables affected each elephant. Overall, the absolute difference between the alternatives had a higher influence than the ratio on the probability of choosing the larger alternative in the easiest prospect, the ratio had a higher influence than the absolute difference on the probability of choosing the larger alternative in the most difficult prospect, and the relevance of the effects of the variables was mixed in the prospect in between.

For Chova and Mussina, the absolute difference was slightly more decisive than the ratio in the easiest prospect, it had less weight in choices of the prospect in between, and it had almost no effect in the most difficult prospect, where the ratio had a much higher weight. For Nuanedi and Shan, the absolute difference was strongly more relevant than the ratio in the easiest prospect, both the variables had a similar weight on choices of the prospect in between, and the ratio between the alternatives became strongly more relevant than the absolute difference in the most difficult prospect.

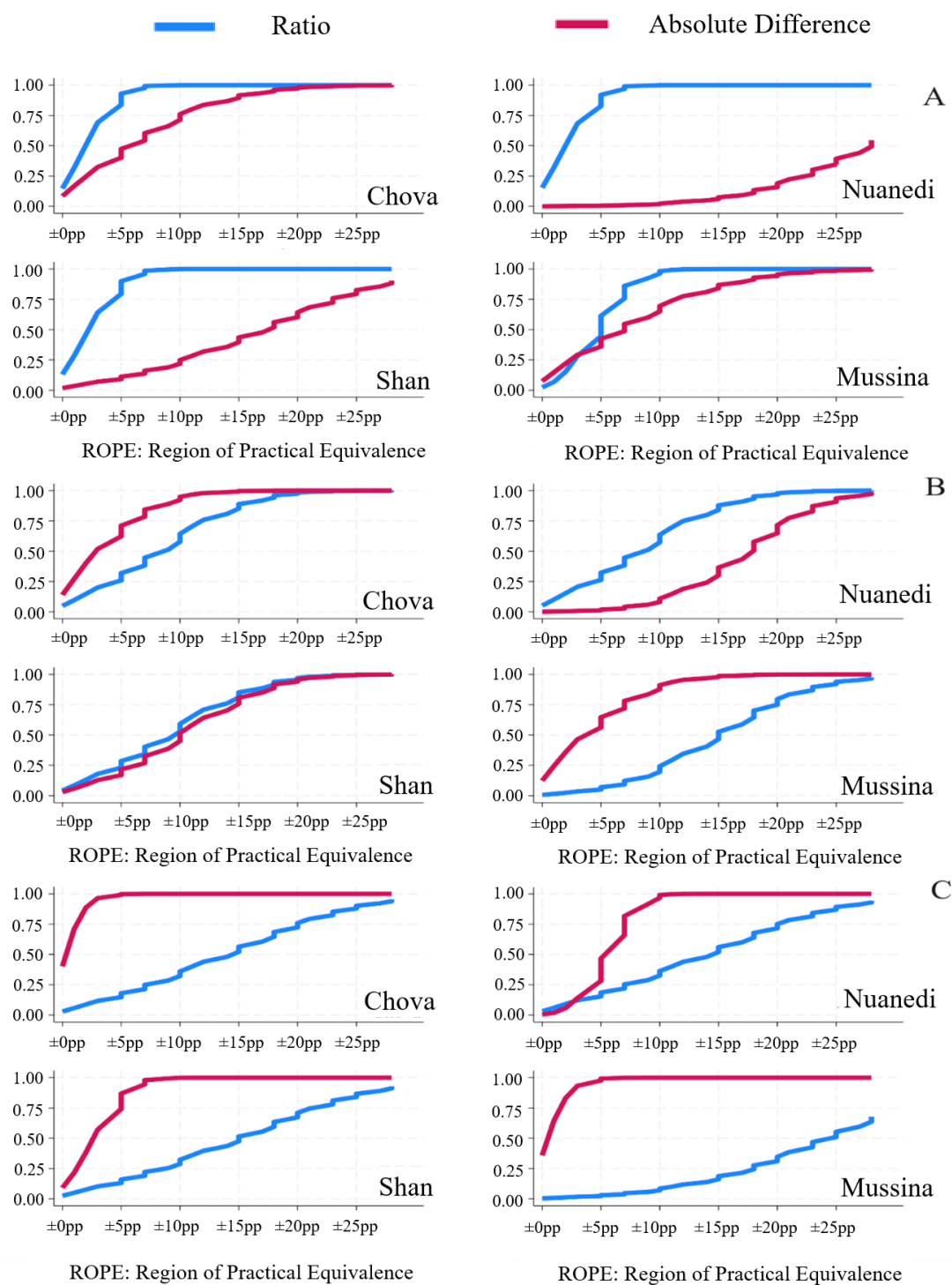


Figure 3.9: The probability that the posterior distribution of the ratio and absolute difference between the alternatives lie inside the ± 25 percentage point changes from not affecting the probability of choosing the larger alternative, calculated at the easiest prospect (A, ratio=0.17, abs.diff.=5), the prospect in between (B, ratio=0.5, abs.diff.=3), and the most difficult prospect (C, ratio=0.83, abs.diff.=1), estimated from the BHMrd in the “boskos experiment”.

Effect of magnitude when alternatives have fixed ratio of 0.5

The effect of magnitude on choices having a ratio of 0.5 was calculated by comparing the effect of small and large magnitude in each condition via Pearson's Chi-square test, following previous elephant literature. Figures 3.10 and 3.11 show the proportion of choices of the larger alternative in both conditions with small and large magnitudes as they appear in the raw data. In general, magnitude did not affect the performance of the elephants at ratio 0.5. The exception shown in Figure 3.10 was Nuanedi in the smell-only condition. She chose the larger alternative significantly more when the magnitude was large (72% of the time) compared to when the magnitude was small (46% of the time).

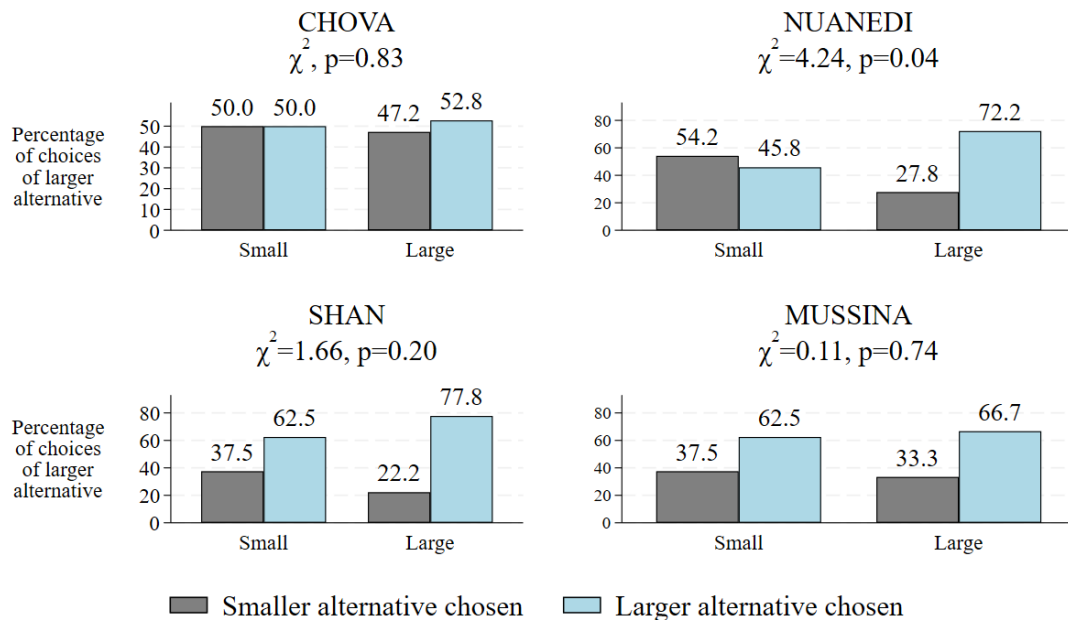


Figure 3.10: The percentage of choices of the larger alternative when the magnitude is small (3 or 6 pieces of boskos) or large (9, 12, or 15 pieces of boskos) at choices having ratio 0.5 (1vs2, 2vs4, 3vs6, 4vs8, and 5vs10) in the smell-only condition of the “boskos experiment”. A Chi-square having a $p < 0.05$ indicates that the number of choices of the larger and smaller alternatives significantly differs between prospects having small and large magnitude.

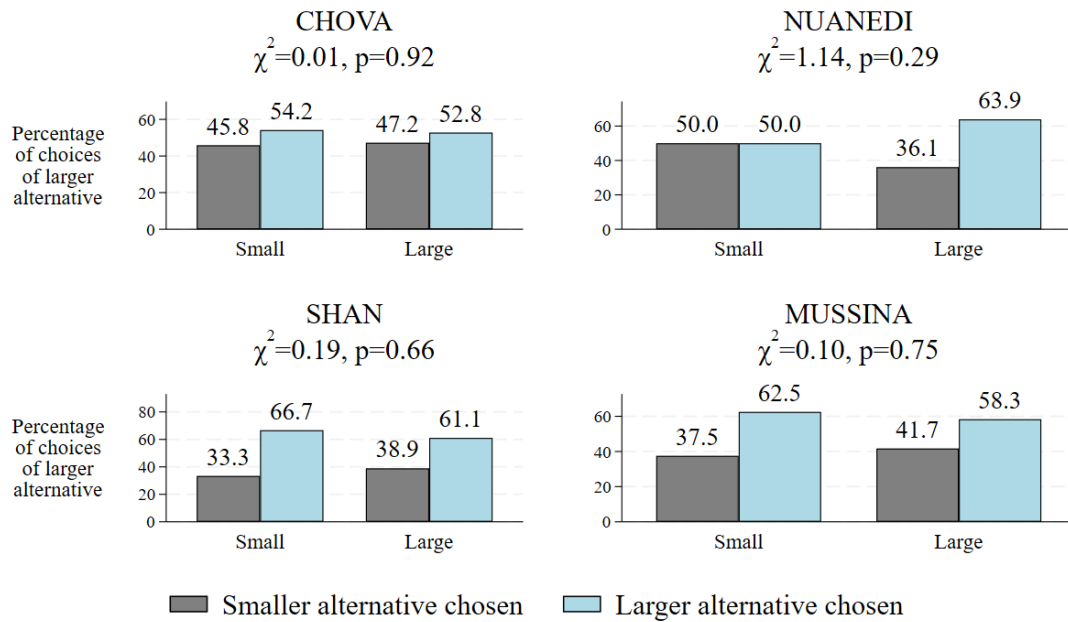


Figure 3.11: The percentage of choices of the larger alternative when the magnitude is small (3 or 6 pieces of boskos) or large (9, 12, or 15 pieces of boskos) at choices having ratio 0.5 (1vs2, 2vs4, 3vs6, 4vs8, and 5vs10) in the smell-plus-sound condition of the “boskos experiment”. A Chi-square having a $p < 0.05$ indicates that the number of choices of the larger and smaller alternatives significantly differs between prospects having small and large magnitude.

The effect of magnitude at a fixed ratio of 0.5 was also analysed via BHMrm. This hierarchical model treats magnitude as a continuous variable and controls for ratio, condition, and side of the larger alternative. The ratio 0.5 represents choices 1vs2, 2vs4, 3vs6, 4vs8, and 5vs10 and the results of the effect of magnitude at ratio 0.5 are shown in Figure 3.12. The plots shown in Figure 3.12 resemble Figure 3.6, which shows the effect of magnitude on the probability of choosing the larger alternative regardless of the ratio of the alternatives. Therefore, the effect of magnitude did not depend on the ratio of the alternatives, and looking at the full range of magnitude by treating it as a continuous variable gives different results than dividing magnitude into subjective small and large categories.

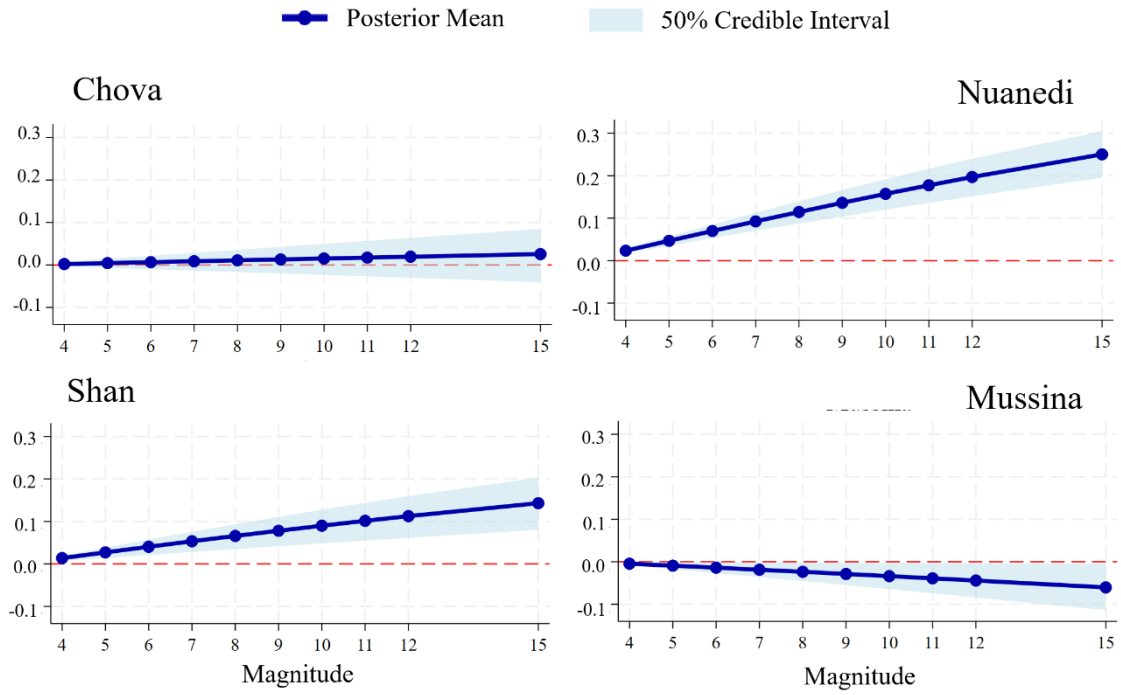


Figure 3.12: The AME of the magnitude of the alternatives on the probability of each elephant choosing the larger alternative in choices having a ratio of 0.5, estimated from the BHMrm in the “boskos experiment”. The dashed red line, being the reference, represents the probability of choosing the larger alternative when the cumulative magnitude of the alternatives is 3.

Learning

The learning ability of the elephants was tested in both conditions by comparing the predictive posterior distributions of their choices without experience and with full experience, i.e. their predicted preferences at the beginning of the experiment and their predicted preferences at the end of the condition. The distributions are shown in Figures 3.13 and 3.14. Each elephant had a higher predicted preference at the end of each condition rather than the predicted preference at the beginning of them, as shown in Table 3.4. Therefore, discrimination of each elephant increased over time.

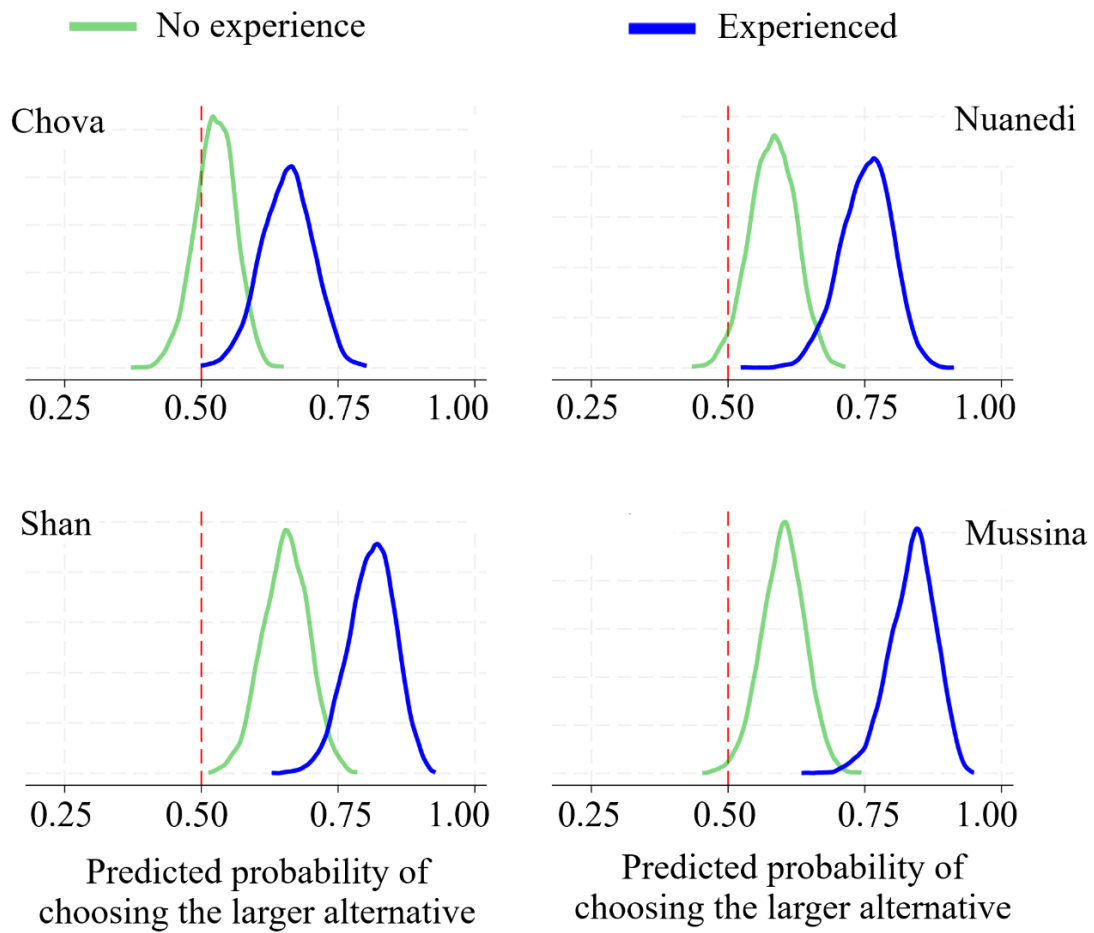


Figure 3.13: The predicted posterior probability of each elephant choosing the larger alternative in the smell-only condition in the first trial (green) and in the last trial (blue) of the condition, estimated from the BHMt in the “boskos experiment”. The red dashed line represents the probability of choosing the larger alternative by chance.

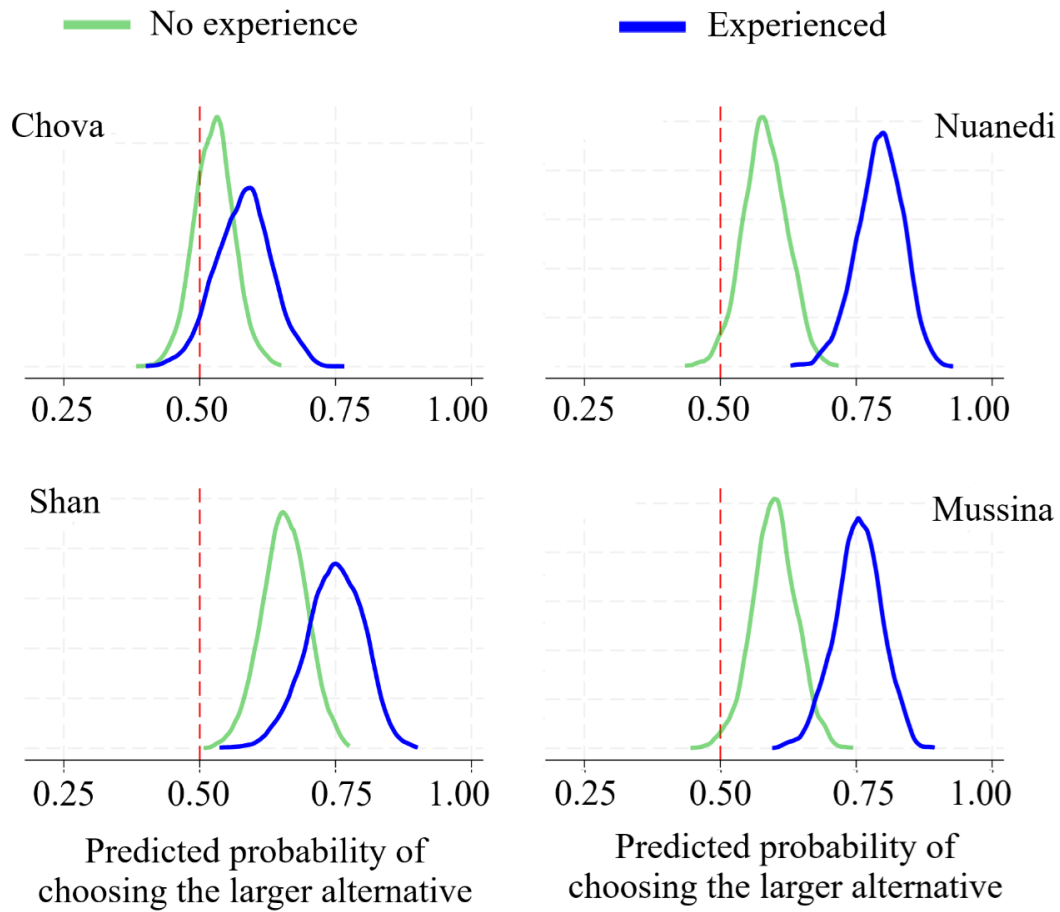


Figure 3.14: The predicted posterior probability of each elephant choosing the larger alternative smell-plus-sound condition in the first trial (green) and in the last trial (blue) of the condition, estimated from the BHMt in the “boskos experiment”. The red dashed line represents the probability of choosing the larger alternative by chance.

Table 3.4: The predictive posterior probability of each elephant choosing the larger alternative in the smell-only and the smell-plus-sound condition in the first and last choice of the conditions, estimated from the BHMt in the “boskos experiment”. Mean is the mean of the posterior distribution, “Prob > 0.50” represents the probability of the predictive posterior distribution being greater than 0.50.

Smell-only condition				
	Without experience		With full experience	
Subject	Mean	Prob > 0.50	Mean	Prob > 0.50
Chova	0.53	0.71	0.66	1.00
Nuanedi	0.58	0.97	0.75	1.00
Shan	0.66	1.00	0.81	1.00
Mussina	0.60	0.99	0.84	1.00
Smell-plus-sound condition				
	Without experience		With full experience	
Subject	Mean	Prob > 0.50	Mean	Prob > 0.50
Chova	0.53	0.71	0.58	0.95
Nuanedi	0.58	0.97	0.80	1.00
Shan	0.66	1.00	0.75	1.00
Mussina	0.60	0.99	0.75	1.00

Discussion

Overall, all the elephants chose the larger quantity of boskos more than by chance in both experimental conditions. These results are similar to previous findings in African elephants tested in visual or auditory domains (Perdue et al., 2012), and in Asian elephants tested in the olfactory domain (Plotnik et al., 2019). Possibly, discrimination in Asian and African elephants follows the same mechanisms and it does not vary based on the sense used to investigate the alternatives. We found an expected negative effect of the ratio of the alternatives on the probability of choosing the larger

reward for each elephant, and a positive effect of the absolute difference between the alternatives for two of the elephants.

Our results are inconsistent with those of a series of studies conducted on Asian elephants (Irie-Sugimoto et al., 2009; Irie and Hasegawa, 2012; Irie et al., 2019) where ratio, absolute difference, and magnitude did not affect the ability of elephants to discriminate between two different quantities. On the other hand, the results of the current study are consistent with several other studies on Asian (Plotnik et al., 2019; Snyder et al., 2021) and African elephants (Perdue et al., 2012), finding a negative effect of the ratio of the alternatives.

The results also showed that the elephants based their decisions more on the absolute difference or on the ratio of the alternatives based on the different combinations of pieces of boskos they were discriminating between. When the absolute difference was high, such as in 1 vs 6, it had a strong effect on choosing 6 boskos, while when the ratio was high, such as in 5 vs 6, it had a strong effect on choosing 6 boskos. This is an interesting starting point to be more deeply studied in the future, possibly with the use of mixture models.

Surprisingly, the effect of the cumulative magnitude in general was irrelevant for Chova, slightly negative for Mussina, positive for Shan, and strongly positive for Nuanedi. Nuanedi's higher probability of choosing the larger reward when more pieces of boskos were at stake could depend on her motivation. She might be indifferent between small quantities of boskos, and start to value larger quantities of boskos only when these exceeded a certain amount and were considerably different from the smaller reward. This explanation is also supported by the fact that in combinations having a

fixed 0.5 ratio in the smell-only condition Nuanedi was the only elephant choosing the larger reward more often when the prospects had a larger magnitude.

The elephants chose the larger alternative slightly more often in the smell-only condition than in the smell-plus-sound condition, on average by about 3.5%, as reported in Table 3.3. Since it is known that elephants base their feeding choices on olfactory cues (Schmitt et al., 2018), it is possible that the addition of sound did not add any information but rather elongated the waiting time while the buckets got loaded by the researcher. The addition of a longer wait to the experimental routine could be perceived by the elephants as a period in which they were prevented from reaching the reward they expected to receive, leading to frustration (Amsel, 1958). Such frustration might have lowered the elephants' attention leading to a higher number of inattentive choices. However, the difference in performance between the different conditions was small, and as expected, each elephant had a higher probability of choosing the larger reward at the end rather than at the beginning of each condition.

Each elephant had a right-side preference. The preference for one side over another has been previously observed in elephants (Plotnik et al., 2013). Previous studies on the quantity discrimination of elephants did not formally analyse the effect of the location of the larger alternative on the probability of choosing it. However, Plotnik et al. (2013), comparing the effect of visual and vocal cues in guiding elephants' choices and using different analyses from this paper, found that Asian elephants could show a side preference for either side. To know whether elephants have a common side preference or show individual variation, for example as humans do (Porac and Coren, 1981), is a topic that needs further research.

Among the four tested elephants, Chova always chose the larger alternative less than the others in any task. This might be due to the serious injury he suffered in the trunk, which might have damaged his olfactory capacity. It is quite interesting that though his ability to discriminate was lower than that of the females, he was still able to discriminate better than by chance on average, suggesting that though his olfaction might be compromised, it is still a valuable sense to make optimal foraging choices, at least at short smelling distances.

In conclusion, this study confirms that the untrained tendency of African elephants to choose the larger alternative in binary choices over different quantities of the same edible item is mainly affected by the ratio and absolute difference between the alternatives (the more different the alternatives, the higher the probability of choosing the larger one). The effect of magnitude depends more on the individual, with Nuanedi being the only elephant choosing much better when discriminating between larger quantities of boskos.

In addition, the average accuracy of African elephants in this study did not differ from the average accuracy of African and Asian elephants in studies where alternatives were presented through different senses, and it did not differ substantially between the two conditions of the experiment. This suggests that discrimination ability does not depend on the sense used to investigate the alternatives. The differences found in the performances of single individuals highlight the importance of using a large sample size to be able to make conclusions that might apply to the species. To the best of our knowledge, only six studies have focused on the quantity discrimination ability of elephants so far, of which, only two tested more than three individuals (Irie-Sugimoto et al., 2009; Plotnik et al., 2019).

References

- Agrillo, C., Bisazza, A., 2014. Spontaneous versus trained numerical abilities. A comparison between the two main tools to study numerical competence in non-human animals. *Journal of Neuroscience Methods* 234, 82–91.
- Agrillo, C., Dadda, M., Bisazza, A., 2007. Quantity discrimination in female mosquitofish. *Animal Cognition* 10, 63–70.
- Agrillo, C., Dadda, M., Serena, G., 2008. Choice of Female Groups by Male Mosquitofish (*Gambusia holbrooki*). *Ethology* 114(5), 479–488.
- Amsel, A., 1958. The role of frustrative nonreward in noncontinuous reward situations. *Psychological bulletin* 55(2), 102.
- Bánszegi, O., Urrutia, A., Szenczi, P., Hudson, R., 2016. More or less: spontaneous quantity discrimination in the domestic cat. *Animal Cognition* 19, 879–888.
- Bates, L.A., Sayialel, K.N., Njiraini, N.W., Poole, J.H., Moss, C.J., Byrne, R.W., 2008. African elephants have expectations about the locations of out-of-sight family members. *Biology Letters* 4(1), 34–36.
- Battalio, R.C., Kagel, J.H., MacDonald, D.N., 1985. Animals' choices over uncertain outcomes: Some initial experimental results. *The American Economic Review* 75(4), 597–613.
- Benson-Amram, S., Gilfillan, G., McComb, K., 2018. Numerical assessment in the wild: insights from social carnivores. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373(1740), 20160508.
- Bester, T., Schmitt, M.H., Shrader, A.M., 2023. The deterrent effects of individual monoterpene odours on the dietary decisions of African elephants. *Animal Cognition* 26(3), 1049–1063.
- Bisazza, A., Gatto, E., 2021. Continuous versus discrete quantity discrimination in dune snail (Mollusca: Gastropoda) seeking thermal refuges. *Scientific Report* 11(1), 3757.
- Butterworth, B., 2022. *Can Fish Count?: What Animals Reveal about Our Uniquely Mathematical Mind*. Hachette UK.
- Caraco, T., Martindale, S., Whittam, T.S., 1980. An empirical demonstration of risk-sensitive foraging preferences. *Animal Behaviour* 28(3), 820–830.
- Davis, H., 1984. Discrimination of the number three by a raccoon (*Procyon lotor*). *Animal Learning & Behavior* 12(4), 409–413.
- Hauser, M.D., Carey, S., Hauser, L.B., 2000. Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267(1445), 829–833.
- Irie, N., Hasegawa, T., 2012. Summation by Asian Elephants (*Elephas maximus*). *Behavioral Sciences* 2(2), 50–56.
- Irie, N., Hiraiwa-Hasegawa, M., Kutsukake, N., 2019. Unique numerical competence of Asian elephants on the relative numerosity judgment task. *Journal of Ethology* 37, 111–115.
- Irie-Sugimoto, N., Kobayashi, T., Sato, T., Hasegawa, T., 2009. Relative quantity judgment by Asian elephants (*Elephas maximus*). *Animal Cognition* 12, 193–199.
- Kilian, A., Yaman, S., von Fersen, L., Güntürkün, O., 2003. A bottlenose dolphin discriminates visual stimuli differing in numerosity. *Animal Learning & Behavior* 31, 133–142.

- McComb, K., Reby, D., Baker, L., Moss, C., Sayialel, S., 2003. Long-distance communication of acoustic cues to social identity in African elephants. *Animal Behaviour* 65(2), 317–329.
- Miletto Petrazzini, M.E., Fraccaroli, I., Gariboldi, F., Agrillo, C., Bisazza, A., Bertolucci, C., Foà, A., 2017. Quantitative abilities in a reptile (*Podarcis sicula*). *Biology Letters* 13(4), 20160899.
- Miller, A.K., Hensman, M.C., Hensman, S., Schultz, K., Reid, P., Shore, M., Brown, J., Furton, K.G., Lee, S., 2015. African elephants (*Loxodonta africana*) can detect TNT using olfaction: Implications for biosensor application. *Applied Animal Behaviour Science* 171, 177–183.
- Perdue, B.M., Talbot, C.F., Stone, A.M., Beran, M.J., 2012. Putting the elephant back in the herd: elephant relative quantity judgments match those of other species. *Animal Cognition* 15, 955–961.
- Plotnik, J.M., Brubaker, D.L., Dale, R., Tiller, L.N., Mumby, H.S., Clayton, N.S., 2019. Elephants have a nose for quantity. *Proceedings of the National Academy of Sciences* 116(25), 12566–12571.
- Plotnik, J.M., Pokorny, J.J., Keratimanochaya, T., Webb, C., Beronja, H.F., Hennessy, A., Hill, J., Hill, V.J., Kiss, R., Maguire, C., Melville, B.L., Morrison, V.M.B., Seecoomar, D., Singer, B., Ukehaxhaj, J., Vlahakis, S.K., Ylli, D., Clayton, N.S., Roberts, J., Fure, E.L., Duchatelier, A.P., Getz, D., 2013. Visual Cues Given by Humans Are Not Sufficient for Asian Elephants (*Elephas maximus*) to Find Hidden Food. *PLoS One* 8, e61174.
- Plotnik, J.M., Shaw, R.C., Brubaker, D.L., Tiller, L.N., Clayton, N.S., 2014. Thinking with their trunks: elephants use smell but not sound to locate food and exclude nonrewarding alternatives. *Animal Behaviour* 88, 91–98.
- Porac, C., Coren, S., 1981. *Lateral Preferences and Human Behavior*. Springer, New York, NY.
- Pyke, G., 1984. Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology, Evolution and Systematic* 15(1), 523–575.
- Rizvanovic, A., Amundin, M., Laska, M., 2013. Olfactory Discrimination Ability of Asian Elephants (*Elephas maximus*) for Structurally Related Odorants. *Chemical Senses* 38(2), 107–118.
- Schmitt, M.H., Shuttleworth, A., Ward, D., Shrader, A.M., 2018. African elephants use plant odours to make foraging decisions across multiple spatial scales. *Animal Behaviour* 141, 17–27.
- Snyder, R.J., Barrett, L.P., Emory, R.A., Perdue, B.M., 2021. Performance of Asian elephants (*Elephas maximus*) on a quantity discrimination task is similar to that of African savanna elephants (*Loxodonta africana*). *Animal Cognition* 24(5), 1121–1131.
- StataCorp, 2023. *Stata 18 Bayesian Analysis Reference Manual*. College Station, TX: Stata Press.
- Vonk, J., Beran, M.J., 2012. Bears ‘count’ too: quantity estimation and comparison in black bears, *Ursus americanus*. *Animal Behaviour* 84(1), 231–238.
- Wood, M., Chamailé-Jammes, S., Hammerbacher, A., Shrader, A.M., 2022. African elephants can detect water from natural and artificial sources via olfactory cues. *Animal Cognition* 25(1), 53–61.

CHAPTER 4: African Elephant Olfactory Quantity Discrimination of Fruits With or Without Direct Contact With the Source of Smell

Introduction

Quantity discrimination ability is widespread in animals' kingdoms due to the advantages it brings (Agrillo and Bisazza, 2014), such as supporting foraging choices (Caraco et al., 1980; Farnsworth and Smolinski, 2006), or planning territorial defence based on the estimated number of intruders (McComb et al., 1994). Different taxa, from molluscs (Bisazza and Gatto, 2021) to mammals (Kilian et al., 2003; Hanus and Call, 2007; Beran et al., 2008) have been demonstrated to have at least the numerical competence required to discriminate between two different quantities of the same item. Unsurprisingly, Asian (*Elephas maximus*) and African elephants (*Loxodonta africana*) are among the animals that have been demonstrated to successfully quantitatively discriminate.

Previous studies have focused on Asian elephants (Irie-Sugimoto et al., 2009; Irie and Hasegawa, 2012; Snyder et al., 2021) and African (Perdue et al., 2012) elephants ability to discriminate between quantities of a specific food that they could see and/or hear falling in a container. The elephants were expected to choose the alternative that maximised their net energy intake (Pyke, 1984), and were considered successful at discriminating between two alternatives if they chose the larger reward more than by chance. The authors of each study investigated the effect of the ratio of the alternatives, i.e. the smaller divided by the larger alternative, the absolute difference between the alternatives, i.e. the larger minus the smaller alternative, and the magnitude

of the alternatives, i.e. the smaller plus the larger alternative, on the probability of the elephants choosing the larger reward.

One group of studies found that both Asian and African elephants behaved in ways that support an accumulator model: their accuracy was negatively correlated with the ratio and positively correlated with the absolute difference between the alternatives (Perdue et al., 2012; Snyder et al., 2021). According to the accumulator model, the magnitudes of the alternatives are spaced linearly with scalar variability (Gallistel and Gelman, 1992). This means that an animal can approximately represent numbers that are quite large (Sulkowski and Hauser, 2001), with representation becoming less exact the larger the numbers are (Butterworth, 2022: Chapter 1). The more similar the two alternatives are, the higher the expected overlap between represented intervals. Therefore, according to the accumulator model, the ratio of the alternatives is the primary limiting factor on the ability of an animal to discriminate between different quantities (Butterworth, 2022: Chapter 1).

The second group of studies, on the other hand, found that the accuracy of Asian elephants in discriminating between different numbers of shapes on a screen or real food was not affected by either the ratio, absolute difference, or magnitude of the alternatives (Irie-Sugimoto et al., 2009; Irie and Hasegawa, 2012; Irie et al., 2019). The authors suggest that the large memory of Asian elephants might allow them to store and compare a precise representation of many objects, which would make their discrimination ability very accurate even when the alternatives are similar to each other (Irie-Sugimoto et al., 2009).

None of the studies cited above cancelled or masked the smell of the alternatives, always giving the elephants redundant cues (Snyder et al., 2021). Therefore, it is possible that in each of these studies, elephants used olfactory information to discriminate. One study investigated the quantity discrimination ability of Asian elephants when only olfactory information about the rewards was available (Plotnik et al., 2019). The researchers offered the elephants a series of binary choices between different quantities of sunflower seeds concealed in two opaque buckets. The elephants could only assess the alternatives by smelling the top of the buckets, where a perforated lid allowed the content smell to be perceived. The elephants' performance supported the accumulator model, increasing with a decrease in ratio value and an increase in absolute difference between the alternatives (Plotnik et al., 2019).

It is surprising that only one study focussed on elephant quantity discrimination based on olfaction only. Olfaction is generally thought to be the most relevant sensory modality to elephants in social (Jacobson and Plotnik, 2020) and foraging decision-making (Plotnik et al., 2014; Schmitt et al., 2018). From a physiological point of view, the African elephant is the mammal species possessing the most olfactory genes (Niimura et al., 2014). They use olfaction to obtain information from the environment, to learn about an individual's sexual stage (Jacobson and Plotnik, 2020), and to detect the presence of potential aggressors (Bates et al., 2007). In addition, African elephants could locate their favourite food using olfactory cues only, even when the smell was deliberately masked by other stronger scents (McArthur et al., 2019). African elephants have also been trained to detect the presence of TNT with success rates higher than dogs (Miller et al., 2015). Finally, a study by Schmitt et al. (2018) demonstrated that African elephants can perceive olfactory cues coming from plant parts and make foraging

decisions based on them, both when the cue was in a box by the elephant trunk and from a ~7 m distance (Schmitt et al., 2018).

The current study represents the first attempt to assess the quantity discrimination ability of African elephants when the stimuli are represented by different numbers of one fruit type, only olfactory cues about the size of the rewards are available, and in a condition in which the alternatives cannot be inspected by directly smelling the container of the alternatives. Indeed, the discrimination ability of the elephants was compared between apples and oranges, and by adding a new “condition” never tested before. A comparison was made between the performance of the elephants smelling directly on the top of perforated buckets containing the rewards (contact condition), as done by Plotnik et al. (2019) with Asian elephants, with the performance of the elephants choosing the reward from a distance, without the possibility of placing the trunk on top of the buckets (no-contact condition).

The study aims to determine whether the different nature and intensity of the smell of fruits in a contact and a no-contact condition affect the choices of the elephants. Suppose the olfactory discrimination of African elephants is as acute as many believe; in that case, elephants should be able to discriminate in contact and no-contact conditions and be as accurate with both types of fruits. In addition, the effects of ratio, absolute difference, and cumulative magnitude of the alternatives were tested. From the literature (Perdue et al., 2012; Plotnik et al., 2019; Snyder et al., 2021) and my previous results (Chapter 3), we expected elephants to successfully discriminate via olfaction only, and to be negatively affected by the ratio and positively affected by the absolute difference between the alternatives. The learning ability of the elephants was also tested by comparing their performance at the start and end of each task. Finally, it was

assessed whether the individual elephants showed side preferences, indicated by their performance being better on one side than the other, by testing the effect of the side of the larger reward on the probability of the elephants choosing it.

Methods

Data collection

The subjects of the study were the four semi-tame adult African elephants hosted at Adventures with Elephants (AwE), in Limpopo, South Africa, presented in the General Methodology section of Chapter 1. The materials used in this experiment were a canvas mat and the two plastic buckets used in the previous Chapter, as can be seen in Figure 4.1.



Figure 4.1: One of the two perforated buckets containing oranges used in the “apple-orange discrimination experiment”.

Apples were selected as a fruit to use as they were the favourite fruit of most of the elephants in a fruit preference experiment (see Chapter 2). Oranges had been used as the reward for the elephants in many different training sessions before this study, and all the elephants liked them. As presented in Chapter 2, when allowed to choose between half an apple or half an orange, Chova and Nuanedi had a slight preference for apples, while Mussina and Shan had a strong preference for oranges.

The elephants were presented with each possible combination of pairs between 1 and 5 fruits, and a few choices between 1 and 6 fruits, for a total of 11 prospects shown in Table A2 in Appendix 1. To avoid possible Clever Hans effects, the handlers did not know how many fruits were in the buckets until the elephant chose, and the researcher, who prepared the buckets, stood behind the handlers looking to the opposite side of the elephant.

Either 1, 2 or 3 trials a day per elephant were performed, depending on the availability of fruits. Trials with apples were performed from June 2021 to May 2022 starting with the contact condition, and trials with oranges from February to October 2022, also starting with the contact condition. This implies the temporal overlap of some trials of the no-contact condition with apples and trials of the contact condition with oranges.

Contact condition: Each elephant was presented with a binary choice between two different quantities of apples or oranges that they could smell directly from the bucket but not see. The canvas mat was located roughly four metres from the buckets and the buckets were 50 cm from each other (Figure 4.2). The elephant started the experiment on the mat and when released with the command “Walk up and smell”, the

elephant approached the alternatives, smelled both of them by placing the trunk on the lid of the buckets alternatively and indicated a choice by touching the preferred bucket with the trunk. Each bucket was kept in place by one handler who placed his foot on top of the bucket as can be seen in Figure 4.3. The elephant was given the content of the chosen bucket and the unchosen bucket and its content were removed.



Figure 4.2: A view of the setup of the contact condition of the “apple-orange discrimination experiment”.

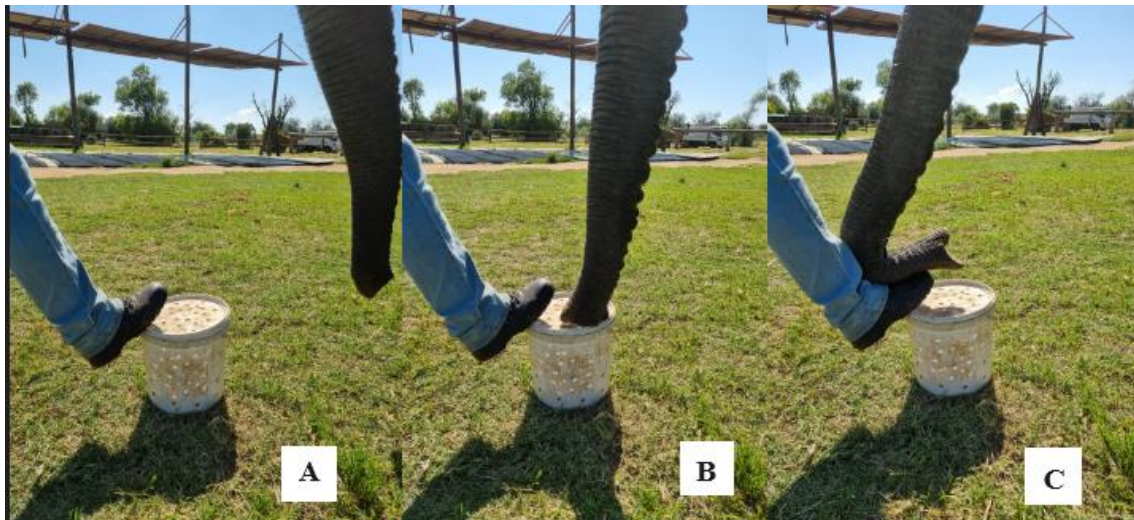


Figure 4.3: An overview of the choosing phase of the “apple-orange discrimination experiment”. a) The handlers keep the buckets containing the alternatives in place with a foot while the elephant approaches them; b) the elephant smells the top of the buckets to acquire information about the number of oranges or apples they contain; c) the elephant chooses one of the buckets. Usually, the elephant expresses the choice by touching the chosen bucket, however Shan (the elephant in the picture) behaves differently, always expressing her choice by pushing on the handler’s leg.

No-contact condition: The elephants could not investigate the alternatives by smelling directly on top of the bucket’s lid, but they could only smell the content of the buckets from 5 metres away. The only difference in set-up from the contact condition is that the perforated buckets were now located five metres from the elephant and three metres from each other.

The researcher positioned the mat and buckets so that the wind always blew from the alternatives toward the elephant. A small flag was used to identify the wind direction. The elephant stayed stationary on the mat for 10 seconds or until she or he had pointed the trunk in the direction of the buckets and had smelt the air. After being released by a handler with the word “Choose”, the elephant reached the chosen alternative and received it. The alternatives were the same combination of pairs of apples or oranges used in the contact condition.

Data analysis

The statistical analysis has been conducted with Stata 18, documented in StataCorp (2023), using Bayesian Hierarchical Models (BHM) with a probit likelihood (see Chapter 1 for details on the Bayesian approach). The dependent variable used was the binomial variable “choice of the larger alternative” (1 for yes or 0 for no).

To assess if each elephant chose the larger alternative more than by chance, two BHM with no covariates, one per fruit type, were estimated using a single-chain MCMC of 100,000 samples and an additional 50,000 burn-in samples for each model. They will be referred to as BHMapple and BHMorange, and their results are presented per condition.

To assess whether the probability of each elephant choosing the larger alternative *improved over time*, two BHM, one per fruit type, with a continuous covariate added to measure the experience interacted with the condition of the experiment and the binary variable for each elephant, were estimated. Experience was measured by the sequential choice number over time for each elephant. These models will be referred to as BHMta for apples and BHMto for oranges. Both models were estimated using a single-chain MCMC of 100,000 samples and an additional 50,000 burn-in samples. To determine if the elephants learned through the experiment, predictive posterior distributions of the choice of the larger alternative have been estimated using all the data, and by setting the “experience” variable to the first and the last trial of the condition, so as to simulate a choice without experience and a choice with full experience of the task. These simulations considered choices that spanned all possible prospects used in the experiment. This means that the simulated choices

without experience and with full experience are comparable and representative of all possible choices.

To assess what *variables* affected the probability of the elephants choosing the larger alternative, two more BHMs were estimated using the relevant explanatory variables (continuous ratio and absolute difference, and categorical condition and chosen side) in interaction with the binary variable for individual elephants. These models will be referred to as BHM_{rda} for apples and BHM_{rdo} for oranges. The simulation for these models was done with 5 MCMC chains of 500,000 samples per chain, plus 50,000 burn-in samples per chain.

Each of the BHM simulations converged satisfactorily. The convergence displays are not presented here but are available upon request.

The effect of experience, ratio, absolute difference, condition of the experiment, and location of the larger alternative are presented in the form of the Average Marginal Effect (AME). In addition, the strength of the effect of the ratio of the alternatives and the absolute difference between the alternatives at specific prospects is compared and presented using the Region Of Practical Equivalence (ROPE). See Chapter 1 for details on the definition and calculation of AME and ROPE.

Results

Choosing the larger alternative more than by chance

A total of 1320 observations were collected, 166 choices made by each elephant with apples, and 164 choices made by each elephant with oranges. The raw data show that, on average, the elephants chose the larger quantity of apples 63% of the time in the

contact condition and 51% of the time in the no-contact condition. The bucket containing more oranges was chosen on average 70% of the time in the contact condition and 51% of the time in the no-contact condition.

The plots of the posterior distributions of the probability of choosing the larger alternative from models BHMApple and BHMOrange are presented in Figure 4.4. These plots show that each elephant almost certainly chose better than by chance in the contact condition using either fruit, with the lowest probability of preferring the larger reward being 0.97 for Chova discriminating between apples. Table 4.1 shows the exact values for each elephant, fruit type, and condition.

By contrast, the elephants as a group did not choose better than by chance when they could *not* smell the alternatives directly (no-contact condition), as shown in Figure 4.4. However, this pooled result conceals substantial heterogeneity across individuals. Chova and Nuanedi chose the larger reward more than by chance with apples (with a probability of 0.76 and 0.63 respectively) and Shan chose similarly well with oranges (with a probability of 0.86), as can be seen in Table 4.1.

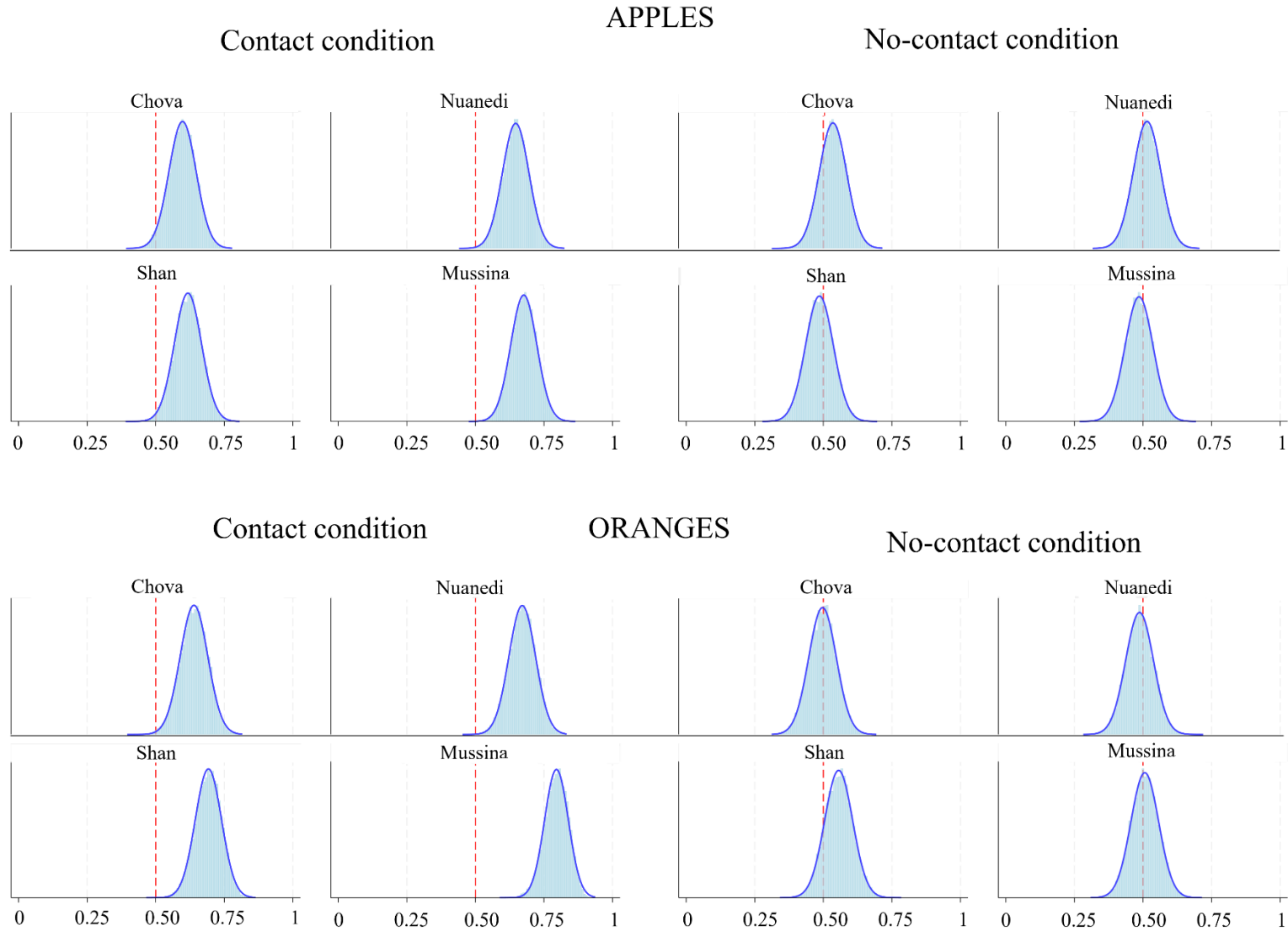


Figure 4.4: The posterior distribution of the elephant probabilities of choosing the larger alternative estimated from the BHMs without covariates, BHMapple (top panel) and BHMorange (bottom panel), in the “apple-orange discrimination experiment”. The dashed red line represents the probability of choosing the larger alternative by chance.

Table 4.1: The posterior estimates of the probability of choosing the larger alternative for each elephant estimated from the BHMs without covariates, BHMapple and BHMorange, per condition, in the “apple-orange discrimination experiment”. Mean and Sd represent the mean and standard deviation of the posterior distribution, 50% HPD low and 50% HPD high represent the thresholds of the 50% Highest Probability Density of the posterior. The last column represents the probability of the posterior probability being greater than 0.50.

Subject	Mean	Sd	50% HPD low	50% HPD high	Prob > 0.50
Apples, contact condition					
Chova	0.60	0.05	0.57	0.63	0.97
Nuanedi	0.65	0.05	0.62	0.68	1.00
Shan	0.62	0.05	0.58	0.65	0.99
Mussina	0.68	0.05	0.65	0.71	1.00
Apples, no-contact condition					
Chova	0.53	0.05	0.50	0.57	0.76
Nuanedi	0.52	0.05	0.48	0.55	0.63
Shan	0.49	0.05	0.45	0.52	0.39
Mussina	0.49	0.05	0.46	0.52	0.39
Oranges, contact condition					
Chova	0.63	0.05	0.61	0.68	1.00
Nuanedi	0.67	0.05	0.64	0.71	1.00
Shan	0.69	0.05	0.66	0.73	1.00
Mussina	0.80	0.04	0.77	0.77	1.00
Oranges, no-contact condition					
Chova	0.50	0.05	0.46	0.53	0.48
Nuanedi	0.49	0.05	0.45	0.52	0.40
Shan	0.56	0.05	0.52	0.59	0.86
Mussina	0.51	0.05	0.47	0.54	0.55

Learning

The estimates from models BHMta and BHMto are presented in Table 4.2. An elephant having a larger probability of choosing the larger reward at the end than at the beginning of a task suggests that learning took place throughout the task. In the contact condition with apples (panel A of Table 4.2), Chova was the only elephant not having a higher predicted preference for the larger alternative in the last trial than in the first trial, going from a 0.86 to a 0.73 probability of preferring the larger reward at the beginning and the end of the condition respectively. All the other elephants chose the larger reward more at the end than at the beginning of the condition, as can also be seen in Figures 4.5 and 4.6 from the distance between the green and blue lines in the top panel of the plot. In the no-contact condition with apples (panel C of Table 4.2), each elephant had a higher predicted preference for the larger reward at the beginning rather than at the end of the condition.

In the contact condition with oranges (panel B of Table 4.2), Chova's predicted preference for the larger alternative drastically dropped from a probability of 1.00 in the first trial of the condition to a probability of 0.61 in the last trial. The predicted preference for the larger alternative for Nuanedi was slightly higher at the beginning compared to the end of the condition, and Shan and Mussina had the same predicted preferences at the start and end of the contact condition with oranges. In the no-contact condition with oranges (panel D of Table 4.2), each elephant had higher predicted preferences for the larger alternative in the first compared to the last trial of the condition, as can be seen in Figures 4.7 and 4.8. The difference was particularly strong for Chova and Mussina, who went from having a predicted probability of preferring the

larger alternative in the first trial of the no-contact condition of 0.99 and 1.00 respectively, to a probability of 0.06 in the last trial of the condition for both elephants.

Table 4.2: The predictive posterior probability of each elephant choosing the larger alternative in the first and last trials of the contact condition with apples (A) and oranges (B) and of the no-contact condition with apples (C) and oranges (D). Mean is the mean of the predicted posterior distribution, “P > 0.50” represents the probability of the predictive posterior distribution being greater than 0.50. The table below is coloured to help visualise the four different combinations of conditions and fruits per elephant.

	A				B			
	<u>APPLES</u> Contact condition				ORANGES Contact condition			
	Without experience		With full experience		Without experience		With full experience	
Subject	Mean	P > 0.50	Mean	P > 0.50	Mean	P > 0.50	Mean	P > 0.50
Chova	0.59	0.86	0.56	0.73	0.67	1.00	0.57	0.61
Nuanedi	0.57	0.79	0.72	0.99	0.65	1.00	0.65	0.95
Shan	0.53	0.64	0.69	0.97	0.67	0.95	0.69	0.96
Mussina	0.57	0.79	0.79	1.00	0.79	1.00	0.77	1.00
	C				D			
	APPLES No-contact condition				ORANGES No-contact condition			
	Without experience		With full experience		Without experience		With full experience	
Subject	Mean	P > 0.50	Mean	P > 0.50	Mean	P > 0.50	Mean	P > 0.50
Chova	0.56	0.91	0.53	0.67	0.56	0.99	0.45	0.06
Nuanedi	0.53	0.76	0.49	0.49	0.55	0.90	0.45	0.19
Shan	0.50	0.51	0.47	0.35	0.61	0.99	0.54	0.76
Mussina	0.51	0.57	0.45	0.25	0.62	1.00	0.43	0.06

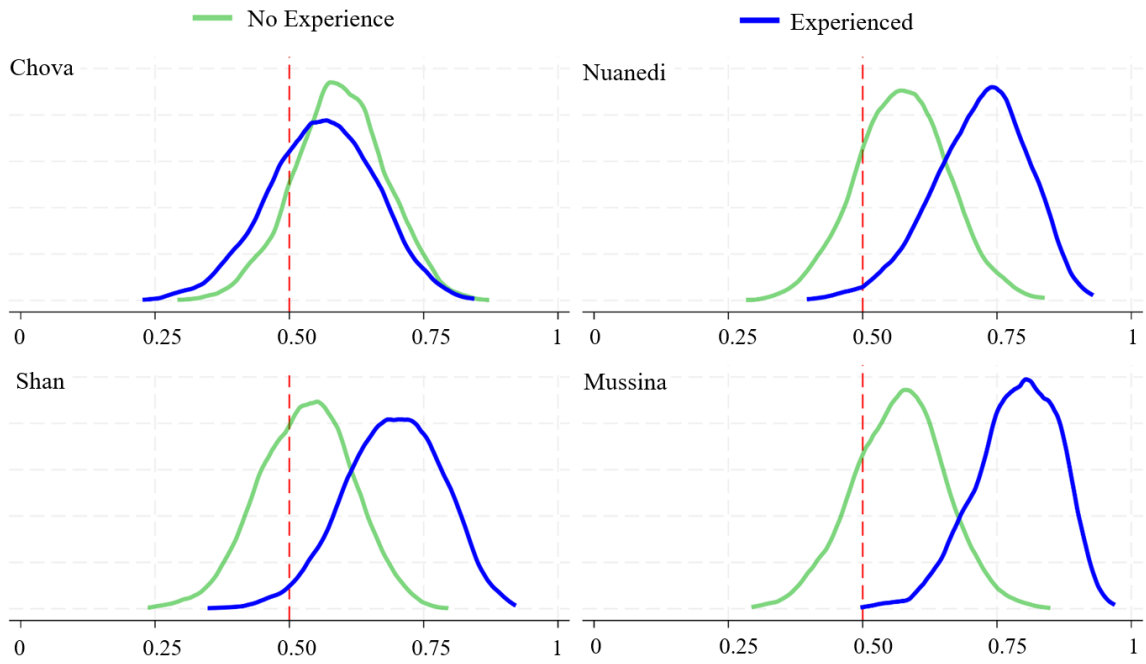


Figure 4.5: The predictive posterior probability of each elephant choosing the larger alternative in the contact condition in the first trial (green) and the last trial (blue) of the condition when choosing between different quantities of apples, estimated from the BHMta in the “apple-orange discrimination experiment”. The dashed red line represents the probability of choosing the larger alternative by chance. The blue curve lying to the right side of the green line suggests learning took place throughout the condition.

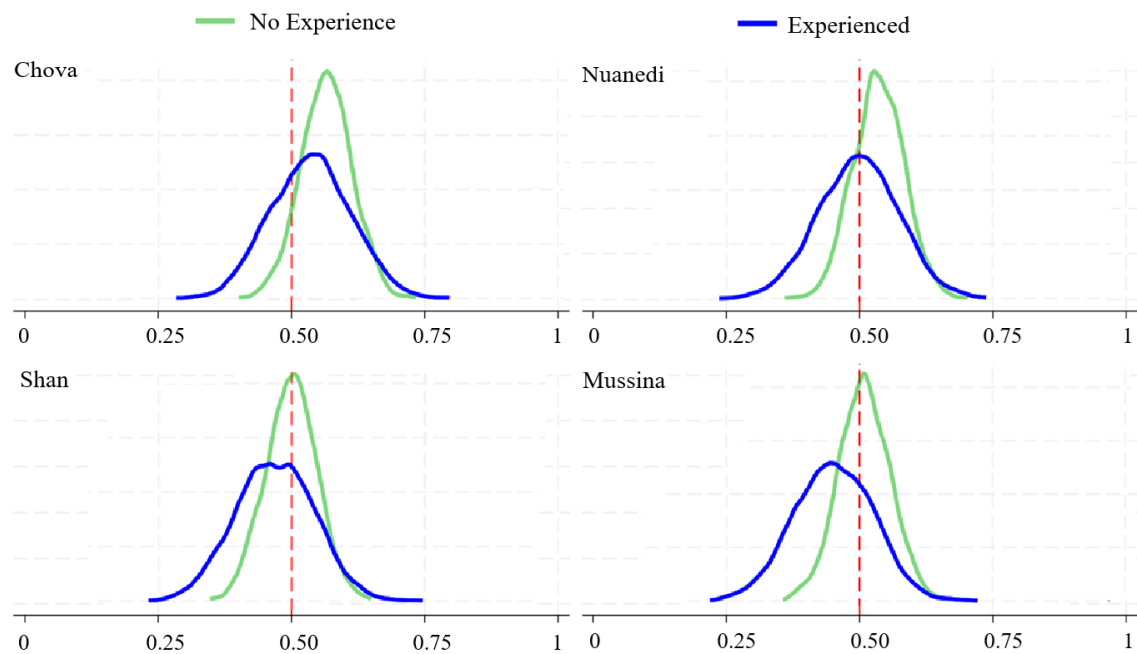


Figure 4.6: The predictive posterior probability of each elephant choosing the larger alternative in the no-contact condition in the first trial (green) and the last trial (blue) of the condition when choosing between different quantities of apples, estimated from the BHMta in the “apple-orange discrimination experiment”. The dashed red line represents the probability of choosing the larger alternative by chance. The blue curve lying to the right side of the green line suggests learning took place throughout the condition.

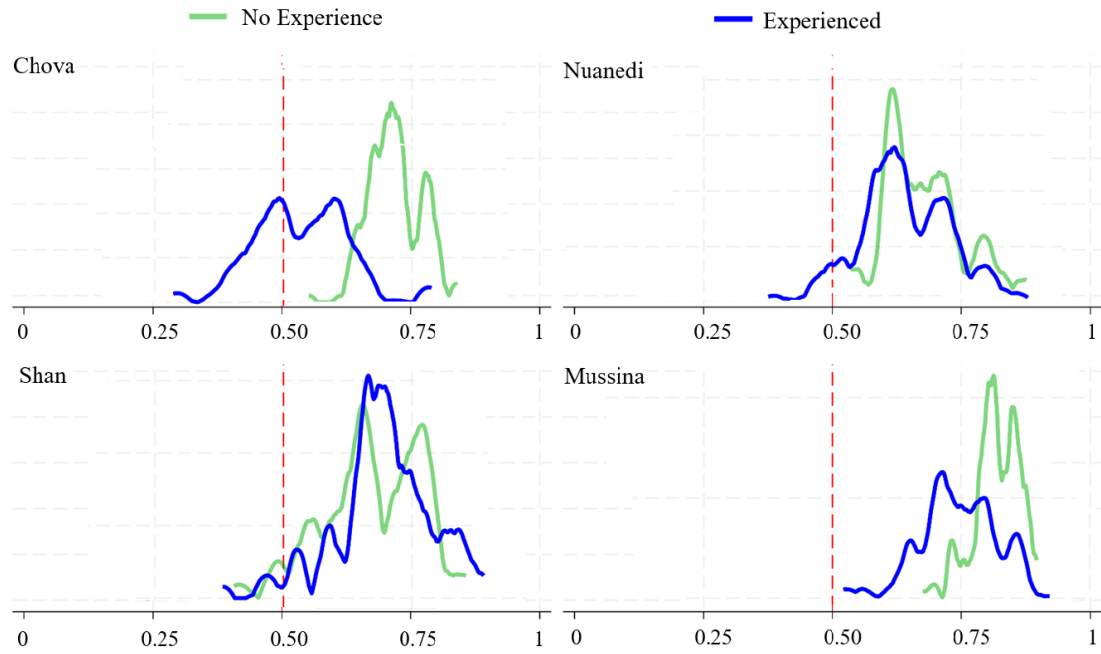


Figure 4.7: The predictive posterior probability of each elephant choosing the larger alternative in the contact condition in the first trial (green) and the last trial (blue) of the condition when choosing between different quantities of oranges, estimated from the BHMto in the “apple-orange discrimination experiment”. The dashed red line represents the probability of choosing the larger alternative by chance. The blue curve lying to the *left* side of the green line suggests *no* learning took place throughout the condition.

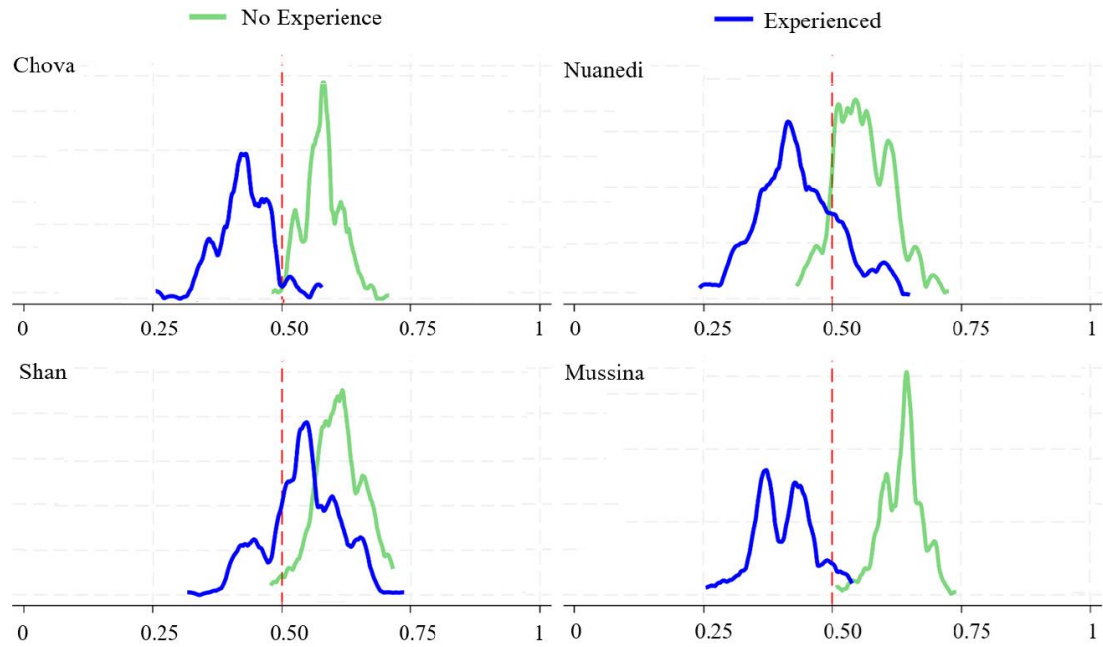


Figure 4.8: The predictive posterior probability of each elephant choosing the larger alternative in the no-contact condition in the first trial (green) and the last trial (blue) of the condition when choosing between different quantities of oranges, estimated from the BHMto in the “apple-orange discrimination experiment”. The dashed red line represents the probability of choosing the larger alternative by chance. The blue curve lying to the left of the green line suggests *no* learning took place throughout the condition.

Effects on choice

Estimates from the models BHM_{rda} and BHM_{rdo} show that the *ratio* of the alternatives did not have a strong effect on the probability of any elephant choosing the larger alternative, as shown in the left section of Figure 4.9. The ratio of the alternatives had an expected, though slight, negative effect on the elephants choosing the larger reward when discriminating between apples, except for Chova, whose discrimination was virtually unaffected by the ratio of the alternatives (top left panel of Figure 4.9). When discriminating between oranges (bottom left panel of Figure 4.9) the ratio of the alternatives had a negative effect on Shan choosing the larger reward and it had an unexpected positive effect on the other elephants.

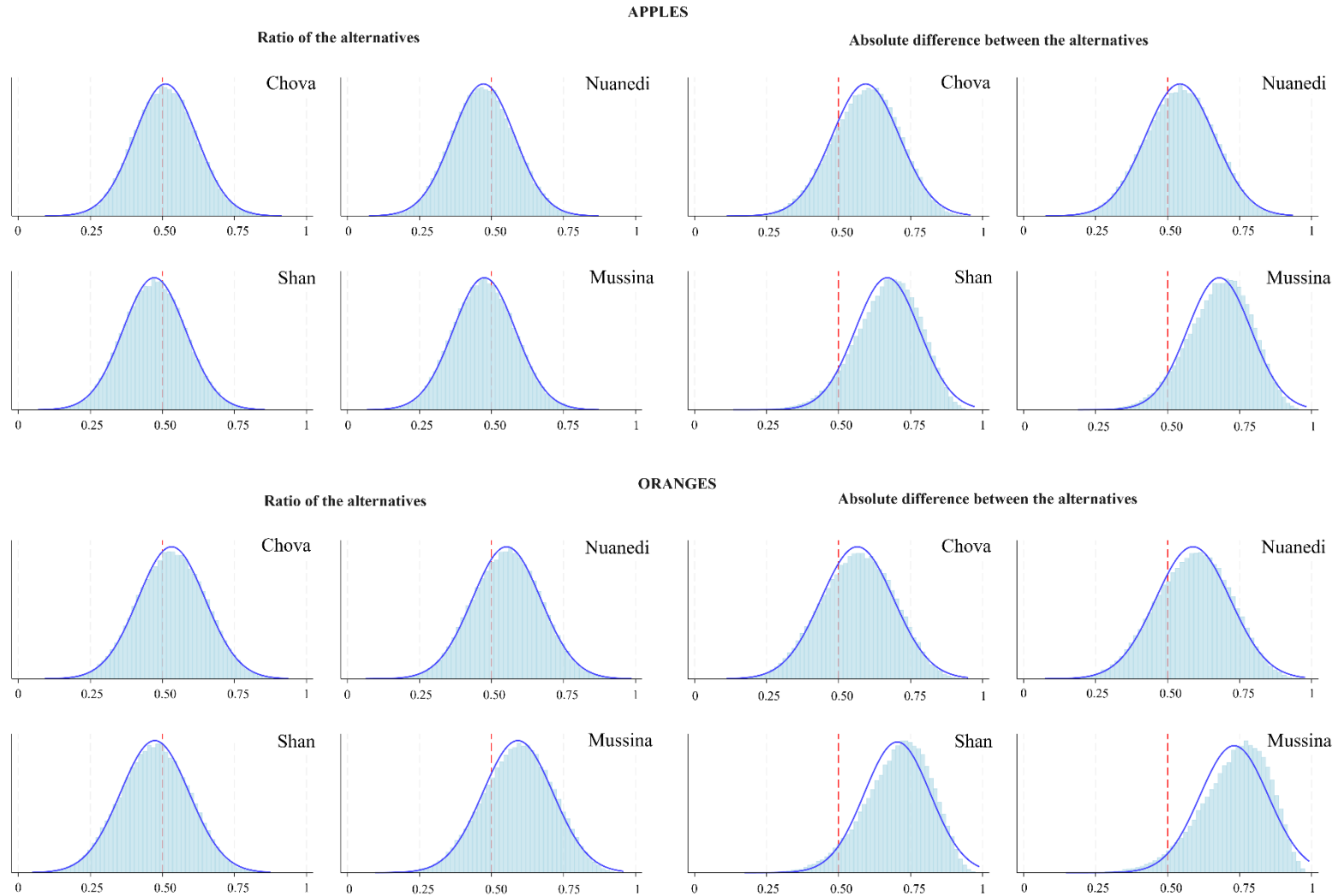


Figure 4.9: The posterior distribution of the effect of the ratio between the alternatives (left section) and the absolute difference of the alternatives (right section) on the elephant probabilities of choosing the larger alternative when discriminating between apples, estimated from the BHMrd (top panel), or when discriminating between oranges, estimated from the BHMrd (bottom panel) in the “apple-orange discrimination experiment”. The dashed red line represents the probability of choosing the larger alternative by chance.

The *absolute difference* between the alternatives had an expected positive effect on the probability of each elephant choosing the larger alternative with both fruits, as shown in the right section of Figure 4.9. The effect was more evident for Mussina and Shan than for Chova and Nuanedi, regardless of the fruit involved in the experiment.

The *side* where the larger alternative was located affected the elephants in different ways, depending on the fruit at stake. This can be seen in Figure 4.10, showing the AME distributions of the elephants in the apples (left section) and oranges (right section) discrimination. The AME distributions represent the difference in the probability of each elephant choosing the larger reward when it was located on their left side compared to when it was located on their right side. A distribution centred to the left of the reference line, i.e. being negative, means that the elephant had a preference for the right side. *Mutatis mutandis*, when the distribution is centred to the right of the reference line, the elephant had a preference for the left side.

With both fruits, each elephant showed a clear preference for one side, but not always the same side. When discriminating between different quantities of apples, Chova, Mussina, and Shan had a preference for the right side. Nuanedi, on the contrary, had a left-side preference. When discriminating between different quantities of oranges, as shown in the right panel of Figure 4.10, Mussina and Nuanedi maintained their side preference, to the right and left side respectively, while Chova and Shan switched their side preference from preferring the right side with apples to preferring the left side with oranges.

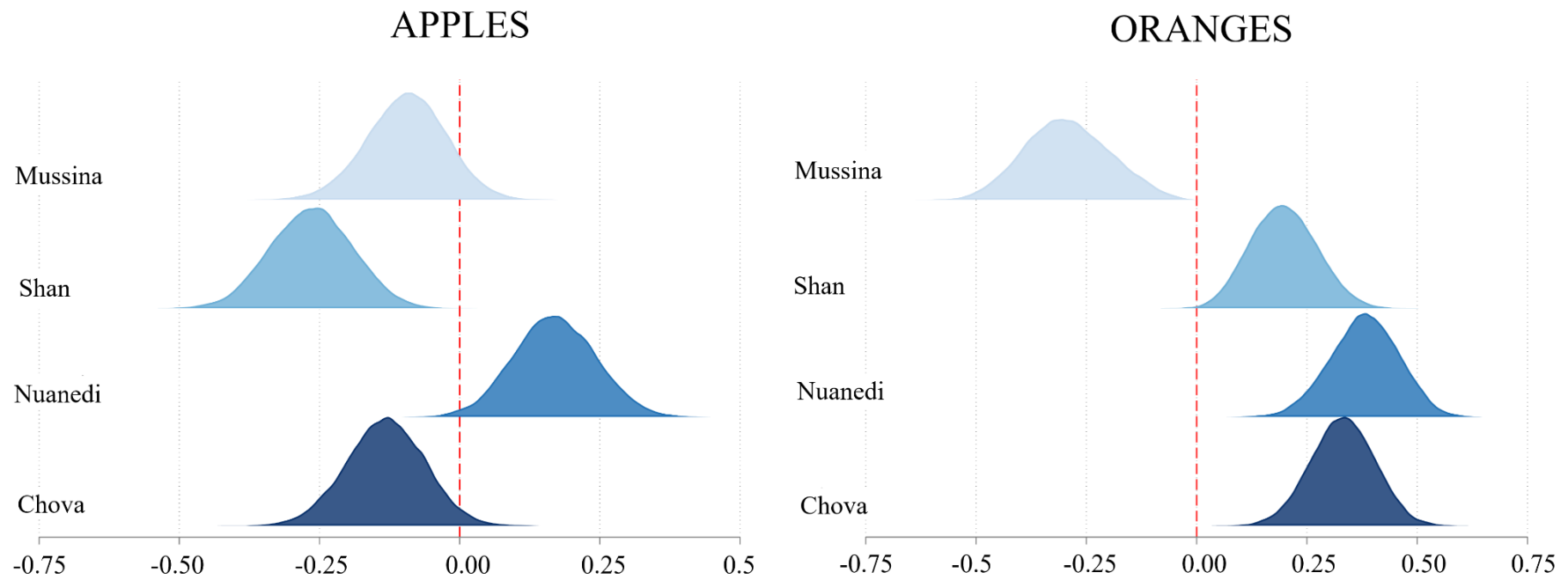


Figure 4.10: The AME of the larger alternative being to the left side on the probability of each elephant choosing the larger alternative when discriminating between apples, estimated from the BHMrdA (left panel) and when discriminating between oranges, estimated from the BHMrdO (right panel) in the “apple-orange discrimination experiment”. The dashed red line represents a 0 AME.

The *condition* of the experiment, being with or without contact with the bucket containing the rewards when smelling to assess the quantities of fruit in the prospect, affected each elephant alike. As shown in Figure 4.11, each elephant had a higher probability of choosing the larger alternative in the contact condition compared to the no-contact condition, with both apples and oranges. This result was also evident from the estimates of the BHMs without covariates represented numerically in Table 4.1 and visually in Figure 4.4. The difference is that Figure 4.11 shows results from BHM_{rda} and BHM_{rdo} where the ratio, absolute difference, and chosen side are controlled for, offering a clearer representation of the effect of the contact vs no-contact condition on the choice of the elephants.

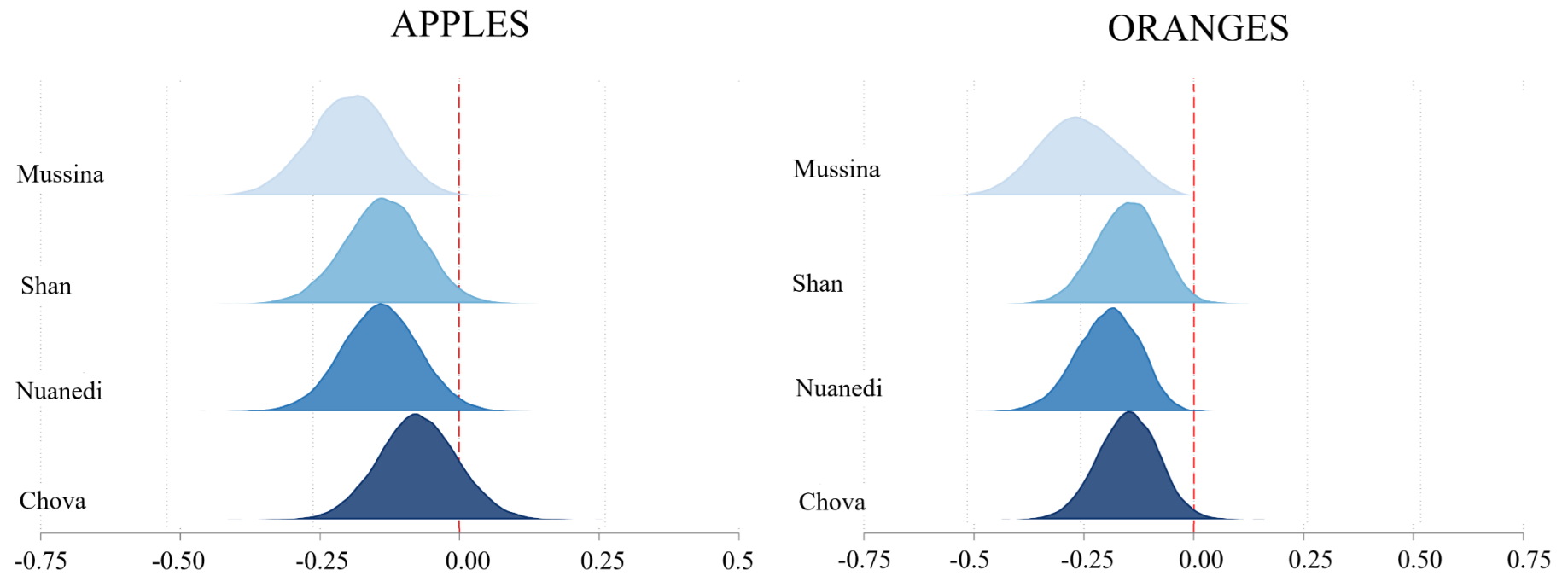


Figure 4.11: The AME of the condition being no-contact on the probability of each elephant choosing the larger alternative when discriminating between apples, estimated from the BHMrd (left panel) and when discriminating between oranges, estimated from the BHMrd (right panel) in the “apple-orange discrimination experiment”. The dashed red line represents a 0 AME.

The ROPE

To compare the effect of ratio and absolute difference of the alternatives at specific prospects, the probability that the posterior distributions of each of these variables lay in a range of values for the ROPE in intervals on either side of 0 is reported. The selected prospects were those that should be the *easiest prospect* to discriminate, i.e. the prospect having the smallest ratio and the highest absolute difference: 1 vs 6 (ratio = 0.17, absolute difference = 5), the prospect that should be the *most difficult prospect* to discriminate, i.e. the prospect with the largest ratio and the smallest absolute difference, 4 vs 5 (ratio = 0.80, absolute difference = 1), and the *prospect in between* having the central values of both ratio and absolute difference, i.e. 3 vs 6 (ratio = 0.5 and absolute difference = 3). The results of the ROPEs, reported in Figure 4.12 for apples and Figure 4.13 for oranges, show that ratio and absolute difference affected the choice of the elephants similarly for both fruits, but differently based on the prospect they were discriminating.

In the *easiest prospect*, both with apples and oranges (section A of Figures 4.12 and 4.13), the effect of the ratio of the alternatives was completely included in the ± 10 pp (percentage points) ROPE. On the contrary, the effect of the absolute difference between the alternatives in the easiest prospect was not completely included in the ± 25 pp ROPE shown in section A of Figures 4.12 and 4.13. This indicates that the absolute difference of the alternatives had a stronger effect than the ratio on the probability of choosing the larger reward for each elephant with both fruits.

The effect of the ratio and absolute difference of the alternatives on the probability of choosing the larger reward in the *prospect in between* is shown in section B of Figure 4.12 for apples and Figure 4.13 for oranges. With both fruit types, for

Chova and Nuanedi the effect of the two variables overlap, reflecting the fact that both variables had a similar importance for Chova and Nuanedi when discriminating 3vs6 fruits. Mussina and Shan also chose based on both variables, but for them, the effect of the absolute difference between the alternatives was stronger than for Chova and Nuanedi discriminating 3vs6 fruits.

The effect of the absolute difference between the alternatives on the probability of choosing the larger reward in the *most difficult prospect* lay completely within the ± 15 pp ROPE for each elephant with both fruits, as shown in section C of Figures 4.12 and 4.13. On the other hand, the effect of the ratio of the alternatives was not completely contained in the ± 25 pp ROPE shown in the plots. This reflects a stronger effect of ratio than absolute difference on the probability of choosing the larger reward for each elephant with both fruits.

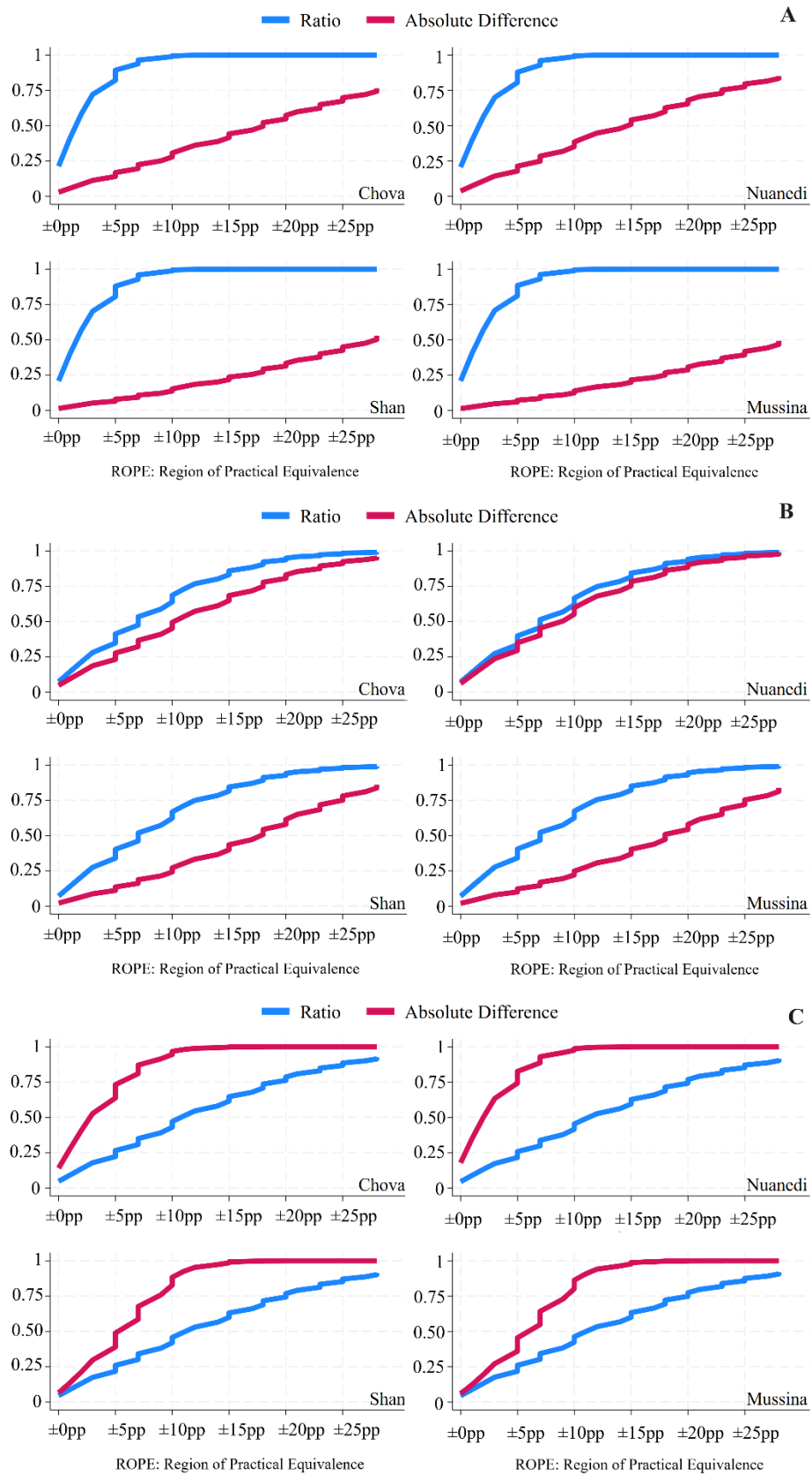


Figure 4.12: The probability that the posterior distribution of the ratio and the absolute difference between the alternatives lie inside the ± 25 percentage points change from not affecting the probability of choosing the larger alternative when discriminating between apples, calculated at the easiest prospect (A, ratio=0.17, abs.diff.=5), the prospect in between (B, ratio=0.5, abs.diff.=3), and the most difficult prospect (C, ratio=0.80, abs.diff.=1), estimated from the BHMrd in the “apple-orange discrimination experiment”.

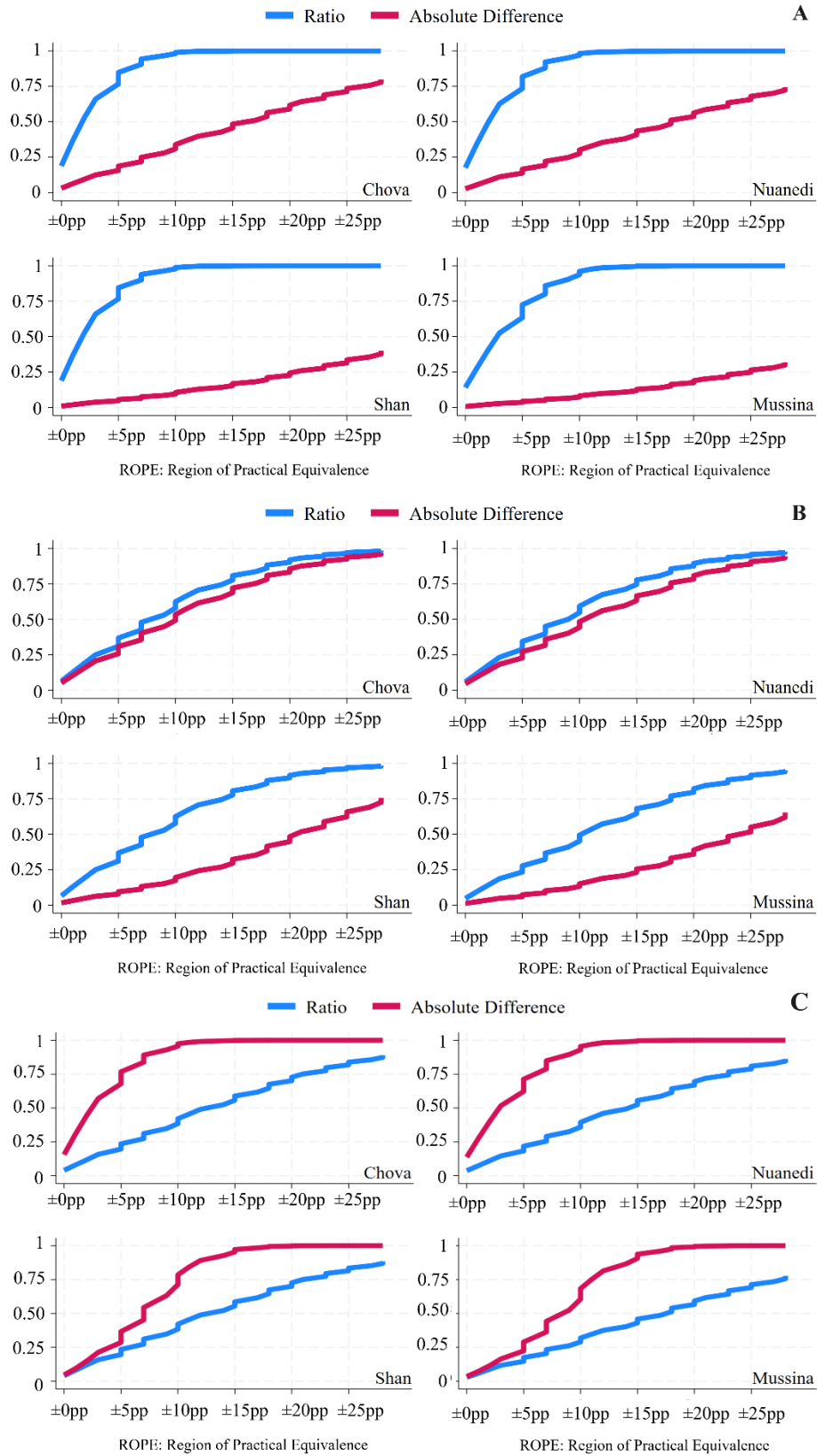


Figure 4.13: The probability that the posterior distribution of the ratio and the absolute difference between the alternatives lie inside the ± 25 percentage point change from not affecting the probability of choosing the larger alternative when discriminating between oranges, calculated at the easiest prospect (A, ratio=0.17, abs.diff.=5), the prospect in between (B, ratio=0.5, abs.diff.=3), and the most difficult prospect (C, ratio=0.80, abs.diff.=1), estimated from the BHMrd0 in the “apple-orange discrimination experiment”.

Discussion

Each of the four adult African elephants participating in this study was able to discriminate between different quantities of either apples or oranges when only olfactory cues were available in the contact condition. The same ability was found in Asian elephants participating in a similar task (Plotnik et al., 2019).

There was not much difference in the accuracy of the elephants when discriminating between different quantities of apples or oranges. The aroma profiles of these fruits are both complex and characterised by different volatile compounds, mainly esters in ripe apples, and monoterpenes such as limonene in oranges (Gonçalves et al., 2018). The fact that the discrimination of the elephants was not affected by the different aromas suggests that the olfaction of African elephants allows them to correctly associate the quantity of different volatile compounds with the number of fruits producing them. This is not surprising since the same group of elephants studied here were able to select marula fruits (*Sclerocarya birra*) of higher sugar content by smelling and assessing the quantity of ethanol and ethyl acetate released by the fruits (Nevo et al., 2020).

However, though highly sensitive, the olfaction acuity of African elephants in discriminating quantitatively seems to decrease quickly when there is some distance between the trunk and the source of the smell. In the no-contact condition, only Chova and Nuanedi with apples, and Shan with oranges, credibly chose the larger reward more than by chance, and each of them was less successful than in the contact condition. This result is unexpected. The rewards were placed only five metres from the elephants' starting position, with the wind always blowing from the fruits to the elephant, and the elephant was not forced to decide which side to choose from the starting position.

Indeed, they could walk straight between the alternatives and get closer to them before choosing one, though this happened rarely. We thought this represented an easy task for the elephants. In addition, in a previous study, these elephants were able to always select their favourite plant in binary choices where only olfactory cues were available from a distance of ~7 m (Schmitt et al., 2018). The ecology of elephants might provide a possible explanation for this unexpected result.

African elephants inhabit savannas where resources are often clumped together and good patches might be far from each other (Du Toit and Cumming, 1999). When deciding which patch to forage next at a large spatial scale, elephants need to compare the costs and benefits of each choice available to them before making a decision (McFarland, 1977). Therefore, elephants use olfaction to detect the presence and assess the location of sources of good quality from a distance. To do so, they use two pieces of information: the quality and the strength of the odour of detectable sources (Hopfield, 1991). Since the strength of the odour is correlated with the abundance of the reward and decreases with distance from its source, it could be easier for elephants to *qualitatively* rather than quantitatively discriminate between different foods from a distance. The larger the distance between the elephant and the source of the smell, the more probable it is for the wind to carry more odours, confounding both the quality and the strength of the focal odour even more.

When comparing the choices of the elephants at the beginning and the end of a task, the female elephants improved their performance by choosing the larger reward more often the longer they made choices in the contact condition with apples. In the no-contact condition with apples and both conditions with oranges, each elephant performed similarly or worse at the end than at the beginning of the task. Expectations

were that by repeating a task animals would improve at it (Shettleworth, 2001), or at least not get worse. One hypothesis is that since the last observations of the no-contact condition with apples temporally overlapped with the first observations of the contact condition with oranges, the elephants could have been less motivated to choose the larger alternative on such days. However, the maximum number of fruits obtainable on such days was 11, a number that will not satiate an adult elephant. In addition, if this might explain the absence of learning in the no-contact condition with apples, it does not explain it in both conditions with oranges. The elephants might become bored with the simple exercise, and even less interested in it when it reached the stage of the no-contact condition with oranges when it was more difficult for them to discriminate in general.

All elephants showed a side preference, but with variation in constancy. Nuanedi and Mussina maintained their side preference regardless of the fruit used, and Chova and Shan had a different side preference depending on whether they were discriminating between apples or oranges. A preference for one side over another has been previously observed in elephants (Plotnik et al., 2013) and other animals (Ward and Smuts, 2007; Aïn et al., 2009; Bánszegi et al., 2016). An animal that chooses one side more than the other might require a larger difference in prospects to induce choice away from the preferred side. This would result in the animal choosing the larger alternative more often when it is on the unpreferred side. A side preference might also have been due to the setup of the no-contact condition of the study. Though wind direction was checked at the beginning of each trial, the wind might have changed during the experiment, so that one elephant could have perceived the smell of one of the rewards first and chosen it, before even investigating the smell of the other alternative. However, none of these

possible options explains why the performance of some elephants would be better on one side or the other depending on the fruit at stake, while other elephants were consistent on the side where they performed better choices. This is an interesting question for future research.

The effect of the ratio and absolute difference between the alternatives has been the main focus of the previous literature, which found controversial results. We found that the absolute difference between the alternatives had an expected positive effect on each elephant choosing the larger reward with both fruits. The effect of the ratio of the alternatives was negative for each elephant with apples and positive for Chova, Nuanedi, and Mussina with oranges. Previous studies found either no effect of ratio (Irie-Sugimoto et al., 2009; Irie and Hasegawa, 2012; Irie et al., 2019) or a negative correlation between the ratio and the proportion of choices of the larger reward (Perdue et al., 2012; Plotnik et al., 2019; Snyder et al., 2021). Since prospects having a large absolute difference also have a small ratio and *vice versa*, it seems counterintuitive to observe a positive effect of both variables for some elephants with oranges. This might depend on the fact that both variables participated in guiding the choices of the elephants and that some elephants were guessing in the no-contact condition.

Comparing the effect of the ratio and absolute difference of the alternatives in specific prospects allows one to estimate how important each variable was for the elephants when making specific choices. The effect of the ratio and absolute difference was reversed in both the easiest and the most difficult prospect for each elephant with both fruits (sections A and C of Figures 4.12 and 4.13). In particular, the absolute difference of the alternatives was more important when discriminating between 1vs6, while the ratio affected choices more when discriminating between 4vs5 fruits. The fact

that the effect of ratio and absolute difference is comparable when discriminating between both apples and oranges suggests that the discrimination of elephants is based on the actual quantities of fruit at stake.

In conclusion, this study demonstrated that African elephants can discriminate between different quantities of either apples or oranges when the available cues are olfactory, but only when they can directly touch the buckets containing the alternatives. To do so, with both fruits, elephants based their decisions more on the absolute difference between the alternatives when the rewards differed by many units, and on the ratio of the alternatives when they differed by one unit only. The individual choices of the elephants also depended on the side where the larger reward was located and on the number of trials already performed in the task. These results highlight the importance of focusing on what affects specific choices of individual elephants as, sometimes, elephants behave similarly, e.g. the effect of absolute difference, ratio, distance, and type of fruit, and sometimes they do not, such as in having different side preferences and learning patterns. This study had two main weaknesses: we could check for the wind direction but we could not stop it from changing during a trial, and we had no power over what and how much the elephants ate before the experiment. It is possible to use setups that strictly control the effect of the wind, such as the one used by Schmitt et al. (2018), though they are laborious. However, restricting elephants from eating before the experiment might increase their motivation to choose the larger alternative, but it would be impracticable with wild elephants and unethical with captive ones.

References

- Agrillo, C., Bisazza, A., 2014. Spontaneous versus trained numerical abilities. A comparison between the two main tools to study numerical competence in non-human animals. *Journal of Neuroscience Methods* 234, 82–91.
- Aïn, S.A., Giret, N., Grand, M., Kreutzer, M., Bovet, D., 2009. The discrimination of discrete and continuous amounts in African grey parrots (*Psittacus erithacus*). *Animal Cognition* 12, 145–154.
- Bánszegi, O., Urrutia, A., Szenczi, P., Hudson, R., 2016. More or less: spontaneous quantity discrimination in the domestic cat. *Animal Cognition* 19, 879–888.
- Bates, L.A., Sayialel, K.N., Njiraini, N.W., Moss, C.J., Poole, J.H., Byrne, R.W., 2007. Elephants Classify Human Ethnic Groups by Odor and Garment Color. *Current Biology* 17(22), 1938–1942.
- Beran, M.J., Evans, T.A., Leighty, K.A., Harris, E.H., Rice, D., 2008. Summation and quantity judgments of sequentially presented sets by capuchin monkeys (*Cebus apella*). *American Journal of Primatology* 70(2), 191–194.
- Bisazza, A., Gatto, E., 2021. Continuous versus discrete quantity discrimination in dune snail (Mollusca: Gastropoda) seeking thermal refuges. *Scientific Report* 11(1), 3757.
- Butterworth, B., 2022. Can Fish Count?: What Animals Reveal about Our Uniquely Mathematical Mind. Hachette UK.
- Caraco, T., Martindale, S., Whittam, T.S., 1980. An empirical demonstration of risk-sensitive foraging preferences. *Animal Behaviour* 28(3), 820–830.
- Du Toit, J.T., Cumming, D.H.M., 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity & Conservation* 8, 1643–1661.
- Farnsworth, G.L., Smolinski, J.L., 2006. Numerical discrimination by wild Northern Mockingbirds. *The Condor* 108(4), 953–957.
- Gallistel, C.R., Gelman, R., 1992. Preverbal and verbal counting and computation. *Cognition* 44(1-2), 43–74.
- Gonçalves, B., Oliveira, I., Bacelar, E., Morais, M.C., Aires, A., Cosme, F., Ventura-Cardoso, J., Anjos, R., Pinto, T., 2018. Aromas and Flavours of Fruits. In *Generation of Aromas and Flavours*. IntechOpen.
- Hanus, D., Call, J., 2007. Discrete quantity judgments in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*): The effect of presenting whole sets versus item-by-item. *Journal of Comparative Psychology* 121(3), 241–249.
- Hopfield, J.J., 1991. Olfactory computation and object perception. *Proceedings of the National Academy of Sciences* 88(15), 6462–6466.
- Irie, N., Hasegawa, T., 2012. Summation by Asian Elephants (*Elephas maximus*). *Behavioral Sciences* 2(2), 50–56.
- Irie, N., Hiraiwa-Hasegawa, M., Kutsukake, N., 2019. Unique numerical competence of Asian elephants on the relative numerosity judgment task. *Journal of Ethology* 37, 111–115.
- Irie-Sugimoto, N., Kobayashi, T., Sato, T., Hasegawa, T., 2009. Relative quantity judgment by Asian elephants (*Elephas maximus*). *Animal Cognition* 12, 193–199.

- Jacobson, S.L., Plotnik, J.M., 2020. The importance of sensory perception in an elephant's cognitive world. *Comparative Cognition & Behavior Reviews* 15, 131–148.
- Kilian, A., Yaman, S., von Fersen, L., Güntürkün, O., 2003. A bottlenose dolphin discriminates visual stimuli differing in numerosity. *Animal Learning & Behavior* 31, 133–142.
- McArthur, C., Finnerty, P.B., Schmitt, M.H., Shuttleworth, A., Shrader, A.M., 2019. Plant volatiles are a salient cue for foraging mammals: elephants target preferred plants despite background plant odour. *Animal Behaviour* 155, 199–216.
- McComb, K., Packer, C., Pusey, A., 1994. Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behaviour* 47(2), 379–387.
- McFarland, D.J., 1977. Decision making in animals. *Nature* 269(5623), 15–21.
- Miller, A.K., Hensman, M.C., Hensman, S., Schultz, K., Reid, P., Shore, M., Brown, J., Furton, K.G., Lee, S., 2015. African elephants (*Loxodonta africana*) can detect TNT using olfaction: Implications for biosensor application. *Applied Animal Behaviour Science* 171, 177–183.
- Nevo, O., Schmitt, M.H., Ayasse, M., Valenta, K., 2020. Sweet tooth: Elephants detect fruit sugar levels based on scent alone. *Ecology and Evolution* 10(20), 11399–11407.
- Niimura, Y., Matsui, A., Touhara, K., 2014. Extreme expansion of the olfactory receptor gene repertoire in African elephants and evolutionary dynamics of orthologous gene groups in 13 placental mammals. *Genome Research* 24(9), 1485–1496.
- Perdue, B.M., Talbot, C.F., Stone, A.M., Beran, M.J., 2012. Putting the elephant back in the herd: elephant relative quantity judgments match those of other species. *Animal Cognition* 15, 955–961.
- Plotnik, J.M., Brubaker, D.L., Dale, R., Tiller, L.N., Mumby, H.S., Clayton, N.S., 2019. Elephants have a nose for quantity. *Proceedings of the National Academy of Sciences* 116(25), 12566–12571.
- Plotnik, J.M., Pokorny, J.J., Keratimanochaya, T., Webb, C., Beronja, H.F., Hennessy, A., Hill, J., Hill, V.J., Kiss, R., Maguire, C., Melville, B.L., Morrison, V.M.B., Seecoomar, D., Singer, B., Ukehaxhaj, J., Vlahakis, S.K., Ylli, D., Clayton, N.S., Roberts, J., Fure, E.L., Duchatelier, A.P., Getz, D., 2013. Visual Cues Given by Humans Are Not Sufficient for Asian Elephants (*Elephas maximus*) to Find Hidden Food. *PLoS One* 8, e61174.
- Plotnik, J.M., Shaw, R.C., Brubaker, D.L., Tiller, L.N., Clayton, N.S., 2014. Thinking with their trunks: elephants use smell but not sound to locate food and exclude nonrewarding alternatives. *Animal Behaviour* 88, 91–98.
- Pyke, G., 1984. Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology, Evolution and Systematic* 15(1), 523–575.
- Schmitt, M.H., Shuttleworth, A., Ward, D., Shrader, A.M., 2018. African elephants use plant odours to make foraging decisions across multiple spatial scales. *Animal Behaviour* 141, 17–27.
- Shuttleworth, S.J., 2001. Animal cognition and animal behaviour. *Animal Behaviour* 61(2), 277–286.
- Snyder, R.J., Barrett, L.P., Emory, R.A., Perdue, B.M., 2021. Performance of Asian elephants (*Elephas maximus*) on a quantity discrimination task is similar to that

- of African savanna elephants (*Loxodonta africana*). *Animal Cognition* 24(5), 1121–1131.
- StataCorp, 2023. *Stata 18 Bayesian Analysis Reference Manual*. College Station, TX: Stata Press.
- Sulkowski, G., Hauser, M.D., 2001. Can rhesus monkeys spontaneously subtract? *Cognition* 79(3), 239–262.
- Ward, C., Smuts, B.B., 2007. Quantity-based judgments in the domestic dog (*Canis lupus familiaris*). *Animal Cognition* 10, 71–80.

CHAPTER 5: Can Elephants Do Simple Arithmetic?

Introduction

The ability to discriminate between different quantities of the same item is widespread among animals. To make ecologically successful choices it is often sufficient to be able to recognise many versus few (Davis and Memmott, 1982). The ability to do simple arithmetic operations is more complex. At the bare minimum, it requires an animal to know what “numerosity” is, defined as the size of a set (as distinguished from the logical and mathematical cardinality) (Butterworth, 2022: p. 16).

To be able to count an array of objects it is necessary to count each object only once, in stable order, and to remember the output value. The process of *partitioning* allows one to distinguish between objects that have been already counted and objects that have not been counted yet, and the process of *tagging* allows one to associate a distinct tag with each item in the array (Gelman and Gallistel, 1978). Tags do not need to be verbal, but they must be applied in a stable order to the objects that are counted, with the tag given to the last object in the group representing the quantity of the array (Davis and Memmott, 1982).

Gallistel (1989: p.183) argued that counting can be identified as occurring when animals can at least do two things: represent the numerosity of a set as a distinct attribute of the set and be able to perform mathematical operations, such as $\geq$, $+$, $-$, $\times$, $\div$, with the representations of numerosities. A counting animal does not need to be able to perform all of these operations, or indeed more than one of them.

The first requirement is known as the *abstraction principle*, which means that numerosity is a distinct property of a set, separable from the properties of the items composing the set (Gallistel, 1989: p. 183). So “threeness” is an attribute shared by any group of three objects, in the same way as “wetness” is an attribute shared by any liquid. This implies that when an animal can count up to a certain numerosity, it does not matter which objects or events the animal is counting. Several animals have been shown as able to treat numerosity as an attribute of sets of different items. For example, Davis (1984) trained a racoon (*Procyon lotor*) to discriminate 3 grapes from 1, 2, 4, and 5 grapes and found that the animal was able to abstract the “concept of threeness” by discriminating 3 metal bells in the same way. Guppies (*Poecilia reticulata*) have similarly been trained to select an array based on “fourness” (Miletto Petrazzini et al., 2015). In particular, guppies were trained to select groups of 4 geometric figures instead of groups of 1, 2, 8, or 10 geometric figures. When presented with new comparisons, i.e. 4vs3 and 4vs6, the guppies chose the group of 4 geometric figures significantly more than by chance.

There are many examples of animals demonstrating mathematical abilities that involve numerosity. For example, Mechner (1958) gave rats (genus *Rattus*) a trained counting task involving the pressing of two levers. After the rat pressed the first lever a specific number of times, the second lever was activated and would release a reward if then pressed by the rat. If the rat left the first lever too soon, it would receive a penalty. The rats could count how many times they pressed the first lever and compare this number with the minimum required number of presses determined by the experimenter. In addition, since the rats were rewarded even if they pressed the first lever more times

than requested, when the animals made mistakes, they tended to do so by performing too many presses rather than fewer (Mechner, 1958).

Capuchin monkeys (*Cebus apella*) were able to discriminate between different quantities of food when addition was needed to determine the comparative quantities in an untrained task (Beran et al., 2008). The monkeys were successively shown two different quantities of raisins in two bowls. After seeing the content, the bowls were covered and some extra visible pieces of raisin were added to one of the non-visible alternatives. The monkeys chose the larger alternative more than by chance, as expected if they were maximising their energy intake (Pyke, 1984). This demonstrated that they were able to compute the summation to obtain the final quantities composed of both visible and non-visible raisins.

Cantlon and Brannon (2007) compared rhesus macaques (*Macaca mulatta*) and humans' mathematical abilities in a trained task. They presented the same task to both species. Two sets of dots appeared consecutively on a screen, for example 1 followed by 4 dots. Then, two different sets of dots appeared simultaneously on a screen, one of which represented the sum of the previous two sets, in the example 5 dots. The correct choice consisted of selecting the set of dots matching the sum of the first two sets of dots. Monkeys were able to sum and choose the correct arrays of dots more than by chance, performing comparably to humans.

Rhesus macaques were also able to subtract in a task in which they made free choices. In a study, they were presented with two visible quantities of plums on two stages (Sulkowski and Hauser, 2001). The plums were then covered, while a researcher performed one or more visible removals of plums from one or both stages. The

monkeys chose one of the stages and received the remaining plums. Rhesus monkeys chose the larger quantity of remaining plums more than by chance. This demonstrates that they could count two different quantities, store them in memory, change their memory after observing removal operations, and base their choice on the final number of plums in each alternative. Another animal that can subtract is the pigeon (*Columba livia domestica*). In one study pigeons discriminated between a constant number and the result of subtraction in a trained task (Brannon et al., 2001).

Previous studies have shown that African elephants (*Loxodonta africana*) can successfully discriminate between different quantities of one item through sight, hearing, and smell (Perdue et al., 2012). However, to have the ability to discriminate does not imply that elephants can do arithmetic. One way to test whether elephants can do simple arithmetic would be to demonstrate that elephants have different utilities for different quantities of food, where the utility is the subjective perception of the relative attractiveness of the attribute “quantity” of the food (McFarland, 1977). If an elephant chooses a specific larger reward, for example 3, more often than a specific smaller reward, for example 2, consistently in binary choices, this is an indication that the elephant assigns a higher utility to the higher reward, and therefore recognises the difference between the numerosities 2 and 3. It would be a demonstration of the ability to do simple arithmetic.

This chapter uses the data presented in Chapters 3 and 4 to evaluate the utility of each elephant for different quantities of boskos, apples, and oranges. From the utility of each quantity, the probability that each quantity is regarded as different from another one is calculated for each elephant. The aim is to assess whether four adult African elephants can do simple arithmetic. To be able to count, elephants should have

statistically different utilities for each quantity of the same item, in the form $x \geq x-1$. To our knowledge, no one has tested an animal's ability to do simple arithmetic in this way, but it is a natural method an economist would use with people whose counting abilities were in doubt, for example, young children.

Methods

The subjects of this chapter are the four adult elephants described in the General Methodology of Chapter 1.

Measuring utilities for choice attributes

The utilities of numerosities from 1 to 6 for the elephants were calculated as “random utility” values using the Bayesian Conditional Logistic (CL) model developed by McFadden (1974) presented in Chapter 1 and applied to the choices for the “fruit preference experiment” in Chapter 2. This application of the CL model to numerosity allows the evaluation of the ability of the elephants to perform simple arithmetic.

In the “fruit preference experiment” the preference of the elephants for different fruit types was evaluated through a BHM using a CL specification of the likelihood of the observation. This model evaluates the likelihood of the choices of all pairwise combinations of fruits, to estimate the utility of each fruit. The probability that each fruit would be chosen by each elephant is then calculated from the utility of each fruit.

In Chapter 2 each elephant was assumed to make choices as if each food type on offer generated utility to the elephant. In the language of these CL models, the “attribute”, a categorical variable, is the *kind* of fruit that was offered for choice. When

an elephant is assumed by this model to be evaluating two fruits on offer, it is only relative utility that matters. So the utility of *one* fruit must be normalised to be some constant, normally 0 or 1, to identify the utility values of all other fruits. In Chapter 2 the option “None”, representing an alternative containing no fruits, was normalised to have utility set to 0. This normalisation choice affects the level of the utility values estimated, but it does not affect the inferred probabilities of choice. By normalising the option with the smallest utility to have utility 0, the utility values of the other fruits will all be positive and easy to visualise in a display. Once the utility U is estimated for each elephant and fruit attribute, one can evaluate the probability of each fruit being chosen. For a full exposition of the model refer back to Chapter 2.

In the current chapter, the same Bayesian CL model is applied to the data described in Chapters 3 and 4. Three Bayesian CL models were estimated using the data collected for both conditions of the “boskos experiment” (Chapter 3), and for the contact condition of the “apples-oranges discrimination experiment” (Chapter 4). The no-contact condition data of Chapter 4 were not used since the elephants did not perform better than by chance in that task. Each model had no covariates, only a dummy for the elephants making the choice and interaction dummies between the elephant and the quantities involved. The boskos model used 4 chains to estimate the posterior, and the models with apples and oranges used 5 chains. Each chain used 50,000 MCMC burn-in simulations, and 100,000 simulations based on these burn-in, resulting in 400,000 simulations for boskos and 500,000 simulations for apples and oranges.

The *number* of items in the choice for a given reward type was here used as the attribute of the model rather than the *type* of fruit. Note that the *number* is still used as a categorical variable, therefore it is convenient to name these attributes one, two, three,

four, five, and six. The reward types were boskos, apples, or oranges. For Chova and one apple, we have

$$U_{\text{chova, one}} = V_{\text{chova, one}} + \varepsilon_{\text{chova, one}} \quad (1)$$

and

$$V_{\text{chova, one}} = \alpha_{\text{one}} + \beta_{\text{one}} \times \text{Chova} + \gamma_{\text{one, chova}} \times (\text{Chova} \times \text{One}) \quad (2)$$

where One is a binary covariate indicating that a choice involved a reward of one item, and

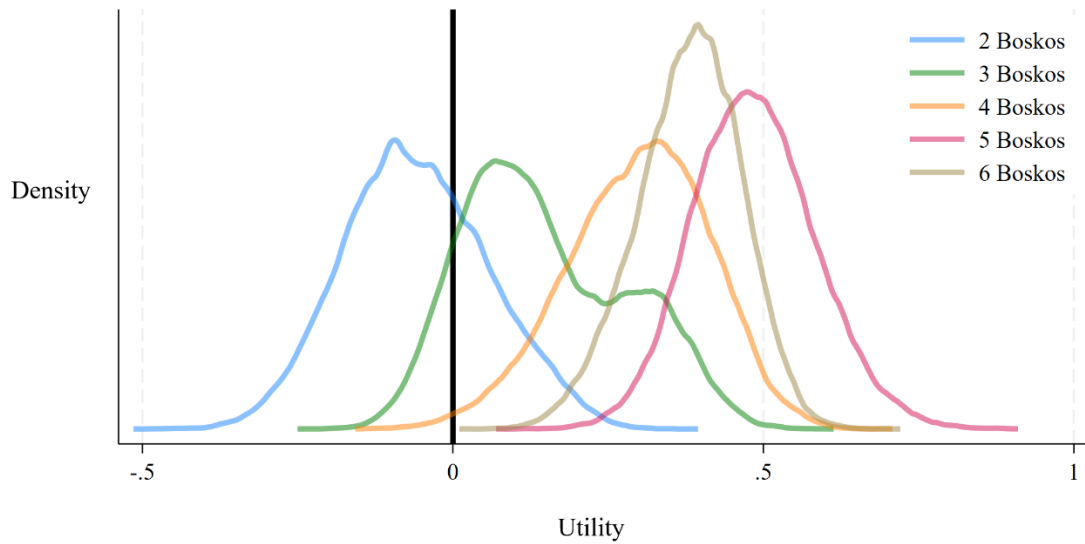
$$\Pr_{\text{chova, two} > \text{one}} = \Pr(U_{\text{chova, two}} > U_{\text{chova, one}}) \quad (3)$$

The utilities of different quantities of boskos for Chova and Mussina are shown in Figure 5.1 as another example. In this case, 1 piece of boskos is normalised to have a utility of 0. The display shows that Chova's utility for 2 boskos is likely lower than the utility for 1 boskos and that the utility for 6 boskos is likely lower than 5 boskos.

Indeed, Figure 5.1 shows that the probability that $2 \geq 1$ and $6 \geq 5$ for Chova with boskos were 0.18 and 0.23 respectively. Mussina, on the other hand, clearly valued 2 boskos more than 1 boskos (probability $2 \geq 1 = 0.99$), but she is unlikely to value 4 more than 3 (probability $4 \geq 3 = 0.23$) and 6 more than 5 pieces of boskos (probability $6 \geq 5 = 0.21$).

Chova

Probability of $2 \geq 1$, $3 \geq 2$, $4 \geq 3$, $5 \geq 4$, and $6 \geq 5$ is 0.30, 0.96, 0.83, 0.89, and 0.19, respectively



Mussina

Probability of $2 \geq 1$, $3 \geq 2$, $4 \geq 3$, $5 \geq 4$, and $6 \geq 5$ is 0.99, 1.00, 0.38, 1.00, and 0.19, respectively

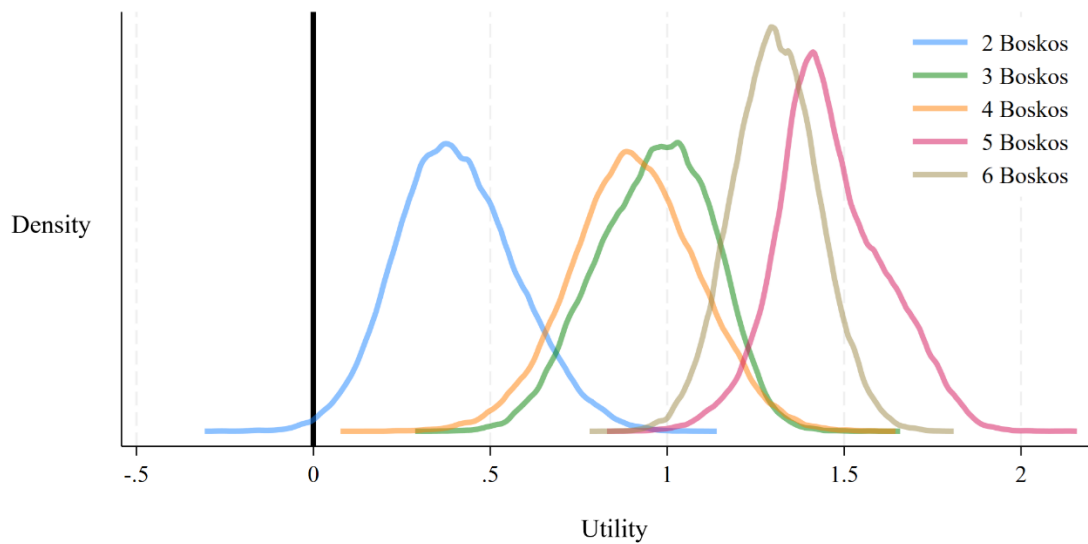


Figure 5.1: The utilities of Chova (top) and Mussina (bottom) for different quantities of boskos, estimated from a Conditional Logit BHM without covariates in the “boskos experiment”. The black vertical line represents the utility zero assigned to the utility of 1 boskos

The probability that each elephant had a preference for numerosity (x) compared to the adjacent smaller numerosity ($x-1$) has been calculated for boskos, apples, and

oranges, following equation (3). The full range of possible probabilities for all elephants and rewards are presented in the results.

In the “boskos experiment” the elephants were offered every possible combination between 1 and 6 boskos. In the “apple-orange discrimination experiment” the elephants choose between every possible combination between 1 and 5, plus some choices of 1vs6 (see Table A2 in Appendix 1). Therefore, the BHM results for comparisons such as 2vs6, 3vs6, 4vs6, and 5vs6 are based on actual observations for boskos, and are *predicted* for apples and oranges. As a consequence, there is less confidence in the results of the comparisons to 6 for apples and oranges than for boskos.

Results

Overall, the elephants tended to assign higher utilities to higher rewards, with some exceptions. The inferred probability of the utility of the larger quantity at stake being greater than the utility of the smaller quantity at stake is shown separately for boskos, apples, and oranges in the form of matrices. The matrices are colour-coded so that probabilities lower than 0.5 have the lightest background, and the background then becomes one tone darker for each 0.1 increase in the inferred probability.

Boskos

The inferred probability that each elephant associated a higher utility to the higher quantity of boskos is shown in Figure 5.2. Overall, the elephants assigned higher utilities to the higher rewards in most of the comparisons. However, there were individual differences. Shan had a higher estimated utility for the higher reward in each comparison. Nuanedi had a similar estimated utility for 3vs4, and for 5vs6 boskos. Chova preferred 1 to 2 boskos, Mussina preferred 3 to 4 boskos, and both Chova and Mussina had a higher estimated utility for 5 than 6 boskos.

Apples

In discriminating between apples, Mussina had a higher estimated utility for the larger reward in each comparison, as shown in Figure 5.3. Nuanedi had a higher estimated utility for the smaller reward in some cases when 6 apples were involved. She preferred 5 and 4 apples to 6, and she had a similar utility for 3vs6, and 2vs6. Shan was indifferent between 3vs4 apples and between 5vs6 apples. Chova had similar estimated utilities for 1vs2 and 4vs5 apples.

Oranges

The discrimination between different quantities of oranges is shown in Figure 5.4. Mussina and Nuanedi had a higher estimated utility for the larger reward in each comparison. On the contrary, Shan was indifferent between 4, 5, and 6 oranges, and she preferred 2 to 3 oranges. Chova was indifferent between many combinations: 2vs4, 2vs6, 3vs6, and 4vs6, and preferred 2 to 3, and 5 to 6 oranges.

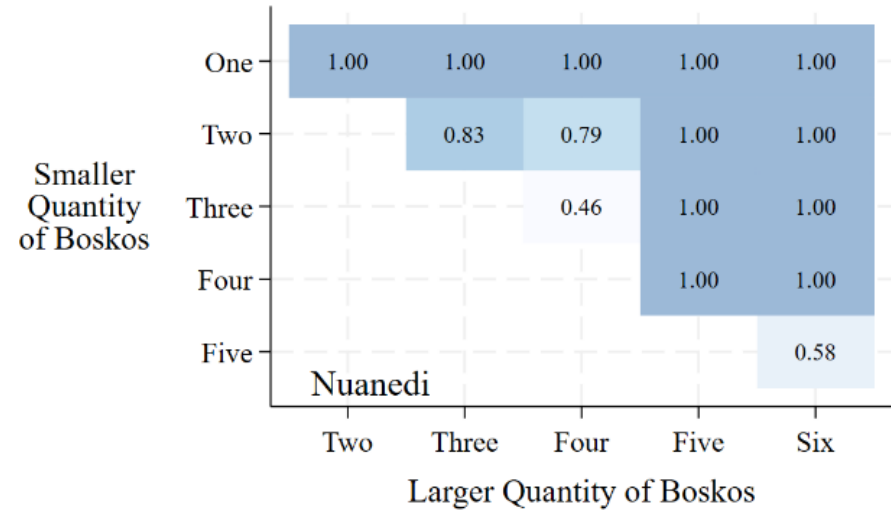
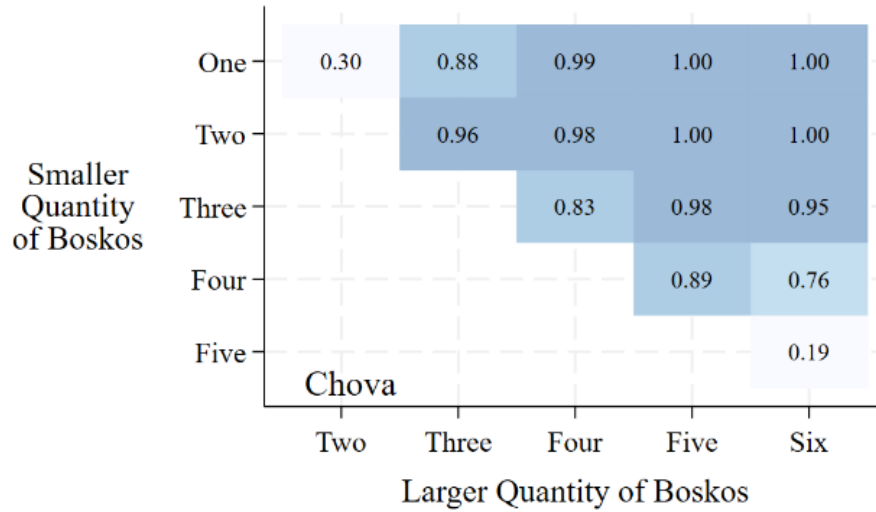


Figure 5.2: The inferred probability of the utility of the larger quantity of boskos being greater than the utility of the smaller quantity of boskos.

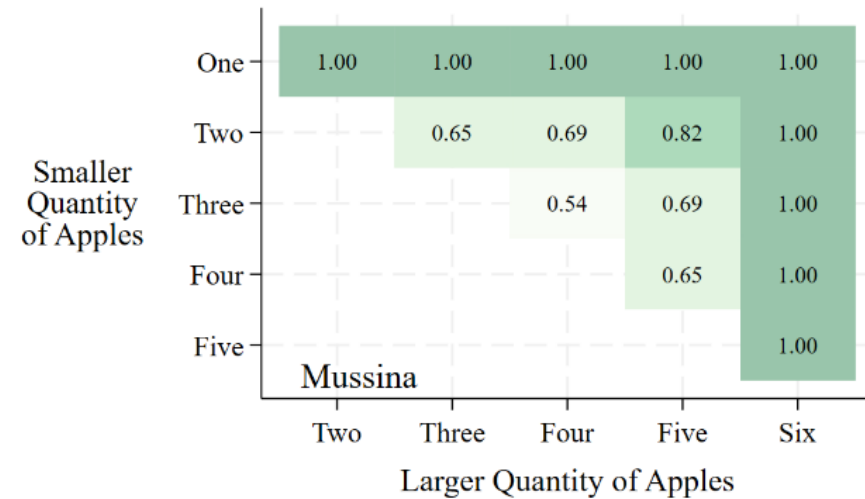
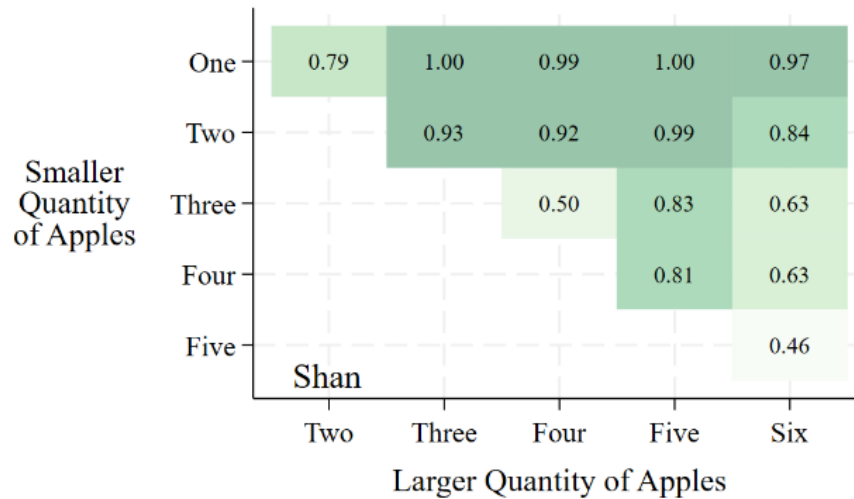
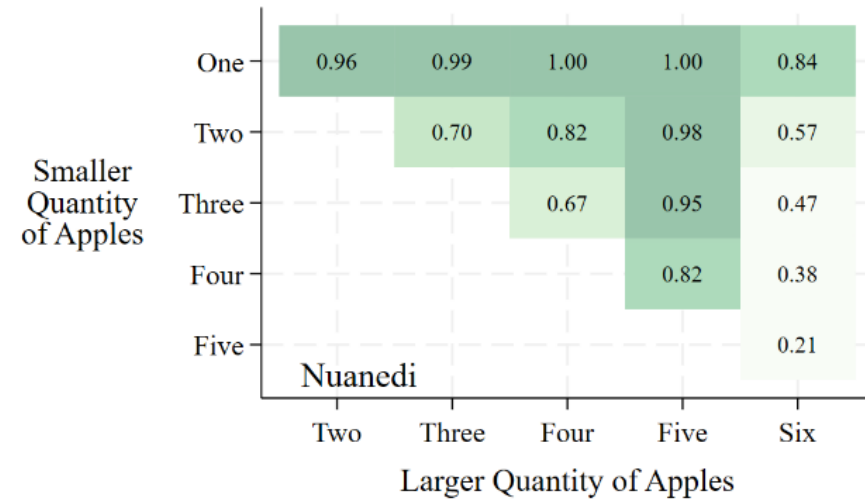
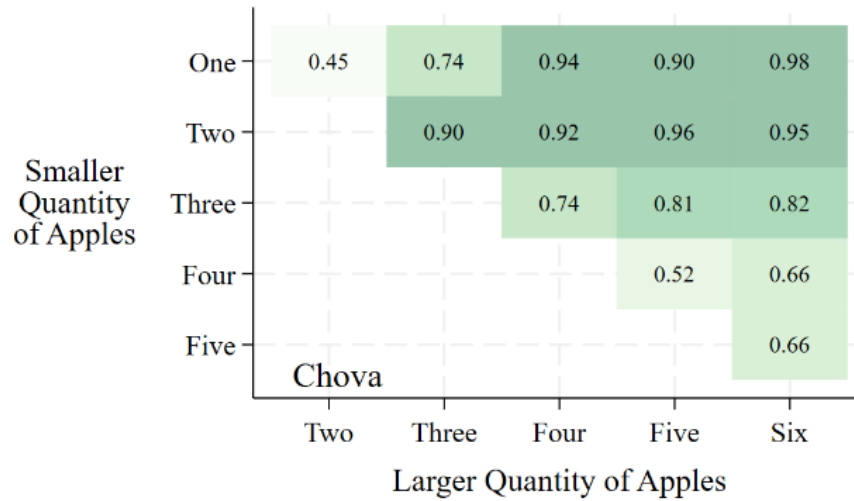


Figure 5.3: The inferred probability of the utility of the larger quantity of apples being greater than the utility of the smaller quantity of apples.

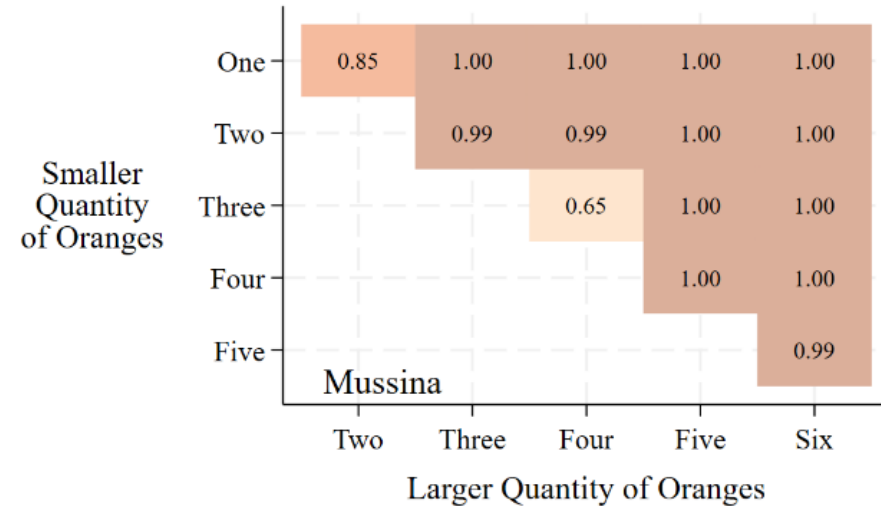
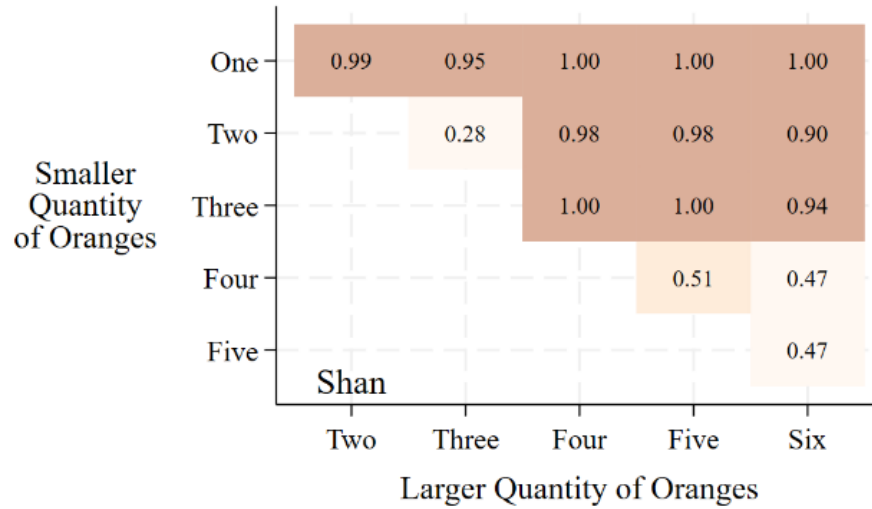
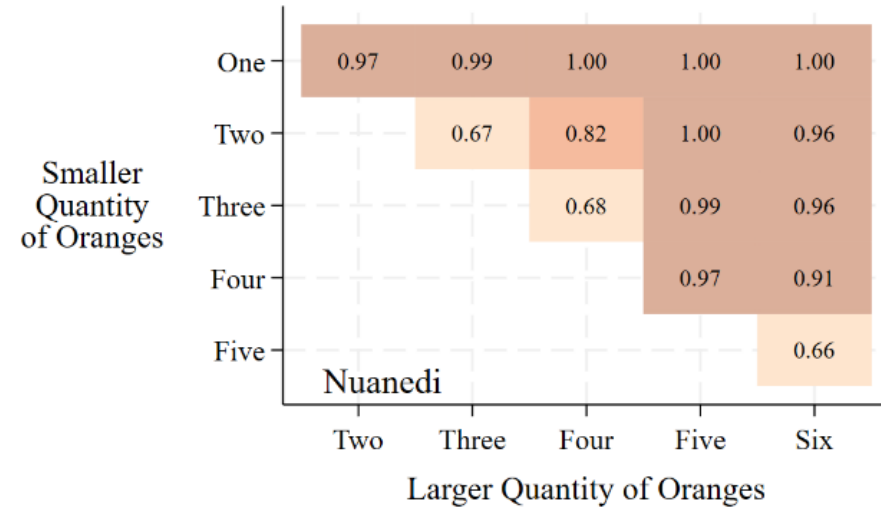
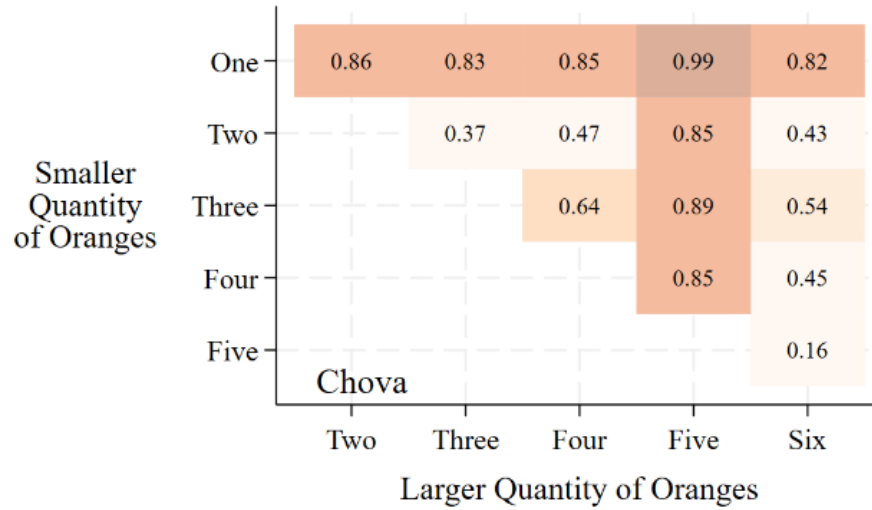


Figure 5.4: The inferred probability of the utility of the larger quantity of oranges being greater than the utility of the smaller quantity of oranges.

Discussion

Each elephant *generally* assigned a higher utility to the higher reward presented to them in binary tasks. However, there was heterogeneity across the behaviour of the individual elephants. The three females showed similar trends, although with different foods. Shan always preferred the higher reward in each comparison with boskos, as did Mussina and Nuanedi with oranges. With boskos, Mussina preferred 3 to 4 and 5 to 6, while Nuanedi was indifferent to these quantities, and Shan was indifferent to the same quantities of apples. Chova also preferred 5 to 6 boskos. In addition, Chova preferred 1 to 2 boskos and apples, and 2 to 4 oranges, and was the only elephant not behaving as if he assigned a larger utility to the larger reward in these comparisons.

The elephants were often indifferent between 2vs6, 3vs6, 4vs6, and 5vs6 apples and oranges. This result might depend on the fact that these probabilities were predicted out of sample and not estimated from direct observation, therefore being less precisely inferred. Otherwise, the most difficult comparisons for the elephants to discriminate between were 5vs6 and 3vs4 with boskos and apples, and 2vs3 with oranges. One possible reason for being indifferent to different quantities of food is that an animal may not perceive the quantities as different. Alternatively, the animal might be able to perceive the difference between 5 and 6 units of food, but is indifferent between them. This could happen because the utilities obtained by the animal from consuming either 5 or 6 units of food are so similar that the animal is not motivated to choose one over the other (Agrillo and Bisazza, 2014).

Chova's preference for 1 over 2 boskos, and his indifference for 1 or 2 apples and 2 or 4 oranges is unexpected. Such a low success rate with these comparisons might depend on the fact that Chova suffered a trunk injury long before the beginning of the

study, which resulted in the loss of the prehensile part of his trunk. This might have affected his sensitivity to odours, such that more units of food are necessary for him to precisely quantify a smell. Indeed, he generally has the lowest probability of assigning a higher utility to the larger alternative in 2vs1 and 3vs1 comparisons, the comparisons with the smallest magnitude in each experiment.

In conclusion, we can affirm that elephants can do simple arithmetic, and they are extremely accurate when the numerosities they compare differ by 2 or more. Indeed, apart from Chova, each elephant behaved as if they had a larger utility for the larger numerosity in comparisons having an absolute difference equal to or greater than 2 with every type of fruit. This chapter shows how to evaluate an animal's ability to do simple arithmetic in a way that, to our knowledge, has never been done before. In the future, it would be useful to collect more data with oranges and apples, especially on comparisons involving 6 fruits. This would allow assessing if the somewhat poor discrimination of elephants in these combinations is due to these probabilities being predicted rather than observed, or if there is a substantial difference in discriminating between fruits and boskos in these comparisons.

References

- Agrillo, C., Bisazza, A., 2014. Spontaneous versus trained numerical abilities. A comparison between the two main tools to study numerical competence in non-human animals. *Journal of Neuroscience Methods* 234, 82–91.
- Beran, M.J., Evans, T.A., Leighty, K.A., Harris, E.H., Rice, D., 2008. Summation and quantity judgments of sequentially presented sets by capuchin monkeys (*Cebus apella*). *American Journal of Primatology* 70(2), 191–194.
- Brannon, E.M., Wusthoff, C.J., Gallistel, C.R., Gibbon, J., 2001. Numerical Subtraction in the Pigeon: Evidence for a Linear Subjective Number Scale. *Psychological Science* 12(3), 238–243.

- Butterworth, B., 2022. Can Fish Count?: What Animals Reveal about Our Uniquely Mathematical Mind. Hachette UK.
- Cantlon, J.F., Brannon, E.M., 2007. Basic Math in Monkeys and College Students. *PLoS Biology* 5(12), e328.
- Davis, H., 1984. Discrimination of the number three by a raccoon (*Procyon lotor*). *Animal Learning & Behavior* 12(4), 409–413.
- Davis, H., Memmott, J., 1982. Counting Behavior in Animals: A Critical Evaluation. *Psychological Bulletin* 92(3), 547–570.
- Gallistel, C.R., 1989. Animal Cognition: The Representation of Space, Time and Number. *Annual Review of Psychology* 40(1), 155–189.
- Gelman, R., Gallistel, C.R., 1978. The Child's Understanding of Number. Cambridge, Mass: Harvard University Press.
- Gumbel, E.J., 1958. Statistics of Extremes. Columbia University Press, New York.
- McFadden, D.L., 1974. Conditional logit analysis of qualitative choice behavior. In: *Frontiers in Econometrics*, ed. P. Zarembka. New York: Academic Press, 105–142.
- McFarland, D.J., 1977. Decision making in animals. *Nature* 269(5623), 15–21.
- Mechner, F., 1958. Probability relations within response sequences under ratio reinforcement. *Journal of the Experimental Analysis of Behavior* 1(2), 109.
- Miletto Petrazzini, M.E., Agrillo, C., Izard, V., Bisazza, A., 2015. Relative versus absolute numerical representation in fish: Can guppies represent “fourness”? *Animal Cognition* 18, 1007–1017.
- Perdue, B.M., Talbot, C.F., Stone, A.M., Beran, M.J., 2012. Putting the elephant back in the herd: elephant relative quantity judgments match those of other species. *Animal Cognition* 15, 955–961.
- Pyke, G., 1984. Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology, Evolution and Systematic* 15(1), 523–575.
- Sulkowski, G., Hauser, M.D., 2001. Can rhesus monkeys spontaneously subtract? *Cognition* 79(3), 239–262.

CHAPTER 6: General Discussion

This thesis assessed the preferences of African elephants (*Loxodonta africana*) between different fruits, investigated what factors drive the quantity discrimination of African elephants, and assessed whether elephants learn throughout a task, always focusing on the performances of the single individuals. Finally, the thesis investigated the ability of elephants to do simple arithmetic, in the sense of attributing distinct increasing utility to increasing quantities of food. The study sample was relatively small (4 or 6 elephants) because we worked with semi-tame elephants who were already used to responding to commands. However, six is the largest number of individuals ever tested in a quantity discrimination task and BHM give robust estimates, even with small samples. This chapter synthesises the main findings of all the chapters, highlighting the novelty of the study and its contribution to science.

Novelty and relevance

The majority of the results and methodologies presented in this thesis are new to the field. This is the first study testing quantity discrimination based on smell alone in African elephants, and the first testing, in any elephant species, quantity discrimination by olfaction when contact with the source of the smell is prevented. It is the first study assessing the fruit preferences of African elephants and testing quantity discrimination using different foods. It is the first study on quantity discrimination by elephants to find signs of learning throughout different tasks and to test for side preferences. Finally, it is

the first study to assess an animal's ability to do simple arithmetic by comparing the utility assigned by the animal to single numerosities.

Some studies tested the mathematical abilities of several animals, for example the ability of rhesus monkeys (*Macaca mulatta*) and pigeons (*Columba livia domestica*) to subtract (Brannon et al., 2001; Sulkowski and Hauser, 2001), or the ability of capuchin (*Cebus apella*) and rhesus monkeys to sum (Cantlon and Brennon, 2007; Beran et al., 2008). However, the analysis reported in Chapter 5 is completely novel in the animal literature, therefore it probably constitutes the most important contribution of the thesis. In addition, the matrices presented in Chapter 5 will be used in the larger project following this study and can be applied to different fields.

Elephants were able to detect the presence of food and chose the larger reward when only olfactory cues were available and they could smell the containers with the alternatives directly. These abilities are shared with Asian elephants (*Elephas maximus*) (Plotnik et al., 2014, 2019). The fact the discrimination by the elephants was lower when they could not touch the containers with their trunks suggests that contact is needed for the smell to be intense enough to discriminate well between different quantities of food.

The fruits most favoured by the elephants from the set considered were apples, oranges, and mangos (Chapter 2), and the ability of African elephants to discriminate between different quantities of the same food was tested using boskos (game pellet) (Chapter 3), and apples or oranges (Chapter 4). The elephants chose the larger alternative more than by chance at a similar rate with the different foods, suggesting that the ability to quantitatively discriminate is not influenced by the food at stake.

The use of Bayesian analysis and the Region of Practical Equivalence (ROPE) (Chapters 3 and 4) allowed us to compare the effect of absolute difference and ratio of the alternatives on the choices of specific combinations of rewards. Both variables affected the choices of the elephants regardless of the food at stake, but depending on the different combinations of rewards. Specifically, the choices of each elephant appeared to be driven by the absolute difference of the alternatives when faced with the easiest prospect (1vs6), and by the ratio of the alternatives when faced with the most difficult prospect (5vs6 or 4vs5). This finding suggests that, as found in other species such as rhesus monkeys, New Zealand robins (*Petroica australis*), and horses *Equus caballus* (Hauser et al., 2000; Hunt et al., 2008; Uller and Lewis, 2009), elephant olfactory quantity discrimination is mainly driven by the numerosity of the rewards rather than by other characteristics of each type of food. Based on this result, the ability of elephants to do simple arithmetic was tested and we found that, though elephants did not always choose the larger reward when the alternatives differed by 1 unit, they consistently treated numerosities as different when rewards differed by 2 or more units (Chapter 5).

The learning ability of elephants depended on both the difficulty and the timeline of the various tasks. When comparing the performance at the end with the performance at the beginning of each task, the female elephants showed evidence of learning in the first tasks they performed, when they did not know how the experiment worked (i.e. when discriminating with boskos and in the contact condition with apples), as would be expected (Shettleworth, 2001). When the contact condition with oranges was later applied, the elephants were accustomed to the experiment, and did comparatively well at the beginning *and* end of the task, not showing signs of learning.

Finally, none of the elephants showed signs of learning in the no-contact condition with either apples or oranges, with our results suggesting that the elephants could just not identify the larger alternative under this condition.

We estimated that each elephant had a preference for the right side in the boskos experiment, which was maintained by some elephants, and switched to a left-side preference for others in other experiments. Previous studies on quantity discrimination (i.e. Irie-Sugimoto et al., 2009; Perdue et al., 2012; Irie et al., 2019; Plotnik et al., 2019; Snyder et al., 2021), as well as ours, avoided the artificial encouragement of a side preference by balancing the presentation of the larger reward on each side of the elephant and avoiding having it on the same side more than 3 consecutive times. It is unclear why the preference for a side would change, but it is important to note, especially for future experiments, that none of the elephants was ever *indifferent* to the side of the choice.

Each of the results of this study is to be used as the building blocks for the first study eliciting the risk preferences of a non-human animal in an untrained setup, which will employ the same study elephants and is close to starting. The elephants will be offered choices between binary rewards varying both in quantities and probability of receiving the reward. For these tasks, apples and oranges will be used as rewards since they appear to be the most preferred fruits available all year.

Statistical considerations

This is the first study on animal quantity discrimination to employ Bayesian methods, and in particular, Bayesian Hierarchical Models (BHMs). Previous studies on

the quantity discrimination of elephants used frequentist analyses to study how the difference in the size of the alternatives was correlated with the choice of the larger reward (e.g. Perdue et al., 2012; Plotnik et al., 2019; Snyder et al., 2021). Bayesian methods, in general, use prior beliefs about the behaviour of the elephants to draw inferences about the behaviour of those elephants. The BHM uses pooled data over *all* of the elephants to estimate posterior beliefs for the herd, which are then used as informative priors to estimate the posteriors of *each* elephant. Bayesian methods use the same specifications of likelihoods as Classical methods, but the interpretation of the estimates is very different (e.g. see Kruschke, 2015). In this thesis, the primary reason for using BHMs is to be able to make more informative inferences about individual elephants, where the “extra information” comes from the behaviour of all the elephants in the herd.

The comparison of the effect of the absolute difference and the ratio of the alternatives is central to much of the literature on animal cognition (see Agrillo and Bisazza, 2014). In Chapters 3 and 4 this issue was examined by estimating a structural BHM that included interactions of covariates for these two variables, and then evaluating the importance of their respective posterior estimates in terms of their effects on the probability of choosing the larger alternative. To directly compare these effects at specific choices, the concept of a ROPE was applied. One limitation of this approach is that it is challenging to precisely draw separate inferences about the variables because both appear together in explaining the behaviour of each elephant.

Alternatively, one could have used the Bayes Factors (BF) (Kruschke, 2015: Chapter 12). That would instead compare one model including the absolute difference covariate with another model including the ratio covariate. While the BF approach has

the advantage of being relatively easy to interpret, it has the weakness of being easily misinterpreted as if “selecting” one model over the other, rather than evaluating the relative ability of the two models to account for the data. Another weakness of the BF approach is that the marginal likelihoods needed to calculate it are hard to reliably calculate, particularly for hierarchical models (Raftery, 1996; Gronau et al., 2017).

The other alternative is to use a “mixture model” of the effects of the ratio and absolute difference of the alternatives (Lee and Wagenmakers, 2013: Chapter 6). A mixture model would also involve the estimation of two models, one for each variable considered. It would then weight the conditional likelihood of each model (conditional on using the difference or the ratio of the alternatives) using a “mixture probability” to be estimated. This mixture probability can be interpreted as the weight that the individual elephant places on either variable. This approach, following Harrison and Rutström (2009) for modelling human risk preferences, allows each elephant to behave as if attaching different weights to the two variables. One elephant could behave as if using the absolute difference between the alternatives most of the time when making choices, another elephant could behave as if using the ratio of the alternatives most of the time, and another elephant might behave as if using both roughly equally.

One of the advantages of the mixture model is that it would allow the addition of covariates for each elephant to vary with whether absolute differences or the ratio of the alternatives are used. The approach used in Chapters 3 and 4 assumed that these additional effects (e.g. for side preference) were the same for each elephant, no matter which reward comparison measure that elephant used. One limitation of the mixture model is that it requires many more parameters in comparison to the other two approaches, making it harder to reliably estimate. It remains a prospect for future work,

by those associated with the currently reported research or by others, to re-analyse the data using one of these alternative methods.

Conclusion

The fact that elephants can successfully discriminate between different quantities of different fruits, that they are relatively precise when the difference between the alternatives is at least 2 units, and they can learn over the course of a novel task, are of fundamental importance. Based on this information we now know that eliciting the risk preferences of elephants might be possible, and what quantities the elephants can do simple arithmetic with. All the observations used to obtain the results presented in this thesis constitute informative priors for the next project and also provide information to start to better understand how elephants make decisions in the wild.

References

- Agrillo, C., Bisazza, A., 2014. Spontaneous versus trained numerical abilities. A comparison between the two main tools to study numerical competence in non-human animals. *Journal of Neuroscience Methods* 234, 82–91.
- Beran, M.J., Evans, T.A., Leighty, K.A., Harris, E.H., Rice, D., 2008. Summation and quantity judgments of sequentially presented sets by capuchin monkeys (*Cebus apella*). *American Journal of Primatology* 70(2), 191–194.
- Brannon, E.M., Wusthoff, C.J., Gallistel, C.R., Gibbon, J., 2001. Numerical Subtraction in the Pigeon: Evidence for a Linear Subjective Number Scale. *Psychological Science* 12(3), 238–243.
- Cantlon, J.F., Brannon, E.M., 2007. Basic Math in Monkeys and College Students. *PLoS Biology* 5(12), e328.
- Gronau, Q.F., Sarafoglou, A., Matzke, D., Ly, A., Boehm, U., Marsman, M., Leslie, D.S., Forster, J.J., Wagenmakers, E., Steingroever, H., 2017. A tutorial on bridge sampling. *Journal of Mathematical Psychology* 81, 80–97.
- Harrison, G.W., Rutström, E.E., 2009. Expected utility theory and prospect theory: One wedding and a decent funeral. *Experimental Economics* 12(2), 133–158.

- Hauser, M.D., Carey, S., Hauser, L.B., 2000. Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267(1445), 829–833.
- Hunt, S., Low, J., Burns, K.C., 2008. Adaptive numerical competency in a food-hoarding songbird. *Proceedings of the Royal Society B: Biological Sciences* 275(1649), 2373–2379.
- Irie, N., Hiraiwa-Hasegawa, M., Kutsukake, N., 2019. Unique numerical competence of Asian elephants on the relative numerosity judgment task. *Journal of Ethology* 37, 111–115.
- Irie-Sugimoto, N., Kobayashi, T., Sato, T., Hasegawa, T., 2009. Relative quantity judgment by Asian elephants (*Elephas maximus*). *Animal Cognition* 12, 193–199.
- Kruschke, J.K., 2015. *Doing Bayesian data analysis: A tutorial with R, JAGS, and Stan*. Academic Press, Second Edition.
- Lee, M.D., Wagenmakers, E.J. 2014. *Bayesian cognitive modeling: A practical course*. Cambridge university press.
- Perdue, B.M., Talbot, C.F., Stone, A.M., Beran, M.J., 2012. Putting the elephant back in the herd: elephant relative quantity judgments match those of other species. *Animal Cognition* 15, 955–961.
- Plotnik, J.M., Brubaker, D.L., Dale, R., Tiller, L.N., Mumby, H.S., Clayton, N.S., 2019. Elephants have a nose for quantity. *Proceedings of the National Academy of Sciences* 116(25), 12566–12571.
- Plotnik, J.M., Shaw, R.C., Brubaker, D.L., Tiller, L.N., Clayton, N.S., 2014. Thinking with their trunks: elephants use smell but not sound to locate food and exclude nonrewarding alternatives. *Animal Behaviour* 88, 91–98.
- Raftery, A.E., 1996. Approximate Bayes factors and accounting for model uncertainty in generalised linear models. *Biometrika* 83(2), 251–266.
- Shettleworth, S.J., 2001. Animal cognition and animal behaviour. *Animal Behaviour* 61(2), 277–286.
- Snyder, R.J., Barrett, L.P., Emory, R.A., Perdue, B.M., 2021. Performance of Asian elephants (*Elephas maximus*) on a quantity discrimination task is similar to that of African savanna elephants (*Loxodonta africana*). *Animal Cognition* 24(5), 1121–1131.
- Sulkowski, G., Hauser, M.D., 2001. Can rhesus monkeys spontaneously subtract? *Cognition* 79(3), 239–262.
- Uller, C., Lewis, J., 2009. Horses (*Equus caballus*) select the greater of two quantities in small numerical contrasts. *Animal Cognition* 12, 733–738.

Appendix 1

Table A1: A summary of some of the relevant literature on animal quantity discrimination. When the effect of one variable was not tested, it appears as a dash. Asterisks indicate that the effect of the variable was not formally tested or it was not statistically significant (but close to) for all or some of the individuals.

Study	Animal class	Species	Type	Stimuli	Presented	Sense	Ratio	Abs diff	Magnitude	Statistical analysis
Abramson et al., 2013	Mammals	Beluga (<i>Delphinapterus leucas</i>), Bottlenose dolphins (<i>Tursiops truncatus</i>)	Trained	Food	Simultaneously	Sight	No	No	No	Binomial tests, Pearson correlation coefficients
		Beluga (<i>Delphinapterus leucas</i>)				Echolocation			Negative	
		Bottlenose dolphins (<i>Tursiops truncatus</i>)			Consecutively	Sight	-	Positive	-	
		Beluga (<i>Delphinapterus leucas</i>)			Item by item		No	No	No	
Agrillo et al., 2007	Fish	Mosquitofish (<i>Gambusia holbrooki</i>)	Untrained	Conspecific	Simultaneously	Sight	Negative	-	No	ANOVAs, Student t-tests
							-	Only 1	Negative	
Agrillo et al., 2010	Fish	Mosquitofish (<i>Gambusia holbrooki</i>)	Trained	Geometric figures	Simultaneously	Sight	Only 1:2	-	No	Student t-tests, Chi-square tests, ANOVAs
							Negative	-	-	
Agrillo et al., 2012	Fish	Guppies (<i>Poecilia reticulata</i>)	Untrained	Conspecific	Simultaneously	Sight	Negative	-	-	ANOVAs, Student t-tests, likelihood ratio analyses
	Mammals	Humans (<i>Homo sapiens</i>)	Trained	Dots on a screen	Consecutively	Sight				

Study	Animal class	Species	Type	Stimuli	Presented	Sense	Ratio	Abs diff	Magnitude	Statistical analysis
Ain et al., 2009	Birds	African grey parrots (<i>Psittacus erithacus</i>)	Untrained	Solid food	Simultaneously	Sight	Negative	Positive	No	Binomial tests, Chi-square tests, Pearson's correlation tests
				Liquid food						
Baker et al., 2011	Mammals	Coyotes (<i>Canis latrans</i>)	Untrained	Food	Simultaneously	Sight	Negative	-	No	Student t-tests, binomial tests, linear regression analyses, binary logistic regressions
Barnard et al., 2013	Mammals	Olive baboons (<i>Papio anubis</i>)	Untrained	Food	Simultaneously	Sight	Negative	-	-	Weber fractions, Pearsons' correlation tests
					Item by item					
Bisazza et al., 2014	Fish	Guppies (<i>Poecilia reticulata</i>)	Trained	3D objects	Simultaneously	Sight	Negative	-		ANOVAs, Tukey's tests, Spearman tests
Bogale et al., 2011	Birds	Jungle crows (<i>Corvus macrorhynchos</i>)	Trained	Printed shapes and symbols	Simultaneously	Sight	Negative	-	Negative	ANOVAs, Wilcoxon signed-ranks tests, Pearson's correlation coefficients
Balestrieri et al., 2019	Amphibians	Green toads (<i>Bufo balearicus</i>), edible frogs (<i>Pelophylax esculentus</i>)	Untrained	Conspecific	Simultaneously	Sight	-	-	-	Wilcoxon tests, Generalised Linear Models
Ba'nszegi et al., 2016	Mammals	Domestic cats (<i>Felis silvestris catus</i>)	Untrained	Food quantity	Simultaneously		Negative	No	No	Binomial tests, Generalised Estimating Equations
				Food size			No	-	No	
				Food quantity		Olfaction	-	-	-	
Beran et al., 2008	Mammals	Capuchin monkeys (<i>Cebus apella</i>)	Untrained	Food	Consecutively	Sight	Negative	-		Sign tests, Pearson's correlation tests, Student t-tests
Bisazza et al., 2014	Fish	Blind cavefish (<i>Phrearichthys andruzzii</i>)	Trained	Sticks	Simultaneously	Touch, lateral line	Negative	-	-	Wilcoxon signed rank tests, Friedman tests

Study	Animal class	Species	Type	Stimuli	Presented	Sense	Ratio	Abs diff	Magnitude	Statistical analysis
Bisazza and Gatto, 2021	Molluscs	Dune snails (<i>Theba pisana</i>)	Untrained	Number of refuges	Simultaneously	Sight	Negative	-	-	Generalised Linear Models, Kendall correlations, Chi-square tests, Bayesian Information Criteria, Bayes Factors
				Objects with a different surface area			No	-	-	
Cantlon and Brennon, 2007	Mammals	Rhesus macaques (<i>Macaca mulatta</i>)	Trained	Dots on a screen	Set + set, then simultaneously	Sight	Negative	-	Negative	Weber fractions
		Humans (<i>Homo sapiens</i>)						-		
Carazo et al., 2009	Insects	Yellow mealworm beetles (<i>Tenebrio molitor</i>)	Untrained	Number of females' odours	Simultaneously	Smell	Negative	-	-	Wilcoxon signed ranks tests
Cox and Montrose, 2016	Mammals	Rats (<i>Rattus norvegicus domestica</i>)	Untrained	Food	Simultaneously	Sight	Negative	-	-	Student t-tests, Spearman rank-order correlation tests
						Olfaction	-	-	-	
						Sight	-	-	-	
Davis, 1984	Mammals	Racoon (<i>Procyon lotor</i>)	Trained	Objects (grapes or metal bells)	Simultaneously	Sight	-	-	-	Binomial expansions
Emmerton, 1998	Birds	Pigeons (<i>Columba livia</i>)	Trained	White dots on a black background	Simultaneously	Sight	-	Positive	-	ANOVAs
Farnsworth and Smolinski, 2006	Birds	Northern Mockingbirds (<i>Mimus polyglottos</i>)	Untrained	Sticks secluding food	Simultaneously	Sight	Negative*	Positive*	No*	Chi-square tests, G-tests of independence, Student t-tests

Study	Animal class	Species	Type	Stimuli	Presented	Sense	Ratio	Abs diff	Magnitude	Statistical analysis
Garland et al., 2012	Birds	North Island robins (<i>Petroica longipes</i>)	Untrained	Food	Item by item	Sight	No	-	Negative	Binary logistic regressions
					Simultaneously	Sight	Negative		No	
Gatto et al., 2017	Fish	Guppies (<i>Poecilia reticulata</i>)	Trained	Dots on a screen	Simultaneously	Sight	-			Chi-square tests, Linear Mixed Models, Student t-tests
				3D objects						
Gazzola et al., 2018	Reptiles	Hermann's tortoises (<i>Testudo hermanni</i>)	Untrained	Food quantity	Simultaneously	Sight	Negative	-	-	Chi-square tests, Mixed Models, Pearson's correlation tests
				Food size						
Gross et al., 2009	Insects	Honeybees (<i>Apis mellifera</i>)	Trained	2D symbols	Consecutively	Sight	No	-	Negative	ANOVAs, Student t-tests
Hanus and Call, 2007	Mammals	Bonobos (<i>Pan paniscus</i>), chimpanzees (<i>Pan troglodytes</i>), gorillas (<i>Gorilla gorilla</i>), and orangutans (<i>Pongo pygmaeus</i>)	Untrained	Food	Simultaneously	Sight	Negative	Positive	No	Wilcoxon tests, Kruskal–Wallis tests, Mann–Whitney tests, Stepwise multiple regressions, Student t-tests, Binomial tests
					Consecutively			No		
					Item by item					
Hauser et al., 2000	Mammals	Rhesus macaques (<i>Macaca mulatta</i>)	Untrained	Food	Item by item	Sight	-	-	Negative	One tail sign tests
Hunt et al., 2008	Birds	New Zealand robins (<i>Petroica australis</i>)	Untrained	Food	Item by item	Sight	Negative*	-	Negative	Binomial tests, Multiple Regression Models
				Food + rocks			Only 1:1	-	Negative	
Irie and Hasegawa, 2012	Mammals	Asian elephants (<i>Elephas maximus</i>)	Untrained	Food	Item by item	Sight	No	No	No	Binomial tests, Pearson's correlation tests

Study	Animal class	Species	Type	Stimuli	Presented	Sense	Ratio	Abs diff	Magnitude	Statistical analysis
Irie et al., 2019	Mammals	Asian elephant (<i>Elephas maximus</i>)	Trained	Shapes on a screen	Simultaneously	Sight	No	No	No	Logistic regressions, Binomial tests
Irie-Sugimoto et al., 2009	Mammals	Asian elephants (<i>Elephas maximus</i>)	Untrained	Food	Simultaneously	Sight	No	-	-	Binomial tests, Pearson's correlation tests
					Item by item	Sight, hearing		No	No	
Kilian et al., 2003	Mammals	Bottlenose dolphin (<i>Tursiops truncatus</i>)	Trained	Two-dimensional shapes on a panel	Simultaneously	Sight	-			Binomial tests
Krusche et al., 2010	Amphibians	Salamanders (<i>Plethodon shermani</i> ; <i>P. metcalfi</i>)	Untrained	Live crickets (Food)	Simultaneously	Sight	Negative	-		Binomial tests
Lin et al., 2021	Reptiles	Asian freshwater turtles (<i>Mauremys sinensis</i>)	Trained	3D objects	Simultaneously	Sight	Negative	-		Wilcoxon signed rank tests, Binomial tests, Linear models
Lucon-Xiccato et al., 2018	Amphibians	Italian treefrogs (<i>Hyla intermedia</i>)	Untrained	Green printed bars	Simultaneously	Sight	Negative	-		Chi-square tests, Generalised Linear Models, Tukey post hoc test
MaBouDi et al., 2020	Insects	Bumblebees (<i>Bombus terrestris audax</i>)	Trained	Artificial flowers	Simultaneously	Sight	-	-	-	Generalised Linear Models
Miletto Petrazzini et al., 2017	Reptiles	Ruin lizards (<i>Podarcis sicula</i>)	Untrained	Food size	Simultaneously	Sight	Negative	-		ANOVAs
				Food number			No			
Panteleeva et al., 2013	Mammals	Striped field mice (<i>Apodemus agrarius</i>)	Untrained	Live food	Simultaneously	Sight, tact, smell	-		No*	Chi-square tests, Wilcoxon signed-rank tests
Perdue et al., 2012	Mammals	African elephants (<i>Loxodonta africana</i>)	Untrained	Food	Item by item	Sight, hearing	Negative	-	No	Binomial distributions, Pearson's correlations tests, Chi-square tests
						Hearing				

Study	Animal class	Species	Type	Stimuli	Presented	Sense	Ratio	Abs diff	Magnitude	Statistical analysis
Pisa and Agrillo, 2009	Mammals	Domestic cats (<i>Felis silvestris catus</i>)	Trained	Dots on a piece of paper	Simultaneously	Sight	-			Chi-square tests, One sample t-tests
Plotnik et al., 2019	Mammals	Asian elephants (<i>Elephas maximus</i>)	Untrained	Food	Simultaneously	Smell	Negative	Positive	-	Logistic regression mixed models, Chi-square tests
							Only 1:2 and 1:3	-	No	
Range et al., 2014	Mammals	Dogs (<i>Canis familiaris</i>)	Trained	Food	Item by item	Sight	Negative*	-		Non-linear mixed effect models, One-sample t-tests
				Food + rocks						
Rugani et al., 2013	Birds	Domestic chicks (<i>Gallus gallus</i>)	Trained	Images on screens	Simultaneously	Sight	Negative	-	No	ANOVAs, One-sample t-tests
Tomonaga, 2008	Mammals	Chimpanzees (<i>Pan troglodites</i>)	Trained	Dots on a screen	Simultaneously	Sight	Negative	Positive	-	Multiple regression analysis, Binomial tests, ANCOVAs
								-	No	
Schmitt and Fischer, 2011	Mammals	Olive baboons (<i>Papio anubis</i>), long-tailed macaques (<i>Macaca fascicularis</i>)	Untrained	Food	Simultaneously	Sight	Negative	Positive	-	Generalised Linear Mixed Models
				Rocks						
Snyder et al., 2021	Mammals	Asian elephants (<i>Elephas maximus</i>)	Untrained	Food	Item by item	Sight and hearing	Negative	-	Negative*	Pearson's correlation tests, Mann-Whitney test, Generalised Linear Models
						Hearing	Negative*		No	
						Both	Only 1:2		No	

Study	Animal class	Species	Type	Stimuli	Presented	Sense	Ratio	Abs diff	Magnitude	Statistical analysis
Stancher et al., 2014	Amphibians	Oriental fire-bellied toads (<i>Bobina orientalis</i>)	Untrained	Live food	Simultaneously	Sight	Negative	-		ANOVAs, Mauchly's sphericity tests, Student t-tests, Fisher's LSD posthoc test
							-			
Tornick et al., 2015	Birds	Clark's nutcrackers (<i>Nucifraga columbiana</i>)	Untrained	Food	Consecutively	Sight	Negative	No	No	Student t-tests, Linear regressions
Uller and Lewis, 2009	Mammals	Horses (<i>Equus caballus</i>)	Untrained	Artificial apples	Item by item	Sight	Only 2:3	-	Negative	Binomial tests
							-			
Uller et al., 2003	Amphibians	Salamanders (<i>Plethodon cinereus</i>)	Untrained	Live food	Simultaneously	Sight	Negative*	-	Negative	Binomial tests
Utrata et al., 2012	Mammals	Timber wolves (<i>Canis lupus</i>)	Untrained	Food	Item by item	Sight	Negative*	-		Non-linear mixed effect models, Student t-tests, Binomial tests
				Food + rocks			No			
Ward and Smuts, 2007	Mammals	Domestic dogs (<i>Canis lupus familiaris</i>)	Untrained	Food	Simultaneously	Sight	Negative	Positive	No	Generalised Estimating Equation Models, Binomial tests
					Consecutively		Negative/No	Positive/No		
							No			

Table A2: A description of the binary comparisons presented to the elephants in this study, with their ratio, absolute difference, and cumulative magnitude. In Chapter 3 the elephants discriminated between all the comparisons, in Chapter 4 the elephants were presented only with the comparisons in the white cells.

Alternatives	Ratio	Absolute difference	Cumulative magnitude
1vs6 – 6vs1	0.17	5	7
1vs5 – 5vs1	0.20	4	6
1vs4 – 4vs1	0.25	3	5
1vs3 – 3vs1	0.33	2	4
2vs6 – 6vs2	0.33	4	8
2vs5 – 5vs2	0.40	3	7
1vs2 – 2vs1	0.50	1	3
2vs4 – 4vs2	0.50	2	6
3vs6 – 6vs3	0.50	3	9
4vs8 – 8vs4	0.50	4	12
5vs10 – 10vs5	0.50	5	15
3vs5 – 5vs3	0.60	2	8
2vs3 – 3vs2	0.67	1	5
4vs6 – 6vs4	0.67	2	10
3vs4 – 4vs3	0.75	1	7
4vs5 – 5vs4	0.80	1	9
5vs6 – 6vs5	0.83	1	11

Table A3: A list of the available studies on quantity discrimination in elephants, indicating the species, the number of tested individuals, the mode of presentation of the stimuli, the sense involved in the choice, and the effect of ratio, absolute difference, and cumulative magnitude of the alternatives on discrimination, the statistical analysis used, and some notes. When the effect of one variable was not tested, it appears as a dash.

Study	Species	N elephants	Presented	Sense	Ratio	Abs diff	Magn	Statistical analysis	Notes
Irie and Hasegawa, 2012	Asian elephants (<i>Elephas maximus</i>)	3	Item by item	Sight	No	No	No	Binomial tests, Pearson's correlation tests	
Irie et al., 2019	Asian elephants (<i>Elephas maximus</i>)	1	Simultaneously	Sight	No	No	No	Logistic regressions, Binomial tests	High ratios and small absolute differences increased the time needed by the elephant to make a decision
Irie-Sugimoto et al., 2009	Asian elephants (<i>Elephas maximus</i>)	5	Simultaneously	Sight	No	-	-	Binomial tests, Pearson's correlation tests	One elephant was negatively affected by absolute difference, and another was positively affected by absolute difference
		4	Item by item	Sight, hearing		No	No		
Perdue et al., 2012	African elephants (<i>Loxodonta africana</i>)	2	Item by item	Sight, hearing Hearing	Negative	-	No	Binomial distributions, Pearson's correlations tests, Chi-square tests	No effect of magnitude at ratio 1:2
Plotnik et al., 2019	Asian elephants (<i>Elephas maximus</i>)	6	Simultaneously	Smell	Negative Only 1:2 and 1:3	Positive -	- No	Logistic regression mixed models, Chi-square tests	
Snyder et al., 2021	Asian elephants (<i>Elephas maximus</i>)	2	Item by item	Sight and hearing	Negative	-	Negative*	Pearson's correlation tests, Mann-Whitney tests, Generalised Linear Models	*Both magnitude and ratio had a negative effect for one elephant, no effect for the other.
				Hearing	Negative*		No		
				Both	Only 1:2		No		