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Does visitor behaviour in front of enclosures differ between captive dogs and wolves?

Master Thesis

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A. Abstract

It has been proposed that our attitudes towards dogs developed out of our negative attitude towards wolves, simultaneously with the domestication process of dogs from wolves. Our attitudes and behaviours became more positive towards tamer individuals, while we maintained negative attitudes towards wolves (Dual Response Hypothesis, DRH). Supposedly, this created a feedback loop with more positive attitudes further advancing the domestication process. If we developed such differential, inherent attitudes, our contemporary behaviour should reflect more negative attitudes towards wolves (i.e. more attentive because of fear, more disruptive, and noisier), compared to more positive attitudes towards dogs (i.e. more interaction attempts). To test the DRH, we compared spontaneous visitor behaviour (across different demographic categories) in front of captive wolves and dogs in a comparable context at the Wolf Science Center, controlling for the animals' visibility and behaviour.

In line with our predictions, interaction attempts were significantly more prevalent (70%) in front of dogs compared to wolves, and shown more often by younger visitors. Contradicting our predictions, adult visitors were more attentive towards dogs, and not significantly more disruptive, or noisier at wolf enclosures. Further, canids' visibility and behaviours revealed systematic differences in visitor reactions towards the two species. Our results suggest that even in a comparable, non-direct contact setting, humans are inclined to interact with dogs, and behave more cautiously around wolves. These differences in behaviour found in our study provide partial support to the DRH.

B. Zusammenfassung

Es wird vermutet, dass unsere Einstellung gegenüber Hunden sich zeitgleich zum Domestizierungsprozess aus der negativen Einstellung gegenüber Wölfen entwickelt hat. Unsere Einstellungen und Verhaltensweisen wurden positiver gegenüber zahmeren Individuen, während wir eine negative Einstellung gegenüber Wölfen beibehielten (Dual-Response Hypothese, DRH). Dies habe eine Feedbackschleife erzeugt, in der die positiveren Einstellungen den Domestikationsprozess weiter förderten. Wenn wir solch differentielle, inherente Einstellungen entwickelt haben, dann sollte unser gegenwärtiges Verhalten negativere Einstellungen gegenüber Wölfen widerspiegeln (d.h. gesteigerte Aufmerksamkeit auf Grund von Angst, mehr störendes und lauteres Verhalten), im Vergleich zu positiveren Einstellungen gegenüber Hunden (d.h. mehr Interaktionsversuche). Um die DRH zu testen haben wir spontanes Besucherverhalten (verschiedene demographische Kategorien berücksichtigend) gegenüber Wölfen und Hunden in einem vergleichbaren Kontext eines Wildparks im Bereich des Wolf Science Centers ausgewertet und dabei die Sichtbarkeit und das Verhalten der Tiere berücksichtigt.

In Übereinstimmung mit unseren Vorhersagen traten Interaktionsversuche signifikant häufiger bei den Hunden im Vergleich zu den Wölfen auf und wurden öfter durch jüngere Besucher gezeigt. Im Kontrast zu unseren Vorhersagen waren erwachsene Besucher aufmerksamer gegenüber Hunden, und nicht signifikant störender oder lauter bei den Wolfsgehegen. Darüber hinaus legte die Miteinbeziehung der Sichtbarkeit und des Verhaltens der Kaniden systematische Unterschiede in den Besucherreaktionen gegenüber den beiden Arten offen. Unsere Ergebnisse deuten darauf hin, dass Menschen selbst in einem vergleichbaren Kontext mit indirektem Kontakt dazu neigen mit Hunden zu interagieren und sich vorsichtiger gegenüber Wölfen zu verhalten. Unsere Ergebnisse unterstützen in Teilen die DRH.

C. List of Figures and Tables

D. Acknowledgements

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1. Introduction

Attitudes are psychological evaluations of an entity as positive or negative (Ajzen & Fishbein, 2005). In the case of animals, humans may consider species that seem very similar, or are even closely related, in an oppositional manner (Taylor & Signal, 2009). An illustrative example of such evaluations may be how we view honey bees and wasps. While the former is considered a useful insect, the latter is often perceived as a nuisance by the public, despite both species fulfilling important ecological functions (Sumner et al., 2018). As a result of these attitudes, protection efforts are more widespread for bees, while killing wasps still seems to be a reasonable action for many. It has been argued that attitudes are an important predictor of how humans behave towards animals (Coleman et al., 2016; Serpell, 2004; but see Heberlein, 2012), with a strong impact on animal lives, both at the individual and at the species level.

In the case of animals, several authors suggest that our attitudes are composed of two factors: affect and utility (for review see Serpell, 2004). Both dimensions are said to range from negative to positive, interact in complex patterns and shape our behaviours towards a species. Since attitudes contain expected benefits and risks of interacting with an entity (Ajzen & Fishbein, 2005), we adapt our behaviour towards a species based on the expected outcome. This expected outcome interacts with our emotions towards a species. Consider an Asian farmer living in the territory of tigers. The farmer may have a positive attitude towards the domestic cats, which hunt mice on his farm (benefit), and the farmer may even enjoy cuddling with cats (emotion). The tiger on the other hand is a predator, and encounters are life-threatening (risk), which is why he fears tigers (emotion), jointly constituting a negative attitude towards tigers.

It has been suggested that protective mechanisms, such as an inherited predisposition to be fearful of dangerous animals, is evolutionarily adaptive, manifest in negative attitudes and facilitate protective behaviours against these species (Öhman & Mineka, 2001). Learning to evaluate the risks of interacting with a deadly species through direct experience would simply be too costly. Examples may be the negative emotions (e.g. fear) towards potentially harmful species like snakes and spiders (Prokop et al., 2009; Rinck & Becker, 2007). This seems to be an inherited predisposition, as infants already display increased attention (indicator of fear) towards snakes and spiders, compared to other non-threatening species (Deloache & LoBue, 2009; Kawai & Koda, 2016; Rakison & Derringer, 2008). What is more, fear of and negative attitudes towards snakes and spiders can be found across cultures (Davey et al., 1998; Landová et al., 2018; Polák et al., 2020; Prokop et al., 2009). But species evolve, and in some instances this changes how they relate to humans and vice versa.

The domestication of dogs may provide one of the most interesting examples of how slight changes in attitudes and concomitant behaviours towards wolves among some of our ancestors may have contributed to a more than tens of thousands year long process bringing about a new species. The Dual-Response Hypothesis by Treves and Bonancic (2016; DRH) suggests that such a shift in attitudes and behaviours intitiated the domestication process, changed our affect towards, and the utility (risks and benefits) of interacting with dogs and wolves respectively, and ultimately shaped our contemporary relation with these two canid species.

1.1. The Dual-Response Hypothesis

The DRH proposes that (while most people feared wolves, David 2009) “attraction to physical proximity” to wolves among some of our ancestors coincided with the benefits of cohabitation in the same territories with these essentially dangerous predators (e.g. following wolf tracks to find a higher abundance of prey). The attraction to wolves supposedly resulted in closer, mutual contact with some wolves that were more tolerant towards humans, initiating the domestication process of dogs. Treves and Bonancic (2016) argue that during the domestication process our attitudes and behaviours towards dogs diverged gradually from our response to wolves. The progression of the domestication process (i.e. the emergence of some tamer individuals) alongside the shift in attitudes towards less aggressive canids could have created a positive feedback loop. More and more people attracted to physical proximity to these less dangerous canids (or the other way around, less people fearing and avoiding them) allowed us to maximise our benefits of close contact with these individuals (e.g. herding, guarding, hunting). There may always be some variability in attitudes and behaviours towards any species. Yet, the DRH proposes that in the case of wolves and dogs the responses towards them contain both negative and positive attitudes (and concomitant behaviours), but with polarised majorities as the domestication process resulted in different risks and benefits in interacting with the two species (Treves & Bonancic, 2016). This polarisation is apparent in the history of our relation to wolves, the evolved role of dogs in our society today, and our contemporary attitudes towards both species.

1.2. The Human-Wolf Relationship

Historically, wolves were our competitors for prey (Perri, 2016; Turner, 2009) and later for our livestock (Lopez, 1978), and posed a threat as predators to us (Linnell et al., 2002). That is the main reason why we have eradicated wolves through direct hunting and habitat destruction in different areas around the world. The significance of competition with wolves for humans may have resulted in a consolidated negative attitude that is represented in fear of wolves across cultures until today (Davey et al., 1998). While in more recent history, direct attacks of wolves on humans have been (Linnell et al., 2002), and are still rare (Linnell et al., 2021), the associated fear of wolves preying on us prevails, as signified by the still popular fairy tale ‘Little Red Riding Hood’. Nevertheless, thanks to laws that have restricted hunting over the last 40 years, wolves did not become extinct, and Europe has seen a rise in their numbers (Convention on the Conservation of European Wildlife and Natural Habitats, 1997). In many regions, however, the return of wolves reignites fear and profound resistance in the form of poaching among parts of the population (Olson et al., 2015), all signs of negative attitudes towards the species.

Indeed, attitudes towards wolves are more negative with increased perceived threat of wolves during their reapperance (Stütz, 2020), and only after some years of experience of little conflict, attitudes of the general population may return to their previous value (Kaczensky, 2006). In rural areas inhabitants are most affected by the reappearance of wolves and experience disadvantages (e.g. competition with livestock-owners and hunters) explaining why negative attitudes are particularly prominent in these regions (Franchini et al., 2021; Grima et al. 2019). Consolidated negative attitudes towards wolves among the most affected stakeholders are counterbalanced by neutral to slightly positive (but not stable) attitudes towards wolves among urban residents, and the positive attitudes of some conservationists, who favour the protection of wolves (Franchini et al., 2021; Kaczensky, 2006). Negative attitudes by livestock-owners and hunters in contrast to positive ones by conservationists can logically be explained by the different instrumental value ascribed to wolves. The former perceive wolves as an economic threat, while the latter value their ecological significance (Boyce, 2018). Both groups act in accordance with these evaluations, with conservationists trying to protect wolves to ensure a successful return, and livestock-owners and hunters following an eradication approach.

Kaczensky (2006) compared attitudes in a German region to which wolves had already returned with attitudes in regions not affected by the wolves’ reappearance. The results demonstrated a consolidated negative attitude of hunters and livestock owners, but surprisingly positive attitudes in the general population in both regions. In comparison to the more rural Norway (Kleiven et al., 2004), German participants were more tolerant to the presence of wolves beyond designated conservation areas. However, the German region to which wolves had returned at the time of the study is a military training ground, and a third of residents of that region were not aware of wolves inhabiting their region. Kaczensky (2006) points out that despite general positive attitudes towards wolves, there was little interest in learning about them. That is why they warned that the slightly positive attitudes towards wolves in the general population in their study could easily be swayed by negative media coverage. Today, the return of wolves is more widespread in Europe, and the former slightly positive attitudes in the general public have reached a neutral level, and negative attitudes among rural inhabitants (particularly hunters and livestock-owners) are increasing (Franchini et al. 2021). Without proper management, experts warn that the arrival of wolves will likely lead to negative attitudes in more and more regions (Franchini et al. 2021; Herzog, 2018). In fact, the recent return of wolves in Upper and Lower Austria has reignited negative attitudes not only among hunters and livestock-owners (Stütz, 2020).

The effect the wolves return has on attitudes seems to be further mediated by gender and age. Women hold more negative attitudes compared to men, and younger people express less negative attitudes across studies (Dressel et al., 2015; Kaczensky, 2006; Kotrschal et al., 2013; Røskaft et al., 2007; Wechselberger & Leizinger, 2018; Wechselberger et al., 2005). One explanation may be that negative attitudes are more pronounced among women, as they are more fearful about wolves, and thus, feel more affected by their reappearance (Kaczensky, 2006). Why age affects attitudes is a question yet to be answered. Nevertheless, it is a factor that should be taken into consideration, when studying attitudes and behaviours towards wolves.

1.3. The Human-Dog Relationship

Concerning the domestication of dogs, the DRH suggests that a shift from a negative attitude towards wolves towards a positive attitude towards proto-dogs allowed humans who sought out contact, to benefit more and more from mutualistic interactions with the latter (Treves & Bonancic, 2016). Even before humans settled, we incorporated dogs in our lives for their instrumental value (hunting, meat supply; Lupo, 2011; Serpell, 2016). With humans settling and domesticating livestock species, dogs gained further roles in our societies, like herding and protecting us from competing predatory species (including ancestral wolves; Lord et al., 2016; Treves & Karanth, 2003).

Today, dogs are “man’s best friend”, and live close to humans all around the world (Serpell, 2016). Although variation across cultures exists, dogs’ most prominent role in western societies (especially those that have eradicated stray dog populations) is that of a companion (Serpell, 2016). Correspondingly, western attitudes towards dogs are predominantly positive (Coleman et al., 2016; Driscoll, 1995; Ellingsen et al., 2010; Lakestani et al., 2011). A study in Austria showed that participants associate companionship, care, and utility (indicators of a positive attitude) with dogs, but not with wolves (Kotrschal et al., 2013). Consequently, behaviours towards dogs are consistent with positive attitudes towards them, that is, they are tolerated within our society and many people enjoy taking care of them. In Europe, one out of four households choose to live with at least one dog (FEDIAF, 2020), per year we spend increasing amounts of money on our pets (FEDIAF, 2017; FEDIAF 2020), and many owners enjoy indulging their dogs in whichever way possible (Serpell, 2016).

Indeed, dogs are perceived by humans in western regions in an extremely positive manner in comparison to other (domesticated) species, while at the same time receiving lower ratings related to safety (Driscoll, 1995). In fact, the risk of being attacked by a dog is considerably larger (Sarenbo & Svensson, 2021) than being attacked by a wolf (Linnell et al., 2021). Nevertheless, we generally fear wolves while attitudes towards dogs are so predominantly positive (even if parts of our society still fear them) that we tolerate them living among us despite the associated risk. A reason for this may be that the benefits associated with living with dogs outweigh these risks. Interestingly, bite victims (on average) have more positive attitudes towards dogs than do people who have never been bitten, mostly because people with more positive attitudes towards dogs seek out contact with them more often, resulting in a higher risk of being bitten (Lakestanti et al., 2011), which is in line with the DRH.

Also in the case of dogs, there are demographic differences in attitudes towards the species. Attitudes towards dogs are more positive among women and the young, compared to men and older people (Boyd et al., 2004; Brandl, 2016; Kotrschal et al., 2013; Lakestani et al., 2011). In the case of women, it seems that their more positive attitude is driven by positive affective evaluations, as opposed to the more utility-based evaluations of dogs by men (Brandl, 2016; Ellingsen et al., 2010; Kotrschal et al., 2013). The influence of age on attitudes towards dogs, again, seems less straightforward. Despite remembering less aggressive encounters with dogs, older people hold more negative attitudes towards dogs (more fearful and perception of dogs as dangerous), while children (especially of dog-owners) and young adults hold more positive attitudes towards dogs (Boyd et al., 2004; Lakestani et al., 2011). While Boyd et al. (2004) suspect a cohort effect, we still lack a tangible explanation as to why children hold more positive attitudes towards dogs compared to older people, despite both groups being at higher risk of dog attacks (Sarenbo & Svensson, 2021). In summary, in western societies dogs are met mostly with positive attitudes and have been incorporated in our everyday life.

1.4. Comparing Attitudes and Behaviours towards Dogs and Wolves

In contrast, wolves face neutral to negative attitudes, with certain groups maintaining a consolidated opposition to wolves translating into political activism against the wolves' return. However, most of the evidence comes from studies investigating attitudes towards dogs and wolves separately. Only few studies attempted to compare attitudes, let alone behaviours, towards the two species within the same human sample. Hence, it is still unclear whether our attitudes and subsequent behaviours towards wolves and dogs differ, as proposed by the DRH. The scarcity of studies might be explained by the fact that potential encounters with the two species differ substantially in the likelihood to occur and in context. Beyond that, we still do not fully understand how experience influences our attitudes towards the two canid species (Boyd et al., 2004; Kaczensky, 2006; Lakestani et al., 2011). This creates a challenge in disentangling how far our behaviour is shaped by experience or an inherited response pattern. Nevertheless, as there is an effect of age on attitudes towards wolves and dogs, it is important to include different age groups to obtain results that are generalizable across age. Arguably, ample experience of interacting with dogs in our everyday life may have shaped our behaviours towards them more intensely than in the case of wolves. Yet, the influence of experience on our behaviour towards dogs should be higher in a context in which we have encountered dogs before, and be less pronounced in a context in which we have not encountered them before. It is reasonable to assume that wolves hold a sense of novelty for most people in any context, as it is so unlikely to ever experience a direct encounter.

Therefore, finding a comparable context, in which most people have not interacted with dogs (nor wolves), would not only enable the direct comparison of behaviours towards the two canid species, but should help to keep the influence of prior experience with dogs at a minimum. The Wolf Science Center (WSC; https://www.wolfscience.at/) offers such a unique setting. The WSC is embedded in the Wildpark Ernstbrunn, a game-park in Lower Austria. There, both wolves and dogs are raised and kept in a standardised and thus comparable manner. The animals live in large enclosures that are visible to visitors of the game park.

Seizing this opportunity, Brandl (2016) conducted the first study comparing human attitudes and behaviours towards wolves and dogs in a direct contact setting. In particular, the study investigated attitudes and behaviours of paying attendees during visitor programs of the WSC. Participants differed in their behaviour towards the two canid species: attendees were more relaxed (indicating less fear) during the dog pack visit, but were also less eager to interact with the animals, compared to when participating in the wolf pack visit. The participants' attitudes (assessed through self-report questionnaires), however, were not associated with these behavioural differences, as they were comparably positive towards both species. These findings contradict the DRH, as it proposes more negative attitudes towards wolves, which should correlate with more cautious behaviour. However, the rare opportunity to interact with wolves and having to pay for the participation most likely attracted a highly biased sample. It is conceivable that only subjects with especially positive attitudes towards wolves were included in the study. Further, paying attendees of the WSC's special visitor program receive safety instructions (Brandl, 2016). For the research purpose of the WSC it is important that experiences of wolves and dogs with humans are comparable, which is why participants are instructed to behave in the same manner in the enclosures of the two species. Beyond that, the safety instructions ensure that attendees only use behaviours towards the dogs that are safe towards wolves as well (e.g. not grabbing the animals). That paying attendees still differed in their behaviour, despite the instructions and self-reported comparable attitudes towards both species, begs the question what caused these differences. Paying attendees still behaving more relaxed during the dog pack visit, despite the safety instructions, demonstrates that their evaluations of the risks involved differed between the two species, which may not have been covered by the attitudes questionnaire used in Brandl's study (2016).

In the field of study of racist behaviours and its attitudinal basis, researchers have been facing a similar paradox. In self-report questionnaires, white participants indicated to not hold negative attitudes towards people of colour (Crosby et al., 1980). Yet, discriminating behaviour against people of colour was (and still is) a widespread phenomenon, although self-report studies indicated that attitudes were not the driving factor (Son Hing et al., 2008). The development of a new behavioural test generated a potential explanation: Attitudes consist of somewhat independent explicit and implicit parts, both influencing our behaviours. Self-report questionnaires can only assess the explicit part of attitudes, which are cognizantly accessible. Yet, spontaneous behaviour reflects both, implicit and explicit attitudes (Perugini, 2005). Participants in Brandl's study (2016) did not differ in their explicit attitudes towards wolves and dogs, as assessed through the questionnaire. As the more or less spontaneous behaviour in direct contact likely reflected a mixture of both implicit and explicit attitudes, it could be that the observed differences (e.g. more relaxed at dogs) arose from differential implicit attitudes towards wolves and dogs. Moreover, revealing the purpose of the study by conducting the attitude questionnaire before the pack visits might have further emphasised the influence of the participants' explicit attitudes (biased by social desirability; van de Mortel, 2008). This might have minimised the influence of implicit attitudes on participants' behaviour towards the animals, resulting in only small differences observed in behaviour towards wolves and dogs (Brandl, 2016). In everyday life, our actions are undoubtedly guided by a mixture of implicit and explicit attitudes (Wilson et al., 2000). Hence, investigating truly spontaneous behaviour as an indicator of attitudes has the potential to diminish the social desirability bias and further increase external validity. This approach, however, requires not to call the participants' attention to their explicit attitudes. The behaviour spontaneously shown by regular park visitors towards the wolves and dogs kept at the WSC might reflect attitudes more universally. In contrast to paying attendees of direct contact programs, visitors of the game park Ernstbrunn may not visit because of a special fascination for wolves, but to encounter any or all of the 18 species exhibited at the Wildpark Ernstbrunn (http://www.wildpark-ernstbrunn.at/de/), and thus can be assumed to be a less biased sample with more heterogeneous attitudes (i.e. more representative of the composition of attitudes in the general population). That is why the current study investigates spontaneous behaviour of game park visitors in front of wolves compared to dogs as a proxy for attitudes towards the two species.

The diversity of spontaneous behaviour confronts us with the challenge of operationalizing positive and negative attitudes using specific behavioural indicators. Deloache and LoBue (2009) faced the same challenge when testing for an inherited predisposition to fear snakes in preverbal infants. The study used attentiveness (operationalized by increased gazing) as an indicator of fear towards snakes. However, attentiveness could also be a sign of an attraction to physical proximity or novelty (Ernst et al., 2020), which is why they used further behavioural indicators (e.g. grasping) to differentiate the emotional valence towards the presented stimuli. Attentiveness because of novelty (i.e. without a negative predisposition) should result in attempts to interact. In this case, one would behave more curious, trying to come closer to the object of one's curiosity. In the case of a negative predisposition, however, one would not expect attempts to establish a positive interaction. Instead, we would expect behaviours indicative of negative affect, which do not exacerbate the risks associated with the species, when exposed to them. The risks are of course highly dependent on context, and our experience with the species in that specific context. In a safe context (e.g. with a fence in between), a negative attitude might show in behaviours that are disruptive to the animals (e.g. to test their reaction towards oneself from a safe position), or might even be considered aggressive. Therefore, any study comparing attitudes and behaviours towards wolves and dogs requires a comparable context, involving similar risks (and benefits) of behaviours shown towards the two species, but with comparable experience with the species in this specific context.

Understanding whether there is indeed an inherent dual response to dogs and wolves (i.e. dogs face a society favourable towards them, while wolves face opposition) would not just further our understanding of how dogs came to be man’s best friend, but would be an important factor to consider in managing wildlife-human conflict and planning educational conservation programs for wolves.

1.5. Hypothesis and Predictions

Throughout history up until today, our treatment of wolves and dogs differs, proposedly because of our differing inherent attitudes (Treves & Bonacic, 2016). Based on competition and threat from wolves, and the mutualism with dogs that evolved through their domestication, the DRH proposes that on average, humans should show disruptive behaviours towards wolves (indicating a negative attitude), while seeking out contact with dogs (Treves & Bonacic, 2016). This coincides with contemporary, western attitudes and behaviours towards the two species respectively. Therefore, we expect spontaneous visitor behaviour towards the two species to differ when facing the animals in a comparable context. Considering the competition with, and threat of wolves compared to dogs, a predisposition to attend to wolves (because of high fear levels) could have been adaptive for our ancestors (and might still be today). That is why we predicted increased attentiveness with less attempts to interact with the animals at wolf enclosures compared to dogs. Accordingly, visitors should

a. take more pictures, and point at wolves more (behaviours indicative of attentiveness) compared to dogs. Complementary, we expected visitors to
b. show more attempts to interact with dogs, compared to wolves (e.g. throw food in the enclosure, attempt to draw the animals' attention through chirruping, imitation of animal voices, or to decrease the proximity to the animals by trespassing from the visitor pathways).
c. Furthermore, we predicted that, if an inherent negative attitude towards wolves still is an influencing factor, visitors should behave more disruptively (indicating more fear and a lack of attraction to physical proximity) in front of wolf enclosures. That is, we expected more throwing of objects into the enclosure, more shouting, and in general, more noise in front of the wolves' compared to dogs' enclosures (i.e. relative to visitor numbers, their noise level should be higher at wolf enclosures). This pattern (more attentive and disruptive, with less attempts to interact with wolves compared to dogs) should
d. be more pronounced in women compared to men, as women have been shown to hold more negative attitudes towards wolves, supposedly because of a higher fear level (Kaczensky, 2006), and hold more positive attitudes towards dogs (Ellingsen et al., 2010).
e. As attitudes towards both species have been shown to be more negative among older compared to younger people, we further expected that older people would show less

attempts to interact with, and more disruptive behaviours towards either species, compared to younger visitors.

2. Materials and Methods

2.1. Setting

We observed regular park visitors of the Wildpark Ernstbrunn, Austria, in the section of the Wolf Science Center (WSC; that is, in predefined areas in front of dog and wolf enclosures). The Wildpark Ernstbrunn is a game-park keeping local domesticated species, and their wild counterparts in a family-friendly setting. Several walk-in enclosures provide direct contact opportunities with non-dangerous species, and visitors can interact with many ungulate species safely through the fences, which is not possible with the kept canids. Furthermore, visitors can buy dried corn at the entrance to feed the animals to facilitate interactions. However, the corn is sold without instructions concerning which animals are allowed to be fed. Therefore, signs at the dog and wolf enclosures warn to not feed them.

The WSC is a scientific institution investigating the social and cognitive capacities of wolves and dogs. For this purpose, 13 adult grey wolves in six packs, and six adult mongrel dogs in three packs were kept during the course of this study. Subjects of both species are hand-raised and kept by the WSC in a standardised manner, enabling comparative studies between the domesticated dog and its wild counterpart (Range & Virányi, 2014). The packs are shifted between species-specific enclosures in a semi-regular manner, which allowed us to control for potential mitigating effects of enclosure design on both animal and human behaviour (as recommended by Sherwen & Hemsworth, 2019). Six of the wolf enclosures were observable to visitors, while for dogs it was only one (Fig. 1). Despite that, the enclosures of both dogs and wolves have similar appearances, as they are structured in a comparable manner. Each enclosure is fenced in with high metal wire along a second wooden railing that delineates the visitor pathway with at least one meter distance to the fence. All enclosures contain areas of lush foliage, as well as more open spaces, giving animals the choice to be visible to visitors or retreat from their view. Moreover, each enclosure is equipped with a water dispenser in the visual range of the visitor pathway, and shelters in the form of huts. Some of the wolf enclosures further contain dens built by the wolves, and dogs can choose to enter a room in a house adjacent to the enclosure at all times for shelter (accounting for species-specific needs). To control for potential influencing effects of different enclosures and individual animals (Sherwen & Hemsworth, 2019), as well as weekdays and daytime, observations were conducted in a semi-randomized manner so that over the course of the study each part of each observation day was equally represented in the final sample for each enclosure and pack.

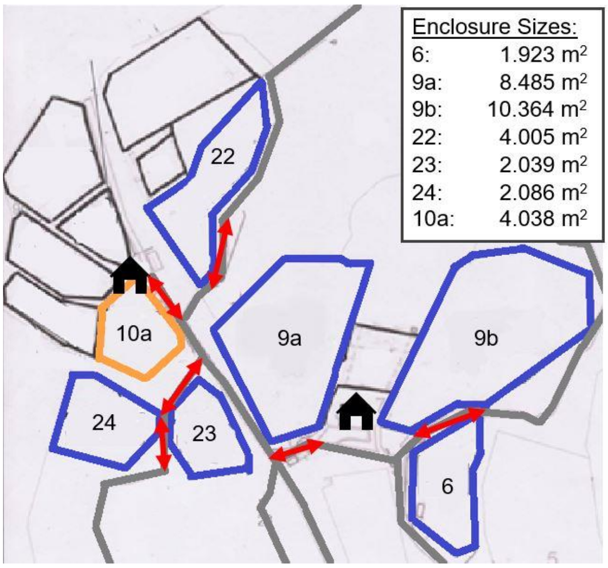

Figure 1: Map of the WSC. Includes position of trainer houses. Observation areas are indicated by red arrows. Wolf enclosures are displayed in blue. The dog enclosure is displayed in orange.

The observations took place over a span of six weeks (August-September 2021) during the parks' opening hours (9am-5pm) on Thursdays, Fridays, and Sundays. Based on staff experience, visitor numbers vary between these weekdays. In total, we conducted 99.08 hours of observations. The observation period was situated during the summer holidays, thus constituting the annual peak season for the game park. Observations took place in predefined areas on the visitor path along seven enclosures (Fig. 1) using landmarks (e.g. trees, fence posts, visitor signs) to delineate the boundaries. The use of landmarks was chosen in order to avoid marking the observation areas, so that they were not recognizable to visitors. The areas were chosen according to highest animal visibility, and thus, visitors were expected to be most abundant. Each observation area contained at least one warning sign to not feed the animals. The main observer positioned herself at a spot along the visitor pathway, allowing her a good view of all visitors within the area. As part of a concomitant study, a second observer collected data on the animals' behaviours. This allowed to control for the influence of some animal parameters on visitors, such as their activity levels (see below). The second observer adjusted her position within the predefined observation area to achieve the best view of the animals. Data was collected directly on a tablet with Excel.

2.2. Observational Procedure

Before data collection, both experimenters completed a training period first observing the animals, and then the visitors (~9 hours of observation time) simultaneously, but independently, for assessing inter-rater reliability. Before each observation started, temperature and weather conditions (i.e. sunny, cloudy, rain) were noted. During data collection, instantaneous and scan sampling with 30 one-minute intervals were applied (Martin & Bateson, 2007), alongside continuous sampling. Noise levels were collected within five-minute intervals. For each one-minute interval we collected data on visitor abundance, as well as animal parameters, which were expected to influence visitors. We were required to reprimand behaviours that are forbidden by park rules due to their potential harm for both visitors and animals (i.e. trespassing, throwing food or objects into the enclosure). Further, the beginning and completion of visitor behaviours could not be defined consistently across all variables. Instances of some behaviours (e.g. pointing, throwing objects) are clearly delimitable, while the duration of other behaviours (e.g. taking image material) is not as easily observable. Therefore, for each behaviour only the first occurrence per visitor was noted per one-minute interval.

2.3. Visitor Variables

We collected data on visitor abundance, and noise levels (Tab. 1), as well as behaviours of individual visitors (Tab. 2). For each visitor behaviour, we further estimated basic demographics of the acting person (i.e. age, gender; Tab. 3). To identify whether an individual visitor displayed several behaviours of interest, we further noted the colour of their clothes. This allowed us to control for non-independece of repeated observations of the same individual. The free movement of visitors and their numerosity made a single count simultaneously with the collection of visitor behaviours unfeasible. But based of the system for individual recognition, we analysed behaviours of interest of N = 2022 individual visitors.

Variable Name	Description	Code
Visitor Abundance	$N_{visitor}$: 0	0
	$N_{visitor}$: <5	1
	$N_{visitor}$: 5-9	2
	$N_{visitor}$: 10-19	3
	$N_{visitor}$: >20	4
Average Noise	A-weighted equivalent continuous sound level	LAeq
Maximum Noise	A-weighted maximum sound level	LAmax

Table 1: General Estimates

2.3.1. Visitor Behaviours

Visitor behaviours were grouped into three categories, indicative of attitudes (Tab. 2). Pointing at and taking pictures of the animals were used as an indicator for attentiveness. Interaction attempts including efforts to decrease the distance to the animals (e.g. trespassing, feeding, lures…) were used as indicators of attraction to physical proximity (i.e. positive attitudes). Behaviours that may be disruptive to the animals (shouting, throwing objects), are thought to indicate more negative attitudes towards the animals, as one would show these behaviours to test the animals without considering a potential negative effect on the animals, or simply act upon a dislike towards the animal from a safe position behind the fence.

Category	Variable Name	Definition	Code
Attentive Behaviours	Pointing at Animal	Visitor points, makes gestures with arms, hands or head towards an animal	P
	Picture	Visitor takes image material of the animals, or of other visitors, with animals in the frame	B
Disruptive Behaviours	Shouting	Talking with a raised voice beyond normal conversational volume (except children crying)	S
	Throwing Objects (into enclosure)	Throwing a non-food object into the enclosure (incl. attempts intercepted through reprimands)	O
Interaction Attempts	Lures (verbal and gestural)	Visitor addresses animal verbally and/or makes luring hand-gestures, while looking at the enclosure	L
	Animal Voice	Visitor imitates wolf or dog vocalisations	V
	Feeding Animals	Throwing food into the enclosure (incl. attempts intercepted through reprimands)	E
	Pet Dog Trespassing	All four paws of a pet dog behind wooden railing demarking the visitor path way (demographics of person holding the leash considered)	DT
	Human Trespassing	Visitor with both feet behind wooden railing demarking the visitor path way, or visitors bending forward over the railing and reaching with arms towards the enclosures, instead of just resting the arms on the railing.	HT

Table 2: Individual Behaviours

Variable Name	Category	Code
Age of Actor	<20 years	1
	20-39 years	2
	>40 years	3
Gender of Actor	Female	F
	Male	M

Table 3: Demographic Estimates

2.3.2. Noise Measurements

The noise measurements provide us with a behavioural estimate at group level (Tab. 1). We chose to collect both the average noise level (LAeq), as well as the maximum noise level (LAmax). The LAeq is an adequate measurement of the general noisiness of a group. Yet, it does not reflect sudden, and short bursts of noise, which is why we included LAmax as well (ANIMA, 2022). Noise levels were collected using the NIOSH Sound Level Meter (EA LAB, 2016) on an iPhone 11, as it provides high accuracy ($R^2 = 0.97$; Crossley et al., 2020). The noise levels were measured by the first observer, due to her stationary position. The continuously collected visitor and animal behaviours of interest, alongside notes of special events, informed the noise data preparation for the statistical analysis (e.g. identifiable sources of loud noises independent from the visitors' behaviours, staff walking by, presence of guided tours, animal feeding and training, or reprimands of visitor behaviours forbidden by park rules). Based on the notes, we excluded the maximum noise level, whenever the loudest noise was produced by the observer herself, the observed animals themselves, visitors talking to the observer, or other loud environmental noises occurring in close proximity to the first experimenter (e.g. closing of metal gates).

2.4. Animal Parameters

Visitor studies in zoos have demonstrated that the animals themselves influence visitor behaviour. Visible and active animals attract more visitors, and catch their attention (Altman, 1998; Davey, 2006; Margulis et al., 2003). Studying visitor behaviour at the WSC allowed us to control for this potential source of variation. To control for animal visibility following Kuhar et al. (2009), the second observer noted whether an individual animal was visible at any time during a one-minute interval (total number of visible animals per one-minute interval). Beyond that, the current activity level of each animal in the enclosure at the start of each one-minute interval was noted following the methodology of Wacker (2020). Animals were categorised as inactive, if they were lying or sitting at the time point of the scan sample, and as active, if they were standing or walking. Based on this, the number of active animals was calculated per scan sample. Beyond the more general estimate of the number of animals active, we expected that some animal behaviours (eating/drinking, affiliative, aggressive, dominant, submissive, vocalisations) would especially catch the visitors' attention, which is why these were observed continuously. The sum of these behaviours shown by all animals in the enclosure was calculated for each interval (number of animal behavious).

2.5. Statistical Analysis

Based on the training period for the oberservational procedure, we analysed inter-rater reliability achieving good to excellent agreement according to Koo and Li (2016; see Appendix A for full results of the intraclass correlation coefficients).

Models were fitted in R (version 4.1.2; R Core Team, 2021) using the function lmer or glmer from the lme4 packages (version 1.1-27.1; Bates et al., 2015) with the optimizer "bobyqa" using 100.000 iterations. Linear mixed models (LMMs) were used for the responses "Average Noise", "Maximum Noise", while generalized linear mixed models (GLMMs) with binomial error structure and logit link function were used for the response "Attentive Behaviours", "Interaction Attempts" and "Disruptive Behaviours".

We ran two separate models for each response variable. For the first model we were interested in the effect the number of visible animals has on the response. For the second model we were interested in the effect of animal's behaviour (number of active animals and number of animal behaviours), and we therefore used a subset of the data were at least one individual was visible (excluding observations were no animals were visible). For the LMMs that cover the noise levels, our key fixed effects of interest were the interaction of species with the number of visible animals, or in the second model the animal's behaviour. For the GLMMs that cover the interaction between humans and animals, we were interested in the interaction between species with gender, age and animal visibility (or in the second model the animal's behaviour). As additional fixed effects that served as control variables we included staff presence (coded as yes, no), weekday, and weather (coded as sunny, cloudy, rainy). Before being included in the model, the covariates number of visible animals (or in the second model: number of active animals), age and visitor abundance were z-transformed to ease model convergence and achieve easier interpretable model coefficients (Schielzeth, 2010).

To avoid pseudoreplication we also included packID and enclosure as random effects, further we included the random effect of the individual combination of pack and date (pack.date) to code for any day to day variation within each pack. To avoid overconfident models and to keep type I error rate at the nominal 5% level, we included all theoretical identifiable random slope components (Schielzeth & Forstmeier, 2009, Barr et al., 2013). The original models also included all correlations between random intercepts and random slopes, but as these seem to be unidentifiable (with correlations being one or close to one), we removed these from the models (Matuschek et al., 2017).

After fitting the full models we confirmed that none of the model assumptions were violated and assessed model stability. We verified absence of collinearity by calculating the Variance Inflation Factor (VIF) using the R package “car” version 3.0-12 (Fox & Weisberg, 2019). This revealed that collinearity was not an issue (all VIFs <1.5). Further, we visually inspected whether the best linear unbiased predictors (BLUPs) per level of the random effects were approximately normally distributed (Baayen, 2008; Harrison et al., 2018). We assessed model stability with regard to the model estimates by comparing the estimates from the model including all data with estimates obtained from models in which the levels of random effects were excluded one at a time (Nieuwenhuis et al., 2012).

We compared each full model with all terms included to their respective null model lacking the key terms of interest, but otherwise being identical in the random effects part, using a likelihood ratio test to avoid ‘cryptic multiple testing’ (Forstmeier & Schielzeth, 2011). If a full-null model comparison revealed clear effects of the predictors of interest, we tested the individual fixed effects to achieve informative estimates of the fixed effects terms using the drop1 function in R. We did so by reducing model complexity, and dropping non-significant interactions from higher order to lower order terms from the model one at a time, and compare the simpler with the more complex model utilizing likelihood ratio tests.

3. Results

3.1. Attentive Behaviours

We analysed 2,228 instances of attentive behaviours ($N_{Picture} = 632$, $N_{Pointing} = 1596$). Attentive behaviour towards the two species differed depending on visitor age (species*age: GLMER: $\chi^2 = 10.03$, $df = 2$, $P = 0.007$; Fig. 2). Young adults were significantly more attentive in front of the dog compared to wolf enclosures ($z = 2.81$, $SE = 0.46$, $P = 0.005$). Further, across species the youngest age class was less attentive compared to both younger adults (wolves: $z = -11.52$, $SE = 0.21$, $P < 0.001$; dogs: $z = -2.40$, $SE = 0.39$, $P = 0.043$) and older adults (wolves: $z = -15.53$, $SE = 0.16$, $P < 0.001$; dogs: $z = -4.53$, $SE = 0.40$, $P < 0.001$). Beyond the age of visitors, their gender influenced attentive behaviour as well (main effect: GLMER: $\chi^2 = 9.44$, $df = 1$, $P = 0.002$), with men being 38% less likely to display attentive behaviours.

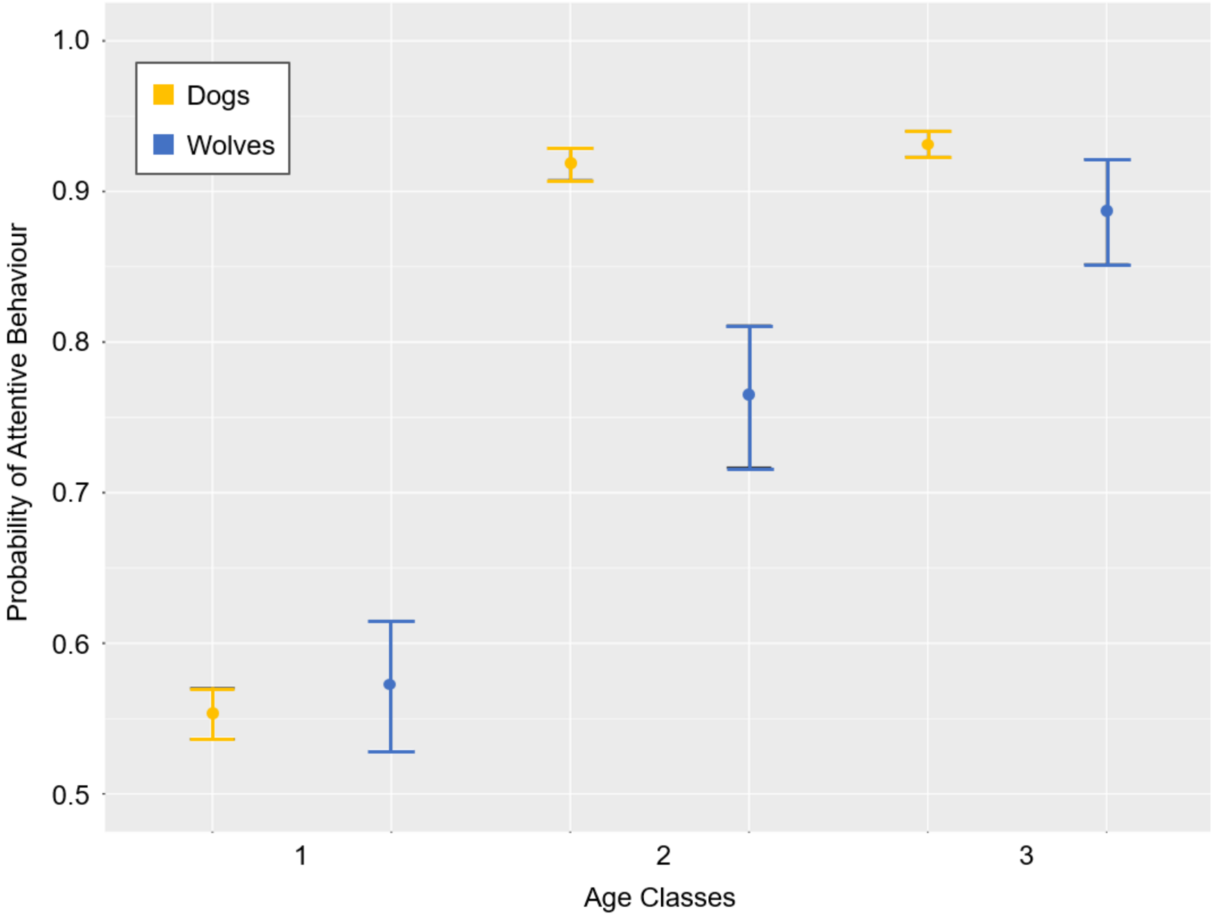

*Figure 1: : Attentive Behaviour in Relation to Animal Visibility: Species*Age. Average probability of attentive behaviour per age class in the first model accounting for the number of visible animals. Error bars indicate standard deviation.*

Furthermore, the number of visible animals modulated attentive behaviours (main effect, GLMER: $\chi^2 = 8.44$, $df = 2$, $P = 0.015$). Visitors tended to be 69% more attentive when one animal was visible compared to when no animal was visible ($z = -2.26$, $SE = 0.35$, $P = 0.062$). When at least two canids were visible compared to none, visitors were 65% more attentive ($z = -2.72$, $SE = 0.22$, $P = 0.018$). The difference between one canid and at least two canids visible was not significant ($z = 0.63$, $SE = 0.30$, $P = 0.81$).

A similar pattern emerged in the second model for attentive behaviour, when considering the number of active animals, and number of animal behaviours, instead of the number of visible animals. Again, the age groups differed in attentive behaviours in front of wolf and dog enclosures (species*age, GLMER: $\chi^2 = 9.37$, $df = 2$, $P = 0.009$; Appendix B). Younger adults were significantly more attentive at the dog compared to the wolves' enclosures ($z = 2.67$, $SE = 0.56$, $P = 0.008$). In front of wolf enclosures, the youngest age class was significantly less attentive compared to both, younger adults ($z = -10.60$, $SE = 0.25$, $P < 0.001$), and older adults ($z = -14.67$, $SE = 0.18$, $P < 0.001$). In front of the dog enclosure, the difference between the youngest age class and younger adults only showed a tendency ($z = -2.10$, $SE = 0.46$, $P = 0.091$), but the youngest age class was significantly less attentive compared to older adults ($z = -4.25$, $SE = 0.42$, $P < 0.001$). Again, the model accounting for the number of active animals, and the number of animal behaviours on visitors' attentiveness towards wolves and dogs, revealed a significant main effect of gender (GLMER: $\chi^2 = 7.67$, $df = 1$, $P = 0.006$). Men were 39% less likely to display attentive behaviours ($z = -3.38$, $SE = 0.14$, $P = 0.001$). In contrast to the number of visible animals, however, the number of active animals, and the number of animal behaviours were not associated with attentiveness towards animals (all $P > 0.05$).

3.2. Interaction Attempts

In total, we analysed 535 interaction attempts ($N_{\text{Lures}} = 154$, $N_{\text{Animal Voice}} = 264$, $N_{\text{Feeding Animals}} = 14$, $N_{\text{Pet Dog Trespassing}} = 30$, $N_{\text{Human Trespassing}} = 73$). The final model for interaction attempts in relation to the number of visible animals only included main effects, after stepwise exclusion of the non-significant interactions. The main effect of species was significant (GLMER: $\chi^2 = 5.50$, $df = 1$, $P = 0.019$), and interaction attempts were 70% more likely at dog enclosures ($z = 2.75$, $SE = 0.31$, $P = 0.006$). Conversely to attentive behaviours, however, the number of visible animals did not affect interaction attempts (GLMER: $\chi^2 = 3.64$, $df = 2$, $P = 0.162$).

The demographic characteristics of visitors correlated with the likelihood to interact with the canids as well (age: GLMER: $\chi^2 = 150.59$, $df = 2$, $P < 0.001$; gender: GLMER: $\chi^2 = 6.64$, $df = 1$, $P = 0.010$). The youngest age class was 17% more likely to display interaction attempts towards canids compared to younger adults ($z = 7.47$, $SE = 0.21$, $P < 0.001$), and 18% more likely compared to older adults ($z = 11.01$, $SE = 0.14$, $P < 0.001$). The adult groups were comparably likely to display interaction attempts ($z = -0.50$, $SE = 0.23$, $P = 0.872$). Concerning gender (GLMER: $\chi^2 = 6.75$, $df = 1$, $P = 0.009$), men were 61% more likely to display interaction attempts towards canids ($z = 3.48$, $SE = 0.13$, $P = 0.001$).

The model for interaction attempts in relation to the number of active animals, and the number of animal behaviours, is consistent with that controlling for the number of visible animals. Species was a significant predictor (GLMER: $\chi^2 = 5.52$, $df = 1$, $P = 0.019$), with visitors being 72% more likely to attempt an interaction with dogs compared to wolves ($z = 2.74$, $SE = 0.34$, $P = 0.006$). Neither the number of animal behaviours (GLMER: $\chi^2 = 0.59$, $df = 1$, $P = 0.44$), nor the number of active animals influenced interaction attempts (GLMER: $\chi^2 = 0.92$, $df = 2$, $P = 0.63$).

The influence of demographic variables in this model again was significant and consistent with the one accounting for the number of visible animals (age, GLMER: $\chi^2 = 145.90$, $df = 2$, $P < 0.001$; gender, GLMER: $\chi^2 = 5.45$, $df = 1$, $P = 0.020$). Again, the youngest age class was more likely to attempt an interaction compared to younger adults (16%, $z = -7.67$, $SE = 0.21$, $P < 0.001$), as well as older adults (17%, $z = -10.71$, $SE = 0.15$, $P < 0.001$). Further, men compared to women were 60% more likely to display interaction attempts ($z = 2.96$, $SE = 0.14$, $P = 0.003$).

3.3. Disruptive Behaviours

We analysed 203 instances of disruptive behaviours ($N_{\text{Shouting}} = 190$, $N_{\text{Throw Object}} = 13$). In the final model for disruptive behaviour in relation to animal visibility, the interaction species*number of visible animals had significant predictive value (GLMER: $\chi^2 = 6.23$, $df = 2$, $P = 0.044$; Fig. 3). This effect seems to be driven by the only significant contrast between no and at least two wolves visible ($z = 3.41$, $SE = 0.30$, $P = 0.002$), as none of the other contrasts were significant (see Appendix C).

Again, the model revealed a significant influence of age (GLMER: $\chi^2 = 178.36$, $df = 2$, $P < 0.001$), with a slightly higher probability of disruptive behaviour by the youngest age class compared to both younger adults (8%, $z = -7.81$, $SE = 0.31$, $P < 0.001$) and older adults (5%, $z = -9.09$, $SE = 0.32$, $P < 0.001$). The effect of gender showed a trend (GLMER: $\chi^2 = 3.55$, $df = 1$, $P = 0.059$), with men being 62% more likely to display disruptive behaviours ($z = 2.40$, $SE = 0.20$, $P = 0.016$).

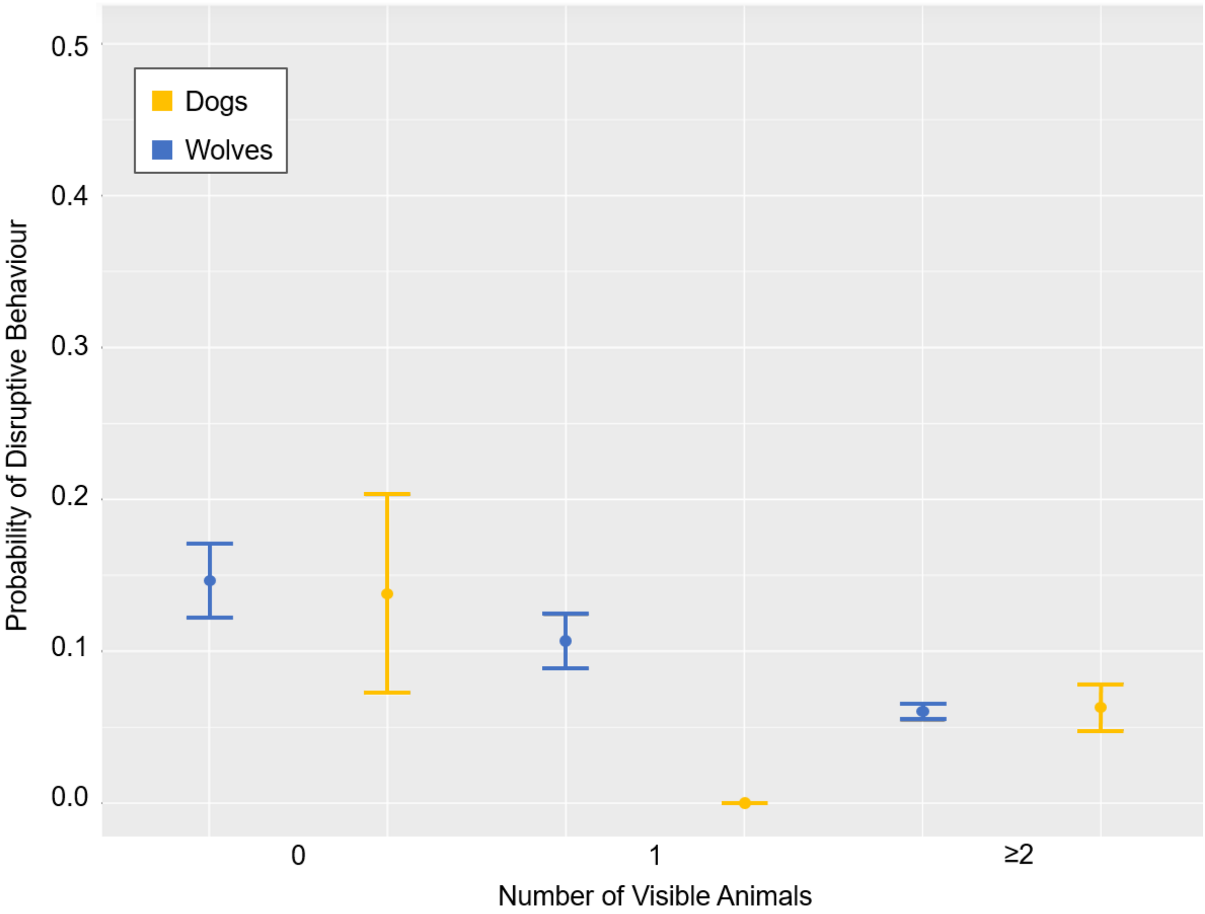

*Figure 3: Disruptive Behaviour: Species*Number of Visible Animals. Average probability of disruptive behaviour in relation the number of visible animals. Error bars indicate standard deviation.*

The second model for disruptive behaviour by visitors revealed a significant influence of species*number of active animals (GLMER: $\chi^2 = 10.70$, *df* = 2, *P* = 0.005; Fig. 4), but not of the number of behaviours shown by the canids (GLMER: $\chi^2 = 1.29$, *df* = 1, *P* = 0.256). The significant interaction of species*number of active animals seems to be driven by the difference in disruptive behaviour between wolves and dogs when no canid was active (*z* = 2.02, *SE* = 1.07, *P* = 0.044), although there was a trend in front of dog enclosures between no and two dogs active (*z* = 2.12, *SE* = 1.12, *P* = 0.087). Disruptive behaviour in front of wolf enclosures is comparable between the different numbers of active animals (all *P* > 0.05; see Appendix C).

Age had a significant predictive value for disruptive behaviour (GLMER: $\chi^2 = 147.83$, *df* = 2, *P* < 0.001). Both younger adults (*z* = -6.02, *SE* = 0.49, *P* < 0.001), and older adults (*z* = -8.46, *SE* = 0.34, *P* < 0.001) were 5% less likely to display disruptive behaviours in comparison to the youngest age class. The difference between the two adult groups was not significant (*z* = -0.15, *SE* = 0.57, *P* = 0.987). The main effect of gender, again, showed a trend (GLMER: χ^2

= 2.88, df = 1, *P* = 0.090), with men being 62% more likely to display disruptive behaviour (*z* = 2.36, *SE* = 0.21, *P* = 0.018).

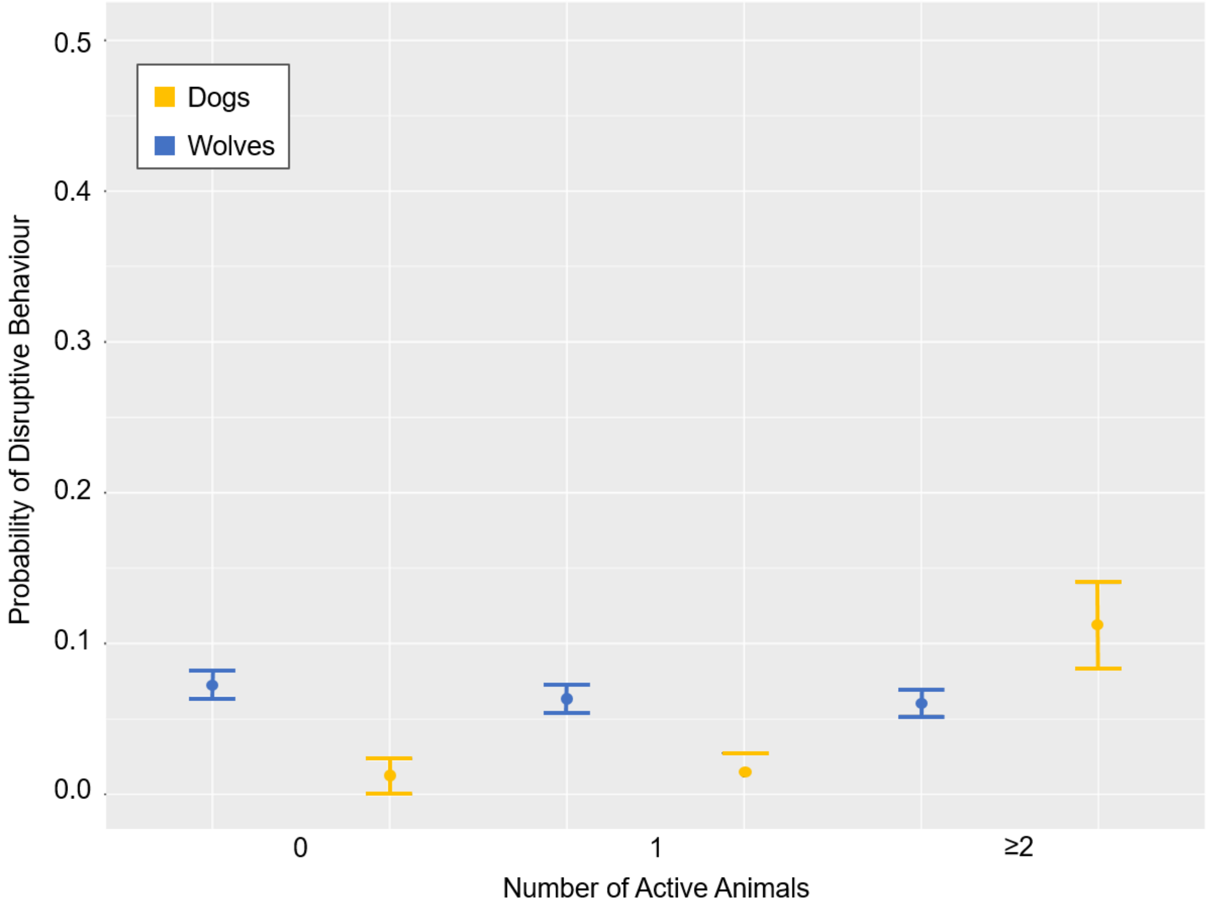

*Figure 4: Disruptive Behaviour: Species*Number of Active Animals. Average probability of disruptive behaviour in relation the number of active animals. Error bars indicate standard deviation.*

3.4. Average Noise

According to the graph displaying average noise levels in relation to the number of visible animals and species, visitors were generally noisier at wolf compared to dog enclosures (Appendix D). Despite the significant interaction (species*number of visible animals, GLMM: χ^2 = 15.73, *df* = 2, *P* < 0.001), this effect seemed to be driven by the low average noise levels when no dog was visible. There was no significant difference between one or two dogs visible, the number of visible wolves did not influence average noise levels either, and the difference in noise between wolves and dogs was not significant at any level of animal visibility (all *P* > 0.05; see Appendix C). Post-hoc contrasts only revealed a significant difference in average noise levels between no dog visible and one (*z* = -2.95, *SE* = 0.65, *P* = 0.009), or two dogs visible (*z* = -5.22, *SE* = 0.31, *P* < 0.001).

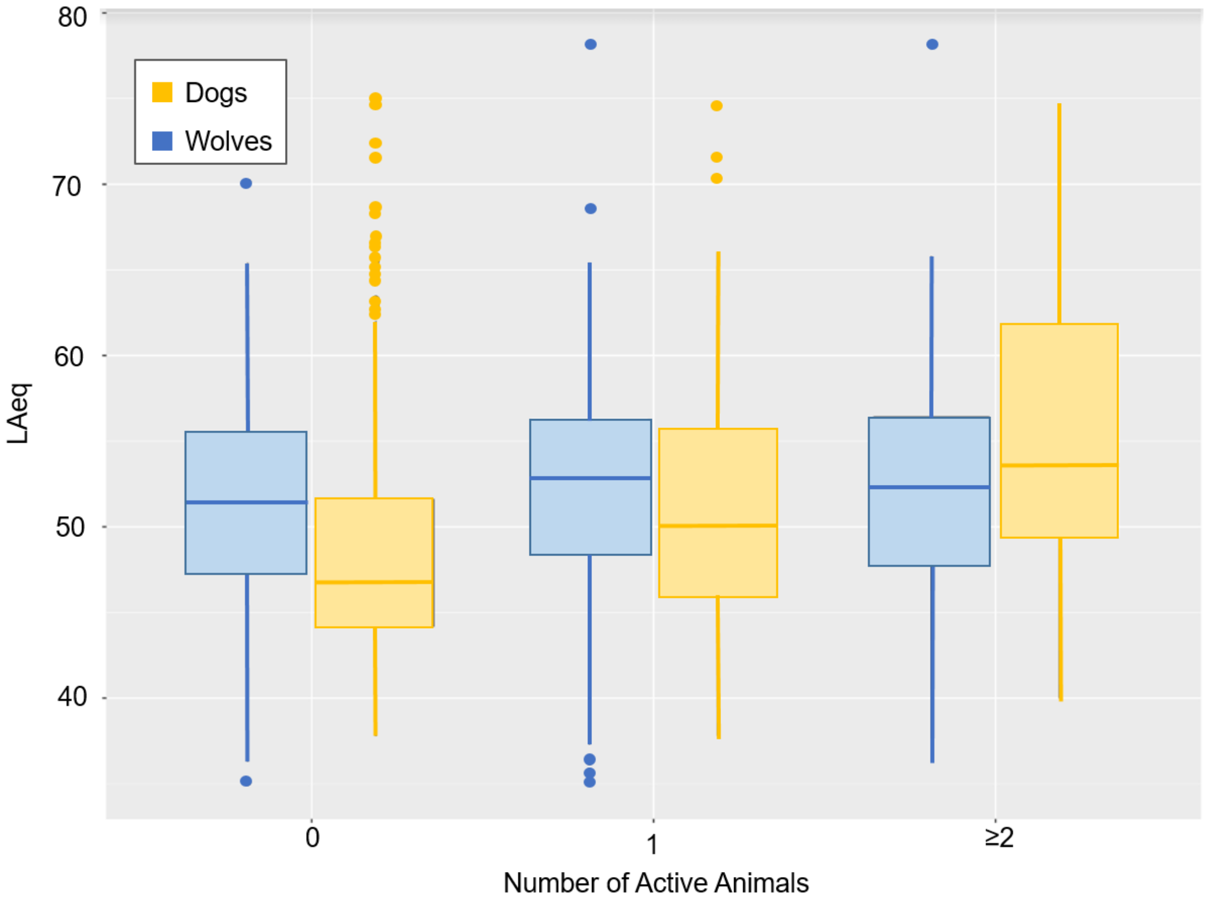

*Figure 5: Average Noise: Species*Number of Active Animals. A-weighted equivalent continuous sound level (LAeq) in relation to the number of active animals. The box represents median and interquartile range (IQR), the lower and upper whiskers represent Q1 - 1.5 IQR, and Q3 + 1.5 IQR. Outliers are represented by dots.*

Taking into consideration the animals' behaviour (species*number of active animals, GLMM: $\chi^2 = 50.96$, $df = 2$, $P < 0.001$; Fig. 5; species*number of animal behaviours, GLMM: $\chi^2 = 6.82$, $df = 1$, $P = 0.009$; Fig. 6) revealed a similar pattern on average visitor noise. Once more, average noise levels did not differ significantly between wolves and dogs between any number of active animals (all $P > 0.05$; see Appendix C). When at least two canids were active, however, the difference in average noise between wolves and dogs showed a trend ($z = -1.68$, $SE = 1.46$, $P = 0.092$). The contrasts revealed that visitors were significantly louder when two dogs were active, compared to only one dog active ($z = -2.73$, $SE = 0.61$, $P = 0.017$), or no dog active ($z = -8.73$, $SE = 0.32$, $P < 0.001$). Interestingly, visitors were quieter, when dogs were showing no, or only a single behaviour, but louder at dog enclosures compared to wolf enclosures, when the dogs displayed multiple behaviours (Fig. 6). In other words, the number of behaviours shown by wolves compared to dogs had less of an influence on average visitor noise.

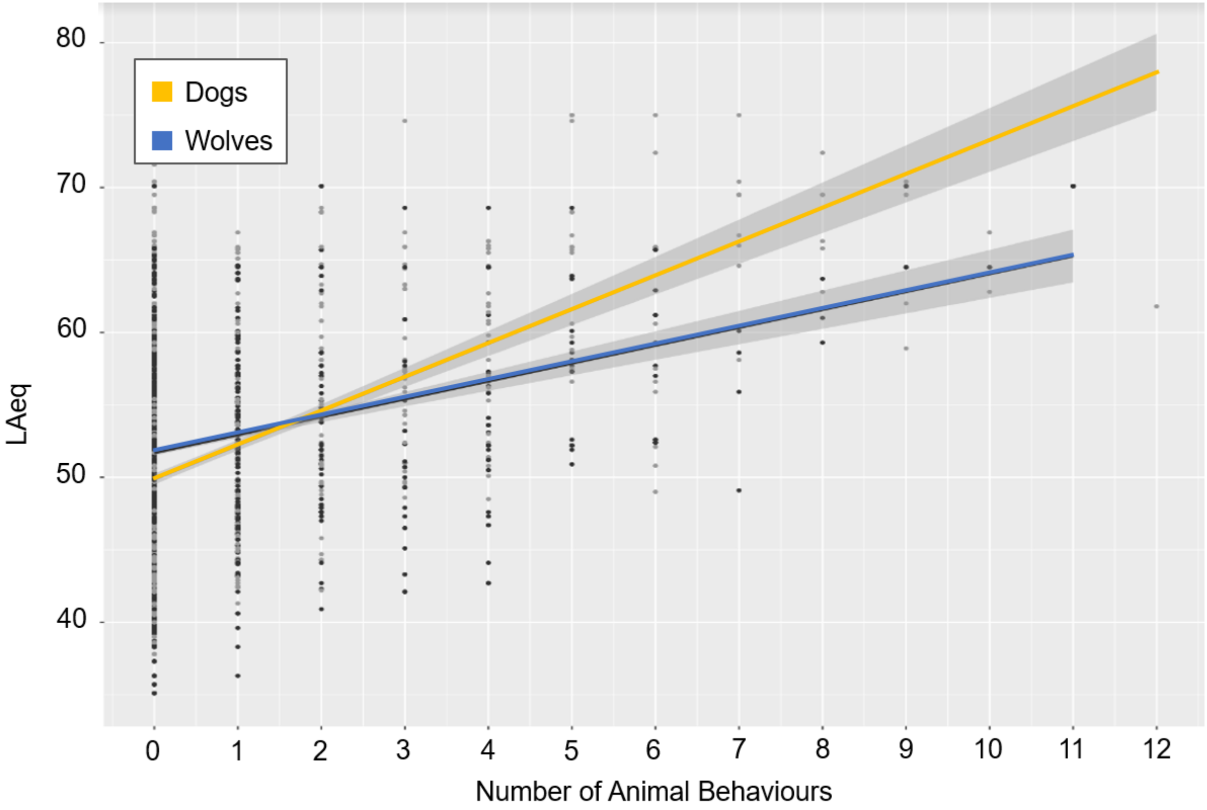

*Figure 6: Average Noise: Species*Number of Animal Behaviours. Association between the A-weighted equivalent continuous sound level (LAeq) and the number of animal behaviours. The shaded zone represents the 95% confidence interval.*

3.5. Maximum Noise

Unlike the average noise level, the interaction of species*number of visible animals was non-significant for the maximum noise level, and therefore removed from the model (GLMM: $\chi^2 = 1.73$, *df* = 2, $P < 0.42$). In the final model, there was a significant effect of the number of visible animals on the maximum noise level (GLMM: $\chi^2 = 27.74$, *df* = 2, $P < 0.001$), but not of species (GLMM: $\chi^2 = 0.64$, *df* = 1, $P < 0.42$). Visitors' maximum noise was significantly louder when at least two canids were visible, compared to when none were visible ($z = -5.34$, *SE* = 0.26, $P < 0.001$). The other contrasts were not significant (all $P > 0.05$; see Appendix C).

The second model for maximum noise levels, accounting for the number of active animals, and the number of animal behaviours, revealed significant effects of both factors in interaction with species (species*number of active animals, GLMM: $\chi^2 = 36.17$, *df* = 2, $P < 0.001$, Appendix E; species*number of animal behaviours, GLMM: $\chi^2 = 4.76$, *df* = 1, $P = 0.029$, Fig. 10). Concerning the interaction of species and the number of active animals, the comparison of maximum noise levels at wolf and dog enclosures between any number of active animals was not significant (all *P* > 0.05; see Appendix C). Again, the interaction seemed to be driven by significantly higher maximum noise levels when two dogs were active (0 vs 2: *z* = -6.69, *SE* = 0.43, *P* < 0.001; 1 vs. 2: *z* = -2.49, *SE* = 0.73, *P* = 0.034). The maximum noise level did not differ between no dog active and only one dog active (*z* = -1.54, *SE* = 0.69, *P* = 0.27). For the wolves, visitors' maximum noise levels were comparable between the different numbers of active animals (all *P* > 0.05; see Appendix C). Again, the number of behaviours displayed by wolves compared to dogs had less of an effect on visitors' maximum noise level (Appendix F).

Predictor of Interest	**Fixed Effect**	χ^2	***df***	***P***
	Attentive Behaviours (GLMM)			
[N] Visible Animals	[N] Visible Animals	8.44	2	0.015*
	Species*Age	10.03	2	0.007**
	Gender	9.44	1	0.002*
[N] Active Animals & [N] Animal Behaviours	Species*Age	9.37	2	0.009**
	[N] Active Animals	0.55	1	0.458
	[N] Animal Behaviours	0.68	2	0.711
	Gender	7.67	1	0.006**
	Interaction Attempts (GLMM)			
[N] Visible Animals	Species	5.50	1	0.019*
	[N] Visible Animals	3.64	2	0.162
	Age	150.59	2	< 0.001**
	Gender	6.64	1	0.010*
[N] Active Animals & [N] Animal Behaviours	Species	5.52	1	0.019*
	[N] Active Animals	0.79	1	0.374
	[N] Animal Behaviours	0.96	2	0.620
	Age	145.90	2	< 0.001**
	Gender	5.45	1	0.020*
	Disruptive Behaviours (GLMM)			
[N] Visible Animals	Species*[N] Visible Animals	6.23	2	0.044*
	Age	178.36	2	< 0.001**
	Gender	3.55	1	0.059
	Species*[N] Active Animals	10.70	2	0.005*

[N] Active Animals & [N] Animal Behaviours	[N] Animal Behaviours	1.29	1		0.256
	Age	147.83	2	<	0.001**
	Gender	2.88	1		0.090
Average Noise (LMM)					
[N] Visible Animals	Species*[N] Visible Animals	15.73	2	<	0.001**
[N] Active Animals & [N] Animal Behaviours	Species*[N] Active Animals	50.96	2	<	0.001**
	Species*[N] Animal Behaviours	6.82	1		0.009**
Maximum Noise (LMM)					
[N] Visible Animals	[N] Visible Animals	27.74	2	<	0.001**
[N] Active Animals & [N] Animal Behaviours	Species*[N] Active Animals	36.17	2	<	0.001**
	Species*[N] Animal Behaviours	4.76	1		0.029*

*Table 4: Results for all final models of the (generalized) linear mixed models fit by likelihood ratio test. For each response variable the separate models for the key fixed effects of interest are displayed. *< 0.05, ** < 0.001.*

4. Discussion

The DRH proposes that during the domestication process our attitudes towards dogs gradually diverged from an overall rather negative attitude towards wolves to a rather positive one towards dogs. Based on contemporary attitudes, we therefore expected more attentive, and disruptive behaviours and more noise towards wolves (indicative of a more negative attitude), and more interaction attempts with dogs (indicative of an overall positive attitude). Due to demographic differences in attitudes, we additionally expected that women compared to men, and older compared to younger visitors, would be more attentive, with more disruptive behaviours and less interaction attempts towards both canid species.

Our results (summarized in Tab. 4) show that adult visitors were generally more attentive in front of dog compared to wolf enclosures. Compared to both adult groups, the youngest age class displayed significantly less attentiveness, but equally so to wolves and dogs. Moreover, across species, men were less attentive compared to women. Plausibly, when the animals were not visible, visitors were significantly less attentive towards them (i.e. pointing, taking pictures). Yet, attentiveness was independent of the number of active animals or animal behaviours. Interaction attempts were 70% more likely towards dogs as opposed to wolves. Across species, they were shown more frequently by the youngest age class and men. In contrast to attentive behaviours, interaction attempts were independent of all animal parameters. For wolves, disruptive behaviours decreased the more animals were visible, and overall, they faced more disruptive behaviours compared to dogs independent of the number of wolves active. In contrast, disruptive behaviours increased in front of dog enclosures as more animals were active. In addition, the youngest age class was slightly more likely to display disruptive behaviours compared to both adult groups, and although this result only tended to be significant, men were 62% more likely to behave disruptivly compared to women. Concerning noise levels, overall, the graphs indicate that visitors were louder at wolf enclosures (Appendices D, E; Fig. 5), but these differences between wolves and dogs were not significant. For the wolves we did not detect an influence of the animal parameters. The significant interactions seemed to be driven mainly by differences in noise levels at the dog enclosures: visitors were louder when more dogs were visible, active, or when the dogs showed more behaviours.

In contrast to our hypothesis and predictions, attentive behaviours were more frequent towards dogs compared to wolves in both adult age classes (although not significant for the older one). We predicted that visitors would be more attentive towards wolves because of higher fear levels (Deloache & LoBue, 2009). However, we may also be more attentive towards something we enjoy. To differentiate the emotional valence towards the presented stimuli, therefore, further behavioural indicators would be required to interpret attentive behaviours as a proxy for attitudes (Ernst et al., 2020). It could be that the attentive behaviours observed in our study (pointing, taking pictures) indicate a positive affect towards the animals. That our attitudes towards dogs in comparison to wolves are indeed more positive, is supported by the result that interaction attempts were more likely in front of dogs compared to wolves (in line with DRH). This is especially striking, as we have so many opportunities to interact with dogs in our everyday life, without a fence preventing direct contact.

The interpretation of disruptive behaviour is more intricate. We cannot clearly support our hypothesis and predictions, as disruptive behaviours were not generally more likely in front of wolves compared to dogs across models. Accounting for the number of visible animals, disruptive behaviours were comparable between species. Yet, for wolves, but not for dogs, the probability of disruptive behaviours was significantly lower when at least two compared to no wolves were visible. Comparing disruptive behaviours across the different levels of visible wolves in Fig. 3, there seems to be an almost linear decrease of disruptive behaviours with increasing numbers of visible wolves. Visitors knew when they were in front of a wolf enclosure, as most of them carried maps of the Wildpark Ernstbrunn with them. It is imaginable that visitors only dared to show disruptive behaviours at wolf enclosures when they did not see any animal. They may have tried to tease the wolves a bit and test, whether they would come into sight to investigate the disturbance. Yet when multiple wolves were visible, the visitors may have been more cautious towards the wolves' reaction, despite the fence in between. Beyond that, disruptive behaviours included throwing objects. We observed some instances during which visitors tried to throw sticks into the dogs' enclosure verbalising that they wanted to play fetch with the dogs, revealing that their intention was to interact, which indicates a positive attitude. For the wolves, visitors seemed to use more pebbles, signifying a rather negative attitude. Conceivably, it may be that a negative intention indicated by disruptive behaviours was overestimated for dogs. This would support the DRH, as we do not have to be as fearful of dogs around us (even if they are active), as we would have to be in an encounter with wolves. Admittedly, this interpretation requires further investigation. That some of the contrasts for dogs just missed the significance level may be due to the infrequency of disruptive behaviour in our sample in comparison to attentive behaviours and interaction attempts.

What is more, the visitors may have behaved in a more orderly manner, because of our obvious presence conducting observations in affiliation with the WSC, and beyond that, the presence of other visitors can reduce negative behaviours towards captive animals (Kemp et al., 2019). Even if we took all possible measures to conceal that we also observed the visitors, and not just the animals, we cannot rule out that we prevented the occurrence of more disruptive behaviours. This is especially true, as we had to interrupt any behaviour prohibited by park rules, which likely prevented further unruly behaviours of other visitors witnessing our reprimands. In order to analyse a bigger and unbiased sample of disruptive behaviours, we therefore recommend that future studies deploy hidden cameras.

Nevertheless, if we take a look at the probability of disruptive behaviours in relation to the number of active animals (Fig. 4; only contains cases in which animals were visible), it seems that in line with our prediction, visitors did not want to disturb dogs as much as wolves. The number of disruptive behaviours towards wolves overall was higher compared to dogs, and is comparable across the different numbers of active wolves. There was, however, a trend of more disruptive behaviours when two dogs were active compared to when no dog was active, a difference not present in wolves. Hence, it may be that visitors were more reactive to dogs, when two of them were active, but did not want to disturb them as much, when they were inactive.

The idea that visitors were more reactive to dogs is intriguing. The DRH proposes that the initial shift in attitudes interplayed with the risks and benefits associated with interacting with tamer canids. Sharing a habitat with animals, especially when we have close and direct contact, is only possible, if we can behave freely around them. According to the DRH, this interplay of human and animal factors created a positive feedback loop further promoting the domestication process (Treves & Bonancic, 2016). That domestication changed the behaviour of dogs towards humans is a core element of dog domestication hypotheses (for review see Range & Marshall-Pescini, 2022), one of which suggests that dogs faced a selective pressure for a higher tolerance towards humans (i.e. less fearful and aggressive; Emotional Reactivity Hypothesis: Hare & Tomasello, 2005; Hare et al., 2012). While wolves can be socialised to humans through extensive training as well, wolf pups display more aggression towards their caregivers compared to equally socialised dogs (Gácsi et al., 2005). What is more, socialisation towards humans seems less stable in wolves. Adult dogs seem to generalize their socialisation with familiar humans to strangers, in contrast to wolves (Bentosela et al., 2016; Wirobski et al., 2021). Thus, we may have learned that due to dogs' decreased emotional reactivity, we are freer in our behaviour around them, and do not have to be as cautious as we would have to be around wolves (i.e. we can be more reactive towards dogs). This logic is further supported by the results of our noise measurements.

Based on visiual inspection it seems that visitors were generally louder at wolves compared to dogs. Yet, the differences between wolves and dogs were not significant. The graphs displaying the significant interactions of species*number animal behaviours, as well as the significant differences in average and maximum noise depending on the number of visible or active dogs, clearly show that when it comes to noise, visitors behaved more reactively in front of the dogs' compared to the wolves' enclosures. For the average noise level in relation to the number of active animals an alternative explanation should be considered. Dogs vocalised significantly more often compared to wolves (Kanwischer, 2022). Because the dogs almost always barked when visitors were present, we could not exclude the intervals during which the dogs barked from the average noise at dog enclosures, as we would have lost almost all data. As this measure of noise is averaged over a five-minute interval, peaks of noise (e.g. barking) can be assumed to have a limited effect. Nevertheless, the average noise level might have been biased by the barking of dogs, and it could be that the significant differences between two and no, or only one dog active respectively is attributable to the noise the dogs elicited themselves. The anecdotal evidence that the dogs almost always barked in pairs strengthens this alternative explanation. Yet, the maximum noise level reflects the peaks of noise within a five-minute interval. The maximum noise level, therefore, was cleaned from any instance, in which the dogs themselves elicited the loudest noise. That average noise and the cleanded maximum noise show the same pattern with the same significant contrasts, indicates that our average noise was not biased by barking.

Although the results for noise (no significant difference between wolves and dogs, but a significant increase in noise with more dogs active, and more behaviours) are not in line with our hypothesis and prediction, it is fathomable that a more complex pattern of differences in visitor behaviours towards wolves and dogs is present. Indeed, the pattern we did find is consistent with the DRH. We expected that visitors would be noisier and show more disruptive behaviours towards wolves, because of the safe context. However, despite the fence in between, with more wolves visible, visitors seem to have dared less to disrupt. Additionally, visitors may have been more controlled in their behaviour towards wolves, as disruptive behaviour was comparable across different number of active wolves, and noise levels increased less with wolves showing more behaviours, compared to dogs. This is surprising, as seeing a wolf in action in contrast to dogs should be more of a sensation, and one would expect less controlled behaviours at the wild canids. Instead, we observed less controlled visitor behaviour at the dogs, when they were active and showing behaviours (louder and more disruptive behaviours with the verbal remarks of wanting to play fetch indicating the expectation of a positive interaction). The fence objectively would have allowed the visitors to behave in whichever way they wanted towards both species. Subjectively, visitors might have still associated a higher risk with wolves, which is why they were more controlled in their behaviour at wolf enclosures. This would indicate a more negative attitude based on fear. In contrast, behaving more reactively (i.e. less controlled) towards dogs may reflect the decreased risks of interacting with this domesticated species. Hence, the visitor behaviour reflects the risks (and benefits) associated with the two species, as predicted by the DRH (Treves & Bonancic, 2016).

This critical inspection of alternative explanations demonstrates the importance of controlling for animal parameters when investigating spontaneous behaviours by humans towards an itself spontaneously acting entity. Visitor studies in zoos evince that animal behaviour and visibility influence visitor behaviour (Altman, 1998; Davey, 2006; Margulis et al., 2003), stressing the importance of controlling for these factors. Beyond that, a closer look at the animal parameters and how they relate to visitor behaviour provides added depth to our analysis. While it is logical that visitors displayed less attentive behaviours, when no canids were visible, because there was nothing to point at or take photos of, it seems paradox at first glance that interaction attempts were just as likely when no animals were visible. After a closer look at the variables included in interaction attempts, however, one can imagine that visitors displayed lures, the imitation of animal voices and threw food into the enclosure when no animals were visible as an attempt to lure them into sight. In this instance, but also in the analysis of disruptive behaviours, the animal parameters might serve as an explanation to why visitors behaved the way they did.

Beyond these external factors, the demographic characteristics gender and age systematically influenced visitor behaviour, although not always as we expected. Women in comparison to men hold more positive attitudes towards dogs (Brandl, 2016; Ellingsen et al., 2010; Kotrschal et al., 2013), and more negative attitudes towards wolves, supposedly because of increased fearfulness (Dressel et al., 2015; Kaczensky, 2006; Kotrschal et al., 2013; Røskaft et al., 2007; Wechselberger & Leizinger, 2018; Wechselberger et al., 2005). Yet, we only found significant main effects of gender, but no interactions. Towards both species, men were less attentive, tried to interact more, and tended to more likely display disruptive behaviours. This pattern might indicate a general tendency of men to behave less cautiously towards animals. It could be that a gender-specific effect of attitudes on behaviour towards wolves and dogs was overshadowed by a more general effect of gender on behaviour towards animals. Indeed, Herzog (2007) demonstrated that the effect sizes of gender-specific behaviours outrank those of gender-specific attitudes towards animals. But Herzog (2007) also stressed that gender differences are moderated by a myriad of other factors, and are likely to change over time. This may explain conflicting results of the influence of gender on attention even in front of the same animal enclosures (Ross & Lukas, 2005; Ross et al., 2012). Beyond that, Kemp et al. (2022) found that men did display more disruptive behaviours to reptiles, Tasmanian devils, meerkats, and wild birds, but women were more disruptive towards macropods, challenging the idea of an overarching gender-effect on behaviours towards animals across species. In a real-life setting like zoos and game-parks, visitors not only face the animals, but are also interacting with and influencing each other. To understand how gender affects spontaneous behaviour towards different species as a proxy for attitudes, we therefore recommend to control for visitor-visitor interactions as well. Unfortunately, we had to leave out this aspect of visitor behaviour, as data-collection took place at a group-level, and without recordings allowing us to revisit time-points with heavy visitor traffic.

Just like for gender, the interpretation of the factor age is more intricate than we initially expected. Consistent with more positive attitudes towards both dogs and wolves in younger people, interaction attempts were more likely among the youngest age class across species compared to both adult age classes. Contrary to our prediction, however, the youngest age class also displayed significantly more disruptive behaviours, even if the effect size was rather small with only 5-8% difference in comparison to the older age classes. Similar patterns were found in other studies (Kemp et al., 2022; Ross et al., 2012), and it seems plausible that children simply adhere less to societal and institutional rules. In line with previous findings (Bitgood, 2002; East et al., 2017; Ridgway et al., 2005; Ross & Lukas, 2005; Ross et al. 2012), the youngest age class was significantly less attentive compared to both adult age classes. Interestingly though, the youngest age class was comparably attentive to dogs and wolves, while both adult age classes were more attentive towards dogs. Usually humans show more attention towards novel entities (which should have been the wolves), which is why our result seems counterintuitive (Ernst et al., 2020). One explanation, why adults were more attentive towards dogs would be that the contextual novelty of seeing a dog in an enclosure outweighed the stimulus novelty of wolves (Barto et al., 2013). While many visitors of the WSC likely never saw a wolf first-hand, they also likely never saw a dog in a zoo-like setting, and indeed many visitors voiced their surprise about this circumstance.

This raises the difficult question how experience (or lack thereof) shapes our behaviours towards animals in relation to our attitudes. People with more positive attitudes towards dogs have more negative experiences with them (i.e. bites; Lakestani et al., 2011).

And although we eradicated wolves in many regions, the negative stereotypes as signified by the still popular Little-Red Riding Hood prevail. The reappearance of wolves, despite a lack of direct experience reignites negative attitudes (Herzog, 2018; Kaczensky, 2006; Stütz, 2020). If the risks of being bitten by dogs are manifold (Sarenbo & Svensson, 2021), compared to the risks of a wolf attack (Linnell et al., 2021), it seems that the to this end contrary attitudes towards the two species must be based on an inherent factor as proposed by the DRH (Treves & Bonancic, 2016). Previous studies investigating inherent predispositions towards other species used infants as their sample based on the idea that this would reduce the influence of prior experience with the species (Deloache & LoBue, 2009; Rakison & Derringer, 2008; Kawai & Koda, 2016). Following this logic, children should have more negative attitudes towards wolves, and more positive attitudes towards dogs compared to adults, if there is an inherent predisposition. Yet in fact, children hold more positive attitudes towards both canids (Boyd et al., 2004; Dressel et al., 2015; Lakestani et al., 2011), and as outlined before the effect of experience on attitudes towards wolves and dogs is not as straight-forward.

The DRH proposes a predisposition for negative attitudes towards wolves. Given that the vast majority of people never have had direct experience with a wolf, potentially inherited negative attitudes should not be reinforced, and thus the initial expectation should be that older people hold less negative attitudes towards wolves. However, in the case of political attitudes, we know from longitudinal twin studies that while attitudes are in part heritable, they will only manifest progressively from adulthood onwards (Dawes & Weinschenk, 2020). It could be that our attitudes towards canids, if they are indeed inherited, follow a similar pattern, and manifest with increasing age, despite of our direct experience. This logic would offer an explanation why younger people express less negative attitudes towards wolves compared to older people, and why the youngest age group in our study were just as likely to attend to wolves as to dogs.

Earlier, we speculated that the adult classes in our research displaying increased attentive behaviour towards dogs, may also be an indication of a more positive attitude, consistent with increased interaction attempts. If we have predisposed negative attitudes towards wolves, and more positive ones towards dogs as proposed by the DRH (Treves & Bonancic, 2016), and beyond that our attitudes only manifest over time, this would also explain why both adult groups displayed more attentive behaviours towards dogs compared to wolves, despite the novelty of the latter. Disentangling whether the results in our study can be explained by novelty effects, or by inherent attitudes manifesting over time, would elucidate in how far our attitudes and behaviours towards canids are dependent on and thus influenceable through experience. In light of the wolves return to many western European regions this would be important knowledge to inform conservation efforts.

Future studies should examine how attitudes towards wolves and dogs relate to behaviour on an individual level. Focal observations using hidden cameras of spontaneous visitor behaviours at the WSC, with subsequent completion of attitude questionnaires (including prior experience with the species) would not only reduce observation bias, but could clarify which behaviours are indicative of positive and negative attitudes. The bottom-up approach deployed in this study to collect visitor behaviours that are typically and spontaneously shown, allowed us to capture systematic differences in behaviours towards wolves and dogs. Not revealing the true purpose of the study, and focusing on spontaneous behaviour arguably provided an approach with higher external validity in contrast to a more controlled experimental set-up. Additionally, the study period was situated during the summer holidays, a typical time for family outings. Therefore, we expect that we observed a sample representative of the general population despite the somewhat remote location of the game-park Ernstbrunn. Unfortunately, as we did not want to reveal the purpose of the study by handing out questionnaires, we cannot confirm this assumption, as we could only estimate basic demographics. What is more, controlling for animal parameters added value to the interpretation of visitor behaviour. However, with the study period lying in summer, it could be that the animals were less active, which may also have limited the number of visitor reactions to the canids, and might have further contributed to the low number of disruptive behaviours. Our presence likely influenced this type of behaviour most. Hence, using simultaneous video recordings of both animal and visitor behaviour would not only reduce the bias caused by our presence, but would also allow for a more detailed analysis of visitor behaviour.

All in all, our research was able to detect systematic differences in human behaviour towards wolves and dogs as a proxy for attitudes, even in a context with comparable risks and benefits. Most strikingly, and in line with our prediction, visitors interacted more with these out of reach dogs despite the ample opportunitiy for direct contact with dogs in our everyday life. Beyond that, visitors were more attentive towards dogs (although we initially expected attentive behaviours to be indicative of fear as part of a negative attitude), pointing to a more positive attitude towards dogs in contrast to wolves. Finally, the disruptive behaviours and noise levels indicate that visitors, in line with our hypothesis and predictions, behaved less considerate towards wolves and used this safe context to test for the wolves' reaction towards them. For dogs on the other hand, the visitors showed less disruptive behaviours, when they were inactive, but were more reactive when the opportunity arose to interact with the dogs. Although our predictions concerning the influence of demographic factors were not met, the more complex pattern visible in our data is consistent with the DRH (Treves & Bonancic, 2016). It seems that the influence of experience on our attitudes and behaviours towards dogs and their wild counterpart cannot be explained by simple associative mechanisms. Therefore, it is worthwhile further exploring the possibility of inherent predispositions shaping our differential attitudes and behaviours towards wolves and dogs. Especially important are the questions whether a negative inherent predisposition towards wolves shapes our behaviours, manifests with age, and in how far our attitudes as a mitigating factor can be influenced (for example through experience and knowledge). Such a predisposition for a negative attitude towards wolves should be further explored, as it would be a curcial factor to consider in planning successful conservation interventions, as the wolf is returning to more and more regions in Europe.

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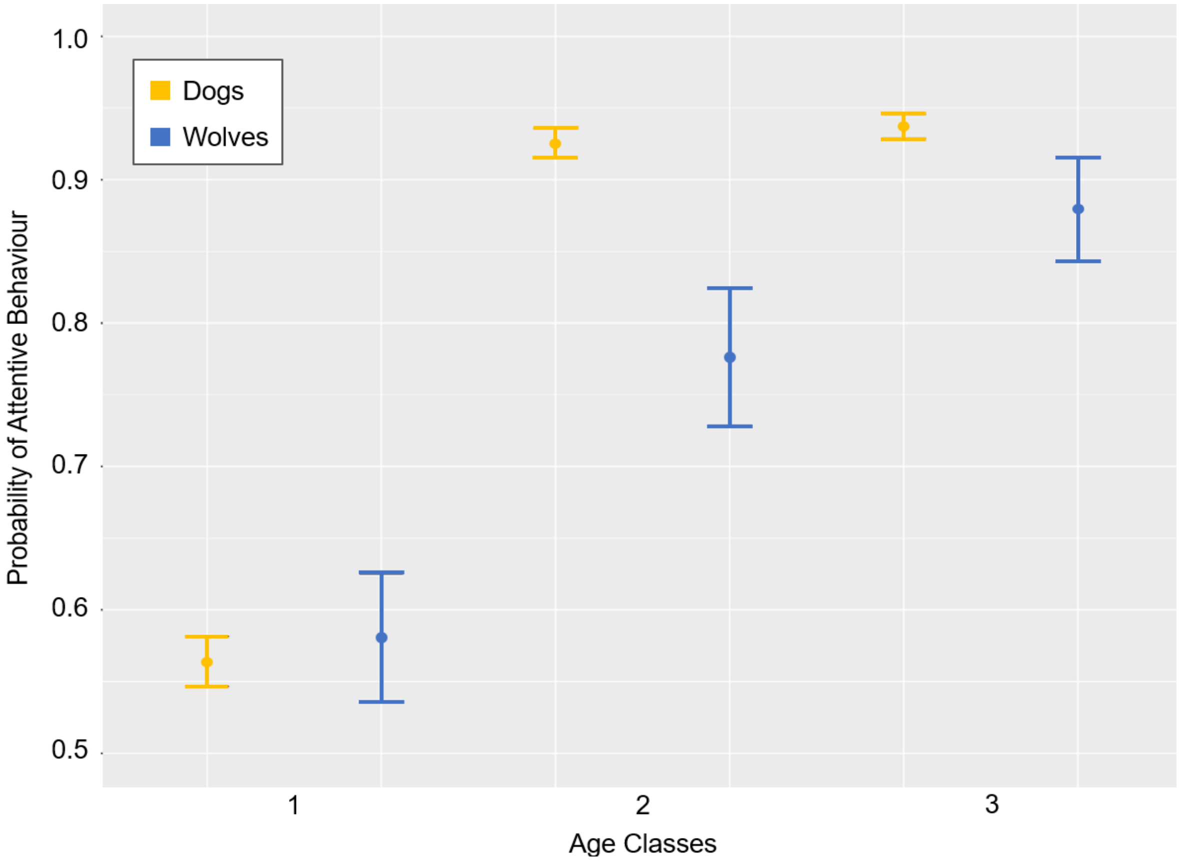
6. Appendices

Appendix A

Variables	ICC (95% confidence interval)	F-test with true value 0			
		Value	*df1*	*df2*	P-Value
Visitor Number	0.957 (0.951-0.962)	45.6	835	835	0
Gender	0.943 (0.932-0.952)	34.1	493	494	<0.001
Age	0.942 (0.931-0.951)	33.2	493	493	<0.001
Attentive Behaviours					
Picture	0.920 (0.909-0.930)	24.1	836	836	0
Pointing at Animal	0.895 (0.881-0.908)	18.1	836	837	<0.001
Disruptive Behaviours					
Throwing	-	-	-	-	-
Shouting	0.976 (0.972-0.979)	80.9	836	836	0
Interaction Attempts					
Feeding Animals	-	-	-	-	-
Human Trespassing	0.915 (0.903-0.925)	22.5	836	836	0
Pet Dog Trespassing	0.933 (0.923-0.941)	28.8	836	837	0
Lures	0.959 (0.953-0.964)	48.0	836	836	0
Animal Voice	0.957 (0.951-0.963)	45.9	836	837	0

Results of the Inter-Rater Reliability Test by use of intraclass correlation coefficients (ICC). Average measures for two-way random effects model. Degrees of freedom (df). Throwing and Feeding Animals occurred to infrequent to calculate ICC.

Appendix B



*Attentive Behaviour in Relation to Animal Behaviour: Species*Age. Average probability of attentive behaviour per age class in the second model accounting for the number of active animals and number of animal behaviours. Error bars indicate standard deviation.*

Appendix C

Contrasts

Predictors of Interest	Contrast	Interaction	Estimate	*SE*	*z*	*P*
			Attentive Behaviours			
[N] Visible Animals	Species	Age				
	W vs. D	1	-0.19	0.36	-0.54	0.593
	W vs. D	2	1.29	0.46	2.81	0.005*
	W vs. D	3	0.47	0.48	1.00	0.319
	Age	Species				
	1 vs. 2	W	-2.43	0.21	-11.52	<0.001*
	1 vs. 3	W	-2.48	0.16	-15.53	<0.001*
	2 vs. 3	W	-0.05	0.24	-0.22	0.974
	1 vs. 2	D	-0.95	0.39	-2.40	0.043*
	1 vs. 3	D	-1.81	0.40	-4.52	<0.001*
	2 vs. 3	D	-0.87	0.49	-1.76	0.183
	[N] Visible Animals					
	0 vs. 1	-	-0.79	0.35	-2.26	0.062
	0 vs. ≥2	-	-0.60	0.22	-2.72	0.018*
	1 vs. ≥2	-	0.19	0.30	0.63	0.805
[N] Active Animals & [N] Animal Behaviours	Species	Age				
	W vs. D	1	-0.16	0.45	-0.35	0.729
	W vs. D	2	1.51	0.56	2.67	0.008*
	W vs. D	3	0.64	0.55	1.17	0.243
	Age	Species				
	1 vs. 2	W	-2.62	0.25	-10.60	<0.001*
	1 vs. 3	W	-2.57	0.18	-14.66	<0.001*
	2 vs. 3	W	0.05	0.27	0.19	0.980
	1 vs. 2	D	-0.96	0.46	-2.10	0.091
	1 vs. 3	D	-1.77	0.42	-4.25	<0.001*
	2 vs. 3	D	-0.82	0.54	-1.50	0.291
	[N] Active Animals					
	0 vs. 1	-	0.15	0.23	0.67	0.783
	0 vs. ≥2	-	-0.05	0.17	-0.28	0.959
	1 vs. ≥2	-	-0.20	0.23	-0.87	0.656
			Interaction Attempts			
[N] Visible Animals	Age					
	1 vs. 2	-	1.61	0.22	7.47	<0.001*
	1 vs. 3	-	1.49	0.14	11.01	<0.001*
	2 vs. 3	-	-0.12	0.23	-0.50	0.872

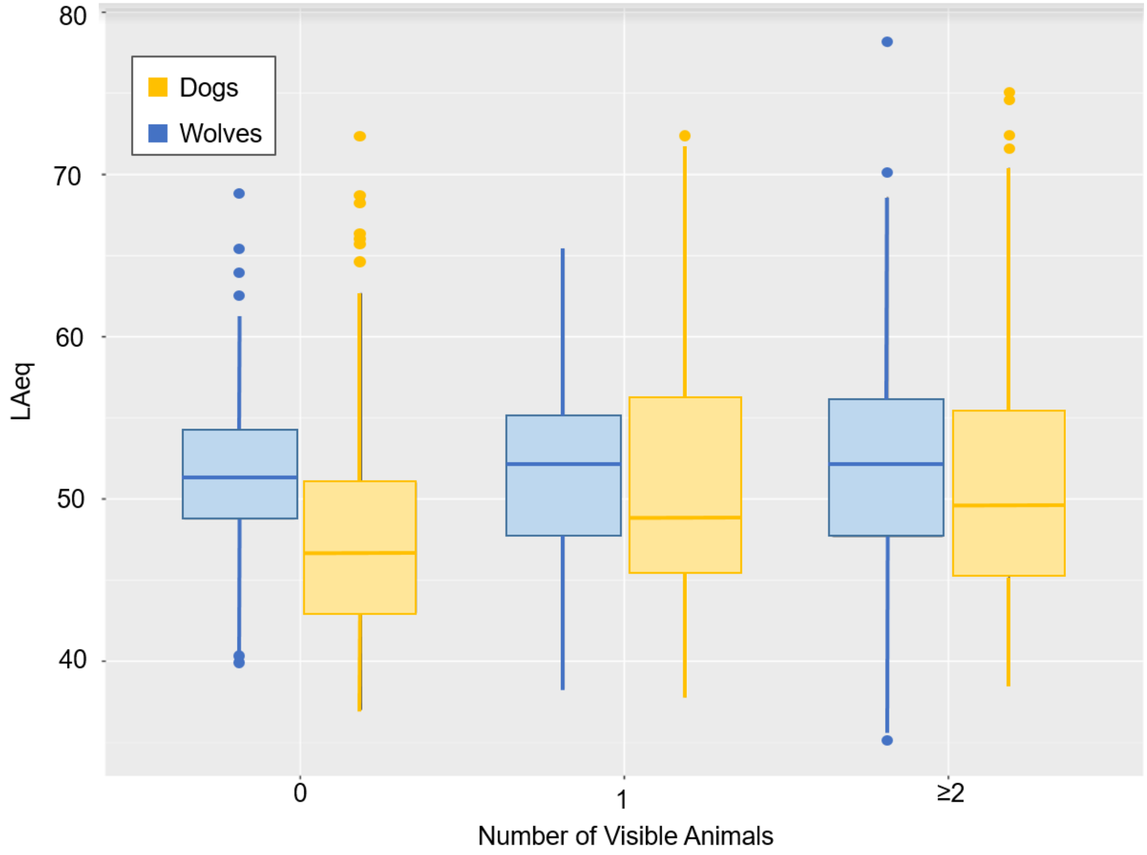
	[N] Visible Animals					
	0 vs. 1	-	0.41	0.27	1.51	0.284
	0 vs. ≥2	-	0.34	0.22	1.56	0.264
	1 vs. ≥2	-	-0.06	0.20	-0.31	0.948
[N] Active Animals & [N] Animal Behaviours	Age					
	1 vs. 2	-	1.63	0.21	7.67	<0.001*
	1 vs. 3	-	1.60	0.15	10.71	<0.001*
	2 vs. 3	-	-0.03	0.23	-0.15	0.988
	[N] Active Animals					
	0 vs. 1	-	-0.16	0.21	-0.77	0.723
	0 vs. ≥2	-	-0.14	0.17	-0.85	0.675
	1 vs. ≥2	-	0.02	0.21	0.08	0.997
			Disruptive Behaviours			
[N] Visible Animals	Species	[N] Visible Animals				
	W vs. D	0	0.20	0.73	0.27	0.783
	W vs. D	1	16.61	120.68	0.14	0.891
	W vs. D	≥2	0.19	0.39	0.49	0.624
	[N] Visible Animals	Species				
	0 vs. 1	W	0.46	0.44	1.04	0.551
	0 vs. ≥2	W	1.03	0.30	3.41	0.002*
	1 vs. ≥2	W	0.57	0.39	1.46	0.310
	0 vs. 1	D	16.87	120.68	0.14	0.989
	0 vs. ≥2	D	1.02	0.72	1.42	0.330
	1 vs. ≥2	D	-15.85	120.68	-0.13	0.991
	Age					
	1 vs. 2	-	2.41	0.31	7.81	<0.001*
	1 vs. 3	-	2.92	0.32	9.09	<0.001*
	2 vs. 3	-	0.51	0.42	1.21	0.449
[N] Active Animals & [N] Animal Behaviours	Species	[N] Active Animals				
	W vs. D	0	2.16	1.07	2.02	0.044*
	W vs. D	1	1.88	1.14	1.65	0.100
	W vs. D	≥2	-0.59	0.50	-1.18	0.237
	[N] Active Animals	Species				
	0 vs. 1	W	0.28	0.34	0.83	0.681
	0 vs. ≥2	W	0.39	0.27	1.47	0.305
	1 vs. ≥2	W	0.11	0.35	0.30	0.952
	0 vs. 1	D	0.00	1.53	0.00	1.000
	0 vs. ≥2	D	-2.36	1.12	-2.12	0.087

	1 vs. ≥2	D	-2.37	1.20	-1.97	0.121
	Age					
	1 vs. 2	-	2.96	0.49	6.02	<0.001*
	1 vs. 3	-	2.87	0.34	8.46	<0.001*
	2 vs. 3	-	-0.09	0.57	-0.15	0.987
		Average Noise				
[N] Visible Animals	Species	[N] Visible Animals				
	W vs. D	0	0.74	1.89	0.39	0.694
	W vs. D	1	-1.47	1.97	-0.75	0.455
	W vs. D	≥2	-0.83	1.87	-0.44	0.657
	[N] Visible Animals	Species				
	0 vs. 1	W	0.30	0.45	0.65	0.792
	0 vs. ≥2	W	-0.04	0.30	-0.14	0.989
	1 vs. ≥2	W	-0.34	0.43	-0.78	0.716
	0 vs. 1	D	-1.92	0.65	-2.95	0.009*
	0 vs. ≥2	D	-1.62	0.31	-5.22	<0.001*
	1 vs. ≥2	D	0.30	0.62	0.49	0.874
[N] Active Animals & [N] Animal Behaviours	Species	[N] Active Animals				
	W vs. D	0	0.46	1.44	0.32	0.751
	W vs. D	1	-0.83	1.51	-0.55	0.582
	W vs. D	≥2	-2.45	1.46	-1.68	0.092
	[N] Active Animals	Species				
	0 vs. 1	W	0.19	0.36	0.54	0.854
	0 vs. ≥2	W	0.14	0.25	0.56	0.842
	1 vs. ≥2	W	-0.05	0.37	-0.14	0.989
	0 vs. 1	D	-1.09	0.59	-1.87	0.147
	0 vs. ≥2	D	-2.77	0.32	-8.73	<0.001*
	1 vs. ≥2	D	-1.67	0.61	-2.73	0.017*
		Maximum Noise				
[N] Visible Animals	[N] Visible Animals					
	0 vs. 1	-	-1.03	0.68	-1.50	0.290
	0 vs. ≥2	-	-1.37	0.26	-5.34	<0.001*
	1 vs. ≥2	-	-0.34	0.67	-0.52	0.864
[N] Active Animal & [N] Animal Behaviours	Species	[N] Active Animals				
	W vs. D	0	1.67	1.27	1.31	0.189
	W vs. D	1	1.13	1.36	0.83	0.407
	W vs. D	≥2	-1.51	1.30	-1.16	0.247

[N] Active Animals	Species				
0 vs. 1	W	-0.52	0.39	-1.32	0.386
0 vs. ≥2	W	0.29	0.31	0.96	0.603
1 vs. ≥2	W	0.81	0.41	2.00	0.113
0 vs. 1	D	-1.06	0.68	-1.54	0.272
0 vs. ≥2	D	-2.88	0.43	-6.69	<0.001*
1 vs. ≥2	D	-1.83	0.73	-2.49	0.034*

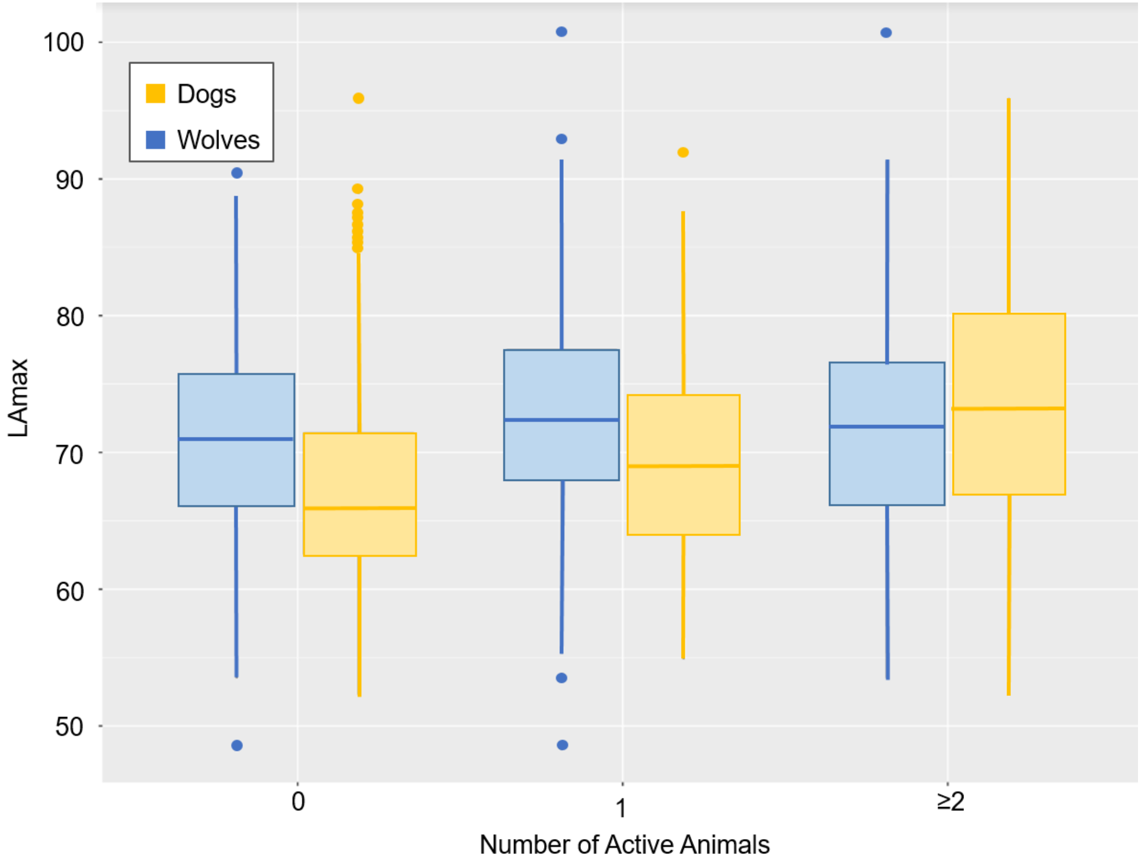
*Note. Table of all contrasts. In case of main effects the column ‘Interaction’ contains a ‘-‘. Standard Error (SE). Significant results at P > 0.05 indicated by *.*

Appendix D



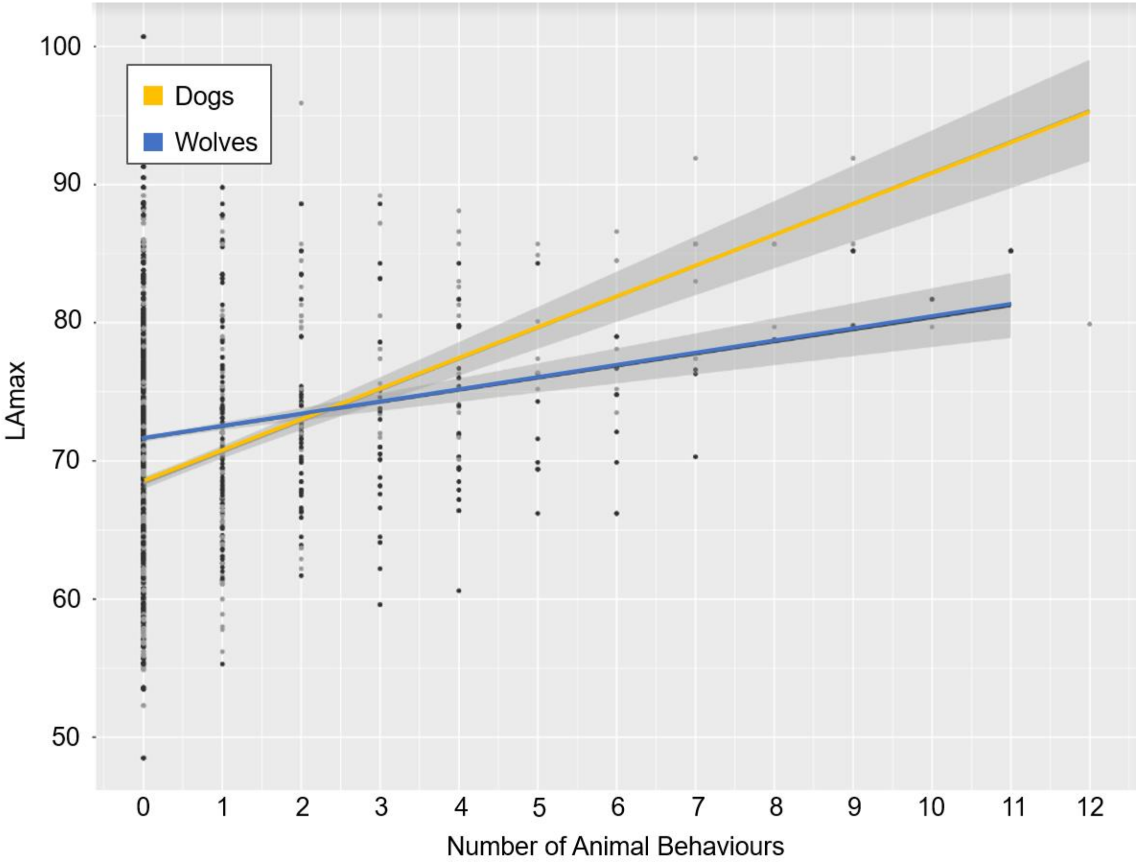
*Average Noise: Species*Number of Visible Animals. A-weighted equivalent continuous sound level (LAeq) in relation to the number of visible animals. The box represents median and interquartile range (IQR), the lower and upper whiskers represent Q1 - 1.5 IQR, and Q3 + 1.5 IQR. Outliers are represented by dots.*

Appendix E



*Maximum Noise: Species*Number of Active Animals. A-weighted maximum sound level (LAmax) in relation to the number of active animals. The box represents median and interquartile range (IQR), the lower and upper whiskers represent Q1 - 1.5 IQR, and Q3 + 1.5 IQR. Outliers are represented by dots.*

Appendix F



*Maximum Noise: Species*Number of Animal Behaviours. Association between the A-weighted maximum sound level (LAmax) and the number of animal behaviours. The shaded zone represents the 95% confidence interval.*