# Farm Animal Cognition

## Physico- and Socio-Cognitive Capabilities of Ungulate Livestock

**Dissertation**
**zur Erlangung des**
**Doktorgrades der Agrarwissenschaften (Dr. agr.)**
der
Naturwissenschaftlichen Fakultät III
Agrar- und Ernährungswissenschaften,
Geowissenschaften und Informatik
der Martin-Luther-Universität Halle-Wittenberg

vorgelegt von
Diplombiologe Christian Nawroth
geboren am 15.10.1982 in Elsterwerda

Gutachter: Prof. Dr. Eberhard von Borell
Prof. Dr. Birger Puppe

Verteidigung am: 02.02.2015

Halle/Saale 2015

# Acknowledgment

My first sincere gratitude goes to my supervisor at the Martin-Luther-University, Prof. Eberhard von Borell, for giving me the opportunity to work with him at the Department of Animal Husbandry and Ecology.

I also want to acknowledge the support I received from my department colleagues.

I am very grateful to my external collaborators, Mirjam Ebersbach and Jan Langbein. My gratitude also goes to Judith Benz-Schwarzburg, Ludwig Huber, Juliane Kaminski and Christian Schlögl, whose dedication to the field of animal cognition was contagious.

I want to thank all the animals that participated in the experiments for all the joy, excitement, and these moments of "well, this is strange…".

Finally, I would like to thank Svenja Knipphals for her never ending support during my doctoral study and beyond.

This dissertation is dedicated to my parents.

# Summary

This thesis aims to investigate physico- and socio-cognitive capabilities of ungulate livestock species, in particular those of domestic pigs (*Sus scrofa domestica*), dwarf goats (*Capra aegagrus hircus*) and sheep (*Ovis orientalis aries*), to gain a better understanding of how these animals mentally represent their physical and social environment. Test paradigms from recent comparative psychological research in primates and dogs were used and modified to the behavioural needs and constraints of the tested species. The thesis is divided into eight chapters.

**Chapter I** gives a general introduction to the topic of physical and social cognition. It also provides a brief history of previous studies on livestock species focusing on behavioural aspects in general and cognition in particular. An additional section reports on the intersection of animal cognition research and animal welfare science. Finally, Chapter I states the objectives of the thesis and briefly introduces the administered test paradigms of the various experiments.

**Chapter II** provides an extensive introduction to the topic of exclusion performance and is published in the journal *PLOS ONE*. The objective in this study was to compare dwarf goats and sheep in their ability to choose a hidden reward by means of absent and therefore indirect information (i.e. to choose by exclusion). The results show that goats performed better than sheep when only indirect information was available. These results may be caused by the different feeding ecologies of the two species, with goats expressing a higher feeding flexibility and higher loss aversion.

**Chapter III** presents a series of experiments investigating the ability to choose by exclusion in two perceptual modalities in domestic pigs and is published in the journal *Animal Cognition*. The objective of this study was to test the ability of domestic pigs to choose by exclusion in the visual and auditory domain. The results showed that pigs were able to use indirect visual and, to some degree, indirect auditory cues to infer the location of a hidden reward.

**Chapter IV** provides a detailed introduction covering several aspects of social cognition in human-animal interactions. It presents investigations on various socio-cognitive abilities of dwarf goats and is published in the Journal *Animal Cognition*. The objectives of this study were to investigate the ability of dwarf goats to differentiate between attentive states of humans using a food-anticipation paradigm and to investigate which human-given cues goats are able to use in an object choice task. The results indicated that subjects changed their anticipatory behaviour depending on the presence and absence of an experimenter in general and his attentive state in particular as a means for reward delivery. In addition, goats were able to use cues like pointing and touching to find a hidden food reward, but failed to use head direction of the experimenter as a cue in a food-related context.

**Chapter V** presents research on the ability of domestic pigs to differentiate between attentive states of humans in a choice task and is published in the Journal *Behavioural Processes*. An impulsive approach style with short response times and a non-impulsive approach style where response times were relatively long could be distinguished. Pigs applying the non-impulsive approach style chose the attentive person above chance level, which was not the case when subjects chose impulsively.

**Chapter VI** provides knowledge on the use of human-given cues in juvenile domestic pigs in a series of experiments and is published in the Journal *Animal Cognition*. The results showed that pigs are able to use a wide variety of pointing cues as well as the head orientation of an experimenter to find a hidden reward.

**Chapter VII** gives a brief summary of the adaptability of the test paradigms and a brief cross-species comparison about the results obtained. Additional sections report implications for animal welfare as well as an outlook on future studies.

**Chapter VIII** provides the final conclusions of the thesis.

**Keywords:** animal welfare; human-animal interaction; physical cognition; pigs; small ruminants; social cognition

# ZUSAMMENFASSUNG

Im Zentrum der vorliegenden Dissertation steht die Untersuchung physikalisch- und sozial-kognitiver Fähigkeiten von Nutztieren, insbesondere die von Hausschweinen (*Sus scrofa domestica*), Zwergziegen (*Capra aegagrus hircus*) und Schafen (*Ovis orientalis aries*). Zu diesem Zweck wurden verschiedene, bisher ausschließlich bei Primaten und Hunden erfolgreich angewandte, Testparadigmen aus der vergleichenden Psychologie auf Nutztiere übertragen. Die Arbeit ist in acht Kapitel unterteilt.

**Kapitel I** gibt eine generelle Einführung in die Bereiche der physikalischen und sozialen Kognition sowie eine kurze Zusammenfassung vorheriger Verhaltens- und Kognitionsstudien an Nutztieren. Es werden zusätzlich die Zusammenhänge von Kognitionsstudien und artgerechter Tierhaltung diskutiert. Die Zielsetzungen des Dissertationsprojekts und die verwendeten Testaufbauten werden dargestellt.

**Kapitel II** beinhaltet eine ausführliche Einleitung zur kognitiven Fähigkeit ‚Wahl durch Ausschluss' und wurde in der Zeitschrift *PLOS ONE* veröffentlicht. In dieser Studie wurden die Fähigkeiten von Zwergziegen und Schafen verglichen, durch Ausschlussprinzip eine Wahl zu treffen. Die Ergebnisse zeigen, dass der Wahlerfolg bei nicht-verfügbarer und somit indirekter Information bei Ziegen höher ist als bei Schafen. Dieses Resultat kann durch die Unterschiede in der Nahrungsselektivität beider Arten erklärt werden, da Ziegen selektiver als Schafe Nahrung aufnehmen und als Konsequenz darauf sensibler auf mögliche Futterverluste reagieren.

**Kapitel III** präsentiert eine Serie von Experimenten, welche die Fähigkeiten von Hausschweinen untersuchten, indirekte akustische und visuelle Reize zum Auffinden eines Futterverstecks zu nutzen. Es wurde in der Zeitschrift *Animal Cognition* veröffentlicht. Hier zeigte sich, dass die Tiere indirekte visuelle Reize zur Ausschlusswahl nutzten. Allerdings war lediglich ein Tier in der Lage auch negative akustische Reize in den Wahlprozess zu integrieren.

**Kapitel IV** beginnt mit einer detaillierten Einführung in spezifische sozio-kognitive Aspekte der Mensch-Tier-Interaktionen. Untersuchungsschwerpunkte waren verschiedene sozio-kognitiven Fähigkeiten von Zwergziegen. Das Kapitel wurde in der Zeitschrift *Animal*

*Cognition* veröffentlicht. Diese Studie beinhaltet Untersuchungen zur Differenzierung zwischen verschiedenen Aufmerksamkeitszuständen eines Menschen sowie zum Nutzen von menschlichen Zeigegesten beim Auffinden einer versteckten Futterbelohnung. Die Ergebnisse weisen darauf hin, dass Ziegen ihr Antizipationsverhalten in Abhängigkeit zur menschlichen Aufmerksamkeit ändern. Zudem sind sie in der Lage, Zeigegesten eines menschlichen Experimentators zu nutzen − allerdings nicht dessen Kopforientierung.

**Kapitel V** stellt eine Studie vor, in welcher die Fähigkeit junger Hausschweine, zwischen verschiedenen Aufmerksamkeitszuständen eines Menschen zu unterscheiden, untersucht wurde. Diese wurde in der Zeitschrift *Behavioural Processes* veröffentlicht. Im Verhalten der Tiere konnte zwischen einer impulsiven Wahl, mit kurzen Antwortzeiten, und einer nicht-impulsiven Wahl, mit relativ langen Antwortzeiten, unterschieden werden. Tiere mit nicht-impulsivem Wahlverhalten wählten die aufmerksame Person signifikant über einer Zufallswahl von 50%.

**Kapitel VI** gibt die Untersuchungen zur Nutzung von menschlichen Hinweisreizen durch junge Hausschweine wieder und wurde in der Zeitschrift *Animal Cognition* veröffentlicht. Die Ergebnisse zeigen, dass Schweine in der Lage sind, eine Vielzahl von menschlichen Zeigegesten, einschließlich der Kopforientierung eines menschlichen Experimentators, zum Auffinden einer versteckten Futterbelohnung nutzen.

**Kapitel VII** enthält eine kurze Zusammenfassung über die Anwendbarkeit neuer Testaufbauten und einen artübergreifenden Vergleich der gewonnenen Ergebnisse. Des Weiteren werden mögliche Auswirkungen auf das Tierwohl und die Haltungsbedingungen von Nutztieren diskutiert. Ein Ausblick beleuchtet Ansätze für zukünftige Studien.

**Kapitel VIII** beinhaltet das Fazit der Dissertation.

**Schlagwörter:** kleine Wiederkäuer; Mensch-Tier-Interaktion; physikalische Kognition; Schweine; soziale Kognition; Tierwohl

# TABLE OF CONTENTS

# List of Tables

# CHAPTER I: INTRODUCTION

The welfare of an animal includes its physical and mental state, and all animals must at least be protected from unnecessary suffering. The Farm Animal Welfare Council in the UK has therefore proposed the 'five freedoms' (Wathes 2010; Farm Animal Welfare Council 2013) which consist of: 1. the freedom from hunger and thirst, 2. the freedom from discomfort, 3. the freedom from pain, injury or disease, 4. the freedom to express normal behaviour, and 5. the freedom from fear and distress.

Other welfare-related approaches to the treatment of animals emerged, covering affective states (Désiré et al. 2002; Marchant-Forde et al. 2009; Mendl et al. 2010), motivation (Kirkden & Pajor 2006; Buijs et al. 2011), coping behaviour (Forkman et al. 1995) and biological/cognitive functioning of farm animals (Duncan & Petherick 1991; Fraser et al. 1997). All of them are in agreement that a detailed understanding of the perceptive and cognitive abilities of non-human animals is necessary for understanding their normal behavioural expressions and for avoiding exposing them to mental distress.

Although it is epistemologically not possible to gain access to the subjective states of another individual (Nagel 1974), objective measures of behaviour can serve as a gateway for researchers to investigate the cognitive mechanisms underlying the perception of the environment in human and non-human individuals. In the last two decades, this field of research has gained increased attention. Most studies here focus on our closest living relatives, primates in general and great apes in particular, and, in terms of convergent cognitive evolution, on corvids and dogs (*Canis familiaris*). However, compared with the amount of studies conducted with the aforementioned species – and despite noteworthy examples (e.g. Albiach-Serrano et al. 2012; Held et al. 2001, 2000; Meyer et al. 2012) - studies on the cognitive capabilities of farm animals are still underrepresented (Shettleworth 2009).

The term 'cognition' can be defined as the mental process of acquiring knowledge and understanding through thought, experience, and the senses and can be divided into two broader domains: physical and social cognition.

## I.I Physical Cognition

The term ‘physical cognition’ refers to an organism’s understanding of objects and their various spatial and causal relationships. For most animal species, the biggest problem that is faced is locating and obtaining food. Thus, many important cognitive skills evolved in the context of foraging (Tomasello & Call 1997).

Most importantly, animals have to navigate in space during the search and relocation of food, shelter and mates - for instance by remembering distinct features, such as size and colour, of specific locations or by spatially representing the environment, using local or global landmarks or the inter-array constellation of specific objects (Shettleworth 2010).

Numerical competence (e.g. Pepperberg 2006), object permanence (i.e., the notion that objects continue to exist even when they are out of an observer’s sight, see Jaakkola 2014) and causal reasoning and learning are other topics usually investigated in this domain (e.g., Premack & Premack 1994). Moreover, the ability to use tools, i.e., to manipulate an inanimate object to reach a goal, is a topic that has gained interest in recent decades (e.g., Vaesen 2012).

## I.II Social Cognition

Conspecifics are physical objects that must be located and identified and that create additional cognitive problems that are not present in the world of inanimate objects (Tomasello & Call 1997). For example, living in groups requires the discrimination of con- and heterospecifics, either on an individual or a group level. Being a social animal also requires some particular form of social intelligence as manipulating conspecifics‘ behaviour, in contrast to manipulating inanimate physical objects, involves the implementation of various social strategies (Barton & Dunbar 1997). Moreover, another individual might behave spontaneously on its own. Thus, the ability to infer the motivations and desires of others will be advantageous for lowering the level of uncertainty in predicting other´s behaviour. Knowledge of perceptive (perception and knowledge) and motivational (desires) states of others, summarized as the so-called ‘Theory of Mind’ (Call & Tomasello 2008), can also be used for more advanced forms of social behaviours and tactics, e.g., intentional deception and cooperation.

An additional crucial part of social cognition involves the ability to socially learn, either through stimulus enhancement, social facilitation, emulation and/or imitation (Huber et al. 2009).

Finally, the domain of social cognition also involves questions regarding the cognitive foundations of morality, e.g. actions involving the welfare of conspecifics, e.g., pro-social choice (Horner et al. 2011) and empathy (Preston & de Waal 2002) or fairness, e.g., inequity aversion (Brosnan & Waal 2003).

## I.III Behavioural Studies on Livestock Species

Previous studies in livestock species have investigated their ability to discriminate between visual, olfactory and acoustic stimuli (e.g., discrimination of shapes in dwarf goats, see Langbein et al. 2008; discrimination of different colours in pigs, see Tanida et al. 1991). This is important for understanding how these animals perceive their environment since their perceptual and discriminatory abilities can differ from our own.

Another line of recent research focuses on emotion and affective states in livestock species because emotionally positive experiences are an important part of good welfare. Here, it is of special concern which environmental and social parameters can affect these variables.

An emotional response consists of behavioural as well as physiological changes and can be investigated using a subject’s anticipation behaviour. For example, an animal can be conditioned to expect a positive or a negative outcome following a formerly neutral stimulus and subjects´ arousal can be assessed based on behavioural as well as heart rate and heart rate variability measures (Zebunke et al. 2011; Imfeld-Mueller et al. 2011). Moreover, this approach can also be used to investigate subjects´ general arousal in different housing conditions or during handling procedures (de Jong et al. 1998; Lensink et al. 2001; Zebunke et al. 2013).

The cognitive components of animals´ emotions are another important aspect and can be studied in experiments using a so-called cognitive or judgment bias (Mendl et al. 2009). Negative affective states are accompanied by greater attention to threatening stimuli and an increased likelihood that ambiguous information will be interpreted pessimistically, whereas more positive states are accompanied by more optimistic judgments. Therefore, this cognitive bias could be a useful tool for measuring the impact of an animal’s environment on its affective state. Currently, there is evidence for an emotion-related judgment bias in decision making in a range of species including rats (Harding et al. 2004; Brydges et al. 2011), sheep (Doyle et al. 2010a, 2010b), cattle (Neave et al. 2013; Daros et al. 2014), domestic pigs (Douglas et al. 2012), and even honeybees (Bateson et al. 2011).

### *I.III.I Cognitive Studies on Livestock Species*

A detailed list of comparable cognitive studies conducted on primates, birds, dogs and livestock species can be found in Table 1.

Several studies showed that pigs seem to be exceptionally good in using spatial information to find hidden food (Mendl et al. 1997; Laughlin & Mendl 2000; Bolhuis et al. 2013). Moreover, they are also able to use feature cues like colour or odour to relocate a rewarded option in space (Croney et al. 2003; Gieling et al. 2012). Other studies conducted on dwarf goats implementing the use of a touch screen have shown their ability to use the oddity principle (Roitberg & Franz 2004) or to form categories of objects (Meyer et al. 2012).

Causal reasoning in livestock species is not well studied and demands further investigations. Albiach-Serrano et al. (2012) presented domestic pigs with a series of tasks covering the social and physical domain of cognition. One of the tasks involved the presentation of a slighted board, covering a hidden reward, while another one involved a baited cup that was shaken and therefore produced some noise. Subjects here had to infer the position of the reward by using the causal relationships between the reward and the board/cup, i.e., the inclination of the board or the noise while shaking the cup. Pigs were able to solve these tasks, though it was not clear if they only used stimulus enhancement cues.

For livestock species, numerical competence was only a subject of investigation in horses (Uller & Lewis 2009; Gabor & Gerken 2014). Studies on other farm livestock species still have to be conducted. To date, no studies involving tool use are available for livestock species (but for dogs see Smith et al. 2012).

Finally, some recent studies suggest some quite sophisticated cognitive abilities in ungulate livestock, such as problem solving and long-term memory in domestic goats (Briefer et al. 2012, 2014) and the use of a mirror to obtain information (Broom et al. 2009; but see Gieling et al. 2014).

In the social domain, many studies on ungulate livestock confirmed that they can discriminate between familiar and unfamiliar conspecifics, as well as between individual group members (cattle (*Bos taurus*): Hagen and Broom 2003; Coulon et al. 2011; goats (*Capra hircus*): Briefer & McElligott 2011; Keil et al. 2012; Briefer et al. 2012; sheep (*Ovis* *aries*): Ligout & Porter; Kendrick et al. 1995; horses (*Equus caballus*): Proops et al. 2009; Krueger & Flauger 2011; pigs (*Sus scrofa*): Mendl et al. 2002; McLeman et al. 2005). Moreover, studies of pigs and cattle have shown that body height and/or facial features can be sufficient to discriminate between humans (Koba & Tanida 2001; Rybarczyk et al. 2001).

Using an informed forager paradigm (Coussi-Korbel 1994), Held and colleagues (2002) found that the approach time to a baited container of a subordinate but knowledgeable pig depends on the body position of a dominant but ignorant conspecific. Overall, the subordinates were more likely to show food-directed behaviour when the chances of arriving at the food source ahead of their exploiters were higher. In one very well controlled study, Held et al. (2001) allowed pigs to follow two companion pigs. One was able to see the baiting of food and the other was not. Most pigs did not follow their companions, probably to avoid competitive and aggressive behaviour. Nonetheless, out of ten pigs, two subjects followed their conspecifics and one of them followed the 'knowing' individual significantly more often than the 'not knowing' individual, suggesting that pigs, to some degree, might be able to take the visual perspective of others.

To date, only a few studies have investigated interspecies communication between ungulate livestock and humans. For example, Kaminski et al. (2005) tested domestic goats in their ability to follow various human-given cues, including pointing and head direction, in an object choice task. Similar studies were conducted with horses (Maros et al. 2008; Proops et al. 2010) and pigs (Albiach-Serrano et al. 2012). These studies found that goats and horses were able to utilize pointing, but not head cues of a human experimenter towards a target location to find a hidden reward whereas domesticated pigs performed poorly with pointing and head cues. Moreover, horses were tested in other studies, in which it was investigated if and how they differentiate between different degrees of human attention (Proops & McComb 2010; Andre & Hausberger 2011). It was found that they behaved differently when a human experimenter was not looking at them, e.g., when the human head was turned away from the subject. Except for dogs (Call et al. 2003), no other domesticated species has been tested with similar test paradigms. Moreover, studies investigating more complex human-animal communication in other domesticated species than dogs are rare (see for dogs: Miklósi et al. 2003; Call et al. 2009; Bräuer et al. 2013).

**Table 1** Overview covering experimental studies on primates, corvids, dogs and ungulate livestock species. Fields marked bold refer to the target area of investigation in the studies conducted within this thesis. + marks positive results, +/- marks inconclusive results, - marks negative results

| Topic | Sub-Topic | Primates | Corvids and Psittacines | Canids | Livestock species |
|---|---|---|---|---|---|
| Discrimination between | Arbitrary stimuli | (1) Chimpanzee + | (2) Raven + | (3) Dogs + | (4) Goats +<br>(5) Pigs + |
| | Conspecifics | (6) Chimpanzee + | (7) Carrion crows + | (8) Dogs + | (9) Cattle +<br>(10) Goats +<br>(11) Pigs + |
| | Humans | (12) Chimpanzee + | (13) Crows + | (8) Dogs + | (14) Cattle +<br>(15) Pigs + |
| Exclusion performance in an object choice task | Indirect visual cues | (16) Great apes +<br>(17) Capuchin + | (18) Carrion crows +<br>(19) Keas –<br>(19) Raven + | (20) Dogs + | n/a |
| | Indirect auditory cues | (16) Great apes +<br>(17) Chapuchins +/- | (21) Grey parrots + | (22) Dogs - | (23) Pigs - |
| Use of human-given cues in an object choice task | Point & touch (local enhancement) | (24) Chimpanzee +/- | (25) Jackdaws +<br>(26) Raven - | (27) Dogs +<br>(28) Wolves +/- | (29) Goats +<br>(30) Horses +<br>(23) Pigs +/- |
| | Head orientation (without local enhancement) | (31) Chimpanzee +/- | (25) Jackdaws +<br>(26) Raven -<br>(32) Rooks +/- | (27) Dogs +<br>(27) Wolves - | (29) Goats –<br>(30) Horses –<br>(23) Pigs – |
| Differentiation between attentive states | Choice task | (33) Chimpanzee +<br>(34) Rhesus macaques + | (35) Robins + | (36) Dogs +<br>(36) Wolves + | (37) Horses + |
| | Obedience task | n/a | n/a | (38) Dogs + | (39) Horses + |
| | Food request task | (40) Great apes +<br>(41) Mangabeys +<br>(42) Baboons + | (25) Jackdaws + | n/a | n/a |

| | | | | | |
|---|---|---|---|---|---|
| Differentiation between intentional and accidental actions | | (43) Chimpanzee +<br>(44) Capuchins + | (45) Grey parrots +/- | (46) Dogs + | n/a |
| Cooperation | | (47) Chimpanzee + | (48) Grey parrots +/- | (49) Dogs +/- | n/a |
| Welfare of others | | (50) Chimpanzee +<br>(51) Capuchins + | n/a | n/a | n/a |
| Fairness/Inequity aversion | | (52) Chimpanzee +<br>(53) Rhesus macaques + | n/a | (54) Dogs + | n/a |

(1) Hayes et al. 1953 (2) Range et al. 2008 (3) Aust et al. 2008 (4) Langbein et al. 2004 (5) Gieling et al. 2012 (6) Campbell & de Waal 2011 (7) Wascher et al. 2012 (8) Racca et al. 2010 (9) Coulon et al. 2011 (10) Keil et al. 2012 (11) McLeman et al. 2005 (12) Parr et al. 1998 (13) Cornell et al. 2012 (14) Rybarczyk et al. 2001 (15) Koba & Tanida 2001 (16) Call 2004 (17) Sabbatini & Visalberghi 2008 (18) Mikolasch et al. 2012 (19) Schloegl et al. 2009 (20) Erdőhegyi et al. 2007 (21) Schloegl et al. 2012 (22) Bräuer et al. 2006 (23) Albiach-Serrano et al. 2012 (24) Mulcahy & Call 2009 (25) von Bayern & Emery 2009 (26) Schloegl et al. 2008 (27) Hare et al. 2002 (28) Virányi et al. 2008 (29) Kaminski et al. 2005 (30) Proops et al. 2010 (31) Call et al. 1998 (32) Schmidt et al. 2011 (33) Bulloch et al. 2008 (34) Flombaum & Santos 2005 (35) Garland et al. 2014 (36) Udell et al. 2011 (37) Proops & McComb 2010 (38) Call et al. 2003 (39) Andre & Hausberger 2011 (40) Kaminski et al. 2004 (41) Maille et al. 2012 (42) Bourjade et al. 2014 (43) Call et al. 2004 (44) Phillips et al. 2009 (45) Peron et al. 2010 (46) Kaminski et al. 2012 (47) Melis et al. 2006 (48) Péron et al. 2011 (49) Bräuer et al. 2013 (50) Horner et al. 2011 (51) Lakshminarayanan & Santos 2008 (52) Brosnan et al. 2005 (53) Brosnan & Waal 2003 (54) Range et al. 2009

### *I.III.II Animal Cognition and Animal Welfare*

Animal welfare is a major concern for society and food production. Good animal welfare is not only determined by the standard of husbandry, but also by both physical and mental health. Although most attempts to investigate the cognitive capabilities of non-human animals represent basic research, general knowledge of how farm animals perceive and deal with their physical and social environment are of importance for applied ethology. Studies covering an individual's learning mechanisms and its understanding of its physical surroundings can provide valuable information for how to design high-standard husbandry conditions (Mendl et al. 1997; Laughlin & Mendl 2000) and to design more appropriate cognitive enrichment, thus improving animal welfare (Puppe et al. 2007; Kalbe & Puppe 2010; Meyer & Langbein 2010; Zebunke et al. 2011). Additionally, studies investigating complex human-animal interactions (e.g., interspecific communication) can contribute to reducing stress during handling and transport (Jago et al. 1999; Waiblinger et al. 2006; Probst et al. 2012). For example, previous studies have shown that early direct interactions between calves/heifers and their handlers (e.g., stroking) led to positive physiological outcomes, including less stress and fear of humans (Boissy & Bouissou 1988; Stewart et al. 2013) which was previously linked to negative effects on welfare (Rushen et al. 1999; de la Lama & Mattiello 2010). Positive human-animal interactions may also increase productivity of livestock (Breuer et al. 2000; Hemsworth 2003). Finally, preventing poor welfare is not the same as providing animals with good welfare. Gaining a better understanding of how livestock species represent their environment will help to provide positive animal welfare and is therefore critical for progress.

## I.IV Objectives

The experimental studies of this thesis focused on several aspects of the physico- and socio-cognitive domain in different species of ungulate livestock. Chapters II and III present investigations covering the ability to choose by exclusion in domestic pigs, dwarf goats and sheep. Chapters IV, V and VI present experiments focusing on the attribution of attentive states in heterospecifics (i.e., humans) and the use of human-given cues by domestic pigs and dwarf goats.

### *I.IV.I Physical Cognition – Exclusion Performance*

In a first set of studies, different species of ungulate livestock were tested in the physico-cognitive domain on their ability to choose by exclusion the location of a hidden reward. A test subject selects the correct location by excluding other potential alternatives even though only indirect information is available (i.e., the absence of a specific cue). For example, Call (2004) used a test setup in which different primate species were presented with two opaque cups of which only one was baited. The subjects were given different kinds of information: full information (content of both cups), direct information (content of baited cup) and indirect information (content of non-baited cup) or no information (control condition). In the case of providing indirect information, it can be tested whether the subjects are able to reason by means of exclusion about the location of the hidden reward or not.

Several explanations for differences in species-specific performances in exclusion tasks are currently proposed (see Table 1). For example, the use of extractive skills to capture prey might explain why great apes and capuchin monkeys (*Cebus apella*) solve the acoustic version of the cup task whereas other primate species do not (Call 2004, 2006; Sabbatini & Visalberghi 2008; Schmitt & Fischer 2009; Heimbauer et al. 2012). In another approach, caching in corvids was linked to their ability to solve a visual exclusion task (Schloegl et al. 2009; Schloegl 2011; Mikolasch et al. 2012). Yet another, more general, explanation focuses on species-specific foraging flexibility – in particular on differences in loss aversion in food acquisition.

Chapters II and III present investigations concerning if, and under which circumstances, domestic pigs, dwarf goats, and sheep are able to choose a hidden reward when they are presented with indirect information only. The paper in Chapter II (Nawroth et al. 2014a) used a comparative approach, testing dwarf goats and sheep with an identical setup. As browsing species, feral and wild goats exhibit highly selective feeding behaviour compared with the rather unselective grazing sheep (Hofmann 1989). This leads to the hypothesis that goats are more flexible in their decision making than sheep and should perform better when confronted with indirect information. In the paper covered by Chapter III (Nawroth & von Borell 2015), juvenile pigs were tested in a slightly different task. Pigs were free to enter a test area where they had to choose between two possible baiting locations. Unlike in the study comparing dwarf goats and sheep, direct and indirect auditory cues were provided to the subjects. As omnivorous and opportunistic feeders, pigs were expected to show a high flexibility in their foraging decisions.

According to the 'foraging flexibility' hypothesis, differences in the use of indirect information were expected between pigs, goats and sheep. Domestic pigs and goats should show better performance in using indirect information due to a higher aversion to losses in food acquisition compared with sheep (Hosoi et al. 1995).

### *I.IV.II Social Cognition – Attentive States and Human-Given Cues*

In a second set of studies within the frame of this thesis, a set of socio-cognitive capacities concerning the differentiation between attentive states and the use of social cues of humans was investigated (Chapter IV-VI). Two kinds of test paradigms are commonly used to study the recognition of attentive states. The first is a choice paradigm in which subjects, in order to receive a reward, are able to choose between two individuals which differ in their attentive state towards the subject. Here, subjects choose the person that pays attention to them (Bania and Stromberg, 2013; Botting et al., 2011; Bulloch et al., 2008; Gácsi et al., 2004; Povinelli and Eddy, 1996; Proops and McComb, 2010) – expecting to receive a food reward or receive one faster. The second is a food-requesting paradigm, in which the subject is facing a human experimenter who engages in different attentive states before a reward is delivered after a certain delay (Kaminski et al. 2004; Hattori et al. 2007; Tempelmann et al. 2011; Maille et al. 2012; Bourjade et al. 2014).

For dwarf goats, a food-requesting paradigm (Chapter IV) was applied to investigate if dwarf goats alter their behaviour depending on different levels of human attention (Nawroth et al. 2015). Additionally, domestic pigs were tested using a choice paradigm (Chapter V) to investigate if they are able to discriminate between different human attentive states (Nawroth et al. 2013). Since goats and pigs are prey species, they should pay attention towards the attentive state of heterospecifics and therefore differences in their behavioural reactions across test conditions were expected

Following the gaze of others might be, in some situations, crucial for survival as well. One mechanism is to co-orient with another individual´s gaze direction to share attention towards a specific object that the other individual is looking at. In a so-called object choice task, a subject can choose between two or more containers, only one of which contains a hidden food reward. A human experimenter administers a communicative cue (e.g. pointing or gazing) towards the correct container while the tested subject is free to choose one (for a review see Miklósi & Soproni 2006).

It was examined if, and under which circumstances, dwarf goats (Chapter IV) and domestic pigs (Chapter VI) were able to choose the correct location of a hidden reward when a human experimenter was providing communicative cues like a pointing gesture towards the baited location (Nawroth et al. 2014b, 2015). It was expected that both species are able to utilize human-given cues.

### *I.IV.III GOALS*

The main objective of this thesis was to (re-)evaluate how farm animals perceive and deal with their physical and social world. The thesis covered three areas of interest. First, it was investigated if and how commonly used test paradigms from comparative psychological work were applicable to various farm animal species (Chapter VII.I). For this reason, test paradigms formerly used in work with dogs, primates, and corvids, were modified according to the perceptual and behavioural needs and constraints of various farm animals (mainly domestic pigs and dwarf goats). The cognitive tests that were used focused on both the physico- and socio-cognitive domain. Second, when test setups were adequately adapted to test a specific species, the data was discussed in a cross-species fashion, i.e., by comparing the results across species (Chapter VII.II). Third and last, potential applied implications of the results are considered and how these may impact housing conditions, production techniques, animal welfare standards and ethical considerations (Chapter VII.III).

# CHAPTER II: EXCLUSION PERFORMANCE IN DWARF GOATS (*CAPRA AEGAGRUS HIRCUS*) AND SHEEP (*OVIS ORIENTALIS ARIES*)

This chapter includes the Paper "Exclusion performance in dwarf goats (*Capra aegagrus hircus*) and sheep (*Ovis orientalis aries*)" written by Nawroth, Christian, von Borell, Eberhard and Langbein, Jan. It has been published in the journal *PLOS ONE*.

Reference: Nawroth, C., von Borell, E., Langbein, J. (2014) *Exclusion performance in dwarf goats (Capra aegagrus hircus) and sheep (Ovis orientalis aries).* PLOS ONE 9(4): e93534.

doi: 10.1371/journal.pone.0093534

# Chapter III: Domestic pigs´ (*Sus scrofa domestica*) use of direct and indirect visual and auditory cues in an object choice task

This chapter includes the Paper "Domestic pigs´ (*Sus scrofa domestica*) use of direct and indirect visual and auditory cues in an object choice task" written by Nawroth, Christian, and von Borell, Eberhard. It has been published in the journal *Animal Cognition*.

Reference: Nawroth, C. & von Borell, E. (2015) *Domestic pigs´ (Sus scrofa domestica) use of direct and indirect visual and auditory cues in an object choice task.* Animal Cognition. Available online.

doi: 10.1007/s10071-015-0842-8

# Chapter IV: 'Goats that stare at men': Dwarf goats alter their behaviour in response to human head orientation, but do not spontaneously use head direction as a cue in a food-related context

This chapter includes the Paper "'Goats that stare at men': Dwarf goats alter their behaviour in response to human head orientation, but do not spontaneously use head direction as a cue in a food-related context" written by Nawroth, Christian, von Borell, Eberhard and Langbein, Jan. It has been published in the journal *Animal Cognition*.

Reference: Nawroth, C., von Borell, E., Langbein, J. (2015) '*Goats that stare at men' – Dwarf goats alter their behaviour in response to human head orientation but do not spontaneously use head direction as a cue in a food-related context.* Animal Cognition 18(1): 65–73.

doi: 10.1007/s10071-014-0777-5

# CHAPTER V: ARE JUVENILE DOMESTIC PIGS (*SUS SCROFA DOMESTICA*) SENSITIVE TO THE ATTENTIVE STATES OF HUMANS? - THE IMPACT OF IMPULSIVE CHOICE ON PERFORMANCE

This chapter includes the Paper "Are juvenile domestic pigs (*Sus scrofa domestica*) sensitive to the attentive states of humans? - The impact of impulsive choice on performance." written by Nawroth, Christian, Ebersbach, Mirjam, and von Borell, Eberhard. It has been published in the journal *Behavioural Processes*.

Reference: Nawroth, C., Ebersbach, M., von Borell, E. (2013) *Are juvenile domestic pigs (Sus scrofa domestica) sensitive to the attentive states of humans? - The impact of impulsive choice on performance.* Behavioural Processes 96: 53–58.

doi: 10.1016/j.beproc.2013.03.002

# CHAPTER VI: JUVENILE DOMESTIC PIGS (*SUS SCROFA DOMESTICA*) USE HUMAN-GIVEN CUES IN AN OBJECT CHOICE TASK

This chapter includes the Paper "Juvenile domestic pigs (*Sus scrofa domestica*) use human-given cues in an object choice task." written by Nawroth, Christian, Ebersbach, Mirjam, and von Borell, Eberhard. It has been published in the journal *Animal Cognition*.

Reference: Nawroth, C., Ebersbach, M., von Borell, E. (2014) *Juvenile domestic pigs (Sus scrofa domestica) use human-given cues in an object choice task.* Animal Cognition 17(3): 701–713.

doi: 10.1007/s10071-013-0702-3

# Chapter VII: General Discussion

## VII.I Adaptability of Cognitive Test Setups to Ungulate Livestock

The studies presented in this thesis found that several standard cognitive test paradigms that were previously used in behavioural experiments with canids and primates were also suitable to test several livestock species. Nonetheless, care has to be taken to adapt these paradigms to the perceptual and behavioural needs and constraints of ungulate livestock species. For example, young domestic pigs had problems using human-given cues that were administered by a standing, and not kneeling, experimenter (Chapter VI), which was not the case with dogs (e.g., McKinley & Sambrook, 2000). It is hypothesized that these differences occurred because of pigs' rooting feeding ecology, leading them to focus primarily on the ground level when searching for food. Concerning the food anticipation paradigm, the behavioural analysis should not solely focus on behavioural patterns recorded in other species, e.g., primates. Due to different morphologies, some behavioural patterns ('begging' in primates) might not be suitable for analyzing the behaviour of other, non-primate, species (see Chapter IV). Lastly, since no restraining was possible (as it is with dogs or horses), the testing behind a mesh (Chapter II and IV) or the use of a corridor leading into a test area (Chapter III, V and VI) proved to be useful and should be implemented in future object choice studies focusing on ungulate livestock.

## VII.II Cross-Species Comparisons

### *Exclusion Performance*

Domestic pigs, dwarf goats and sheep were able to use direct information (presence of food) in a two-way object choice task. In accordance with the 'foraging flexibility' hypothesis, pigs and goats, but not sheep, were able to use indirect information (i.e., the absence of food) to find a hidden reward.

Additionally, pigs were able to use direct visual, but not auditory, information to infer the location of a reward spontaneously. However, four individuals learned to use auditory information after some training and one of the subjects solved all of the subsequent auditory test conditions, including the presentation of indirect auditory information, to infer the location of the reward.

Importantly, the actual test setups could not clarify if dwarf goats and pigs were able to inferentially reason about the content of the baited bucket when only having information about the content of the non-baited bucket (high-level explanation) or if they were simply avoiding the empty bucket in this situation due to learned contingencies (low-level explanation; Call, 2004). More elaborate test designs are necessary to differentiate between the different mechanism in future studies (Aust et al. 2008; Schloegl et al. 2012).

The results of the papers presented in this thesis (Chapter II and III) are consistent with the hypothesis that foraging flexibility explains, at least partly, the ability to use indirect information during a foraging task. This suggests that the species-specific feeding ecology shaped cognitive traits in closely related species like goats and sheep and that these differences remained through the process of domestication. On the other hand, knowledge about the ability to use indirect information of non-domesticated or feral pigs, goats and sheep is lacking and needs further attention.

## *Differentiation of Attentive States*

In the food-anticipation paradigm applied to dwarf goats (Chapter IV), different levels of active anticipation behaviour suggested that goats´ perceived and processed the different attentive states of the human experimenter. In addition, goats stood alert significantly more in the experimental setup as the experimenter gradually decreased attention, at least as long as he was present at all. Both parameters were interpreted as indicating that subjects tailored their anticipatory behaviour depending of the presence and absence of the experimenter in general and his attentive state in particular as a means of reward delivery.

Data for domestic pigs in the choice paradigm was less clear (Chapter V). Here, two approach styles could be distinguished − an impulsive style with short response times and an attentive style where response times were relatively long. With the latter, pigs chose the attentive person above chance level − which was not the case when subjects chose impulsively. These results suggest that pigs, despite their poor performance in the choice task, may be able to use head cues to discriminate between different attentive states of humans. However, better controlled experiments are needed for a detailed evaluation of pigs’ and dwarf goats’ ability to differentiate between different human attentive states.

Additionally, functional properties of others’ perception have to be investigated for both species. The question still remains whether subjects solely responded using fixed behavioural patterns (e.g. to the presence of eyes) or whether they had a genuine understanding of the perceptive input of other individuals (Flombaum & Santos 2005; von Bayern & Emery 2009).

## *Utilization of Human-Given Cues*

Chapter VI provides evidence that juvenile pigs are able to utilize various pointing gestures as well as the body and head orientation of a human experimenter in an object choice task, contrasting the results of a former study by Albiach-Serrano and colleagues (2012). Moreover, Chapter IV shows that dwarf goats were able to use ‘touch’ and ‘point’ cues to infer the correct location of a hidden reward, whereas they remained at chance level in a 'head only' condition. This validates the previous finding of Kaminski and colleagues (2005) of goats´ use of human-given cues in an object choice task. For horses, previous studies also found negative results for the use of 'head only' cues in an object choice task (Proops et al. 2010, 2013).

From an evolutionary perspective, detecting individuals that are paying attention to one is useful in e.g. predator avoidance. Additionally, using head or gaze cues of con- or heterospecifics that are directed towards food sources can be useful in cooperative and/or competitive contexts. As food sources for goats and horses are likely to be distributed in an abundant manner, there is probably no strong adaptive need to share attention to particular food sources with other individuals. On the other hand, species like dogs (McKinley & Sambrook 2000; Soproni et al. 2001; Hare et al. 2002) and pigs (Nawroth et al. 2014b), which rely more on patchily distributed food sources, have been shown to be able to use the head direction of a human experimenter in object choice tasks.

By comparing the outcomes of socio-cognitive studies testing different domestic species, one has to keep in mind that different selective pressures through domestication may likely play a role in explaining their performance. While some species were selected for working purposes or companionship (e.g. dogs and horses) − which probably enhanced their skills in reading human communicative cues − others (e.g., pigs) were mainly selected for growth and meat quality. In contrast, the results of the papers presented in this thesis (Chapters IV, V and VI) suggest that a fundamental knowledge about the perception of heterospecific individuals (i.e., humans) is more closely related to the species-specific socio-ecological niche of the non-domesticated ancestor of a particular domesticated species rather than to their domestication history itself.

## VII.III Implications

Basic research on how farm animals perceive and deal with their physical and social environment is of high importance for a detailed understanding of livestock behaviour. Hence knowledge about the cognitive capabilities of livestock species has the potential to improve animal welfare in the long term. Moreover, a lack of knowledge about their behavioural repertoire can lead to misguided handling practices and designs of husbandry conditions.

For example, when designing cognitively enriching environments, it is crucial to know how aspects of foraging behaviour can differ between (even closely related) livestock species (Chapters II and III). Furthermore, the development and validation of future studies on personality traits (e.g., person approach tests) may build up on the findings obtained in this thesis (Chapters IV and V). Lastly, studies on complex human-animal interaction (e.g., interspecies communication) may also contribute to reduce stress during handling and transport (Jago et al. 1999; Waiblinger et al. 2006; Probst et al. 2012).

Especially in applied ethics it is of high concern how we should treat subjects that see other individuals as distinct entities with their own perceptions, motivations and desires (Benz-Schwarzburg 2011, 2012) or that exhibit episodic memory and therefore do not only live in the 'present' (Mendl & Paul 2008). Part of this thesis focuses on investigations on if and how livestock species attribute perceptions to other individuals (Chapters IV, V and VI). The ability to recognize others' perceptions − and also desires and beliefs − different from one's own, are linked to 'Theory of Mind'-like capabilities (see Chapter I.III) and, together with the abilities to emphasize and to cooperate, are important in the philosophical discussion of how to treat (farm) animals (Benz-Schwarzburg 2012).

The results presented here may also be a step toward a re-evaluation of consumers´ perception of mind in farm animals. Psychological studies have shown that the lack of desire to eat a specific kind of meat rises with the increase of human-like cognitive capacities attributed to a species (Ruby & Heine 2012). Moreover, there is a gap in people's attribution of mind towards farm animals compared to pets (Bastian et al. 2012). However, as species comparisons show there is no *a priori* reason to assume that pets like dogs, cats or horses are somehow ‘smarter’ than animals that are bred for meat or milk production. These differences in public perception of mental capabilities of animals are socially and psychologically constructed. One important factor is that pets are commonly kept in close proximity to people, making them more present in their everyday experiences. Additionally, humans form close bonds to their pets and seek social comfort from them. Therefore people are more prone to anthropomorphize their pets’ behaviour, which leads to changing attitudes towards them, e.g., perceiving them as more intelligent than they actually are (Howell et al. 2013). An additional reason for this gap can be explained by cognitive dissonance − a bias induced to reduce the dissonance between meat eaters’ behaviour and their concern for animal welfare. This dissonance is specifically due to meat eaters’ commitment to meat-eating behaviour which has the potential to contribute to animal suffering. The dissonance reduction brings cognitions in line with behavioural commitments and thus facilitates the execution of non-conflicted actions (Bastian et al. 2012).

## VII.IV OUTLOOK

The study of farm animal cognition is still in development but has received increased attention in recent years. The experiments presented in this thesis will help to develop more complex test setups for future investigations of livestock behaviour. For example, an interesting step towards more detailed studies of domestication effects on cognitive performance can question how domesticated species other than dogs understand the referential nature of human-given cues, e.g. through a pointing gesture. The studies presented here may also facilitate the development of experiments investigating more complex socio-cognitive phenomena in livestock species, like deception, cooperation and empathy – topics that formerly mainly focused on primates and therefore lack comparison (see Chapter I.III.I). Moreover, further comparisons between the behaviour of goats and sheep can help to understand how feeding ecology shapes cognitive capabilities (Chapter II) like risk sensitivity (Heilbronner et al. 2008; Haun et al. 2011). This will improve methods of cognitive enrichment and housing conditions for both species. Moreover, the studies on farm animal cognition can serve as a starting point for how the results of these studies in general may be able to alter public perception and consumer behaviour (Bastian et al. 2012).

# CHAPTER VIII: CONCLUSIONS

Gaining better knowledge of livestock cognitive capacities is of importance for improving their husbandry and welfare. To achieve this, it is important to shift away from an anthropocentric point of view and to focus on the animals' view of their environment and their interactions with it and other individuals. The studies that are presented in Chapters II-VI show that paradigms previously used with primates and dogs can be adapted to livestock species. Moreover, the results obtained indicate that ungulate livestock species have sophisticated cognitive capabilities in dealing with their physical and social environment. The better understanding of how livestock species comprehend their environment will ultimately lead to an improvement in animal welfare in the long term. Despite their high numbers in husbandry, livestock species are still underrepresented in animal cognition research and the experiments presented in this thesis will serve as an additional starting point for further investigations. Finally, an increasing number of cognitive studies conducted on farm animals will likely have effects on public perception and therefore consumer behaviour – leading to a higher level of awareness of how farm animals are housed and how these housing conditions may potentially inhibit the expression of the complex species-specific behavioural and cognitive repertoires not only manifested through an individual´s action but also embedded in its mind.

# BIBLIOGRAPHY

**Albiach-Serrano, A., Bräuer, J., Cacchione, T., Zickert, N. & Amici, F.** 2012. The effect of domestication and ontogeny in swine cognition (*Sus scrofa scrofa* and *S. s. domestica*). *Applied Animal Behaviour Science*, **141**, 25–35.

**Andre, N. & Hausberger, M.** 2011. Do Horses Have a Concept of Person ? *PLOS ONE*, **6**, e18331.

**Aust, U., Range, F., Steurer, M. & Huber, L.** 2008. Inferential reasoning by exclusion in pigeons, dogs, and humans. *Animal Cognition*, **11**, 587–597.

**Bania, A. E. & Stromberg, E. E.** 2013. The effect of body orientation on judgments of human visual attention in western lowland gorillas (*Gorilla gorilla gorilla*). *Journal of Comparative Psychology*, **127**, 82–90.

**Barton, R. A. & Dunbar, R. I. M.** 1997. Evolution of the social brain. In: *Machiavellian Intelligence II*, 2nd edn. (Ed. by A. Whiten & R. W. Byrne), pp. 240–263. Cambridge: Cambridge University Press.

**Bastian, B., Loughnan, S., Haslam, N. & Radke, H. R. M.** 2012. Don't mind meat? The denial of mind to animals used for human consumption. *Personality & Social Psychology Bulletin*, **38**, 247–56.

**Bateson, M., Desire, S., Gartside, S. E. & Wright, G. A.** 2011. Agitated Honeybees Exhibit Pessimistic Cognitive Biases. *Current Biology*, **21**, 1070–1073.

**Benz-Schwarzburg, J.** 2011. Cognitive relatives yet moral strangers? *Journal of Animal Ethics*, **1**, 9–36.

**Benz-Schwarzburg, J.** 2012. *Verwandte im Geiste - Fremde im Recht : Sozio-kognitive Fähigkeiten bei Tieren und ihre Relevanz für Tierethik und Tierschutz.* Erlangen: Erlangen : Fischer.

**Boissy, A. & Bouissou, M.-F.** 1988. Effects of early handling on heifers' subsequent reactivity to humans and to unfamiliar situations. *Applied Animal Behaviour Science*, **20**, 259–273.

**Bolhuis, E. J., Oostindjer, M., Hoeks, C. W. F., de Haas, E. N., Bartels, A. C., Ooms, M. & Kemp, B.** 2013. Working and reference memory of pigs (*Sus scrofa domesticus*) in a holeboard spatial discrimination task: the influence of environmental enrichment. *Animal Cognition*, **16**, 845–850.

**Botting, J. L., Wiper, M. L. & Anderson, J. R.** 2011. Brown (*Eulemur fulvus*) and ring-tailed lemurs (*Lemur catta*) use human head orientation as a cue to gaze direction in a food choice task. *Folia Primatologica*, **82**, 165–176.

**Bourjade, M., Meguerditchian, A., Maille, A., Gaunet, F. & Vauclair, J.** 2014. Olive baboons, Papio anubis, adjust their visual and auditory intentional gestures to the visual attention of others. *Animal Behaviour*, **87**, 121–128.

**Bräuer, J., Kaminski, J., Riedel, J., Call, J. & Tomasello, M.** 2006. Making Inferences About the Location of Hidden Food: Social Dog, Causal Ape. *Journal of Comparative Psychology*, **120**, 38–47.

**Bräuer, J., Schönefeld, K. & Call, J.** 2013. When do dogs help humans? *Applied Animal Behaviour Science*, **148**, 138–149.

**Breuer, K., Hemsworth, P. H., Barnett, J. L., Matthews, L. R. & Coleman, G. J.** 2000. Behavioural response to humans and the productivity of commercial dairy cows. *Applied Animal Behaviour Science*, **66**, 273–288.

**Briefer, E. & McElligott, A. G.** 2011. Mutual mother-offspring vocal recognition in an ungulate hider species (*Capra hircus*). *Animal Cognition*, **14**, 585–98.

**Briefer, E. F., Padilla de la Torre, M. & McElligott, A. G.** 2012. Mother goats do not forget their kids' calls. *Proceedings of the Royal Society B*, **279**, 3749–55.

**Briefer, E. F., Haque, S., Baciadonna, L. & McElligott, A. G.** 2014. Goats excel at learning and remembering a highly novel cognitive task. *Frontiers in Zoology*, **11**, 20.

**Broom, D. M., Sena, H. & Moynihan, K. L.** 2009. Pigs learn what a mirror image represents and use it to obtain information. *Animal Behaviour*, **78**, 1037–1041.

**Brosnan, S. F. & Waal, F. B. M. De**. 2003. Monkeys reject unequal pay. *Nature*, 297–299.

**Brosnan, S. F., Schiff, H. C. & de Waal, F. B. M.** 2005. Tolerance for inequity may increase with social closeness in chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 253–258.

**Brydges, N. M., Leach, M., Nicol, K., Wright, R. & Bateson, M.** 2011. Environmental enrichment induces optimistic cognitive bias in rats. *Animal Behaviour*, **81**, 169–175.

**Buijs, S., Keeling, L. J. & Tuyttens, F. a. M.** 2011. Using motivation to feed as a way to assess the importance of space for broiler chickens. *Animal Behaviour*, **81**, 145–151.

**Bulloch, M. J., Boysen, S. T. & Furlong, E. E.** 2008. Visual attention and its relation to knowledge states in chimpanzees, Pan troglodytes. *Animal Behaviour*, **76**, 1147–1155.

**Call, J.** 2004. Inferences About the Location of Food in the Great Apes (Pan paniscus, Pan troglodytes, Gorilla gorilla, and Pongo pygmaeus). *Journal of Comparative Psychology*, **118**, 232–241.

**Call, J.** 2006. Inferences by exclusion in the great apes: the effect of age and species. *Animal Cognition*, **9**, 393–403.

**Call, J. & Tomasello, M.** 2008. Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences*, **12**, 187–192.

**Call, J., Hare, B. a & Tomasello, M.** 1998. Chimpanzee gaze following in an object-choice task. *Animal Cognition*, **1**, 89–99.

**Call, J., Bräuer, J., Kaminski, J. & Tomasello, M.** 2003. Domestic Dogs (*Canis familiaris*) Are Sensitive to the Attentional State of Humans. *Journal of Comparative Psychology*, **117**, 257–263.

**Call, J., Hare, B., Carpenter, M. & Tomasello, M.** 2004. "Unwilling" versus "unable": chimpanzees' understanding of human intentional action. *Developmental Science*, **7**, 488–498.

**Call, J., Kaminski, J., Bräuer, J. & Tomasello, M.** 2009. Domestic dogs are sensitive to a human's perspective. *Behaviour*, **146**, 979–998.

**Campbell, M. W. & de Waal, F. B. M.** 2011. Ingroup-Outgroup Bias in Contagious Yawning by Chimpanzees Supports Link to Empathy. *PLOS ONE*, **6**, e18283.

**Cornell, H. N., Marzluff, J. M. & Pecoraro, S.** 2012. Social learning spreads knowledge about dangerous humans among American crows. *Proceedings of the Royal Society B: Biological Science*, **279**, 499–508.

**Coulon, M., Baudoin, C., Heyman, Y. & Deputte, B.** 2011. Cattle discriminate between familiar and unfamiliar conspecifics by using only head visual cues. *Animal Cognition*, **14**, 279–290.

**Coussi-Korbel, S.** 1994. Learning to Outwit a Competitor in Mangabeys (*Cercocebus torquatus torquatus*). *Journal of Comparative Psychology*, **108**, 164–171.

**Croney, C. C., Adams, K. M., Washington, C. G. & Stricklin, W. R.** 2003. A note on visual, olfactory and spatial cue use in foraging behavior of pigs: indirectly assessing cognitive abilities. *Applied Animal Behaviour Science*, **83**, 303–308.

**Daros, R. R., Costa, J. H. C., von Keyserlingk, M. a G., Hötzel, M. J. & Weary, D. M.** 2014. Separation from the dam causes negative judgement bias in dairy calves. *PLOS ONE*, **9**, e98429.

**De Jong, I. C., Ekkel, E. D., Burgwal, J. A. van de, Lambooij, E., Korte, S. M., Ruis, M. A. W., Koolhaas, J. M. & Blokhuis, H. J.** 1998. Effects of strawbedding on physiological responses to stressors and behavior in growing pigs. *Applied Animal Behaviour Science*, **64**, 303–310.

**De la Lama, G. C. M. & Mattiello, S.** 2010. The importance of social behaviour for goat welfare in livestock farming. *Small Ruminant Research*, **90**, 1–10.

**Désiré, L., Boissy, A. & Veissier, I.** 2002. Emotions in farm animals: a new approach to animal welfare in applied ethology. *Behavioural Processes*, **60**, 165–180.

**Douglas, C., Bateson, M., Walsh, C., Bédué, A. & Edwards, S. A.** 2012. Environmental enrichment induces optimistic cognitive biases in pigs. *Applied Animal Behaviour Science*, **139**, 65–73.

**Doyle, R. E., Vidal, S., Hinch, G. N. & Fisher, A. D.** 2010a. The effect of repeated testing on judgement biases in sheep. *Behavioural Processes*, **83**, 349–352.

**Doyle, R. E., Fisher, A. D., Hinch, G. N., Boissy, A. & Lee, C.** 2010b. Release from restraint generates a positive judgement bias in sheep. *Applied Animal Behaviour Science*, **122**, 28–34.

**Duncan, I. J. H. & Petherick, J. C.** 1991. The implications of cognitive processes for animal welfare. *Journal of Animal Science*, **69**, 5017–5022.

**Erdőhegyi, Á., Topál, J., Virányi, Z. & Miklósi, Á.** 2007. Dog-logic: inferential reasoning in a two-way choice task and its restricted use. *Animal Behaviour*, **74**, 725–737.

**Farm Animal Welfare Council**. 2013. *The five freedoms.* Surbiton (United Kingdom).

**Flombaum, J. I. & Santos, L. R.** 2005. Rhesus Monkeys Attribute Perceptions to Others. *Current Biology*, **15**, 447–452.

**Forkman, B., Furuhaug, I. L. & Jensen, P.** 1995. Personality, coping patterns, and aggression in piglets. *Applied Animal Behaviour Science*, **45**, 31–42.

**Fraser, D., Weary, D. M., Pajor, E. A. & Milligan, B. N.** 1997. A scientific conception of animal welfare that reflects ethical concerns. *Animal Welfare*, **6**, 187–205.

**Gabor, V. & Gerken, M.** 2014. Shetland ponies (*Equus caballus*) show quantity discrimination in a matching-to-sample design. *Animal Cognition*, **17**, 1233–1243.

**Gácsi, M., Miklosi, A., Varga, O., Topal, J. & Csanyi, V.** 2004. Are readers of our face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent recognition of human's attention. *Animal Cognition*, **7**, 144–153.

**Garland, A., Low, J., Armstrong, N. & Burns, K. C.** 2014. Wild robins (*Petroica longipes*) respond to human gaze. *Animal Cognition*, **17**, 1149–1156.

**Gieling, E. T., Musschenga, M. A., Nordquist, R. E. & van der Staay, F. J.** 2012. Juvenile pigs use simple geometric 2D shapes but not portrait photographs of conspecifics as visual discriminative stimuli. *Applied Animal Behaviour Science*, **142**, 142–153.

**Gieling, E. T., Mijdam, E., Josef van der Staay, F. & Nordquist, R. E.** 2014. Lack of mirror use by pigs to locate food. *Applied Animal Behaviour Science*, **154**, 22–29.

**Hagen, K. & Broom, D. M.** 2003. Cattle discriminate between individual familiar herd members in a learning experiment. *Applied Animal Behaviour Science*, **82**, 13–28.

**Harding, E. J., Paul, E. S. & Mendl, M.** 2004. Cognitive bias and affective state. *Nature*, **427**, 312.

**Hare, B., Brown, M., Williamson, C. & Tomasello, M.** 2002. The domestication of social cognition in dogs. *Science*, **298**, 1634–1636.

**Hattori, Y., Kuroshima, H. & Fujita, K.** 2007. I know you are not looking at me: capuchin monkeys´ (*Cebus apella*) sensitivity to human attentional states. *Animal Cognition*, **10**, 141–148.

**Haun, D. B. M., Nawroth, C. & Call, J.** 2011. Great Apes' Risk-Taking Strategies in a Decision Making Task. *PLOS ONE*, **6**, e28801.

**Hayes, K. J., Thompson, R. & Hayes, C.** 1953. Discrimination learning set in chimpanzees. *Journal of Comparative and Physiological Psychology*, **46**, 99–104.

**Heilbronner, S. R., Rosati, A. G., Stevens, J. R., Hare, B. & Hauser, M. D.** 2008. A Fruit in the Hand or Two in the Bush? Divergent Risk Preferences in Chimpanzees and Bonobos. *Biology Letters*, **4**, 246–249.

**Heimbauer, L., Antworth, R. L. & Owren, M. J.** 2012. Capuchin monkeys (*Cebus apella*) use positive, but not negative, auditory cues to infer food location. *Animal Cognition*, **15**, 45–55.

**Held, S., Mendl, M., Devereux, C. & Byrne, R. W.** 2000. Social tactics of pigs in a competitive foraging task: the "informed forager" paradigm. *Animal Behaviour*, **59**, 569–576.

**Held, S., Mendl, M., Devereux, C. & Byrne, R. W.** 2001. Behaviour of Domestic Pigs in a Visual Perspective Taking Task. *Behaviour*, **138**, 1337–1354.

**Held, S., Mendl, M., Devereux, C. & Byrne, R. W.** 2002. Foraging pigs alter their behaviour in response to exploitation. *Animal Behaviour*, **64**, 157–166.

**Hemsworth, P. .** 2003. Human–animal interactions in livestock production. *Applied Animal Behaviour Science*, **81**, 185–198.

**Hofmann, R. R.** 1989. Evolutionary steps of eco-physiological adaptation and diversification of ruminants - a comparative view of their digestive system. *Oecologia*, **78**, 443–457.

**Horner, V., Carter, J. D., Suchak, M. & de Waal, F. B. M.** 2011. Spontaneous prosocial choice by chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 13847–51.

**Hosoi, E., Swift, D. M., Rittenhouse, L. R. & Richards, R. W.** 1995. Comparative foraging strategies of sheep and goats in a T-maze apparatus. *Applied Animal Behaviour Science*, **44**, 37–45.

**Howell, T. J., Toukhsati, S., Conduit, R. & Bennett, P.** 2013. The perceptions of dog intelligence and cognitive skills (PoDIaCS) survey. *Journal of Veterinary Behavior: Clinical Applications and Research*, **8**, 418–424.

**Huber, L., Range, F., Voelkl, B., Szucsich, A., Virányi, Z. & Miklosi, A.** 2009. The evolution of imitation: what do the capacities of non-human animals tell us about the mechanisms of imitation? *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences*, **364**, 2299–309.

**Imfeld-Mueller, S., Van Wezemael, L., Stauffacher, M., Gygax, L. & Hillmann, E.** 2011. Do pigs distinguish between situations of different emotional valences during anticipation? *Applied Animal Behaviour Science*, **131**, 86–93.

**Jaakkola, K.** 2014. Do Animals Understand Invisible Displacement? A Critical Review. *Journal of Comparative Psychology*, **128**, 1–15.

**Jago, J., Krohn, C. & Matthews, L.** 1999. The influence of feeding and handling on the development of the human–animal interactions in young cattle. *Applied Animal Behaviour Science*, **62**, 137–151.

**Kalbe, C. & Puppe, B.** 2010. Long-term cognitive enrichment affects opioid receptor expression in the amygdala of domestic pigs. *Genes, Brain & Behavior*, **9**, 75–83.

**Kaminski, J., Call, J. & Tomasello, M.** 2004. Body orientation and face orientation: two factors controlling apes' behavior from humans. *Animal Cognition*, **7**, 216–23.

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

**Kaminski, J., Schulz, L. & Tomasello, M.** 2012. How dogs know when communication is intended for them. *Developmental Science*, **15**, 222–32.

**Keil, N. M., Imfeld-Mueller, S., Aschwanden, J. & Wechsler, B.** 2012. Are head cues necessary for goats (*Capra hircus*) in recognising group members? *Animal Cognition*, **15**, 913–921.

**Kendrick, K. M., Atkins, K., Hinton, M. R., Broad, K. D., Fabre-Nys, C. & Keverne, B.** 1995. Facial and vocal discrimination in sheep. *Animal Behaviour*, **49**, 1665–1676.

**Kirkden, R. D. & Pajor, E. a.** 2006. Using preference, motivation and aversion tests to ask scientific questions about animals' feelings. *Applied Animal Behaviour Science*, **100**, 29–47.

**Koba, Y. & Tanida, H.** 2001. How do miniature pigs discriminate between people?: Discrimination between people wearing coveralls of the same colour. *Applied Animal Behaviour Science*, **73**, 45–58.

**Krueger, K. & Flauger, B.** 2011. Olfactory recognition of individual competitors by means of faeces in horse (*Equus caballus*). *Animal Cognition*, **14**, 245–57.

**Lakshminarayanan, V. R. & Santos, L. R.** 2008. Capuchin monkeys are sensitive to others' welfare. *Current Biology*, **18**, R999–1000.

**Langbein, J., Nürnberg, G. & Manteuffel, G.** 2004. Visual discrimination learning in dwarf goats and associated changes in heart rate and heart rate variability. *Physiology & Behavior*, **82**, 601–9.

**Langbein, J., Siebert, K. & Nuernberg, G.** 2008. Concurrent recall of serially learned visual discrimination problems in dwarf goats (*Capra hircus*). *Behavioural Processes*, **79**, 156–64.

**Laughlin, K. & Mendl, M.** 2000. Pigs shift too: foraging strategies and spatial memory in the domestic pig. *Animal Behaviour*, **60**, 403–410.

**Lensink, B. J., Fernandez, X., Cozzi, G., Florand, L. & Veissier, I.** 2001. The influence of farmers' behaviour on calves' reactions to transport and quality of veal meat. *Journal of Animal Science*, **79**, 642–652.

**Ligout, S. & Porter, R. H.** 2004. The role of visual cues in lambs' discrimination between individual agemates. *Behaviour*, **141**, 617–632.

**Maille, A., Engelhart, L., Bourjade, M. & Blois-Heulin, C.** 2012. To beg, or not to beg? That is the question: mangabeys modify their production of requesting gestures in response to human's attentional states. *PlOS ONE*, **7**, e41197.

**Marchant-Forde, J. N., Held, S., Cooper, J. J. & Mendl, M. T.** 2009. Advances in the study of cognition, behavioural priorities and emotions. In: *The Welfare of Pigs*, Vol 7 pp. 47–94. Springer Netherlands.

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

**McKinley, J. & Sambrook, T. D.** 2000. Use of human-given cues by domestic dogs (*Canis familiaris*) and horses (*Equus caballus*). *Animal Cognition*, **3**, 13–22.

**McLeman, M. A., Mendl, M., Jones, R. B., White, R. & Wathes, C. M.** 2005. Discrimination of conspecifics by juvenile domestic pigs, *Sus scrofa*. *Animal Behaviour*, **70**, 451–461.

**Melis, A. P., Hare, B. & Tomasello, M.** 2006. Chimpanzees recruit the best collaborators. *Science*, **311**, 1297–300.

**Mendl, M. & Paul, E. S.** 2008. Do animals live in the present?: Current evidence and implications for welfare. *Applied Animal Behaviour Science*, **113**, 357–382.

**Mendl, M., Laughlin, K. & Hitchcock, D.** 1997. Pigs in space: spatial memory and its susceptibility to interference. *Animal Behaviour*, **54**, 1491–1508.

**Mendl, M., Randle, K. & Pope, S.** 2002. Young female pigs can discriminate individual differences in odours from conspecific urine. *Animal Behaviour*, **64**, 97–101.

**Mendl, M., Burman, O. H. P., Parker, R. M. A. & Paul, E. S.** 2009. Cognitive bias as an indicator of animal emotion and welfare: emerging evidence and underlying mechanisms. *Applied Animal Behaviour Science*, **118**, 161–181.

**Mendl, M., Burman, O. H. P. & Paul, E. S.** 2010. An integrative and functional framework for the study of animal emotion and mood. *Proceedings of the Royal Society B*, **277**, 2895–904.

**Meyer, S. & Langbein, B. P.** 2010. Kognitive Umweltanreicherung bei Zoo- und Nutztieren - Implikationen für Verhalten und Wohlbefinden der Tiere. *Berliner und Münchener tierärztliche Wochenschrift*, **12**, 446–456.

**Meyer, S., Nürnberg, G., Puppe, B. & Langbein, J.** 2012. The cognitive capabilities of farm animals: categorisation learning in dwarf goats (*Capra hircus*). *Animal Cognition*, **15**, 567–576.

**Miklósi, A. & Soproni, K.** 2006. A comparative analysis of animals' understanding of the human pointing gesture. *Animal Cognition*, **9**, 81–93.

**Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z. & Csányi, V.** 2003. A simple reason for a big difference: wolves do not look back at humans, but dogs do. *Current Biology*, **13**, 763–766.

**Mikolasch, S., Kotrschal, K. & Schloegl, C.** 2012. Is caching the key to exclusion in corvids? The case of carrion crows (*Corvus corone corone*). *Animal Cognition*, **15**, 73–82.

**Mulcahy, N. J. & Call, J.** 2009. The performance of bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), and orangutans (*Pongo pygmaeus*) in two versions of an object-choice task. *Journal of Comparative Psychology*, **123**, 304–9.

**Nagel, T.** 1974. What Is It Like to Be a Bat? *The Philosophical Review*, **83**, 435–450.

**Nawroth, C. & von Borell, E.** 2015. Domestic pigs´ (*Sus scrofa domestica*) use of direct and indirect visual and auditory cues in an object choice task. *Animal Cognition*, online available

**Nawroth, C., Ebersbach, M. & von Borell, E.** 2013. Are juvenile domestic pigs (*Sus scrofa domestica*) sensitive to the attentive states of humans? - The impact of impulsivity on choice behaviour. *Behavioural Processes*, **96**, 53–58.

**Nawroth, C., von Borell, E. & Langbein, J.** 2014a. Exclusion performance in dwarf goats (*Capra aegagrus hircus*) and sheep (*Ovis orientalis aries*). *PLOS ONE*, **9**, e93534.

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

**Nawroth, C., von Borell, E. & Langbein, J.** 2015. "Goats that stare at men": dwarf goats alter their behaviour in response to human head orientation, but do not spontaneously use head direction as a cue in a food-related context. *Animal Cognition*, **18**, 65–73.

**Neave, H. W., Daros, R. R., Costa, J. H. C., von Keyserlingk, M. a G. & Weary, D. M.** 2013. Pain and Pessimism: Dairy Calves Exhibit Negative Judgement Bias following Hot-Iron Disbudding. *PlOS ONE*, **8**, e80556.

**Parr, L., Dove, T. & Hopkins, W. D.** 1998. Why Faces May Be Special: Evidence of the Inversion Effect in Chimpanzees. *Journal of Cognitive Neuroscience*, **10**, 615–622.

**Pepperberg, I.** 2006. Grey parrot numerical competence: a review. *Animal Cognition*, **9**, 377–391.

**Peron, F., Rat-Fischer, L., Nagle, L. & Bovet, D.** 2010. "Unwilling" versus "unable" Do grey parrots understand human intentional actions? *Interaction Studies*, **11**, 428–441.

**Péron, F., Rat-Fischer, L., Lalot, M., Nagle, L. & Bovet, D.** 2011. Cooperative problem solving in African grey parrots (*Psittacus erithacus*). *Animal Cognition*, **14**, 545–553.

**Phillips, W., Barnes, J. L., Mahajan, N., Yamaguchi, M. & Santos, L. R.** 2009. "Unwilling" versus "unable": capuchin monkeys' (*Cebus apella*) understanding of human intentional action. *Developmental Science*, **12**, 938–945.

**Povinelli, D. J. & Eddy, T. J.** 1996. What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development*, **61**, 1–191.

**Premack, D. & Premack, A. J.** 1994. Levels of causal understanding in chimpanzees and children. *Cognition*, **50**, 347–362.

**Preston, S. D. & de Waal, F. B. M.** 2002. Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences*, **25**, 1–20.

**Probst, J. K., Spengler Neff, A., Leiber, F., Kreuzer, M. & Hillmann, E.** 2012. Gentle touching in early life reduces avoidance distance and slaughter stress in beef cattle. *Applied Animal Behaviour Science*, **139**, 42–49.

**Proops, L. & McComb, K.** 2010. Attributing attention: the use of human-given cues by domestic horses (*Equus caballus*). *Animal Cognition*, **13**, 197–205.

**Proops, L., McComb, K. & Reby, D.** 2009. Cross-modal individual recognition in domestic horses (*Equus caballus*). *Proceedings of the National Academy of Sciences, USA*, **106**, 947–951.

**Proops, L., Walton, M. & McComb, K.** 2010. The use of human-given cues by domestic horses, *Equus caballus*, during an object choice task. *Animal Behaviour*, **79**, 1205–1209.

**Proops, L., Rayner, J., Taylor, A. M. & McComb, K.** 2013. The responses of young domestic horses to human-given cues. *PLOS ONE*, **8**, e67000.

**Puppe, B., Ernst, K., Schön, P. C. & Manteuffel, G.** 2007. Cognitive enrichment affects behavioural reactivity in domestic pigs. *Applied Animal Behaviour Science*, **105**, 75–86.

**Racca, A., Amadei, E., Ligout, S., Guo, K., Meints, K. & Mills, D.** 2010. Discrimination of human and dog faces and inversion responses in domestic dogs (*Canis familiaris*). *Animal Cognition*, **13**, 525–33.

**Range, F., Bugnyar, T. & Kotrschal, K.** 2008. The performance of ravens on simple discrimination tasks: a preliminary study. *Acta ethologica*, **11**, 34–41.

**Range, F., Horn, L., Viranyi, Z. & Huber, L.** 2009. The absence of reward induces inequity aversion in dogs. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 340–5.

**Roitberg, E. & Franz, H.** 2004. Oddity learning by African dwarf goats (*Capra hircus*). *Animal Cognition*, **7**, 61–67.

**Ruby, M. B. & Heine, S. J.** 2012. Too close to home. Factors predicting meat avoidance. *Appetite*, **59**, 47–52.

**Rushen, J., Taylor, A. A. & de Passillé, A. M.** 1999. Domestic animals' fear of humans and its effect on their welfare. *Applied Animal Behaviour Science*, **65**, 285–303.

**Rybarczyk, P., Koba, Y., Rushen, J., Tanida, H. & de Passillá, A. M.** 2001. Can cows discriminate people by their faces? *Applied Animal Behaviour Science*, **74**, 175–189.

**Sabbatini, G. & Visalberghi, E.** 2008. Inferences About the Location of Food in Capuchin Monkeys (*Cebus apella*) in Two Sensory Modalities. *Journal of Comparative Psychology*, **122**, 156–166.

**Schloegl, C.** 2011. What You See Is What You Get—Reloaded: Can Jackdaws (*Corvus monedula*) Find Hidden Food Through Exclusion? *Journal of Comparative Psychology*, **125**, 162–174.

**Schloegl, C., Kotrschal, K. & Bugnyar, T.** 2008. Do common ravens (*Corvus corax*) rely on human or conspecific gaze cues to detect hidden food? *Animal Cognition*, **11**, 231–241.

**Schloegl, C., Dierks, A., Gajdon, G. K., Huber, L., Kotrschal, K. & Bugnyar, T.** 2009. What You See Is What You Get? Exclusion Performances in Ravens and Keas. *PLOS ONE*, **4**, e6368.

**Schloegl, C., Schmidt, J., Boeckle, M., Weiß, B. M. & Kotrschal, K.** 2012. Grey parrots use inferential reasoning based on acoustic cues alone. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4135–42.

**Schmidt, J., Scheid, C., Kotrschal, K., Bugnyar, T. & Schloegl, C.** 2011. Gaze direction: A cue for hidden food in rooks (*Corvus frugilegus*)? *Behavioural Processes*, **88**, 88–93.

**Schmitt, V. & Fischer, J.** 2009. Inferential Reasoning and Modality Dependent Discrimination Learning in Olive Baboons (*Papio hamadryas anubis*). *Journal of Comparative Psychology*, **123**, 316–325.

**Shettleworth, S. J.** 2009. The evolution of comparative cognition: Is the snark still a boojum? *Behavioural Processes*, **80**, 210–217.

**Shettleworth, S. J.** 2010. Getting Around: Spatial Cognition. In: *Cognition, Evolution, and Behavior*, second edn. pp. 261–312. Oxford: Oxford University Press.

**Smith, B. P., Appleby, R. G. & Litchfield, C. A.** 2012. Spontaneous tool-use: an observation of a dingo (*Canis dingo*) using a table to access an out-of-reach food reward. *Behavioural Processes*, **89**, 219–24.

**Soproni, K., Miklósi, Á., Topál, J. & Csányi, V.** 2001. Comprehension of human communicative signs in pet dogs (*Canis familiaris*). *Journal of Comparative Psychology*, **115**, 122–126.

**Stewart, M., Shepherd, H. M., Webster, J. R., Waas, J. R., McLeay, L. M. & Schütz, K. E.** 2013. Effect of previous handling experiences on responses of dairy calves to routine husbandry procedures. *Animal*, **7**, 828–33.

**Tanida, H., Senda, K., Suzuki, S., Tanaka, T. & Yoshimoto, T.** 1991. Colour discrimination in weanling pigs. *Animal Science and Technology*, **62**, 1029–1034.

**Tempelmann, S., Kaminski, J. & Liebal, K.** 2011. Focus on the essential: all great apes know when others are being attentive. *Animal Cognition*, **14**, 433–439.

**Tomasello, M. & Call, J.** 1997. *Primate Cognition.* 1st edn. New York: Oxford University Press.

**Udell, M., Dorey, N. & Wynne, C.** 2011. Can your dog read your mind? Understanding the causes of canine perspective taking. *Learning & Behavior*, **39**, 289–302.

**Uller, C. & Lewis, J.** 2009. Horses (*Equus caballus*) select the greater of two quantities in small numerical contrasts. *Animal Cognition*, **12**, 733–738.

**Vaesen, K.** 2012. The cognitive bases of human tool use. *Behavioral and Brain Sciences*, **35**, 203–18.

**Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D. & Miklósi, Á.** 2008. Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Animal Cognition*, **11**, 373–387.

**Von Bayern, A. M. P. & Emery, N. J.** 2009. Jackdaws respond to human attentional states and communicative cues in different contexts. *Current Biology*, **19**, 602–6.

**Waiblinger, S., Boivin, X., Pedersen, V., Tosi, M.-V., Janczak, A. M., Visser, E. K. & Jones, R. B.** 2006. Assessing the human-animal relationship in farmed species: A critical review. *Applied Animal Behaviour Science*, **101**, 185–242.

**Wascher, C. a F., Szipl, G., Boeckle, M. & Wilkinson, A.** 2012. You sound familiar: carrion crows can differentiate between the calls of known and unknown heterospecifics. *Animal cognition*, **15**, 1015–9.

**Wathes, C.** 2010. Guarding the welfare of farm animals. *The Veterinary record*, **167**, 583–4.

**Zebunke, M., Langbein, J., Manteuffel, G. & Puppe, B.** 2011. Autonomic reactions indicating positive affect during acoustic reward learning in domestic pigs. *Animal Behaviour*, **81**, 481–489.

**Zebunke, M., Puppe, B. & Langbein, J.** 2013. Effects of cognitive enrichment on behavioural and physiological reactions of pigs. *Physiology & Behavior*, **118**, 70–9.

# Eidesstattliche Erklärung

Ich erkläre an Eides statt, dass ich die Arbeit selbstständig und ohne fremde Hilfe verfasst, keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt und die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe. Hiermit erkläre ich, dass mit dieser wissenschaftlichen Arbeit noch keine vergeblichen Promotionsversuche unternommen wurden. Des Weiteren erkläre ich, dass keine Strafverfahren gegen mich anhängig sind.

Halle/Saale, 08.09.2014 Unterschrift:

# Curriculum Vitae

PERSONAL DETAILS:

| | |
|---|---|
| *Name:* | Christian Nawroth |
| *Address:* | Breitscheidstrasse 19 |
| | 04931 Mühlberg |
| | Germany |
| *Date of Birth:* | 15/10/1982 |
| *Nationality:* | German |

EDUCATION

**October, 2010 – February, 2014**
**University of Halle-Wittenberg**, Germany
PhD student

**October, 2009 – September, 2010**
**University of Leipzig**, Germany
Philosophy Studies

**June, 2008 – May, 2009**
**Max-Planck-Institute for Evolutionary Anthropology**, Germany
External Diploma thesis in Biology (thesis marked 1.3)

**October, 2005 – May, 2009**
**University of Wuerzburg**, Germany
Major Topic: Sociobiology (exam marked 1.0)
Minor Topics: Neurobiology (exam marked 1.0), Animal Ecology (exam marked 2.0)

**October, 2003 – September, 2005**
**University of Giessen**, Germany
"Vordiplom" in Biology, August, 2005

RESEARCH EXPERIENCE

**April, 2013 and May, 2014**
**Leibniz Institute for Farm Animal Biology**, Germany
Exchange student: Research at the Institute for Behavioural Physiology

**October, 2010 – October, 2014**
**University of Halle-Wittenberg**, Germany
Research assistant: Research at the Department of Animal Husbandry and Ecology;
Teaching of student courses and seminars

**February, 2010 – April, 2010**
**Helmholtz Environmental Research Centre UFZ**, Germany
Internship at the Department of Conservation Biology

**September, 2008 – March, 2010**
**Max-Planck-Institute for Evolutionary Anthropology**, Germany
Student assistant: Coding; Guiding tours; Literature research; Test assistant

**August, 2007 – September, 2007**
**University of Giessen**, Germany
Internship at the Department of Biophilosophy (Biology)

**February, 2007 – May, 2007**
**Max-Planck-Institute for Evolutionary Anthropology**, Germany
Internship at the Department of Developmental and Comparative Psychology

**September, 2006 - Dezember, 2007**
**University of Wuerzburg**, Germany
Student assistant: Research at the Department of Neurobiology;
Teaching assistant for student courses

TEACHING EXPERIENCE

**September, 2013 – present**
**University of Halle-Wittenberg**, Germany
Voluntary Teaching of the module “Bioethics”

**October, 2010 – present**
**University of Halle-Wittenberg**, Germany
Teaching in module ‘Farm animal behaviour”

**September, 2006 - Dezember, 2007**
**University of Wuerzburg**, Germany ;
Teaching assistant for student courses in Zoology