Motivation and persistence in problem solving in dogs and wolves: effects of different feeding ecologies?

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Akshay Rao, MSc

From the Konrad-Lorenz Institute of Ethology,

University of Veterinary Medicine of Vienna

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PhD Committee

1st Supervisor

Associate Prof. Dr. Friederike Range

Konrad-Lorenz Institute of Ethology,
University of Veterinary Medicine of Vienna

friederike.range@vetmeduni.ac.at

2nd Supervisor

Prof. Dr. Kurt Kotrschal

Department of Behavioural Biology,
University of Vienna

kurt.kotrschal@univie.ac.at

3rd Supervisor

Priv. Doz. Dr. Sarah Marshall-Pescini

Konrad-Lorenz Institute of Ethology,
University of Veterinary Medicine of Vienna

sarah.marshall@vetmeduni.ac.at

List of Publications

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[+] Co-first Author

[*] Corresponding Author

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2 Author Contributions

2.1 Article 1

Rao A, Range F, Kadletz K, Kotrschal K, Marshall-Pescini S.; Food preferences of similarly raised and kept captive dogs and wolves. *PLoS ONE 13(9): e0203165* (DOI: 10.1371/journal.pone.0203165).

A.R. designed the cafeteria paradigm study, collected data, coded videos, analysed data and drafted the manuscript. F.R. helped design both tasks, assisted in interpreting results and draft the manuscript. K. Kadletz collected data and coded videos for the two-choice task and assisted with drafting the manuscript. K. Kotrschal conceived the cafeteria paradigm, assisted with designing the study, helped interpret the results and draft the manuscript. S.M.-P. coordinated the study, assisted in designing both experiments, analysed data for the two-choice task and assisted with analysing data for the cafeteria paradigm, helped interpret the results and draft the manuscript. All authors gave final approval for publication.

2.2 Article 2

Rao A+*, Bernasconi L+, Lazzaroni M, Marshall-Pescini S, Range F.; Differences in persistence between dogs and wolves in an unsolvable task in the absence of humans. *PeerJ 6:e5944* (DOI: 10.7717/peerj.5944).

A.R. conceived, designed and coordinated the study, analysed the data and drafted the manuscript. L.B. and M.L. participated in designing the study. L.B. collected data, designed the ethogram, coded videos and participated in data analyses and drafting the manuscript. M.L. assisted in designing the ethogram and coded part of the videos for inter-observer reliability. S.M.-P. and F.R. helped in designing the study, interpreting the results and drafting the manuscript. All authors gave final approval for publication.

2.3 Article 3

Marshall-Pescini S+*, Rao A+, Virányi Z, Range F.; The role of domestication and experience in 'looking back' towards humans in an unsolvable task. *Sci Rep. Nature Publishing Group; 2017;7: 46636*.
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S.M.-P conceived, designed and coordinated the study, analysed the data and drafted the manuscript. A.R. collected data on free-ranging and pet dogs, coded videos and participated in data analyses and in drafting the manuscript. Z.V. and F.R. helped design the study, analyse the data and draft the manuscript. All authors gave final approval for publication.

3 Declaration

I herewith confirm that I have followed the rules of good scientific practice in all aspects.

4 General Introduction

Animals face a variety of challenges in the wild – coping with conspecifics, avoiding predators, foraging for resources, etc. These challenges act as selection pressures and drive the evolution of various behavioural strategies that animals use to deal with them[1,2]. Problems animals need to tackle can be classified into several "domains". For example, in the social domain, group-living animals may need to puzzle out conspecifics' intentions and evolve strategies to manipulate them[3]; they often need to cooperate, co-feed and mate, each of which pose their own sets of challenges[4]. Animals need to navigate their surroundings and find optimal foraging routes[5] or remember locations of cached foods[6], which pose challenges in the spatial domain. Tool manufacture and use[7], extractive foraging, etc. pose challenges in the physical domain. The strategies that animals evolve to cope with each of these challenges are driven by the animals' environment and the nature of the problems. How successful animals are at tackling them depends on various aspects of their behaviour and cognitive abilities. Studying animals' problem-solving abilities can hence not only be quite interesting *per se* but can show us patterns in the evolution of cognition. Moreover, the problem-solving abilities demonstrated by closely related species inhabiting different ecological niches can provide insights into the way an animal's environment interacts with and shapes its behaviour.

One domain where researchers have tried to understand the interplay between ecology and how animals solve certain problems is the physical domain. Certain psychological propensities or "correlates" have been found to predict physical problem-solving success across taxa. Examples of these correlates are neophobia (the fear of new situations or objects), motor diversity (the repertoire of problem-solving behaviours an animal displays), behavioural flexibility (an animal's ability to find novel solutions to already known problems, or to use known solutions to solve novel problems) and, persistence[8–20] or task-directed motivation (the length of time an animal spends engaged in a task). These propensities are also interconnected among themselves. For instance, persistence, motor diversity and behavioural flexibility are positively correlated[10–12,14,16], and all three are negatively correlated with neophobia[9,10,12,16,18,19,21,22].

Factors such as a species' ecology, social structure, living conditions and domestication influence these propensities[17,23–25]. For example, compared to conspecifics in more stable environments, birds in variable environments and habitats were found to be less neophobic and showed higher motor diversity and behavioural flexibility, potentially because these traits may help exploit new or difficult-to-reach resources[26–29]. Social carnivores were found to be more persistent than closely related non-social ones, and captive hyenas were found to be more persistent than wild conspecifics[10,12,30]. The authors of these studies concluded that differences in the animals' problem-solving abilities may be due to factors such as domain-general social intelligence promoting innovation in non-social tasks[12] and/or captivity resulting in more exposure to and experience with man-made objects (leading to increased exploration and reduced neophobia), and/or the "enculturation effect" of captivity which could promote greater cognitive capacities in animals with more human interaction[30]. Comparative studies with closely related species that occupy different niches form a good framework for understanding and disentangling these connections.

The process of animal domestication is interesting in that it results in species that are very closely related but often occupy different ecological niches. Domesticated animals have been shown to perform differently in several social and cognitive tasks compared to their wild counterparts[31]. There are two major hypotheses that explain the domestication process in animals. The "human-selection" hypothesis postulates that animals were domesticated by humans actively adopting young and selecting desirable traits such as tameness, friendliness, etc.[32] or by herding and hunting. The human-selection hypothesis can be seen as a combination of two pathways: the "prey pathway", where certain animals were hunted for meat and over time, hunting evolved into game-management and herding strategies (such as with bovids, goats, turkeys, etc.) and the "directed pathway" where humans initiated the domestication process deliberately with the intention of utilizing an animal for a purpose other than just food (such as with horses and donkeys)[32,33].

The second, "self-domestication" hypothesis (also known as the "commensal pathway") suggests domestication to be a coevolutionary process. It is thought to have started with populations of wild animals carving out niches around early human settlements. Animals that could exploit resources around human settlements were probably less aggressive, tamer and had shorter fight or flight distances. Eventually, the descendants of these animals may have formed a commensal relationship with humans. This may have been followed by elements of the direct selection pathway where humans favoured individuals with preferable traits from this population of proto-domesticated animals while displacing ones with unfavourable traits[32,33]. Examples of animals thought to be domesticated via this pathway are pigeons, fowl, rodents, pigs, cats and dogs (one of first animals to be domesticated)[33–35]. Wolves and their domestic counterparts, dogs, are species that are often subjects of cognitive research.

Dogs and wolves diverged between 20,000 and 40,000 years ago[36] and have since evolved different socioecologies[37]. Wolves typically live in family packs and are cooperative breeders[38]. They are predominantly hunters and hunt ungulates in groups, but have a success rate of only between 10% and 49%[39]. Dogs rely directly (such as in case of pet dogs) or indirectly (such as in case of free-ranging dogs) on humans. While studies have focussed mostly on pets, free-ranging dogs represent around 75% of the world's dog population. Compared to wolves, these dogs have a more variable social structure. While they are capable of group hunting[40], they rely primarily on solitary scavenging[37,38] and thrive on and around human refuse. The largest components of their diet are grains and human faeces[37,38,41,42].

Dogs and wolves perform differently in many inter and intraspecific problem-solving tasks[8,9,43–47]. Studies with the "unsolvable task" paradigm (which aims at exploring human-directed behaviour) often report that dogs gaze at humans sooner and longer than wolves[20,44] and studies using pointing gestures suggest that dogs are better than wolves at learning and understanding pointing cues[47,48] (but see Udell et al. 2008). Differences in these human-directed social cognition tasks are most often seen as adaptations to the human environment of dogs[20,46,48–53]. The most common explanation for these differences is the "human-reliance hypothesis". This hypothesis postulates that as humans often provide dogs with support in every important domain (such as access to food [38]), dogs expect humans to solve problems for them and instead of persisting at a given task, turn to humans "for help". However, though dogs outperform wolves in terms of human directed behaviour, wolves are better at imitating conspecifics and following their gazes[51,52], and have better problem-solving abilities[8,43,54,55]. For instance, wolves were more task-focussed, showed more behavioural variety, were more persistent and were able to generalise better than dogs in a string-pulling task[8]. They were faster and more successful at obtaining food from puzzle boxes[20,56–58] and performed better at a visual discrimination task than dogs[54]. These findings are more difficult to explain in reference only to the differences in human presence in dogs' and wolves' social environment.

It is important to understand that dogs' and wolves' ecologies differ in more than just the proximity of humans to their habitats. They have evolved different social structures (e.g. unlike dogs, wolves are cooperative breeders[59,60]), have different social partners (dogs accept humans as social partners more readily than wolves[38]) and have different foraging styles. Yet, dog-wolf behavioural differences have hardly been considered in a broader ecological context despite the fact that feeding ecology has been suggested to influence the correlates of problem-solving success[10,11,16,20]. The recently proposed "socioecological hypothesis" suggests that rather than focusing exclusively on what humans may have selected for in dogs during domestication, it is essential to consider changes in dogs' and wolves' social and ecological niches to better understand dog-wolf differences in physical and social domains[38].

A specific example of how basic differences in animals' problem-solving behaviours may muddle the interpretation of experimental outcomes is the body of work comparing dogs and wolves using the unsolvable task paradigm. This paradigm was originally designed to test human-directed behaviour[44]. While several studies using this paradigm have been quick to point out differences in dogs' and wolves' human-directed behaviour and to suggest that dogs' human-directed behaviour may be an indication of help-seeking[44,45,61,62], none have controlled for differences in persistence between the species. Dogs are known to less persistent than wolves in object manipulation[63,64] and this may in turn affect their human-directed behaviour: the human-directed behaviour that dogs show in cognitive experiments[20,44,45,57,65–68] may be a consequence of reduced persistence rather than a strategic choice to get human assistance.

The purpose of this PhD was to investigate differences in motivation and persistence in dogs and wolves to better understand whether differences in their problem-solving success are influenced by their feeding ecology. To this end, we conducted three experiments with similarly raised and kept dogs at the Wolf Science Center, Ernstbrunn, Austria, one of which was also performed with pet dogs in Vienna, Austria and free-ranging dogs in Bombay and Bangalore, India. We used food preferences as a proxy for testing motivation and used three variants of the classic "unsolvable task" paradigm to evaluate persistence.

Study 1: Food preferences of similarly raised and kept dogs and wolves.

The evolution of food preferences may be driven by the habitat a species has evolved in, energetic requirements and resource distribution[69]. For example, the food preferences of captive spider monkeys were correlated positively with the foods' energy content and negatively with its water content, a result in line with what would be expected from their frugivorous feeding niche and opportunistic feeding style[70]. Conversely, differences in food preferences may result in a separation of feeding niche (perhaps eventually even leading to speciation)[71]. An example of this idea is a study on primates in Madagascar where several related species of Lemurs cohabiting a forest showed preferences for leaves with different chemical compositions[72]. Food preferences, feeding niche (or dietary specializations) and foraging style (or strategies used to obtain food)[73] appear to be generally connected in several species[74,75]. Moreover, an animal's task directed motivation may be linked with feeding motivation[16] and consequentially be affected by its food preferences. For example, a study with Capuchin monkeys showed that they were faster at performing a token exchange task when given a more preferred or high value food reward than when they were given a low value food reward[76]. Studies with Corvids[77,78] and a study with cockatoos[79] demonstrated similar findings. Effects of food preferences on motivation have been found in dogs in a few studies – one study by Bentosela et al. 2009 showed that dogs trained to receive a more preferred food from a trainer had a longer gaze duration towards the experimenter than dogs that received a less preferred reward during training and a delay of gratification study found that dogs were significantly more likely to wait for a reward of higher quality than for a greater quantity of a reward of the same quality[81].

Our main aim with this study was to assess the hypothesis that dogs' and wolves' food preferences may have changed during domestication, potentially due to changes in their foraging styles. Specifically, considering that dogs have adapted to a more opportunistic scavenging style during domestication, and show genetic adaptions to starch, they may show a less strict preference for a single food type and show a weaker preference for meat over starch-rich food. To test this hypothesis, we used a classic two-choice task (a common paradigm for testing food preferences in several taxa[69,70,76,78,82–86] including dogs and wolves[87–90]) as well as a multiple choice paradigm to circumvent some shortcomings of the two-choice task[91].

Study 2: Differences in persistence between dogs and wolves in an unsolvable task in the absence of humans.

Persistence, in the context of problem solving, has generally been quantified as the time an animal spends engaged with a task to obtain a reward[10,12,16,18]. It is one of the strongest indicators of problem-solving success. Persistence predicted success in problem-solving tasks in studies with carnivores such as lions, spotted hyenas, leopards, tigers[12] and hyenas[10,30], in birds[14–16], red fronted lemurs[11], meerkats[18], pet dogs[20] and wolves[20,56]. While there is research investigating dogs' and wolves' persistence, studies so far have had a potentially confounding factor in their design – the presence of a human experimenter[20,43–45,56,65–68]. There is ample evidence that when confronted with a problem in the presence of a human, dogs are more likely than wolves to look towards and/or interact with the human instead of engaging in the task[20,44,56,67].

To better understand differences in dogs' and wolves' persistence, it is imperative to test them in the absence of humans. Udell (2015) attempted this by testing subjects in three conditions - alone, with a silent human, and with an encouraging human, and found wolves to be more persistent than pet dogs, even when alone. While this finding could suggest that dogs may have a "generalized dependence on humans" (Pg. 1), it may also be a result of the different life experiences (which are known to affect problem-solving abilities in dogs[92]) of the pet dogs and hand-reared wolves that participated in the experiment. To circumvent these problems and to have a clearer understanding of dogs' and wolves' persistence in an independent problem-solving task, we presented equally raised and kept pack-living dogs and wolves with two different unsolvable tasks in the absence of humans on two separate occasions. The main aim of this study was to test whether dogs and wolves differ in their persistence in an independent problem-solving task in the absence of humans.

Study 3: The role of domestication and experience in ‘looking back’ towards humans in an unsolvable task.

One of the hypotheses that can explain the human directed behaviour that dogs show in problem-solving tasks is the “human reliance hypothesis”: as dogs live in a human dominated niche[38] where humans often provide support in every important domain (such as access to food[38] and social support[45]), dogs expect humans to solve problems for them. Hence, instead of persisting at a given task, they turn to humans “for help”. However, dogs’ and wolves’ ecologies vary in more than just their proximity to humans. Dogs, primarily scavengers[37,38], depend mostly on refuse[37,38,41,42,93] while wolves depend primarily on group-hunting[37] and need to be persistent due to highly variable success rates (between 10% and 49%)[39].

Hence, according to the alternate, “socioecology-based” hypothesis, rather than turning to humans being a strategic choice for support as previous studies suggest [44,45,61,62], this behaviour may be a consequence of dogs’ reduced persistence. Given that dogs are less persistent than wolves in object manipulation, dogs look back towards the person sooner than wolves.

To tease these hypotheses apart, we adopted the classic unsolvable task used by Miklósi et al. (2003) and tested similarly raised and kept pack-living dogs and wolves, pet dogs and free-ranging dogs to assess if varying amounts of experience with humans affects the dogs’ and wolves’ persistence.

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5 Publications

5.1 Article 1:

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Food preferences of similarly raised and kept captive dogs and wolves.

Akshay Rao[a,b]*, Friederike Range[a,b] , Kerstin Kadletz[a], Kurt Kotrschal[a,c], Sarah Marshall-Pescini[a,b]

a: Wolf Science Center, Konrad-Lorenz Institute of Ethology, University of Veterinary Medicine, Vienna, Austria

b: Comparative Cognition, Messerli Research Institute, University of Veterinary Medicine, Vienna, Medical University of Vienna, University of Vienna, Vienna, Austria

c: Department of Behavioural Biology, University of Vienna, Vienna, Austria

*Corresponding author

5.1.1 Abstract

Food preferences may be driven by a species' ecology. Closely related species such as dogs and wolves may have evolved preferences for different foods owing to their differing foraging styles. Wolves have been shown to be more persistent in problem-solving experiments and more risk-prone in a foraging task. A possible element affecting these (and other) results is a potential dog-wolf difference in food preferences. To address this possibility, we tested similarly raised and kept dogs and wolves in two different food choice tasks, a classic two-choice task and a multiple-choice paradigm. We predicted that if dogs have adapted to a more opportunistic scavenging foraging style, they would show a weaker preference for meat over starch rich foods (such as kibble) and be less affected by hunger than wolves. Alternatively, given the recentness of the new niche dogs have created, we predicted no substantial differences between dogs' and wolves' food preferences. We found that our subjects did not differ in their preference for meat over kibble in either paradigm. However, wolves' (but not dogs') choice patterns were affected by satiation: compared to dogs, wolves were less "selective" when hungry and more "selective" when fed before testing. These differences were more noticeable in the multiple-choice paradigm than in the two-choice task. The former novel paradigm may be more sensitive and better capable of evaluating food preferences in a diverse range of species. Overall, we found that the distinct differences in dogs' and wolves' ecology and foraging styles do not appear to have affected their food preferences and are thus unlikely to have influenced results of previous experiments demonstrating dog-wolf differences in cognitive skills.

Key words: Food preferences, wolf dog comparisons, foraging style, satiation.

5.1.2 Introduction

The evolution of food preferences may be driven by the habitat a species has evolved in, by energetic and protein requirements, and by resource distribution[1]. For example, the food preferences of captive spider monkeys were correlated positively with foods' energy content and negatively with its water content, a result in line with what would be expected from their frugivorous feeding niche and opportunistic feeding style[2]. Similarly, several predators (including domestic dogs, cats, mink and fish) have been shown to prefer protein rich foods [3–6] according to their carnivorous feeding niches. Food preferences are the behavioural fingerprints of evolved feeding niches[7]. An example of this phenomenon was shown in a study on primates in Madagascar where several related species of Lemurs cohabiting a forest showed preferences for leaves with different chemical compositions[8]. Hence, food preferences, feeding niches (or dietary specializations) and foraging styles (or strategies used to obtain food)[9] appear to be generally connected in several species[10,11].

Canines are a relevant taxon to study these connections since several closely related canines have fundamentally different foraging styles; for example, domestic dogs and their closest living relatives, wolves[12]. These differences are most prominently noticeable in free-ranging dogs, which make up over 75% of the world's dog population[13,14]. While dogs are capable of hunting[15], they are primarily solitary scavengers[16,17], thrive around human settlements and feed predominantly and indiscriminately on human refuse[18]. Close analyses of free-ranging dogs' diet have revealed that the largest components of their diet are grains and human faeces[16,17,19,20]. Wolves, on the other hand, while occasionally observed scavenging on human refuse, are specialized hunters[16] and often hunt in packs. Considering their variable and often low success rate (between 10% and 49% per chase), hunting is thought to require an extraordinary level of persistence and food-motivation[21]. The dependence on different food resources is also evident in their genes, with dogs showing better starch digestion than wolves[22 (but see 23)]. Another crucial aspect to consider is the effect of hunger, which may affect preference patterns in both dogs and wolves. Hunger is a motivational factor[24,25], may lead to animals consuming novel foods[26] and even modify their foraging styles[27]. The variation in dogs' and wolves' foraging styles could thus be due to motivational changes induced by hunger and may differently affect their preferences for specific food types.

The different socioecology of dogs and wolves is postulated to have shaped the way in which they approach both social and independent problem-solving tasks[17]. For instance, in line with wolves' dependence on cooperation in both hunting and pup-rearing, wolves outperformed dogs in a cooperative string-pulling task[28] and showed more food sharing than dogs[29]. Compared to dogs, wolves were also more persistent in extractive tasks involving food[30–32] and took more risks in a foraging task when the choice was between a safe, low quality food reward, and a less stable/riskier, high quality one[33]. However, considering the different feeding ecology of dogs and wolves, one possible underlying motivation for wolves' increased persistence, better problem-solving skills and more risk-taking behaviour is differences in dogs' and wolves' food preferences.

To address this possibility, we tested similarly raised and kept dogs and wolves in two different food choice tasks in the current study. We first used a classic two-choice paradigm, where subjects could choose one of two presented foods. This is a common paradigm for testing food preferences in several taxa[1,2,34–40] including dogs and wolves[33,41–43]. However, though widely used, this paradigm does have some shortcomings[44]: while it tells us which food an animal prefers from a pair, it is difficult to say whether the animal would choose similarly when presented with multiple choices. Furthermore, task contingencies (e.g. side biases) and experience with other, similar two-choice tasks may affect the animals' behaviour. Using a second paradigm and assessing the consistency in the animals' preferences between tests would provide better insight into the animals' preferences. Hence, we also adopted a "cafeteria" paradigm where subjects could choose three out of five simultaneously presented food types.

Foraging styles may affect food preferences, and as outlined above, dogs and wolves show some differentiation in their foraging styles (group hunting ungulates vs. scavenging of human refuse). Our main aim was to assess the hypothesis that dogs' and wolves' food preferences may have changed during domestication, potentially due to changes in their foraging styles. Specifically, considering that dogs have adapted to a more opportunistic scavenging style during domestication and that they show genetic adaptions to starch, they may show a less strict preference for a single food type, and show a weaker preference for meat over starch-rich food. Based on this hypothesis, we predicted that compared to wolves, dogs (1) would show a weaker preference for meat over starch-rich food (i.e. dog kibble) in the two-choice task and (2) would be less likely to choose meat and chicks as their first choice in the cafeteria paradigm. We also predicted that dogs (3) would have more choice diversity than wolves (i.e., less strict preference than wolves for certain foods) in the cafeteria task, and (4) would choose nearby foods (foods that were in immediate proximity of a previously chosen food) regardless of the food type, while wolves, having a stronger preference for meat than dogs, would be more likely to choose nearby foods if they were meat or chicks.

Although the feeding niche of dogs and wolves has changed during the course of domestication, the new niche dogs produced is recent and there is a continuum in dogs' and wolves' foraging styles (wolves show scavenging behaviours[16,45] and populations of dogs are known to hunt small ungulates in groups[15,46,47]). The null hypothesis then, is that dogs' feeding ecology has not affected their food preferences when compared to wolves, and dogs still prefer food high in energy and protein[6]. Based on this hypothesis no substantial differences in dogs' and wolves' food preference patterns would be expected.

Since preferences may be linked to the nutritive value of food[11], we conducted nutritional analyses of the food types we used. Finally, since hunger may influence food preferences, we tested subjects in two different satiation states in both paradigms. We predicted that when hungry, subjects would spend more time trying to acquire inaccessible food (i.e., during "inspection" and at the end of a test trial when the apparatus is locked) (for definitions, see 5.1.5.3.2 Testing Phase on Page 34).

5.1.3 General Materials and Methods

5.1.3.1 Ethics Statement

Special permission to use animals in cognitive studies (such as this one) is not required in Austria (Tierversuchsgesetz 2012—TVG 2012). The Tierversuchskommission am Bundesministerium für Wissenschaft und Forschung (Austria) allows research without special permissions regarding animals. The ethical approval for this study was obtained from the 'Ethik und Tierschutzcommission' of the University of Veterinary Medicine (Protocol number ETK-10/03/2016). The Wolf Science Center is in the game park Ernstbrunn (License No.: AT00012014). The CITES permits for our animals are: 2008: Zoo Herberstein, Austria: AT08-B-0998, AT08-B-0996, AT08-B-0997; 2009: Zoo Basel, Switzerland: AT09-E-0061, Triple D Farm, USA: AT09-E-0018; 2010: Parc Safari, Canada: AT10-E-0018; 2012: Minnesota Wildlife Connection, USA: 12AT330200INEGCJ93, Haliburton Forest, Canada: AT12-E0020. The individuals appearing in the figures and videos in this manuscript have given written, informed consent to publish these media.

5.1.3.2 Subjects

A total of 14 wolves (6 F, 8 M) and 19 medium sized, mixed-breed dogs (7 F, 12 M) participated in the entire study. These animals were raised and kept similarly in conspecific packs at the Wolf Science Centre, Ernstbrunn Wild Park, Austria. Eleven wolves (5 F, 7 M; mean age 3.5 ± 1.7 years) and 10 dogs (4 F, 6 M; mean age 3 ± 0.6 years) participated in the two-choice task and 12 wolves (4 F, 8 M; mean age 6.3 ± 1.7 years) and 17 dogs (6 F, 10 M; mean age 4 ± 1.6 years), participated in the cafeteria paradigm (Table 1 on Page 24).

All wolves were born in captivity in North America and Europe. Dogs born before 2014 were obtained from animal shelters in Hungary (Tierheim Szeged and Tierheim Paks). The remaining dogs (2014 generation) were offspring of two of our own females (Layla and Nia) and were born at the Wolf Science Center. All animals except the 2014 dog cohort were separated from their mothers within 10 days of birth and then hand-raised with conspecifics in peer groups (dogs and wolves were raised separately and at different times). In the first 5 months of their life, the animals had continuous access to humans who bottle-fed and later hand-fed them. The 2014 dog cohort spent most of the day with the hand-raisers and in peer groups but returned to their mothers at night. All animals were kept indoors during the first weeks of puppyhood and had free access to a 1,000 m^2 outdoor, “puppy” enclosure from their second month on. They were moved to 2,000 – 8,000 m^2 “living” enclosures at five months of age.

All enclosures are equipped with trees, bushes, logs, shelters and permanent sources of drinking water. All animals voluntarily participate in cognitive and behavioural experiments, and/or training, and/or other social events at least once a day and hence have daily social contact with humans. Animals are rewarded with food for participating in these activities (see 5.1.3.2.1 Subjects’ Diet and Food Types on Page 24). This routine ensures that all animals are cooperative and attentive towards humans and allows weekly veterinary checks without sedating the animals. All animals at the WSC are intact and males are vasectomised.

The two-choice task was conducted from October to December 2013. Of the available test subjects at that time, one wolf (Wamblee) and one dog (Nia), could not be tested because they dropped out in the training stage. The cafeteria paradigm was conducted from August to December 2016. Of the available animals at that time, one dog (Bora) was excluded from testing as she would not approach the test apparatus without a trainer being close (and potentially influencing the choice). Two dogs (Kilio and Rafiki: rehomed) and one wolf (Kay: deceased), that had participated in the two-choice task could not participate in the cafeteria paradigm as they were no longer at the WSC. Dogs born in 2014 participated only in the cafeteria paradigm.

Table 1: Details of the subjects that participated in each testing paradigm

Subject	Group	Sex	Date of Birth	Age when tested	
				Two-Choice Task	Cafeteria Paradigm
Amarok	Wolf	M	04/04/2012	1.6	4.7
Kenai	Wolf	M	01/04/2010	3.6	6.6
Geronimo	Wolf	M	02/05/2009	4.5	7.3
Yukon	Wolf	F	02/05/2009	4.6	7.3
Wamblee	Wolf	M	18/04/2012	Not Tested	4.5
Nanuk	Wolf	M	28/04/2009	4.5	7.3
Una	Wolf	F	07/04/2012	1.6	4.3
Chitto	Wolf	M	04/04/2012	1.6	4.3
Tala	Wolf	F	04/04/2012	1.7	4.3
Kaspar	Wolf	M	04/05/2008	5.6	8.6
Kay	Wolf	F	22/04/2012	1.5	Not Tested
Aragorn	Wolf	M	04/05/2008	5.6	8.3
Shima	Wolf	F	04/05/2008	5.6	8.4
Nia	Dog	F	22/07/2011	Not Tested	5.0
Kilio	Dog	M	18/12/2009	3.8	Not Tested
Gombo	Dog	M	21/03/2014	Not Tested	2.4
Sahibu	Dog	M	21/03/2014	Not Tested	2.4
Maisha	Dog	M	18/12/2009	3.9	6.6
Rafiki	Dog	M	30/11/2009	4.0	Not Tested
Binti	Dog	F	15/09/2010	2.2	5.9
Asali	Dog	M	15/09/2010	3.1	5.9
Bora	Dog	F	02/08/2011	2.3	Not Tested
Banzai	Dog	M	02/04/2014	Not Tested	2.4
Meru	Dog	M	01/10/2010	3.0	5.8
Hiari	Dog	M	21/03/2014	Not Tested	2.4
Imara	Dog	F	21/03/2014	Not Tested	2.4
Nuru	Dog	M	24/06/2011	2.4	4.9
Zuri	Dog	F	24/06/2011	2.4	5.1
Layla	Dog	F	03/08/2011	2.3	5.1
Pepeo	Dog	M	02/04/2014	Not Tested	2.3
Panya	Dog	F	02/04/2014	Not Tested	2.4
Enzi	Dog	M	02/04/2014	Not Tested	2.3

5.1.3.2.1 Subjects' Diet and Food Types

Dogs and wolves at the WSC receive a variety of foods ranging from raw meat to dog kibble, both as a part of their meals and as rewards for participating in behavioural tests. Five different food types, all equally familiar to animals, were chosen for the tests. Four foods were used in both the two-choice task and the cafeteria paradigm: 1) dead, one-day old chicks (cut in two or three pieces), 2) fresh cow head-meat, 3) commercially available sausage (Aro™ Extrawurst), 4) commercially available dry food (Royal Canin™ – German Shepherd); and one food was used only in the cafeteria paradigm (commercially available unflavoured tofu).

These foods were chosen because they are routinely used in behavioural tests, and one aim of our study was to investigate if dogs and wolves show different preferences for these food types, thereby affecting their behaviour in other experiments. We analysed the nutritional content of each food type (Table 2, below).

All food was cut in 2 – 3 cm³ pieces and stored separately. Dry food, bits of sausage and meat are used as rewards when the animals participate in both, behavioural experiments as well as touristic events. Bits of sausage are the most common rewards during training procedures involving shaping. Dry food (Royal Canin™ – German Shepherd) is used as the most common reward during touristic events while bits of sausage, meat and chicks are rarer treats. Once a week, animals have an enrichment session where each pack is shifted out of their enclosures and a mixture of various foods is scattered and hidden in their home enclosures for them to search for and consume. The regular feeding regimes of our animals are based on their natural feeding patterns. Dogs receive dry food (Royal Canin™ – Medium Adult) as an evening meal at the end of every day while wolves (as well as dogs, albeit less frequently) receive dead chickens, rabbits or pieces of deer, calf or sheep carcasses twice or thrice a week, depending on body condition, season, etc. The somewhat different feeding regimes and food quantities (smaller more frequent feeding of the dogs compared to wolves) are based on their natural requirements and aimed at insuring the animals' health.

Table 2: Nutritional information for foods (reported on an 'as is' basis) used for testing preferences and as regular feed (values per 100g of homogenized food).

	Energy (Kcal)	Dry Mass (g)	Moisture (g)	Crude Ash (g)	Crude Protein (g)	Crude Protein ÷ Dry Mass	Crude Fat (g)	Crude Fibre (g)
Foods used in routine experiments								
Chicks, one day old	103	22	78	2	15	0.7	4	0
Cow head-meat	290	45	55	1	17	0.4	26	0
Extrawurst	392	44	56	3	11	0.3	30	0
Royal Canin (GS)	384	92	8	8	24	0.3	19	3.8
Tofu	84	15	84.6	1	9	0.6	5	0
Foods used as regular feed								
Royal Canin (MA)	386	92	8	6	25	0.3	14	1.2
Rabbit	158	30	69.6	1	21	0.7	8	0
Chicken	235	43	57.3	5	16	0.4	20	0.4
Deer carcass	125	27	73	1	22	0.8	4	0

5.1.3.2.1.1 Food Sources

One day old chicks were obtained from “naturaldogs der Naturfuttershop”, Einsiedlingerstraße 26, 4655 Vorchdorf (47°59'05.1" N 13°55'55.0" E). The cow head-meat was purchased from “Fleischerei Pfennigbauer Hausleithen”, Hauptplatz 17, 3464 Hausleiten (48°23'45.1" N 16°06'06.7" E). The Sausage was purchased from METRO Cash & Carry Austria GmbH, Wiener Straße 176-196, 2103 Langenzersdorf (48°17'52.4" N, 16°22'22.7" E). Royal Canin Österreich GmbH, Handelskai 92, Rivergate/Gate 1/OG 11, 1200 Wien (48°14'32.5" N 16°23'04.9" E) supplied all dry food. Tofu was purchased from Hofer Kommanditgesellschaft, Wienerstraße 1, 2115 Ernstbrunn (48°31'34.9" N, 16°22'44.6" E). Rabbits were supplied by Baxter, Uferstrasse 15, 2304 Orth/Donau (48°08'07.5" N 16°42'28.4" E). The Ernstbrunn Wildpark provided the deer carcasses, some chickens and some rabbits. All animals used as feed were obtained dead and were not euthanised at the Wolf Science Center.

5.1.3.3 General Procedure

For each task, a training phase preceded the testing phase. As the experimental setups were novel to the subjects, they were trained to operate each apparatus. Subjects were trained by positive reinforcement-based training (with the aid of a clicker). Bits of sausage and dry food were used as rewards during the shaping process. Subjects were tested once they had reached objective, task-specific criteria for being considered “trained” (see 5.1.4.3.1 Training Phase on Page 28 and 5.1.5.3.1 Training Phase on Page 33) in each task. The number of training sessions required for a subject to reach criteria relied solely on the subject’s performance.

Subjects were tested under two conditions: “high satiation” (henceforth called “fed”) and “low satiation” (henceforth called “unfed”). For the fed condition, subjects were fed approximately 15 hours prior (i.e. the previous evening) to the test session. Wolves were fed either one complete rabbit each or similarly sized portions of a deer carcass. Dogs were fed their regular measures of dry food (different from the food used for the test). For the unfed condition, wolves were not fed the evening before testing. Two dogs could not be kept completely unfed overnight for medical reasons. To ensure consistency, all dogs were fed less than half their regular measures of dry food approximately 15 hours prior (i.e. the previous evening) to the test session.

The testing phase for the two-choice task consisted of four sessions each in the fed and in the unfed condition. Each session consisted of six trials (two trials for each of the six possible combinations of the four foods that were used). The testing phase for the cafeteria paradigm consisted of two sessions each in the fed and in the unfed condition. Each session consisted of five trials. We performed only one session per subject per day in both tasks.

5.1.4 Two-Choice Task

5.1.4.1 Apparatus

The apparatus consisted of a low table (57.5 cm × 49.3 cm) with the following features: a sliding “choice tray” with two wooden blocks (henceforth called “targets”, sized 14.7 cm × 5.5 cm × 3.3 cm) fixed to its left and rightmost extremes (on the side that would be closest to the animal) mounted on top of the table, and a flexible plastic tube (henceforth called the “chute”) attached to the central part of the table. The experimenter could deliver food to the subject via the chute. A panel with flaps hid the experimenter from view of the subject while allowing food to be passed through (Figure 1, below). A single, central food delivery system was chosen to reduce the chances of the subject developing a side bias.

Figure 1: Apparatus used for testing food preferences in the two-choice task (rear).

5.1.4.2 Experimental Setup

The experiment took place in an outdoor testing enclosure. The subject was positioned a shifting channel in the test enclosure. It was was free to move around in the channel. The apparatus, experimenter and trainer were positioned outside the shifting channel. The experimenter was positioned behind the apparatus and was occluded from the subject's view by the apparatus's flaps. A trainer was positioned behind the experimenter and was visible to the test subject. Two subjects (Una and Kay) were not comfortable with the experimenter, so a second trainer adopted the role of the experimenter for these subjects.

5.1.4.3 Procedure

5.1.4.3.1 Training Phase

Training was divided into three sub steps for the two-choice task. The criterion for a subject to proceed to the next training step was scoring nine out of twelve trials correctly in two consecutive sessions. Subjects were first trained to touch a target with their nose. Next, training sessions consisting of four "warm-up" trials and one to two sets of twelve single choice trials were performed. The number of single-choice trial sets depended on the motivation of the subject during that training session. Subjects had only one training session per day. During a warm-up trial, a trainer presented food to the subject twice on each side. In a single choice trial, an experimenter showed the subject a piece of food in the middle of the table and placed it in a small cup on one of the sides of the sliding platform, leaving the other cup empty. The order in which the food was presented on the left or right was semi-randomised such that the food was not presented on the same side more than twice. The sliding platform was then extended, allowing the subject to nose one of the targets. Nosing the target adjacent to the food item was considered a "correct" choice. If the subject chose correctly, the experimenter retracted the platform, picked up the food, showed it to the subject and delivered it to the subject via the chute. In case of an incorrect choice, the experimenter retracted the platform and repeated the trial with the food on the same side.

The second training step involved removing human cues from the setup. The experimenter now baited both cups on the platform with identical pieces of food out of view of the subject and extended it partially. The subject was given three seconds to inspect the food after which the platform was extended fully. The subject could then touch either target with its nose to obtain the food on the corresponding side.

The aim of the third step was to allow the subject to understand that the food that was not chosen first was no longer available. The procedure was identical to that of step two, except that each side was baited with a different food item. The location of each food type was semi-randomised such that it was not presented on the same side more than twice in a row. If a subject displayed a side bias (i.e. chose food on the same side in all 12 trials), a "correction" session was performed, in which the subject was given a choice between dry food and no food in the same semi-randomised fashion. The criterion for a subject to proceed to the testing phase was that it did not show a side bias in the third training step.

5.1.4.3.2 Testing Phase

Each test session began with single-choice trials to ensure the subject was still familiar with the working of the apparatus. The test procedure was identical to step three of the training phase. A test session consisted of twelve trials, two for each of the six possible combinations of food. The order in which the food pairs were presented was semi-randomised so that the same pair of food choices did not occur more than twice in a row. Each subject had only one test session per day. Each subject had four test sessions before feeding and four sessions after feeding. See the Supplementary Video linked on Page 106 of the Appendix for an example of a trial.

5.1.4.4 Analyses

Data for the two-choice task were analysed using generalised linear mixed models with Poisson distributions fit by the Laplace approximation. We used the package "lme4"[48] in R (v 2.14.1)[49]. We tested the effects of species, satiation state, sex and food type on the frequency of food choice. To evaluate whether dogs' and wolves' preference varied depending on food type and whether satiation levels affected food choice differently in dogs and wolves, we included a species by food type, and a species by satiation state interaction in the model. Individuals were added as random effects and analyses were normalised for the number of presentations. To better understand the effects that we found in the overall analyses, we used generalised linear mixed models with the binomial distribution to test the effects of species, satiation state and sex on the likelihood of choosing a food for each of the six combinations the subjects were presented with (i.e. chicks and meat, chicks and sausage, chicks and dry food, meat and sausage, meat and dry food, and sausage and dry food). We adopted a backwards stepwise model reduction approach based on p-values starting with interactions. One individual (Nanuk) was excluded from the analyses as he did not consume food after choosing it.

5.1.4.5 Results

Dogs and wolves did not differ in the frequency with which they chose specific foods (species by food type interaction: F = 1.72, P = 0.2) and did not choose differently whether fed or unfed (species by satiation state: F = 0.14, P = 0.7). There were no main effects of sex (F = 0.34, P = 0.6), satiation state (F = 0.06, P = 0.8) or species (F = 0.39, P = 0.5). The frequency of choice was influenced by food type (F= 92.3, P < 0.001): sausage was chosen less often than chick (F = 2.302, P = 0.021), but was not chosen significantly differently from meat (F = 1.518, P = 0.129). No difference emerged in the frequency of choosing chicks and meat (F = 0.798, P = 0.425), but dry food was chosen least often compared to all other food types (dry food: vs. chick F = 11.043, P < 0.001; vs. meat F = 10.477, P < 0.001; vs. sausage F = 9.297, P < 0.001) (Figure 2, below).

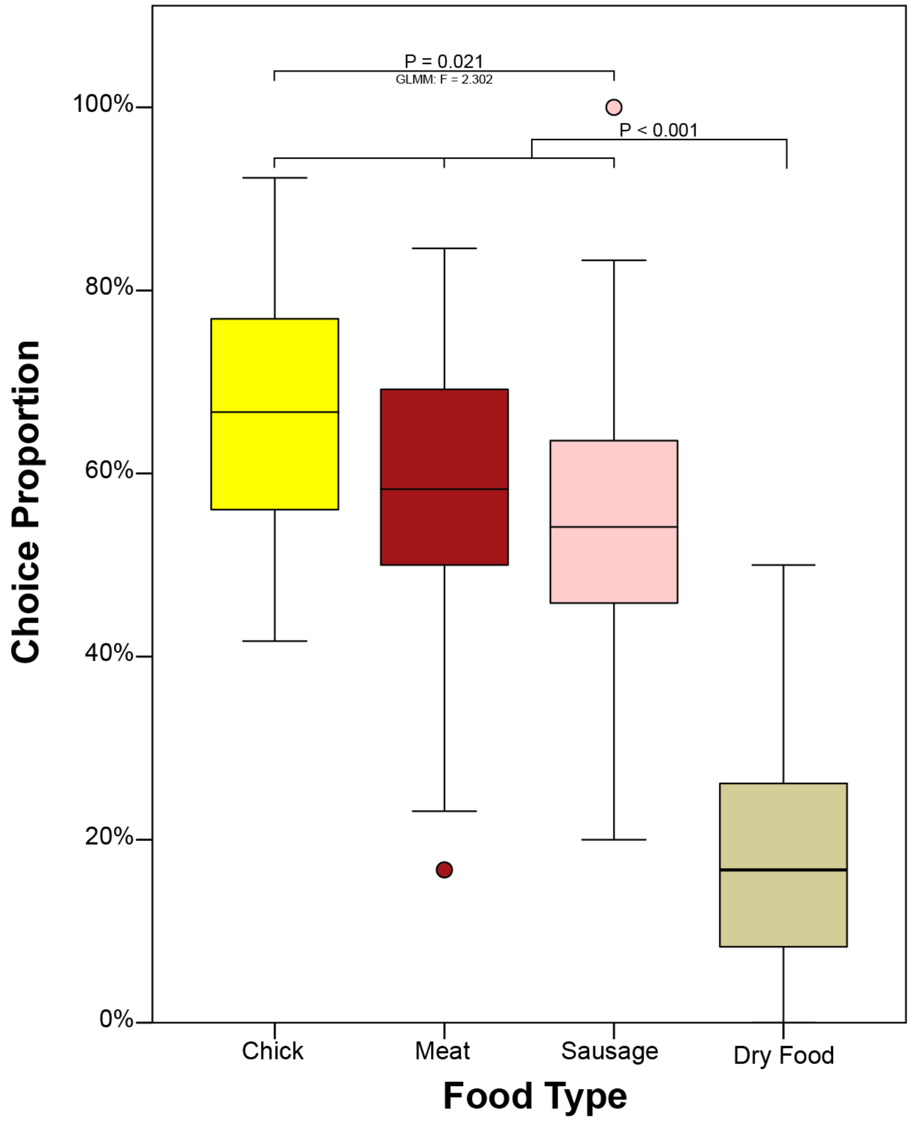

Figure 2: Percentage of food choices, normalised by number of presentations. Circles indicate outliers.

Considering each food pair separately, we found that subjects preferred chicks (z = 7.325, P < 0.001) and meat (z = 8.461, P < 0.001) to the dry food, and this preference was not affected by species (dry food: vs. chicks F = 1.51, P = 0.2; vs. meat F = 0.62, P = 0.4), sex (dry food: vs. chicks F = 0.43, P = 0.5; vs. meat F = 0.14, P = 0.7), or feeding condition (dry food: vs. chicks F = 0.08, P = 0.8; vs. meat F = 0.39, P = 0.5).

Subjects did not prefer meat or chicks significantly to each other (z = 0.982, P = 0.326) and this was not affected by species (F = 2.13, P = 0.16), sex (F = 0.53, P = 0.48) or feeding condition (F = 2.8, P = 0.1).

Subjects preferred chicks to the sausage (z = 4.974, P < 0.001) and this was not affected by species (F = 0.03, P = 0.9), sex (F = 0.01, P = 0.9) or feeding condition (F = 6.2, P = 0.4). Wolves preferred the sausage to the dry food more often than dogs (z = 1.993, P = 0.046) and both dogs and wolves preferred the sausage to the dry food more often when fed than when unfed (z = 2.313, P = 0.021). Both dogs (z = 4.816, P < 0.001) and wolves (z = 6.968, P = 0.001) preferred the sausage to the dry-food regardless of feeding condition (Figure 3, below); and preferences were not affected by sex (F = 0.31, P = 0.58).

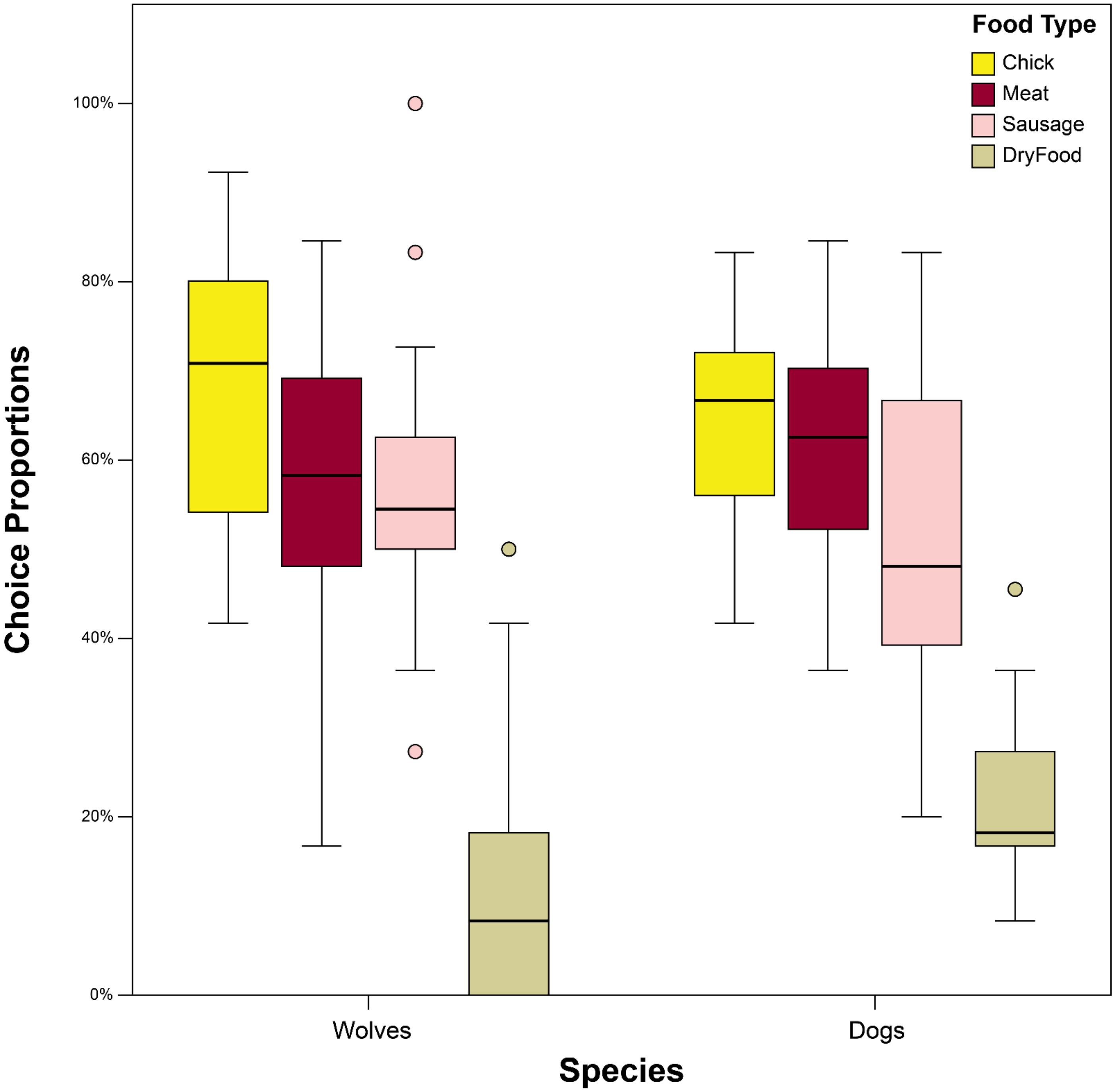

Figure 3: Proportion of food choices, normalised by number of presentations, split by species. Circles indicate outliers.

5.1.5 Cafeteria Paradigm

5.1.5.1 Apparatus

The apparatus consisted of 6 transparent, perforated Plexiglas boxes measuring 20 cm on each side, mounted on an arch-shaped wooden platform (55 cm wide, 5 cm tall and approx. 120 cm in diameter) (Figure 4, below). Commercially available stainless-steel dog-food plates measuring 8 cm in diameter were placed under each Plexiglas box and were fastened to the platform using a screw. Each plate was 75 cm away from the ones adjacent to it. The Plexiglas boxes were mounted with hinges on one side in a way that they could be flipped open. All boxes could be remotely locked, making them impossible to open. Each food plate was used only for a single type of food to prevent potential mixing of food odours and flavours. During the test, a visually equal amount of each food (one to two pieces of meat, sausage, chicks and tofu and four to five pieces of dry food) was used for baiting the boxes.

Figure 4: Apparatus used for the Cafeteria Paradigm.

5.1.5.2 Experimental Setup

The experiment took place in an outdoor testing enclosure. A trainer stood with the subject on a marked spot in the concave part of the arch such that each box was equidistant from the test subject. The experimenter was positioned outside the testing enclosure, in sight of the subject, and re-baited the apparatus between trials (Figure 5, below). One subject (Una) was not comfortable with the experimenter and helper therefore two additional trainers adopted these roles for this subject.

Figure 5: Experimental setup for the cafeteria paradigm. (Left to right) helper, experimenter, trainer and test subject.

5.1.5.3 Procedure

5.1.5.3.1 Training Phase

Each subject received at least one habituation and/or training session to familiarize it with the mechanism of the apparatus and to associate the apparatus with food. A small part of the wooden platform (measuring approx. 100 × 55 cm) containing just one Plexiglas box was used for these sessions. The entire setup was not used to prevent the subjects from developing any preferences for a specific position.

Subjects were trained to flip the Plexiglas box open using their paw or snout by shaping with a clicker. All 5 food types were used to bait the apparatus during training to prevent the subjects from associating the mechanism with a specific kind of food. Bits of dry food and sausage were used as rewards during the shaping process. The objective of the experiment was not to test problem-solving abilities but to assess food preferences. Hence, in cases where the subjects were overly fearful of the movement of the Plexiglas box or in cases where the subjects could not learn to open the boxes on their own after 3 sessions, subjects were trained to indicate their choice by placing their paw on the apparatus following which, the trainer flipped open the box for them (10 dogs and 8 wolves indicated at least once in 4 sessions; 5 dogs and 3 wolves indicated in all sessions).

Subjects were considered "trained" once they required no cues from the trainer and flipped the Plexiglas box open themselves (or placed their paw on the box signalling the trainer to open the box) at least 4 out of 5 times the box was baited.

5.1.5.3.2 Testing Phase

To prevent potential confounding effects of previously eaten foods, the subjects participated in this experiment prior to participating in any other tests. For this test, the subject was either walked to, or shifted (via a series of shifting channels) into the test enclosure, where the un-baited apparatus was present. Subjects were given 2 to 5 minutes to explore the enclosure and inspect the apparatus. This was done to minimise the number of distractions during the test session.

A test session consisted of 1 inspection phase and 5 test trials. Two test sessions were conducted in each satiation condition. The position of foods was changed between sessions but remained constant across trials within each session. Every session was recorded with a video camera mounted on a tripod positioned beside the experimenter behind the first fence. Data for choice of food and duration of attempts to make a choice or extract food when the apparatus was locked were extracted from the recorded videos.

After the subject had explored the test enclosure and apparatus, the trainer called it back and held it on a leash or by a collar. The experimenter entered the test enclosure and baited each box with different food item. One box was left empty and served as a control. The order in which the boxes were baited was randomised. Once baited, the boxes were locked remotely and the experimenter exited the enclosure.

Inspection: The trainer then walked the animal to each box and allowed the subject to see and sniff each one. In case the subject was distracted, the trainer called out to the subject, pointed to each box and ensured that the animal had seen and sniffed it (Figure 6 on Page 35). At this point, the animal could not open the boxes to access the food. The order in which the trainers had subjects inspect the boxes and the box the subjects inspected first was randomised. The trainer then walked the subject back to a marked position from which all foods were equidistant to the subject.

Test trial: A trial started with the boxes being remotely unlocked and the subject being released by the trainer from the marked position.

All subjects could open a maximum of three boxes and could eat the food under each. The remaining boxes were then locked remotely, and the subject was called back by the trainer, ending the trial. At the end of a trial, subjects were rewarded with bits of dry food for returning to the trainer. See the Supplementary Video linked on Page 106 of the Appendix for an example of test trials.

Rebaiting: After each trial, the experimenter entered the test enclosure and replaced the food which the subject had consumed. The experimenter pretended to rebait boxes that still had food under them to prevent potential local enhancement effects. The order in which boxes were rebaited / mock-rebaited was randomised.

Figure 6: Inspection Phase: Trainer pointing at box to ensure test subject sees and sniffs it.

5.1.5.4 Behavioural Coding

Videos were coded using Solomon Coder beta v. 17.02.15 (a behaviour coding software developed by András Péter, Dept. of Ethology, Budapest). See Table 3 (below) for definitions and the supplementary video linked on Page 106 of the Appendix for examples of coded behaviours.

Table 3: Definitions of coded behavioural elements.

Action	Definition
Release	The subject starts moving towards the apparatus after the trainer releases it; the subject is now free to approach the apparatus and make a choice.
Choice #	The subject either flips a box open with its snout or paw, attempts to flip it open more than once or places its paw on or in front of a box indicating that the trainer should open it, followed by the trainer opening the box.
Extra Attempt	The subject attempts to open a box by indicating, pawing, biting, scratching or pulling at it either during ”Inspection” or after Choice 3.

5.1.5.5 Analyses

Food choice data for the cafeteria paradigm were analysed using a Generalised Estimating Equation (GEE) with a multinomial distribution and a cumulative logit link in SPSS (v 23.0). For each choice, we tested whether food choice could be predicted by species, satiation state or an interaction between the two. To better understand how each food type contributed to the effects found in the overall model, we further analysed each food type separately. We tested whether the likelihood of choosing each food type could be significantly predicted by species, satiation state or an interaction between the two (GEE, binomial distribution with a logit link). When analysing Choice 2, we also tested for the effect of foods being adjacent to the previous choice. We accounted for the change in the food types available by factoring Choice 1 into the model. This also allowed us to analyse whether any of the food types chosen first affected the second choice. We were unable to analyse Choice 3 as we did not have enough data to compute the model reliably after controlling for both Choice 1 and Choice 2. We have hence reported only the results for the first two choices.

We calculated each subject's choice diversity in each satiation state (by pooling their choice data in each trial in both sessions) using Shannon's diversity index[50]. Diversity index data were analysed using linear mixed effects models fit by maximum likelihood with the package "lme4" (v 1.1-13)[48] in R (v 3.4.1)[49] . We tested whether choice diversity could be significantly predicted by choice order (whether it was the first or second choice), species or satiation state. We tested interactions between species and satiation state, species and choice order and satiation state and choice order.

We calculated the duration subjects attempted to make "additional" choices in either the initial, inspection phase or after making the three permitted choices ("Extra attempts"- see Table 3 on Page 35 for definition). These data were analysed using generalised additive models for location, scale and shape with the package "gamlss" (v 5.0-5)[51] in R (v 3.4.1). Data distributions were identified using the "gamlss.Dist" package (v 5.0-3). We used a GAMLSS model with the generalised inverse Gaussian distribution to test whether the duration of extra attempts could be significantly predicted by species, satiation state or an interaction between the two. We adopted a model reduction approach based on selecting models by minimising their generalised Akaike information criteria[52].

5.1.5.6 Results

We found an effect of satiation state (Wald χ^2 = 4.7, P = 0.03) but not species (Wald χ^2 = 1.09, P = 0.296) on the proportion of chosen food-types (Figure 7, below). The interaction between species and satiation state was not significant (Wald χ^2 = 0.721, P = 0.396).

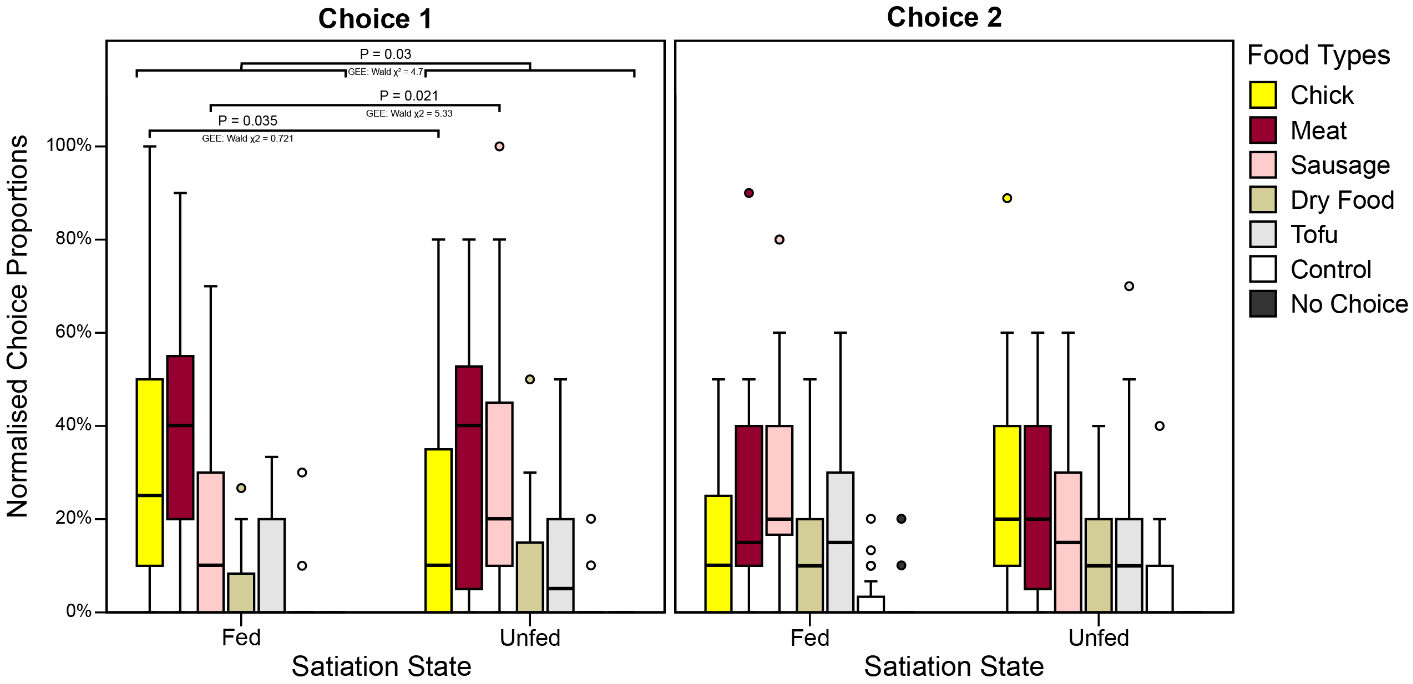

Figure 7: Proportion of food-types chosen first (left) and second (right) in each satiation state, normalised by number of trials. Circles indicate outliers.

A closer analysis of each food type individually (see Table 4 below for a summary of results) showed that the effect of satiation state was driven mainly by two factors: (1) Subjects (both dogs and wolves) chose chicks significantly less when unfed than fed (Wald χ^2 = 4.449, P = 0.035) (Fed: 30%, Unfed: 18.18%); (2) Dogs and wolves chose meat differently between satiation states (Wald χ^2 = 5.33, P = 0.021). A Post hoc Estimated Marginal Means analyses (Wald χ^2 = 11.77, P = 0.008) revealed that wolves chose meat 20% less when unfed (Holm-Bonferroni corrected P = 0.005) than when fed, while dogs did not differ in the proportion of meat chosen between satiation states. For complete model information and parameter estimates for the first choice, see Pages 106 to 113 of the Appendix.

Table 4: Factors predicting the likelihood of a food being chosen as the first choice.

Food Type	Species		Satiation state		Species*Satiation state	
	Wald χ^2	P	Wald χ^2	P	Wald χ^2	P
Chick	0.768	0.381	4.627	0.031	1.683	0.194
Meat	0.002	0.969	1.025	0.311	5.126	0.024
Sausage	0.241	0.623	2.961	0.085	0.73	0.787
Dry Food	0.001	0.979	2.573	0.109	1.905	0.168
Tofu	1.114	0.291	0.949	0.330	0.191	0.662

We found no effect of species (Wald $\chi^2 = 0.231$, $P = 0.631$) or satiation state (Wald $\chi^2 = 3.094$, $P = 0.079$) on the proportion of food chosen by subjects as their second choice. The interaction between species and satiation state was not significant (Wald $\chi^2 = 1.926$, $P = 0.165$). Overall, foods chosen in the second choice were not predicted by their proximity to the first choice (Wald $\chi^2 = 2.254$, $P = 0.133$). There were no significant interactions between the proximity to the first choice and species (Wald $\chi^2 = 2.001$, $P = 0.157$) or proximity to the first choice and satiation state (Wald $\chi^2 = 0.006$, $P = 0.936$). The second choice was significantly affected by the first choice but only if sausage (and not other food types) was chosen as first choice (Wald $\chi^2 = 5.486$, $P = 0.019$).

A closer analysis of each food type individually (for a summary of results, see Table 5 and Table 6 on Page 39) showed that these effects did in fact, differ between food types. A significant species effect emerged in an interaction with feeding condition in the subjects' preference for tofu. Post hoc Estimated Marginal Means analyses (Wald $\chi2 = 24.174$, $P < 0.001$) revealed that when unfed, wolves were less likely than dogs to choose tofu (Holm-Bonferroni corrected $P = 0.035$).

We found a significant interaction between feeding condition and proximity to the first choice in the subjects' preference for meat. Post hoc Estimated Marginal Means analyses (Wald $\chi2 = 20.173$, $P < 0.001$) revealed that subjects were 33.34% less likely to choose meat when it was in proximity to the first choice in the unfed (Holm-Bonferroni corrected $P = 0.008$) but not in the fed condition (Holm-Bonferroni corrected $P = 0.489$).

Proximity to the first choice significantly affected subjects' preference for tofu, dry food and chicks. Tofu was 78.58% more likely to be chosen when in proximity to the first choice. Dry food was 38.88% more likely to be chosen when in proximity to the first choice, but this difference was on the threshold of significance ($P = 0.05$). Chicks were 13.34% more likely to be chosen when they were not close to the first choice.

Further, feeding condition significantly affected subjects' preference for chicks. Regardless of species, subjects were 15% more likely to choose chicks when unfed than when fed (as opposed to the first choice). The likelihood of choosing sausage was significantly higher if chicks, meat or dry food were chosen first. For complete model information and parameter estimates for the second choice, see Pages 114 to 128 of the Appendix.

Table 5: Factors predicting the likelihood of a food being chosen second.

Food Type	Species		Feeding Condition		Species*Feeding Condition		Proximity to Choice 1 (PrC1)		PrC1*Species		PrC1*Condition	
	Wald χ^2	P	Wald χ^2	P	Wald χ^2	P	Wald χ^2	P	Wald χ^2	P	Wald χ^2	P
Chick	0.024	0.877	4.775	0.029	2.019	0.155	6.066	0.014	1.799	0.180	0.755	0.385
Meat	3.590	0.058	0.300	0.584	0.005	0.584	1.913	0.167	1.609	0.205	11.934	0.001
Sausage	0.559	0.455	1.322	0.250	0.291	0.589	10.714	0.001	1.999	0.157	1.393	0.238
Dry Food	0.971	0.324	0.017	0.897	0.056	0.813	*3.858*	*0.05*	0.092	0.761	0.402	0.526
Tofu	6.041	0.014	5.318	0.021	4.523	0.033	19.681	< 0.001	1.243	0.265	2.792	0.95

Table 6: Likelihood of a food being chosen second as predicted by the food chosen first (continued from Table 5).

Food Type	Choice 1: Chick		Choice 1: Meat		Choice 1: Sausage		Choice 1: Dry Food		Choice 1: Tofu	
	Wald χ^2	P	Wald χ^2	P	Wald χ^2	P	Wald χ^2	P	Wald χ^2	P
Chick	-	-	1.053	0.305	6.517	0.011	0.100	0.752	0.083	0.773
Meat	0.253	0.615	-	-	0.077	0.781	0.866	0.352	3.499	0.061
Sausage	9.731	0.002	7.699	0.006	-	-	11.024	0.001	2.348	0.125
Dry Food	2.290	0.130	2.109	0.143	0.419	0.517	-	-	0.042	0.837
Tofu	0.540	0.463	0.258	0.611	0.108	0.742	0.584	0.445	-	-

The interaction between species and satiation state did not have a significant effect on the time subjects spent attempting to get food outside of the permitted choices (t = 0.238, P = 0.514). Overall, regardless of satiation state (t = 0.897, P = 0.372), wolves spent more time than dogs (t = 2.874, P = 0.005) attempting to obtain extra food (median duration wolves = 9.2 sec, dogs = 4.6 sec) (Figure 8, below).

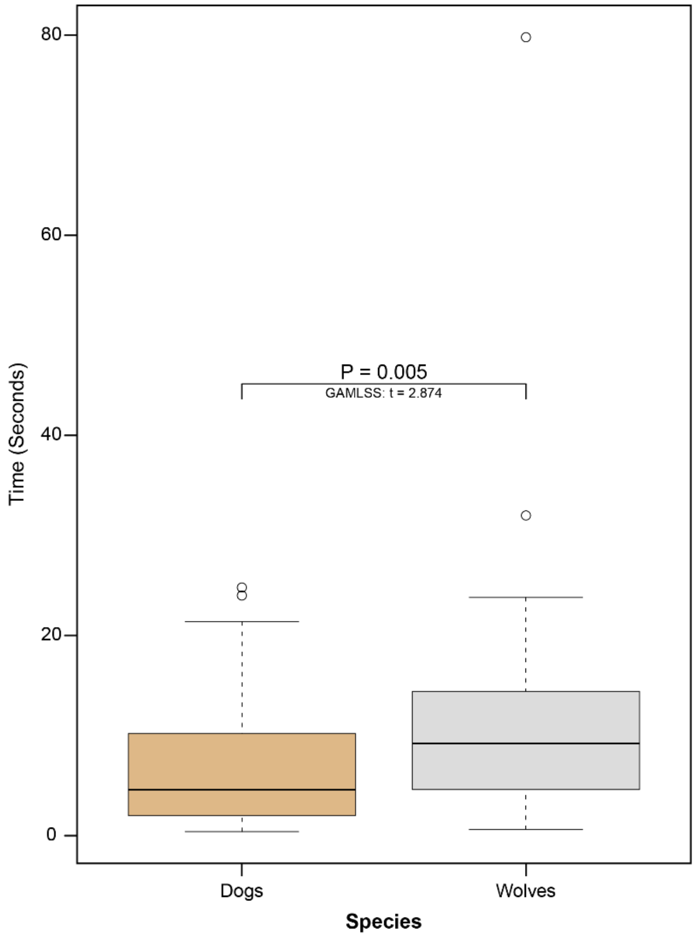

Figure 8: Duration of time subjects spent attempting to obtain inaccessible food. Circles indicate outliers.

There was a significant interaction between species and satiation state on the choice diversity (t = 2.511, P = 0.013). To better understand this interaction, we analysed the effect of satiation state on choice diversity separately for each species. In dogs, choice diversity did not vary significantly between satiation states (t = -0.984, P = 0.348), but in wolves, choice diversity was significantly higher in the unfed condition (t = 2.286, P = 0.028) (Figure 9, below). When unfed, dogs and wolves did not differ significantly in their choice diversity (t = 0.081, P = 0.936) but when fed, wolves were significantly less diverse in their choices than dogs (t = -2.66, P = 0.013).

Overall, choice diversity was significantly lower in the first choice than in the second choice (t = 3.60, P < 0.001). The interactions choice order by species (t = -0.691, P = 0.491) and choice order by satiation state (t = 0.176, P = 0.861) were not significant.

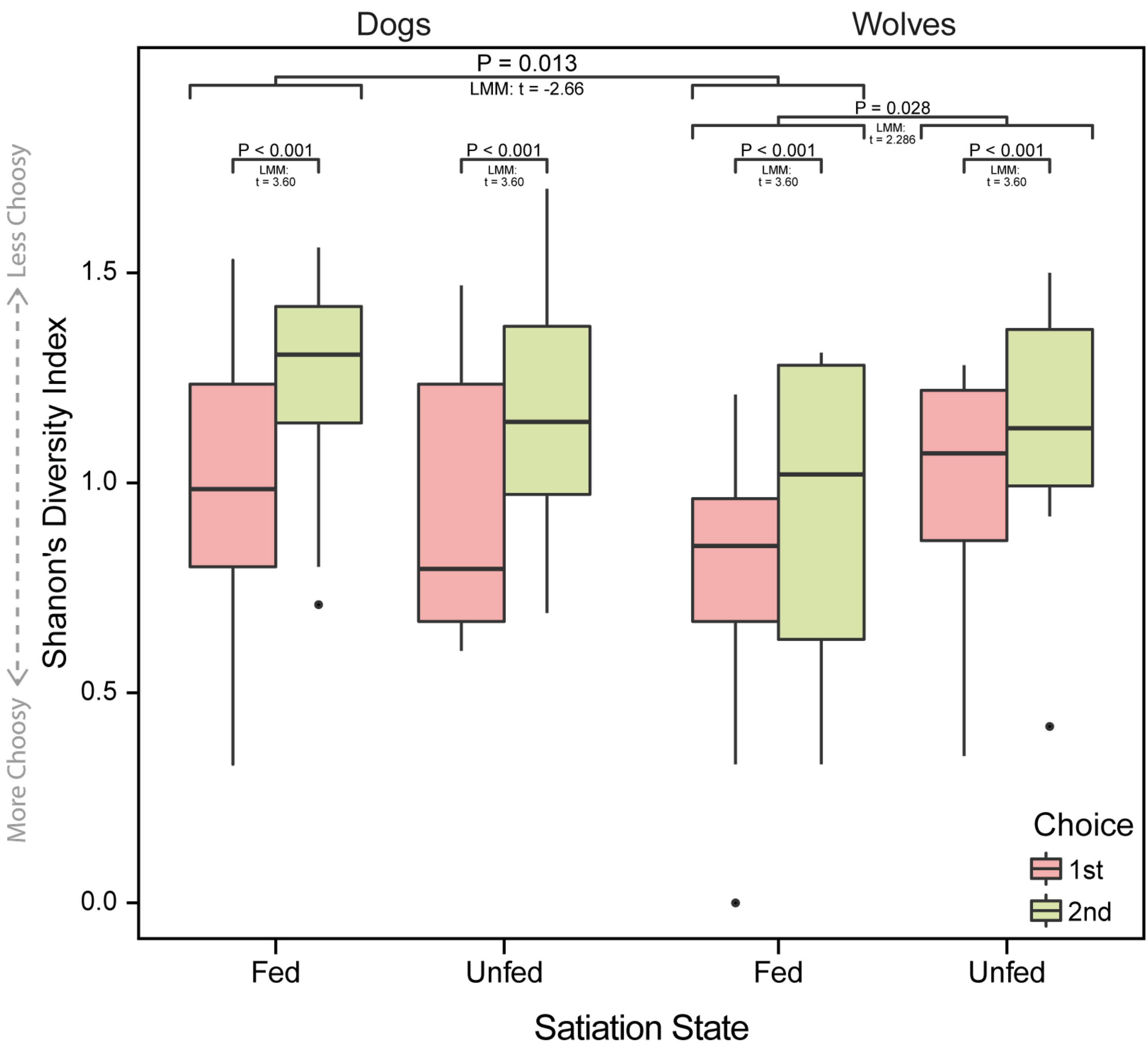

Figure 9: Choice diversity indices across choices, split by species and satiation state. Circles indicate outliers.

5.1.6 Discussion

The current study aimed to investigate the food preferences of dogs and wolves and to this end, we conducted food preference tests in two satiation states with two different paradigms.

We found only minor differences in dogs' and wolves' food preferences. Contrary to our prediction that dogs would show a weaker preference for meat over kibble rich in starch, dogs and wolves did not differ in their preference for meat in either testing paradigm. Both chose nearby foods in the same manner in the cafeteria paradigm. The only observed difference related to choice diversity, where wolves were less diverse (or more "selective") than dogs in the fed condition. Overall it appears that differences in dogs' and wolves' foraging styles have not affected their food preferences. While dogs' better starch digestion has been proposed to be an early effect of their domestication[22], recent studies suggest that this adaptation may have occurred later than previously thought[23]. Of course, "absence of evidence is not evidence of absence", and it is still possible that dogs' and wolves' foraging styles have affected their food preferences, but that these differences are overshadowed by stronger factors, such as the shared feeding habits and food availability of our captive animals, or that the relatively small sample size does not allow for such differences to emerge. Human food preference patterns can be affected by previously consumed meals. Prior to the "fed" condition, dogs were fed kibble and wolves were fed carcasses. It is possible that this may have caused dogs' preference for chicks and meat to increase (and wolves' preference to decrease) the following day and buffered potential differences in dogs' and wolves' food preferences. However, this is unlikely considering we found no differences in dogs' and wolves' preferences in either feeding condition.

We found similar patterns in dogs' and wolves' food preferences in both paradigms. Both chose three kinds of food the most: chicks, meat and sausage. Nutritive value may be one of the explanatory factors for this pattern. The high choice proportion of protein-rich chicks (after correcting for dry mass) is partly in line with work on macronutrient selection[3–6]. However, the tofu had a (corrected) protein content comparable to chicks and higher than meat and sausage, and the kibble had a higher calorific value than all three of the other foods. Yet, tofu and dry food were rarely chosen. If nutritive value was the sole explanatory factor, all protein-rich and high-energy foods should have had comparable choice proportions. That they did not could indicate that the hedonic quality of food (taste/flavour) may override nutritional value. Perhaps subjects avoided foods with extremely low or extremely high moisture contents, which is why tofu and kibble had low choice proportions. The high choice proportions of meat and sausage may have been influenced by their fat content (the highest from the foods we used). Dogs and wolves (like humans and several other animals[53]) may have evolved a preference for fatty foods which may have influenced this choice pattern.

The most important factor that emerges in determining the animals' choice is the rarity of the three most chosen foods in the subjects' daily diet (chicks being the rarest, followed by meat and then sausage). Here, it is also interesting to note that because of the different health requirement of dogs and wolves, their daily feeding regime is somewhat different: dogs receive a higher proportion of dry kibble (which is their staple diet) and only little meat from carcasses, whereas it is the opposite in wolves. 'Rarity' could have been a stronger motivating factor for dogs than wolves. Further, tastes of previously consumed meals are known to affect subsequent food choices in humans[54] and perhaps even in animals: our dogs' and wolves' different feeding regimes could have influenced their food preferences (for example, consuming kibble as a meal the evening prior to a test may increase preference for meat in the test and vice-versa). Yet, no substantial differences emerged in the dogs' and wolves' choices.

Satiation did not affect food choice in the two-choice test and only moderately did so in the cafeteria paradigm. In the latter, subjects were significantly less likely to choose chicks as the first choice when unfed. The proportion of sausage chosen first increased marginally. It is noteworthy that when 'unfed', subjects chose meat and/or chicks as their second choice even when they were not 'nearby' foods. This suggests that subjects sought these foods out, supporting results showing that these were indeed their preferred foods. In contrast, dry food and tofu were more likely to be chosen when they were nearby foods. It is likely that these choices were made impulsively immediately after Choice 1. However, these effects of satiation were not evident in the two-choice task. While widely used[41,42], the two-choice task is known to have shortcomings[44]. In our case, it is likely that task contingencies such as side biases or experiences with similar, two-choice tasks that subjects participated in earlier (such as the numerical competence task[55], for example) may have overshadowed the effects of satiation in the two-choice food preferences task. By offering multiple choices, the cafeteria paradigm allows the construction of a preference scale of foods which can then be understood further with diversity indices. In fact, subjects were significantly more diverse when making their second choice than their first choice. This supports the idea that subjects initially sought out highly preferred foods and were not as choosy afterwards.

While choice diversity did not differ between satiation states in dogs, wolves were significantly more diverse in their choices when unfed compared to when fed. Hunger can affect foraging styles[27]. A proximate explanation for the current results could be that wolves were more "impulsive" when hungry and paid less attention to the position of foods. A number of studies have compared dogs' and wolves' inhibitory control but have not found consistent differences[56,57]. However, satiation level has never been considered in such studies. Current results suggest it may be of interest for future research; orexigenic and/or anorexigenic measures of satiety could be used to objectively quantify "hunger levels"[58–60].

Establishing that dogs and wolves in our facility do not differ in their preferences has significant implications for the studies conducted here. Our subjects have participated in several behavioural and cognitive experiments over their lifetime, many of which have involved food rewards[17,28,30,33,56,61,62]. For example, we found wolves to be more persistent than dogs in trying to obtain inaccessible food, a result that is in line with numerous other studies[17,28,67–69,30–32,56,63–66]. Considering the results from this experiment, we can firmly conclude that the observed dog-wolf differences were not driven by differences in dogs' and wolves' food preferences but were driven more likely by differences in their motivational states regardless of the type of food reward.

Taken together, we found no evidence for the hypothesis that dogs' and wolves' foraging styles have affected their food preferences and conclude that domestication has most likely not affected food preferences significantly in dogs. Choice patterns were mildly affected by hunger in wolves, but not in dogs. We suggest that the cafeteria paradigm is more sensitive than a two-choice task in detecting such differences. Finally, our results indicate that differences in our dogs' and wolves' performance in behavioural/cognitive tests with food rewards is not affected significantly by diverging food preferences in dogs and wolves.

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5.2 Article 2:

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[+] Co-first Author

[*] Corresponding Author

Differences in persistence between dogs and wolves in an unsolvable task in the absence of humans.

Akshay Rao[a,b*+], Lara Bernasconi[b,c +], Martina Lazzaroni[a,b], Sarah Marshall-Pescini[a,b], Friederike Range[a,b]

a: Wolf Science Center, Domestication Lab, Konrad-Lorenz Institute of Ethology, University of Veterinary Medicine of Vienna, Savoyenstraße 1a, A-1160 Vienna, Austria

b: Comparative Cognition, Messerli Research Institute, University of Veterinary Medicine of Vienna, Medical University of Vienna, University of Vienna, Vienna, Austria

c: Department of Comparative Cognition, University of Neuchâtel, Neuchâtel, Switzerland

* Corresponding author

\+ Co-first author

5.2.1 Abstract

Despite being closely related, dogs consistently perform worse than wolves in independent problem-solving tasks. These differences in problem-solving performance have been attributed to dogs' greater reliance on humans, who are usually present when problem-solving tasks are presented. However, more fundamental motivational factors or behavioural traits such as persistence, motor diversity and neophobia may also be responsible for differences in task performance. To better understand what drives dogs' and wolves' different problem-solving performance, it is essential to test them in the absence of humans. Here, we tested equally raised and kept dogs and wolves with two unsolvable tasks, a commonly used paradigm to study problem-solving behaviour in these species. Unlike previous studies, we ensured no humans were present in the testing situation. We also ensured that the task was unsolvable from the start which eliminated the possibility that specific manipulative behaviours were reinforced. This allowed us to measure persistence and motor diversity more accurately. In line with previous studies, we found wolves to be more persistent than dogs. We also found motor diversity to be linked to persistence and persistence to be linked to contact latency. Finally, subjects were consistent in their performance between the two tasks. These results suggest that fundamental differences in the motivation to interact with objects drive the differences in dogs' and wolves' performance in problem-solving tasks. Because correlates of problem-solving success i.e. persistence, neophobia, and motor diversity are influenced by species' ecology, our results support the social ecology hypothesis which postulates that the different ecological niches of the two subspecies (dogs have evolved to primarily be scavengers and thrive on and around human refuse, while wolves have evolved to primarily be group hunters and have a low hunting success rate) have at least partly shaped their behaviours.

Key words: Persistence, Dog-Wolf comparison, Behavioural variety, Comparative cognition, Problem-solving behaviour, Physical Cognition, Individual Consistency.

5.2.2 Introduction

Animals need to solve various ecological and social problems to survive. Studies across taxa have found problem-solving success to depend on several psychological propensities (also referred to as the "correlates of problem-solving success"). These include neophobia (the fear of new situations or objects), motor diversity and behavioural flexibility (the repertoire of problem-solving behaviours an animal displays, and its ability to find novel solutions to already known problems, or use known solutions to solve novel problems) and persistence or task directed motivation[1–13] (quantified as the amount of time an animal spends tackling a task). These correlates are interconnected: motor diversity and behavioural flexibility is positively correlated with persistence[6–8,10,12] and all three are negatively correlated with neophobia[2–4,6,8,12,14,15]. They are influenced by a species' ecology, social structure and living conditions[13,16–18]. For example, birds in variable environments and habitats were less neophobic and had greater motor diversity and behavioural flexibility than conspecifics in more stable environments[19–22]. Persistence was higher in social carnivores than in closely related non-social ones, as well as in captive hyenas than in wild conspecifics[8,23]. Personality (or behavioural type), has also been shown to play a role in problem-solving styles[24]. For instance, in certain contexts, a reactive behavioural type is associated with slower, less exploratory behaviour and lower persistence, while a proactive behavioural type is associated with faster exploratory behaviour and higher persistence[24]. Performing multiple problem-solving experiments over time can help understand consistency in animals' performance and hence, the effect behavioural types have on the correlates of problem-solving success.

Dogs and their closest living relatives, wolves[25], differ strongly in their problem-solving success in various paradigms[1,5,26–36]. For instance, wolves were more task-focussed, showed greater motor diversity, were more persistent and could generalise better than dogs in a string-pulling task[1]. They were faster and more successful at obtaining food from puzzle boxes[5,29,30,32] and performed better at a visual discrimination task than dogs[27]. These differences have partly been attributed to the different ecological niches they live in[30,31,35–40]. Unlike wolves, dogs live in a human dominated niche[31]. They may hence rely on humans more than wolves do, both, in terms of social support[41], and possibly as 'problem-solvers'. Authors often describe dogs displaying copious amounts of human-directed behaviours during problem-solving experiments. There is ample evidence that when confronted with a problem in the presence of a human, dogs are more likely than wolves to look towards and/or interact with the human instead of engaging in the task[5,28,30].

Two hypotheses might explain why dogs engage in and persist less than wolves in these situations. First, it is possible that previous experience with humans, who often solve problems for dogs, drives the dogs' behaviour. In the human-dominated niche that dogs live in, humans often provide support in all important domains including providing access to resources such as food[31]. Hence, dogs might expect humans to solve problems for them and thus turn to humans for help without trying very hard to solve problems by themselves. However, differences in problem-solving success are visible even in dogs and wolves that have identical experiences with humans[32,34–36,40,42–44]. The second, likelier hypothesis that may explain differences in dogs' and wolves' problem-solving performance is that adaptations to their respective feeding ecologies[45] have resulted in dogs and wolves evolving differences in their correlates of problem-solving success, particularly in persistence. Wolves are primarily hunters[45] with very variable success rates (between 10% and 49%) and need to be highly persistent to survive[46]. Dogs, however, are primarily scavengers[31,45], depend mostly on human refuse[31,45,47–49] and may not need to be as persistent. Accordingly, in a problem-solving experiment with a human present, dogs might be less persistent, give up earlier than wolves and then, as there is nothing else to do, explore the test environment, do nothing, or turn towards the human. Following this reasoning, turning to humans might not be a strategic choice to obtain help or support instead of solving the task independently as has been previously suggested[28,41,50,51], but rather a consequence of reduced persistence[32]. Overall, while the socioecology-based hypothesis postulates fundamental differences in motivation (regardless of human presence), the human reliance hypothesis suggests that, while dogs and wolves might have similar problem-solving skills (when alone), dogs turn towards humans as an alternative strategy to solving problems by themselves.

A first step towards teasing these hypotheses apart and better quantifying persistence without direct human influence on dogs' and wolves' performance is to conduct problem-solving tasks in the absence of humans with dogs and wolves with controlled human exposure and rearing histories. Udell (2015) headed in this direction by testing subjects in three conditions - alone, with a silent human, and with an encouraging human. Wolves were more persistent than pet dogs in the task even when alone, suggesting that dogs may have a "generalized dependence on humans" (Pg. 1). However, the authors highlighted that such a dependence may be a result of differences in the life experiences that the pet dogs and hand-reared wolves had. Pet dogs may have been discouraged by their owners to 'problem-solve' the trash-can or kitchen drawers, which may have resulted in dogs being inhibited when confronting a novel object. Differences in life experience are known to affect problem-solving in dogs: highly trained dogs (agility, retriever, search and rescue) showed more independent problem-solving abilities than untrained pet dogs, who conversely looked towards the owner longer[52] in such tasks.

Here, we presented similarly raised and kept pack-living dogs and wolves with two different unsolvable tasks in the absence of humans on two separate occasions. Each task consisted of an object baited with food that was inaccessible to the animal. To avoid animals' expectations regarding the role of a human in the task, we presented the object in their home enclosure where humans rarely enter. Humans entering the enclosure is instead associated with a routine enrichment procedure where the animals are shifted out of the home enclosures, humans scatter food inside, leave, and then shift the animals back in. Apart from removing the expectation of human presence, using an enclosure associated with the enrichment procedure (familiar to all animals) guaranteed a similar motivational state for all subjects. Furthermore, because food motivation is known to influence problem-solving behaviour[12,15,16,53], we tested subjects early in the morning without feeding them the evening prior to the test. Finally, as food motivation is influenced by food quality[54–56]; we used high value food (based on a previously performed preference test[57]) for testing.

We measured persistence as the time spent manipulating the presented objects. We predicted that if human presence during testing and/or general differences in dog-wolf experiences with humans[5] are the main factors responsible for wolves' greater persistence in problem-solving experiments, dogs and wolves would not differ significantly in their persistence in the current study. If, however, adaptations to the respective feeding niches play a bigger role than their experience with humans, wolves would be significantly more persistent than dogs.

Although several studies have compared species[12] and evaluated the effect of different environments on problem-solving behaviour, fewer studies have also examined how problem-solving correlates relate to each other (in birds[12], in mammals[3,6,8]). Therefore, in the current study, apart from persistence, we also measured motor diversity when subjects attempted to extract the food from the presented objects (the number of different object-directed manipulative behaviours our subjects exhibited), the latency for subjects to contact each object (contact latency; typically used as a measure of neophobia[12]) and the body posture subjects exhibited during approach and manipulation (low-insecure vs. high-confident).

Studies have found animals that spend longer engaged in a task to also tend to utilize a greater variety of behaviours[16,58,59]. In line with this, we expected to find a positive correlation between persistence and motor diversity. The relationship between persistence and contact latency may be more multifaceted, as contact latency could be a measure of neophobia but also a measure of (dis)interest in an object. To try teasing these possibilities apart, we included body postures when analysing the data for contact latency. If contact latency was a measure of neophobia, we expected it to be higher in subjects that showed an insecure body posture (known to be related to fear and insecurity[40]) during approach. If no such relationship emerged, it may be that contact latency was a measure of the animal's interest in the task.

Sih & Del Giudice, (2012) proposed that persistence, neophobia and interest may form parts of a behavioural syndrome. If these are indeed personality traits, they would be correlated with each other and be stable over time and context[60]. Hence, regardless of whether contact latency is a measure of neophobia or interest, we expected it to be negatively correlated with persistence in both species. Finally, we evaluated whether individual consistency in persistence and in contact latency would emerge across the two tasks. Considering that may be personality traits[24,58], we predicted that our subjects would indeed be consistent in their persistence and contact latency across tasks.

To sum up, our study had three aims: (1) to test hypotheses about why dogs and wolves (with controlled rearing history and human exposure) differ in their persistence, (2) to assess relationships between the correlates of problem-solving success and (3) test subjects' consistency in their performance across tasks.

5.2.3 Materials and methods

5.2.3.1 Ethics Statement

Special permission to use animals in cognitive studies is not required in Austria (Tierversuchsgesetz 2012—TVG 2012). The "Tierversuchskommission am Bundesministerium für Wissenschaft und Forschung (Austria)" allows research without special permissions regarding animals. We obtained ethical approval for this study from the 'Ethik und Tierschutzcommission' of the University of Veterinary Medicine (Protocol number ETK-07/08/2016).

5.2.3.2 Subjects

We tested 17 adult mixed-breed dogs (*Canis lupus familiaris*) (7 F, 10 M; mean age = 4 ± 1.6 years) and 12 adult grey wolves (*Canis lupus*) (4 F, 8 M; mean age = 6.3 ± 1.7 years) from October 2016 to February 2017 (Table 7 on Page 54). All animals were similarly hand-raised with conspecifics in peer groups by humans (dogs were raised separately from wolves, both at different times) and similarly kept in conspecific packs at the Wolf Science Centre, Austria. They had continuous access to humans who bottle-fed and later hand-fed them in the first 5 months of their life. During the first weeks of puppyhood, they were kept inside. They had free access to a 1,000 m^2 outdoor, "puppy" enclosure from their second month on and were moved to 2,000 – 8,000 m^2 "living" enclosures at five months of age. The animals as adults live in these larger "home enclosures". Packs are regularly moved from one home enclosure to another for logistic reasons (such as to make it easier to walk an animal on leash from its home enclosure to a test conducted indoors, or to a touristic event). All packs have resided in all home enclosures.

Every enclosure is equipped with bushes, trees, logs, shelters and permanent drinking water installations. While humans are not continuously present in living enclosures, all animals do have social contact with them through several means: animals voluntarily participate in cognitive and behavioural experiments, and/or training, and/or other social events at least once a day. Animals are rewarded with food for participating in these activities. This routine ensures that they are cooperative and attentive towards humans and allows weekly veterinary checks without sedating the animals. All animals at the WSC are intact and males are vasectomised. Over the course of their lives, all animals at the WSC have participated in the same behavioural and cognitive experiments and have participated in the same training activities.

Table 7: Subjects.

Subject	Species	Sex	Date of Birth	Age (in years) when tested
Amarok	Wolf	M	04/04/2012	4.7
Aragorn	Wolf	M	04/05/2008	8.3
Chitto	Wolf	M	04/04/2012	4.3
Geronimo	Wolf	M	02/05/2009	7.3
Kaspar	Wolf	M	04/05/2008	8.6
Kenai	Wolf	M	01/04/2010	6.6
Nanuk	Wolf	M	28/04/2009	7.3
Shima	Wolf	F	04/05/2008	8.4
Tala	Wolf	F	04/04/2012	4.3
Una	Wolf	F	07/04/2012	4.3
Wamblee	Wolf	M	18/04/2012	4.5
Yukon	Wolf	F	02/05/2009	7.3
Asali	Dog	M	15/09/2010	5.9
Banzai	Dog	M	02/04/2014	2.4
Binti	Dog	F	15/09/2010	5.9
Bora	Dog	F	02/08/2011	5.0
Enzi	Dog	M	02/04/2014	2.3
Gombo	Dog	M	21/03/2014	2.4
Hiari	Dog	M	21/03/2014	2.4
Imara	Dog	F	21/03/2014	2.4
Layla	Dog	F	03/08/2011	5.1
Maisha	Dog	M	18/12/2009	6.6
Meru	Dog	M	01/10/2010	5.8
Nia	Dog	F	22/07/2011	5.0
Nuru	Dog	M	24/06/2011	4.9
Panya	Dog	F	02/04/2014	2.4
Pepeo	Dog	M	02/04/2014	2.3
Sahibu	Dog	M	21/03/2014	2.4
Zuri	Dog	F	24/06/2011	5.1

5.2.3.3 Apparatus

One object was a perforated, 1.5 kg, hard plastic sphere, 24 cm in diameter (commercially available "Lion Feeder Ball" from www.ottoenvironmental.com; henceforth referred to as the "ball") (Figure 10, below). The other was a modified, perforated PVC sewage pipe (22 cm in diameter, 40 cm in length; henceforth referred to as the "pipe") (Figure 11, below). Prior to the test, each object was baited with large chunks of strongly smelling sausage and meat out of sight of the subject.

Figure 10: Commercially available Lion Feeder Ball

Figure 11: Modified Sewage Pipe

5.2.3.4 Experimental Setup

Before a test session began, we anchored one of the objects to a camping peg driven into the ground in the subjects' home enclosure using a 30-cm long metal chain and marked a two-meter radius around it with a commercially available, bright red timber marking spray. This was done out of sight of the test subject. The peg was positioned such that any interactions the subject had with the object could be recorded from multiple angles without any visual obstructions. Two video cameras (recording at 1920 × 1080 pixels at 50 progressive frames per second) and one smartphone (Samsung Galaxy Note 2) were mounted on tripods at three different angles outside the enclosures. We used "IP Webcam", a freely available app developed by Pavel Khlebovich (http://ip-webcam.appspot.com), to remotely monitor the trial, whilst staying out of sight of the subject during the entire procedure.

Subjects were tested in their home enclosure as they least expect a human to be present inside. Tests at the Wolf Science Centre are normally conducted in specific “testing enclosures” and humans (including trainers) only visit the animals in the home enclosures in very specific contexts (i.e. pack visits, animal care and short, training demonstrations during public guided tours). Subjects were in different home enclosures when they were tested with each object.

5.2.3.5 Procedure

We tested subjects individually between 7:00 a.m. and 10:00 a.m. One animal per pack was tested per session and two to three sessions were conducted per week, never on consecutive days. To ensure high food motivation, the subjects were not fed on the evening before the test. Before the test, we shifted the entire pack out of their home enclosure into an empty enclosure from where their home enclosure was out of sight. The test object was placed in the now empty home enclosure (see 5.2.3.4 Experimental Setup on Page 55). The focal subject was then led back into the home enclosure. We started the test session when the animal entered the 2m-radius (see “Start” in Table 8 under 5.2.3.6 Behavioural Coding on Page 58).

The subject was given 5 minutes to interact with the object. We defined “First Contact” as the first time the subject touched or sniffed the object (in case of a sniff, when the nose was within 5 cm of the object). In case there was no “First Contact” within 5 minutes, the test session was terminated. If the subject did not interact (i.e. “Sniff” or “Manipulate” the object – see Table 8 under 5.2.3.6 Behavioural Coding on Page 58 for definitions of all behaviours and behavioural states) with the apparatus at all for 5 minutes after “First Contact”, the session was terminated. After the subject started interacting with the object, it could continue doing so for as long as it wanted. Each time the subject stopped interacting with the object, we started a 5-minute countdown. If the subject resumed interacting with the object before the countdown expired, we let the test session continue and reset the 5-minute counter. If the subject did not resume interacting with the object by the time the countdown expired, we terminated the test session. To simplify, if a subject started interacting with the object, it could continue doing so for an infinite duration and pause as many times as it liked, as long as the pauses were shorter than 5 minutes; once it paused for over 5 minutes, the test session ended.

After the session ended, we shifted the subject out of the home enclosure and retrieved the object. We carefully washed each object after each session to remove any possible odour cues left by the previously tested subject. Each subject was tested first with the ball and then re-tested with the pipe one and a half to three months later. Two wolves, Chitto and Tala, had to be tested with the pipe six months after their test with the ball due to the onset of the mating season. As we needed to keep our study comparable to a complementary study with free-ranging and pet dogs which were presented with only the ball[61], we were unable to counterbalance the presentation order of the two objects. We used each object only once per subject to avoid object-specific learning effects (e.g. to avoid subjects learning “food from inside this specific green spherical thing cannot be extracted”).

5.2.3.6 Behavioural Coding

We recorded all tests on video and coded behaviours using Solomon Coder beta 100926 (a behaviour coding software developed by András Péter, Dept. of Ethology, Budapest, www.solomoncoder.com). We categorised manipulative behaviours based on the number of body parts they involved and by the nature of the behaviour. For instance, we differentiated between using paws to hold an object while gnawing at it and using paws to scratch vigorously at the object. “Holding” an object with the paws added stability which probably made “Biting” more efficient, while “Scratching” did not add stability, but was probably a different strategy to extract the food within the object. The coded behaviours and their definitions are summarized in Table 8 on Page 58. See the Supplementary Video linked on Page 129 of the Appendix for an example of each behaviour. We defined “Persistence” as the time (in seconds) a subject spent in the “Manipulating” behavioural state. We defined “Contact Latency” as the time (in seconds) a subject took from “Start” to “First Contact”. We defined “Motor Diversity” as the number of unique “Manipulative Behaviours” shown by a subject.

Table 8: Definitions of coded behaviours.

Behaviour	Definition
Approach Posture	
Neutral	Body relaxed; tail relaxed below the plane of the back.
Confident	Body rigid or relaxed, tail above or at the same level of the plane of the back.
Insecure	Tail between the legs (and wagging), and/or back (slightly) lowered, ears can be rearward, and the head can be lowered, approach can be jerky and /or cautious.
Friendly	Body relaxed, tail wagging horizontal or below the plane of the back.
Manipulation Posture	
Insecure	Tail between the legs, even wagging, or back lowered, ears can be rearward, and the head can be lowered, body can be rigid, and movement can be jerky.
Friendly	Tail wagging, not between the legs.
Confident	Body rigid or relaxed, tail above or at the same level of the plane of the back.
Behavioural States	
Sniff	The subject smells or attempts to smell the object with its snout less than 10 cm from the object.
Manipulating	The subject physically manipulates the object using its paws, snout, mouth or any combination of the three and shows any of the “Manipulative Behaviours”.
Markers	
Start	The subject places a paw inside the marked 2-meter radius.
End	The subject stops manipulating the object for 5 minutes or The subject has not started manipulating the object for 5 minutes after making “First Contact” or the subject has not made “First Contact” 5 minutes after “Start”.
Manipulative Behaviours	
Nose	The subject moves the apparatus or tries to lift it with only its nose.
Bite	The subject bites the object / raises the object off the ground by holding it with its mouth by the chain, by the object’s surface or edges, or by the screws / pulls either the chain, the screws or the object’s surface or edges with its mouth.
1 Paw	The subject places its paw on the object without scratching it / uses one paw to scratch at the top of the object while attempting to move the object towards itself / away from itself / laterally.
1 Paw & Bite	The subject places its paw on the object and simultaneously bites the object.
1 Paw & Nose	The subject sniffs / lifts / pushes the object with its nose or licks the object while also manipulating the object with one paw.
Paws On	The subject places both paws on the top of the object and presses the object down.
Scratch	The subject scratches the object’s surface with both its paws by alternating them (without its paws touching the ground).
Scratch & Bite	The subject scratches at the object with both its paws while simultaneously biting it.
Hold & Bite	The subject holds and stabilises the object with both paws on the sides of it or on the top of it for the pipe, while biting it on top.
Dig	The subject uses one or both of its paws to dig at the ground in immediate proximity of the object.
Other Behaviours	
Pee	The subject urinates on the object or on or inside the circle.
Lick	The subject licks the object.
Bark	The subject vocalizes at the object.
Withdraw	The subject jumps away from the object in a neutral or insecure posture after looking at it, approaching it, sniffing it, or manipulating it.
Lay down	The subject lays down or sits next to the object or inside the marked radius.

5.2.3.7 Analyses

We excluded one dog (Gombo) from the analyses for the pipe as he extracted some food from the object due to an apparatus malfunction (a piece of meat that we used had several long fibres that were too close to the holes in the apparatus, which allowed Gombo to easily grab them and pull a piece of meat out through one of the holes). We excluded one wolf (Una) from the latency analyses for the ball as her contact latency was an outlier (28 seconds; $G = 5.09$, $U = 0.007$, $P < 0.001$) (potentially because she was tested at the onset of the breeding season). We excluded one dog (Nuru) from the analyses of the pipe as he was overly persistent with the pipe, making his manipulation duration an outlier (1,361 seconds, $G = 3.10$, $U = 0.63$, $P = 0.008$). We used Grubbs tests[62] implemented with the "outliers" package (v0.14)[64] in R v3.4.3[63] to confirm that these individuals were indeed outliers. See Page 129 of the Appendix for how results changed when these two individuals were included in the analyses. All other subjects were included in the analyses (Ball: N = 11 wolves, 17 dogs, Pipe: N = 12 wolves, 15 dogs).

We used inter-class correlations[64] implemented with the "psych" package (v1.7.8)[66] in R v3.4.3[63] to calculate inter-observer reliability. A second coder coded 20% of the data and all variables achieved reliability coefficients between 0.89 and 0.99 between the two coders.

We first used an exploratory, principal component analysis (PCA) for each object to understand our data. Performing several univariate analyses may not have allowed us to understand the combined effect of all explanatory variables on our subjects' task performance. As we were primarily interested in variables that have previously been shown to relate to problem-solving success, we included persistence, motor diversity, latency to contact, approach posture and likelihood of manipulation as explanatory variables. While we could have included several more variables (such as the frequencies of each manipulative behaviour), we chose to restrict the number of explanatory variables due to our relatively small dataset. We used the PCAmixdata package (v3.1)[67] in R (v3.5.1)[68] which is designed for analysing multivariate data that is a mixture of continuous, discrete and categorical variables.

The PCAmixdata analysis algorithm classified subjects based on our explanatory variables which did not include "Species". The rationale behind leaving species out of the analysis was to allow the algorithm to classify subjects purely based on task performance without any pre-existing bias. This way, if, for example, there were distinct behavioural differences between the two species, it would result in clusters composed entirely of dogs and entirely of wolves, with each cluster having significantly different values of one or more behavioural variables. Conversely, if there were no differences, we may still have found clusters with different variable values, but these clusters would be mixtures of dogs and wolves.

We ran a separate multivariate analysis for each object as including data from both objects in one analysis made it difficult to meaningfully interpret cluster structures. Separating the two objects allowed us to analyse whether subjects performed similarly with both objects. Additionally, we applied an orthogonal rotation to each PCA to make interpretation easier. We used the “PCArot” function which uses a generalization of the varimax procedure for mixed data[69]. This procedure helps associate variables with a selected number of principal components (or dimensions) more clearly by providing either large (almost 1) or small (almost 0) loadings. While the variable loadings on each dimension (and hence the variance explained by each dimension) change after rotation, the total variance explained by the selected dimensions remains unchanged.

The PCA gave us useful insights into patterns in our data but did not let us test whether there was a statistically significant difference in dogs’ and wolves’ performance when interacting with the two objects (we did not make any inferences based on results from the PCA). Hence, we further analysed persistence, motor diversity and contact latency individually using generalised additive models for location, scale and shape (“gamlss” v5.1-0)[70] in R v3.5.1. We used the “gamlss.Dist” package (v5.0-6) to fit distributions to our data. We evaluated the distribution of each response variable and specified the best fitting distribution in the models. We evaluated model fits both by their generalised Akaike information criteria[71] and by the distribution of the model residual quantile-quantile plots. This approach enabled us to analyse the data without using data transformations (transformations could have affected our interpretations of the results[72,73]).

To reduce the risk of our choice of distributions resulting in overfitting models to our data, we validated our models’ results by fitting identical models with other probable distributions and compared models with different distributions but similar AIC values. Further, when our data fit multi-parametric variations of the same distribution equally well, we used the distribution with fewer parameters (e.g. “Persistence” fit Weibull-1, Weibull-2 and Weibull-3 but we used Weibull-1, as this distribution is described with one parameter as against two or three). Results did not change between models, implying that they were robust against choice of distribution. For the sake of brevity, we have only reported results from models with the best fitting distributions here. See the pages 130 to 181 of the Appendix for the complete distribution selection, model reduction and model validation processes, outputs and scripts.

To account for repeated measures, we included the individual as a random factor in all models that included “Object” as a fixed factor. As our subjects’ ages varied, we included “Age” as a factor in all our models to account for any effects this may have on subjects’ task performance[74]. When interactions were not statistically significant, we ran a reduced model that included the same fixed effects but not the interaction term. We have reported the results from these, reduced models whenever interactions were not significant.

Based on the PCA's results, we used a Fisher's Exact Test in R v3.5.1 to investigate whether dogs and wolves differed statistically in their likelihood to manipulate the objects. Our PCA suggested that wolves and dogs may differ in their persistence, but that this difference may be influenced by object type. To investigate this, we used a GAMLSS model to evaluate the effects of species, object type and a two-way interaction between species and object type on persistence, the response variable. To ensure model convergence, we added a miniscule constant (0.00001) to all persistence values. We fit this model with the Gamma distribution and validated it with the Box-Cox T Original, Weibull and Log-normal distributions. This process allowed us to achieve our first aim of testing our hypothesis about dog-wolf differences. We left motor diversity out of this analysis for two reasons: (1) our hypothesis pertained specifically to differences in *persistence* between dogs and wolves and (2) from our PCA (and from further analysis for our second aim), persistence and motor diversity appeared to be correlated; this collinearity may have negatively impacted our interpretation of model results[75].

For our second aim, we focussed on understanding the relationships between the correlates of problem-solving success within dogs and within wolves. We analysed data for both species separately by running separate GAMLSS models for dogs and for wolves. The rationale behind this decision was that the only hypothesis we had pertaining to dog-wolf differences was about persistence and did not encompass other behavioural measures.

We ran two GAMLSS models with contact latency as the response variable. Our PCA suggested that contact latency may be related to object type, and that approach posture and persistence may influence contact latency differently in both objects. Hence, we included object type, persistence, approach posture and two two-way interactions (object type by persistence and object type by approach posture) as explanatory variables. For dogs, we fit the model with the Inverse Gaussian distribution and validated it with the Inverse Gamma, Log-normal and Gamma distributions. For wolves, we fit the model with the Log-normal distribution and validated it with the Gamma, Weibull and Box-Cox Cole-Green distributions.

We ran two GAMLSS models with motor diversity as the response variable. As our PCA suggested that persistence and motor diversity may be correlated, and because this correlation appeared slightly different between the two objects, we included persistence, object type and a two-way interaction between persistence and object type as explanatory variables. For dogs, we fit the model with the Zero Adjusted Poisson distribution and validated it with the Zero Inflated Poisson, Zero Adjusted Negative Binomial (Type I) and Zero Inflated Negative Binomial (Type I) distributions. For wolves, we fit the model with the Poisson distribution and validated it with the Zero Adjusted Poisson, Negative Binomial type I and Generalised Poisson Distributions.

Our last aim was to test subjects' consistency in performance between the two tasks. As we had not restricted the duration a subject could manipulate both objects and as contact latency could have varied due to the layout of the enclosure subjects were tested in, absolute persistence and latency values may not have been meaningfully comparable. Hence, we scaled these values from 0 to 1 in each task separately using the following formula for both variables: $V_s = \frac{V_i - Min\,(V_{all})}{Max\,(V_{all}) - Min\,(V_{all})}$ where V_s = scaled value (persistence or contact latency), V_i = individual's unscaled value, Min / Max (V_{all}) = the minimum / maximum values for that object. We used a Spearman's rank correlation on the scaled persistence and scaled contact latency data to test whether subjects were consistent in their persistence and contact latency between the two objects. We calculated a consistency score for persistence and contact latency by taking the absolute value of the difference between subjects' scaled persistence scores (or scaled contract latency scores) for the ball and for the pipe. We used separate GAMLSS models to assess the effect of species on the consistency scores for persistence and contact latency. For persistence, we fit the model with the Generalised Beta Type 1 distribution and validated it with the Logit Normal distribution. For contact latency, we fit the model with the Simplex distribution and validated it with the Logit Normal and Beta Original distributions.

5.2.4 Results

5.2.4.1 Multivariate approach to wolf-dog comparison

The PCA for the ball produced five dimensions, the first three of which explained 83.28% of the variance in our data. Pre and post orthogonal rotation results are summarised in Table 9, below. The rotation significantly improved variable loadings on dimensions 1 and 3. Hence, we investigated these dimensions further.

Table 9: Summary of the PCA results for the Ball.

Before Orthogonal Rotation								
Dimension	**Eigenvalue**	**Variance Explained**		**Variable Loadings**				
		Individual	**Cumulative**	**Contact Latency**	**Persistence**	**Motor Diversity**	**Approach Posture**	**Manipulation Likelihood**
1	2.1059	42.1187	-	0.1925	0.6168	0.7670	0.0353	0.4944
2	1.0595	21.1904	63.3091	0.5968	0.1596	0.0696	0.0934	0.1401
3	0.9985	19.9693	83.2783	0.0046	0.0454	0.0496	0.8473	0.0516
4	0.6380	12.7605	96.0388	0.2010	0.1117	0.0156	0.0215	0.2882
5	0.1981	3.9612	100.0000	0.0051	0.0665	0.0982	0.0025	0.0257
After Orthogonal Rotation								
1	1.8086	36.1719	-	0.0001	0.8191	0.8548	0.0008	0.1337
2	1.3214	26.4285	62.6003	0.7849	0.0003	0.0312	0.0000	0.5050
3	1.0339	20.6780	83.2783	0.0089	0.0023	0.0002	0.9751	0.0474

We found that dogs and wolves segregated into two near-distinct clusters along dimension 1, but not along dimension 3 (Panel A of Figure 12 on Page 64). Persistence (0.82) and motor diversity (0.85) loaded very strongly on dimension 1 (Panel B of Figure 12 on Page 64), suggesting that the segregation between dogs and wolves was likely due to differences in either persistence, motor diversity, or both, and that these two variables may be correlated. We found two distinct clusters along dimension 3, but each of these clusters were composed of both dogs and wolves. Approach posture loaded very strongly (0.98) on dimension 3 (as did contact latency, but to an almost negligible extent: 0.009) (Table 9 on Page 62 and Panel B of Figure 12 on Page 64). This suggested that there may be a very weak (if any) connection between contact latency and approach posture, and that neither of these variables were likely to be responsible for dog-wolf differences. The PCA for the pipe also produced five dimensions, the first three of which explained 87.03% of the variance in our data. Pre and post orthogonal rotation results are summarised in Table 10, below. We investigated dimensions 1 and 2 further as the rotation significantly improved variable loadings on them.

Table 10: Summary of the PCA results for the Pipe.

Before Orthogonal Rotation

Dimension	Eigenvalue	Variance Explained		Variable Loadings				
		Individual	Cumulative	Contact Latency	Persistence	Motor Diversity	Approach Posture	Manipulation Likelihood
1	2.3801	47.6022	-	0.2343	0.6770	0.8871	0.1554	0.4262
2	1.3100	26.1996	73.8018	0.4153	0.0922	0.0064	0.4906	0.3055
3	0.6613	13.2266	87.0284	0.2499	0.0330	0.0275	0.2972	0.0537
4	0.5132	10.2645	97.2929	0.0985	0.1593	0.0005	0.0567	0.1983
5	0.1354	2.7071	100.0000	0.0020	0.0386	0.0785	0.0000	0.0163
After Orthogonal Rotation								
1	2.0270	40.5395	-	0.0525	0.6832	0.8414	0.0062	0.4437
2	1.1986	23.9721	64.5116	0.0002	0.0032	0.0243	0.9370	0.2339
3	1.1258	22.5167	87.0284	0.8468	0.1158	0.0553	0.0001	0.1079

Unlike with the ball, dogs and wolves did not segregate into distinct clusters along either dimension (Panel A of Figure 13 on Page 65). Like with the ball, persistence (0.68) and motor diversity (0.84) loaded strongly on dimension 1 (Panel B of Figure 13 on Page 65), suggesting that these variables may be correlated. Approach posture and contact latency loaded strongly on different dimensions (Table 10, above, and Panel B of Figure 13 on Page 65). This supported results with the ball and suggested that there may not be a connection between contact latency and approach posture and that neither variable contributed to dog-wolf differences.

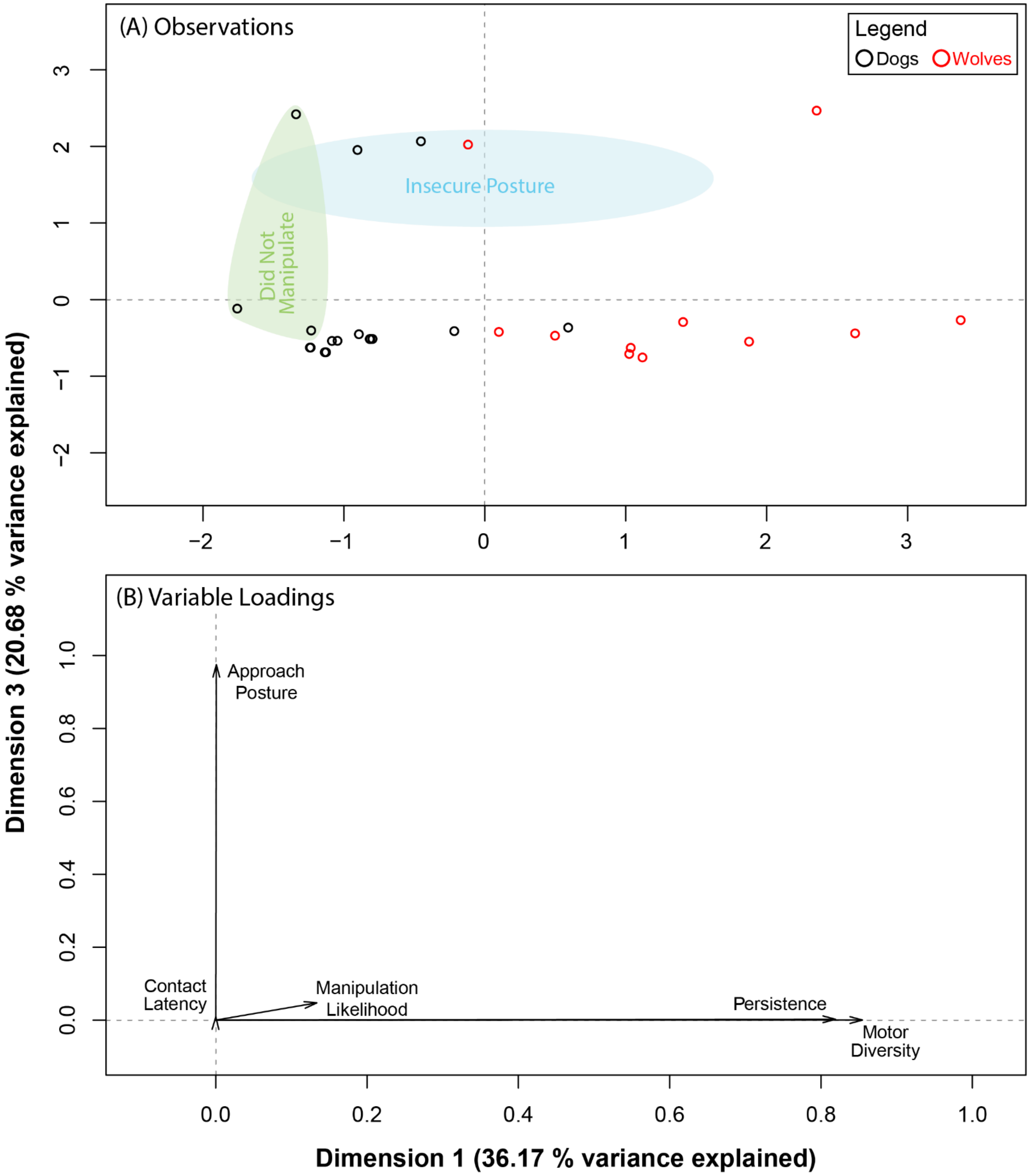

Figure 12: Results for the PCA for the Ball.

Panel A shows where each data point placed with respect to dimensions 1 and 3 (after orthogonal rotation).

Panel B shows how behavioural variables loaded on dimensions 1 and 3 (after orthogonal rotation).

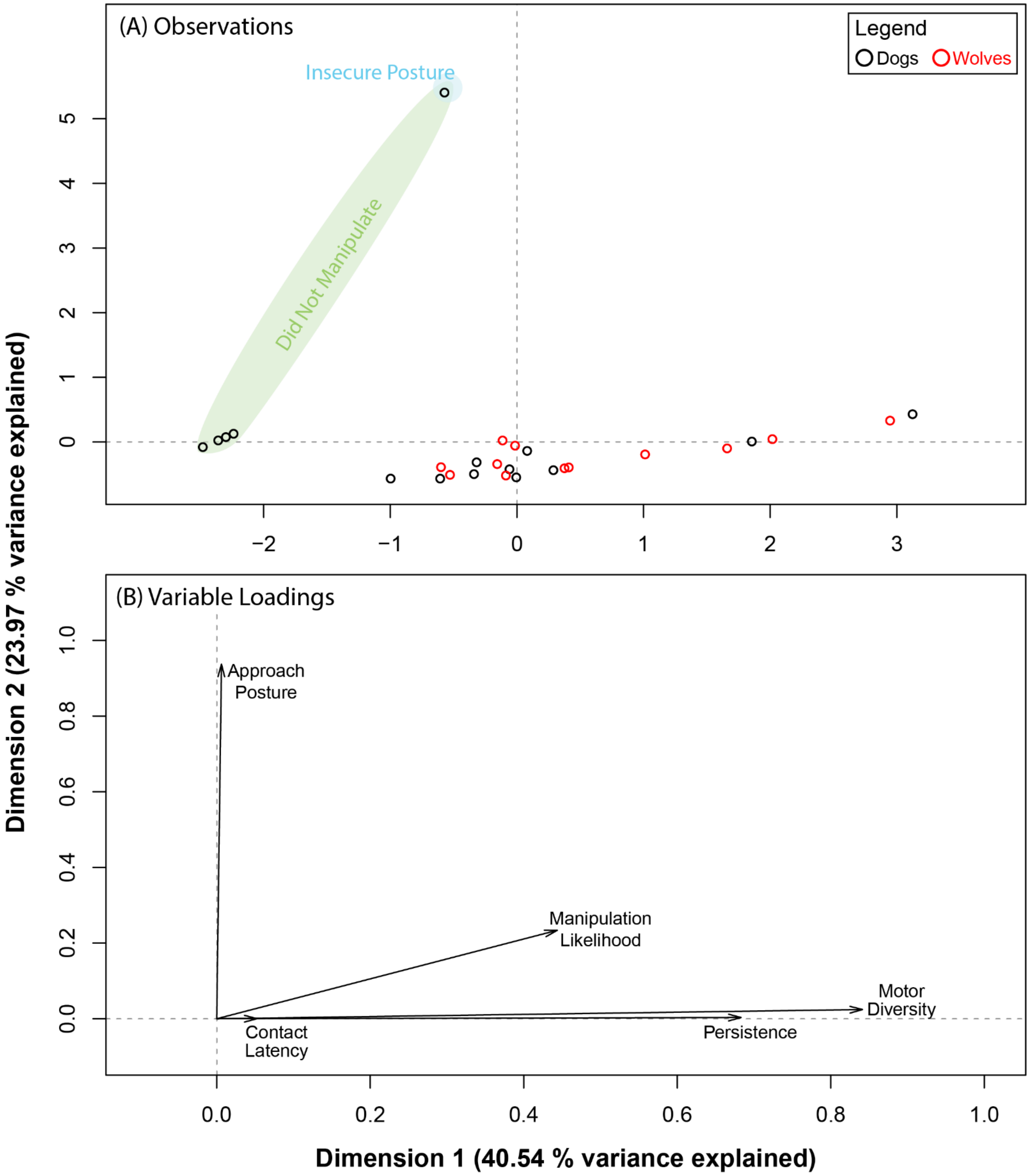

Figure 13: Results for the PCA for the Pipe.

Panel A shows where each data point placed with respect to dimensions 1 and 2 (after orthogonal rotation).

Panel B shows how behavioural variables loaded on dimensions 1 and 2 (after orthogonal rotation).

5.2.4.2 Differences in persistence between wolves and dogs (GAMLSS)

Overall, 14 out of 17 dogs manipulated the ball and 10 out of 15 dogs manipulated the pipe. In contrast, all 11 wolves manipulated the ball and all 12 wolves manipulated the pipe. Wolves were significantly more likely to manipulate objects than dogs (Fisher's Exact Test, Odds Ratio = 0.0, 95% conf. interval 0.00 – 0.71, P = 0.015). Though the PCA suggested that persistence may have been affected by object type, the interaction between species and object was not significant (GAMLSS: t = -1.47, P = 0.15). Wolves were more persistent than dogs (GAMLSS: t = 3.73, P < 0.001) in their manipulation of the objects regardless of object type (Panel A of Figure 14, below). Neither subjects' age (GAMLSS: t = 0.76, P = 0.45) nor object type (GAMLSS: t = 1.06, P = 0.29) affected persistence (Panel B of Figure 14, below).

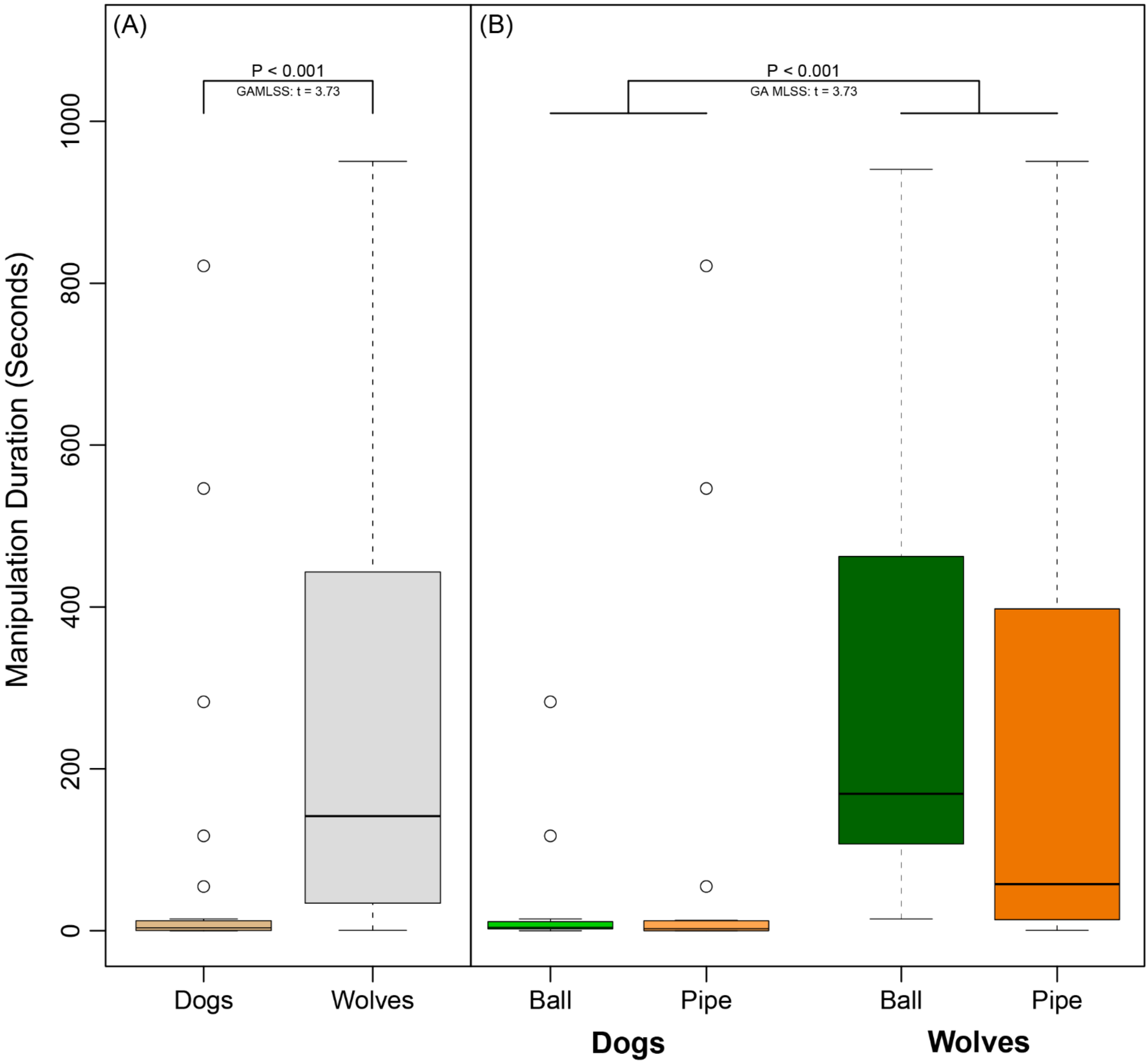

Figure 14: Differences in persistence between dogs and wolves.

Panel A shows the time (in seconds) dogs and wolves spent manipulating both apparatuses combined.

Panel B shows the time (in seconds) dogs and wolves spent manipulating each object separately.

Circles indicate data points that were outside the upper quartile plus 1.5 times the interquartile distance.

5.2.4.3 Relationship between correlates of problem-solving within wolves and dogs

Contact latency decreased with persistence in both dogs (GAMLSS: t = -4.35, P < 0.001; Figure 15, below) and wolves (GAMLSS: t = -3.42, P < 0.01; Figure 16, below). Neither the interaction between object type and persistence (GAMLSS; Dogs: t = 1.91, P = 0.07, Wolves: t = -0.96, P = 0.35) nor that between object type and approach posture significantly affected contact latency (GAMLSS; Dogs: t = -1.32, P = 0.20, Wolves: t = -1.61, P = 0.13). Neither object type (GAMLSS; Dogs: t = 1.44, P = 0.16, Wolves: t = -0.96, P = 0.35) nor approach posture (GAMLSS; Dogs: t = 0.43, P = 0.67, Wolves: t = -1.72, P = 0.10) significantly affected contact latency in either species. Contact latency decreased with age in dogs (GAMLSS: t = -2.85, P < 0.001; Figure 17, below) but not in wolves (GAMLSS: t = -0.04, P = 0.97).

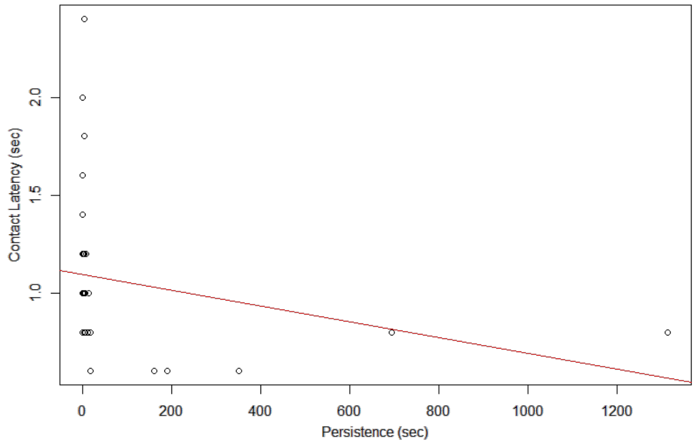

Figure 15: Contact latency vs. Persistence (Dogs)

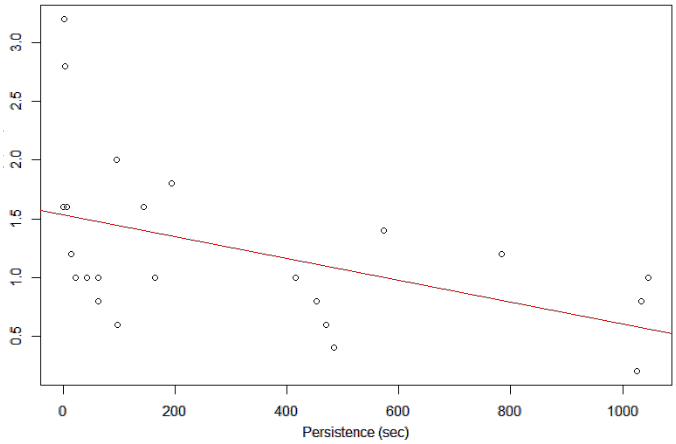

Figure 16: Contact latency vs. Persistence (Wolves)

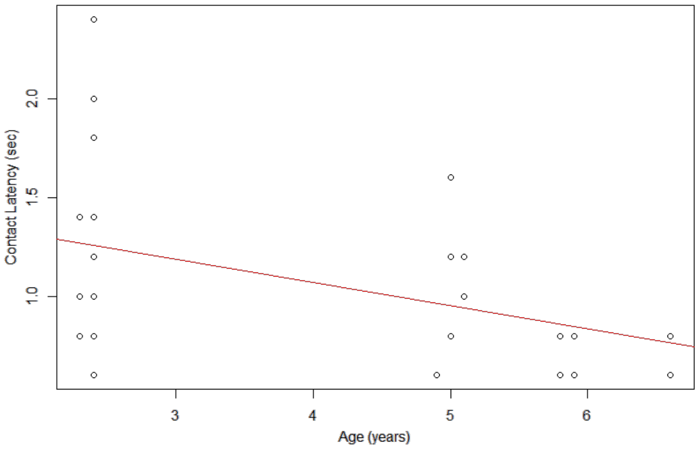

Figure 17: Contact latency vs. Age (Dogs)

Motor diversity increased with persistence in both dogs (GAMLSS: t = 3.74, P < 0.001; Figure 18, below) and wolves (GAMLSS: t = 3.72, P = 0.001; Figure 19, below). The interaction between object type and persistence was not significant (GAMLSS; Dogs: t = -1.67, P = 0.11, Wolves: t = 1.62, P = 0.12). Neither object type (GAMLSS; Dogs: t = -1.74, P = 0.09, Wolves: t = -1.61, P = 0.12) nor age (GAMLSS; Dogs: t = -0.58, P = 0.57, Wolves: t = 1.20, P = 0.24) significantly affected motor diversity in either species.

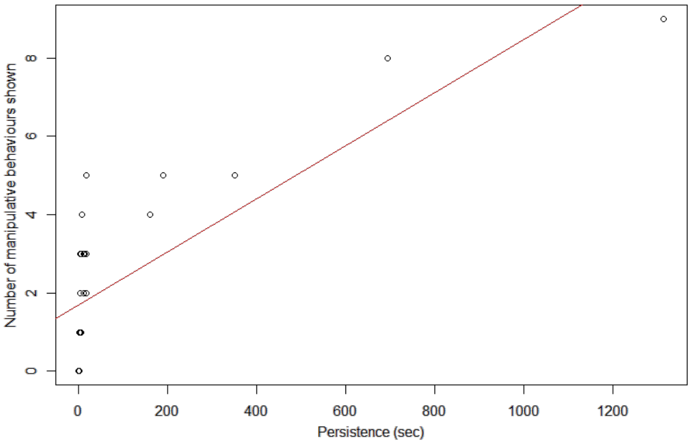

Figure 18: Motor diversity vs. Persistence (Dogs)

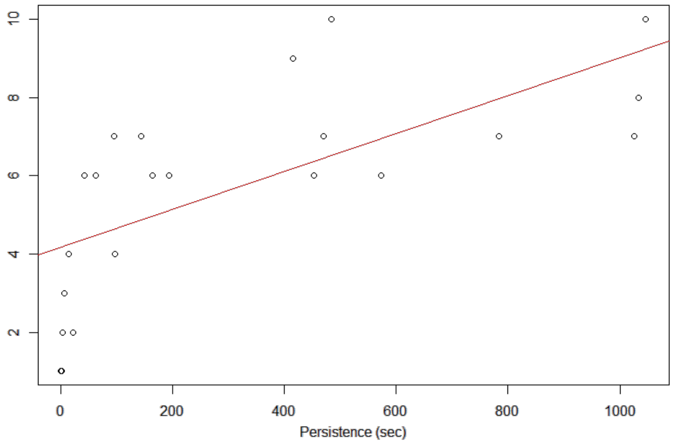

Figure 19: Motor diversity vs. Persistence (Wolves)

5.2.4.4 Individual consistency

Subjects' persistence (Spearman's ρ = 0.71, P < 0.001) as well as contact latency (Spearman's ρ = 0.64, P < 0.001) across tasks were significantly correlated. Figure 20, below shows the subjects' scaled persistence in both tasks.

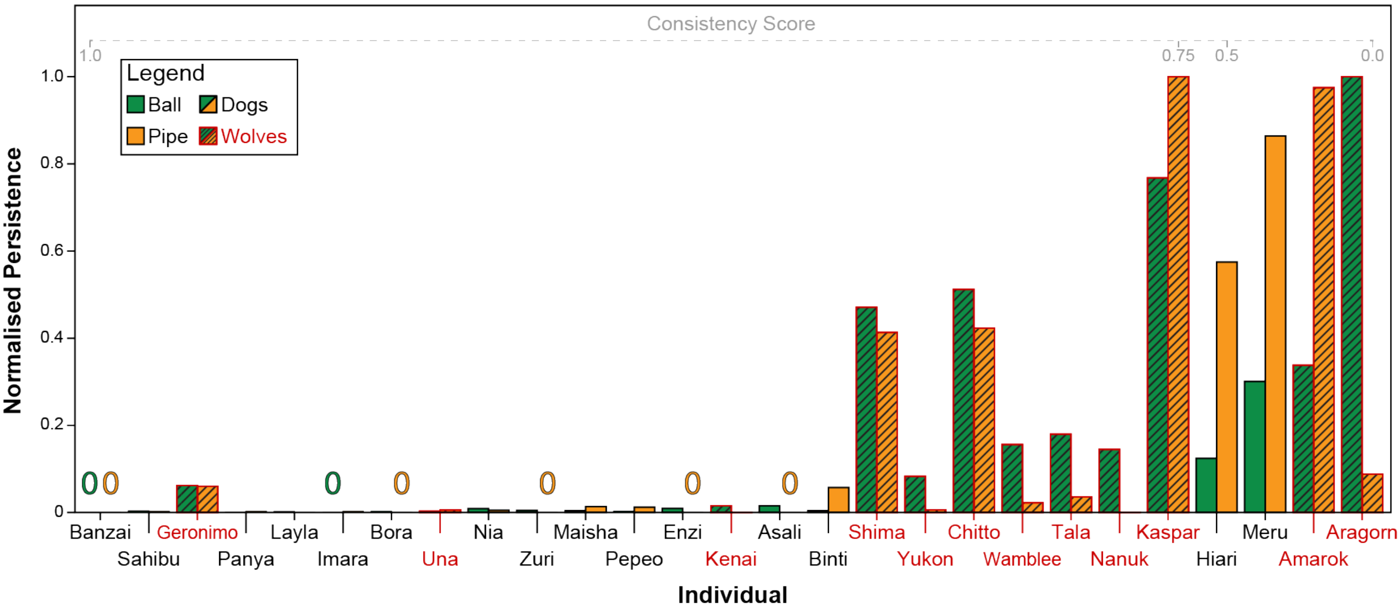

Figure 20: Every individual's persistence in both tasks, re-scaled from 0 to 1 for comparability.
Green bars indicate persistence with the ball, *orange bars* indicate persistence with the pipe.
Zeros indicate that the individual did not manipulate the object at all.
Individuals with *red names and hashed bars* are wolves, individuals with *black names and non-hashed bars* are dogs.
Individuals are arranged from left to right in descending order of consistency in persistence across tasks.

Overall, dogs were significantly more than consistent wolves in both, their persistence (GAMLSS: t = -2.31, P = 0.031) as well as in their contact latency (GAMLSS: t = -2.62, P = 0.02; Figure 21, below).

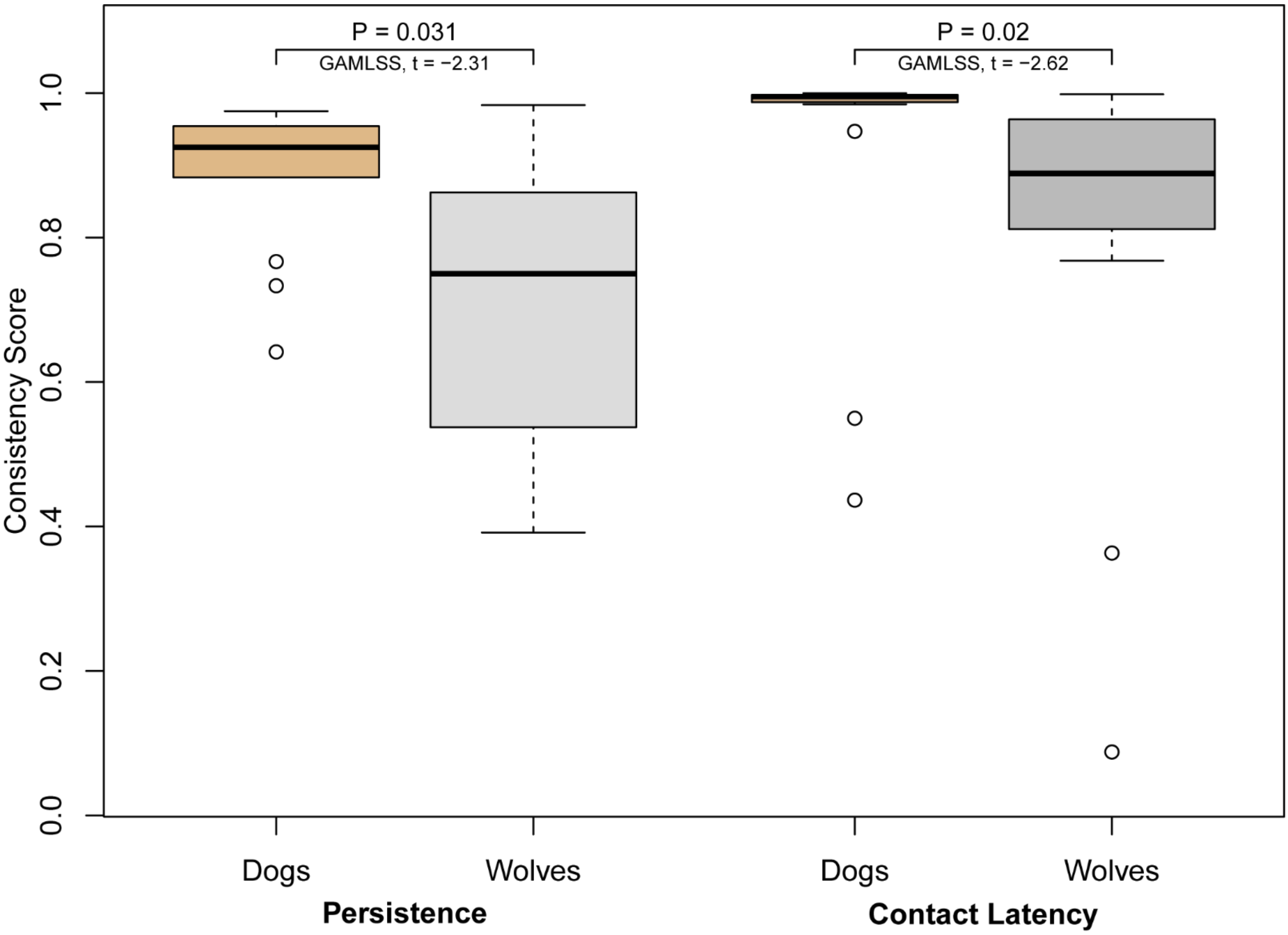

Figure 21: Intra-individual consistency in correlates of problem-solving success.
Circles indicate data points that were outside the upper quartile plus 1.5 times the interquartile distance.

For descriptive statistics of both groups' performance in each task and for complete model information, see the Page 129 of the Appendix.

5.2.5 Discussion

We tested similarly raised and kept dogs and wolves with two unsolvable tasks in the absence of humans on two separate occasions with three aims: First, to test hypotheses about why dogs and wolves with controlled rearing history and human exposure differ in their persistence in an independent problem-solving task; second, to evaluate relationships between correlates of problem-solving success in our subjects and third, to assess our subjects' consistency in task performance. We used two approaches when analysing our data: first, a multivariate principal component analysis and second, a set of univariate mixed models.

Results from the multivariate approach showed wolves to be more persistent and to have greater motor diversity with the ball than with the pipe. This could have been due to wolves' ability to generalise[1]. Wolves may have learned that trying to solve a task presented in that specific setting was futile and did not persist as long with the pipe which was presented as the second task. Alternatively, it is possible that a neophobic response may have affected wolves' persistence and motor diversity negatively[3,12,21] with the pipe.

However, wolves' contact latency, their persistence and motor diversity did not differ significantly between the ball and pipe when these measures were analysed with mixed models. Accordingly, it is unlikely that a neophobic response affected wolves' persistence and motor diversity. This lack of neophobic response may either be due to the objects themselves not being "intimidating" enough, or due to our subjects' experience with several novel objects over their lives. It is possible that like in the study by Moretti et al. (2015), contact latency was a measure of interest in novel objects rather than neophobia. While counterbalancing the order in which the two objects were presented would have allowed better control over novelty, neophobia and generalisation, we had to ensure that all subjects interacted with the ball first to keep this study comparable to a parallel one being run on free-ranging dogs (where testing an individual repeatedly with a gap of two or more weeks was impossible).

Our first, bottom-up, descriptive, multivariate approach categorized wolves and dogs according to behavioural measures (contact latency, approach posture, manipulation likelihood, motor diversity and persistence). This approach allowed us to see how our subjects differed in their behaviour and how behavioural aspects may be correlated. Importantly, as "species" did not factor into this analysis, clusters of dog/wolf data points were exclusively due to behavioural variables. Results from this analysis helped us compare wolves and dogs directly in their persistence and to decide which factors to include when modelling the other behaviour variables. However, as the multivariate analysis was a purely exploratory approach, we made our inferences and conclusions based on mixed models.

When directly comparing wolves' and dogs' persistence in the two tasks using mixed models, our results confirm numerous other studies[1,5,31–33,40,76] that have found wolves to be more persistent than dogs in object manipulation. These differences held even in the absence of humans during testing, and importantly, with dogs and wolves that have the same level of experience with both, humans and with interacting with different objects. A potential concern with using food as a motivator in comparative problem-solving studies is that different species may have different preferences for the same food. In our case, dogs and wolves did not differ in their preference for meat and sausage[57].

A related concern is whether these tasks truly test persistence or motivation to work for food. Persistence has been defined as “task-directed motivation”[12], but it is important to note that disentangling these two concepts is virtually impossible (and is not the focus of this study). Overall, our results can be explained neither by dogs’ (but not wolves) having been inhibited from interacting with objects in their daily lives (e.g. pet dogs), nor by dogs preferring to use a social problem-solving strategy in the presence of a human (i.e. by asking for help instead of solving the problem alone), nor by differences in dogs’ and wolves’ preference for the food used to bait the objects.

Contrary to Siwak (2001), we found older dogs to be more interested in test objects. Dogs at the WSC are kept differently from the beagle colony at the University of Toronto (WSC dogs live in groups while the beagles in Toronto are housed individually) and potentially have different life experiences. It is possible that at the WSC, older dogs have grown more accustomed to cognitive testing and are more task focussed than younger dogs, who may be more interested in exploring their environment instead.

We suggest that the results (wolves being more persistent than dogs) are in line with the hypothesis that differences in dogs’ and wolves’ problem-solving performance is due to adaptations to their respective feeding ecologies. Dogs have been proposed to be selected against directly manipulating their environment and potentially for lower persistence[1] with humans being intermediaries between dogs and their environment[77]. Wolves, however, require high levels of persistence to survive in the wild[46,78,79]. Further, wolves are more sensitive to their environment[1]; while they are more neophobic, they are also more explorative than dogs[2,40]. Considering animals in the current study had the same experience of human provisioning and interaction during object manipulation, we suggest that differences in persistence are more likely due to dogs’ and wolves’ adaptations to their respective ecological niches. The current results cannot reveal the extent to which dogs’ persistence is affected by their generalist-foraging style and by the active role being played by humans in their feeding ecology (such as humans providing dogs with food[79] or actively inhibiting them from interacting with objects, which may be the case with pet dogs). Comparing dog populations with varying levels of experience with humans (such as pet dogs and free-ranging dogs) may help to better understand whether dogs’ reduced persistence could be a result of humans inhibiting their interactiveness with objects.

In line with previous studies[6–8,10], we found motor diversity to be positively linked to persistence in both tasks in both dogs and wolves. Motor diversity and behavioural flexibility is important during foraging. Being able to employ and switch between different strategies both when hunting and when scavenging may increase success rates regardless of foraging style. We found persistence and contact latency to be negatively correlated. Our results are in line with predictions based on the concept of behavioural types[24]. Individuals that were faster to contact the apparatus, presumably were more interested and proactive in their approach and were persistent.

Finally, we found that our subjects were consistent in their persistence and contact latency between the two tasks. Persistence is an important aspect of animal personality[24,81–84]. We found dogs to be more consistent in their persistence (or lack thereof) and in their contact latency than wolves. A likely explanation for this could be that selection against persistence[1] and direct manipulation of the environment[2,30] may have resulted in a more consistent reactive-type personality. Wolves, having faced no such selection, may be more variable in their behaviour. Alternatively, wolves' ability to better generalise and understand that the task is unsolvable may have influenced the consistency in their performance. To disentangle these possibilities, it would be necessary to test subjects in tasks that are similar in concept but in different test settings. Further, utilising multiple tests would provide a better insight into inter-task performance consistency.

Our study was the first to test differences in persistence between similarly raised and experienced dogs and wolves in an unsolvable task in the absence of humans. Past studies have used tasks that have initially been solvable and later become unsolvable. It is possible that persistence may differ between these two designs. The "unsolvable task" paradigm has been widely used with dogs and wolves[5,28,32,41,85–88]. It involves repeatedly allowing a subject to find a solution to a simple foraging task, and then modifying the task to make it unsolvable. Data about persistence are usually collected in the unsolvable trial. This approach has certain drawbacks when studying the correlates of problem-solving success. First, it reinforces certain manipulative behaviours, potentially reducing the motor diversity that the subject would show in the unsolvable trial. Second, reinforcing task-engagement with solvable trials may potentially increase persistence in the unsolvable trial. A task that is unsolvable from the start may provide a more reliable measure of persistence. Third, as human presence affects dogs' and wolves' behaviour differently during the test, testing subjects in the presence of a human may make directly comparing wolves' and dogs' persistence difficult.

While several studies have investigated problem-solving behaviour in dogs and wolves, few have analysed consistency in problem-solving success in dogs[89,90], and none have done so in wolves. By testing dogs and wolves in independent problem-solving tasks with and without the presence of a human, using tasks that offer either controlled or random reinforcement and by using a battery of various physical problem-solving tasks, future studies could improve our understanding of how the domestication process has affected the problem-solving behaviour in the two canids, and the role personality traits play in their problem-solving behaviour. Our study provides an interesting starting point in this direction.

5.2.6 Conclusions

We compared equally raised and kept pack-living dogs and wolves in an independent problem-solving task using the unsolvable task paradigm in the absence of humans. Wolves were more likely than dogs to engage in the presented tasks and were more persistent at attempting to extract food from the presented objects. Results from this study support the socioecology-based hypothesis: fundamental differences in dogs' and wolves' correlates of problem-solving success have evolved due to differences in their feeding ecologies and are responsible for differences in their problem-solving performance. Further, persistence and motor diversity were positively correlated, and subjects were consistent (dogs more so than wolves) in their persistence and approach latency across tasks.

Comparing dog populations that have different experiences with humans (e.g. pets and free-ranging dogs) and testing subjects in identical tasks both, with and without humans present in the test setting may help further disentangle the human-reliance and socioecology-based hypotheses. Using a battery of conceptually similar tests across varying test settings may provide better insight into the role of behavioural types or personality in problem-solving success.

5.2.7 Acknowledgments

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5.3 Article 3:

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The role of domestication and experience in 'looking back' towards humans in an unsolvable task.

Sarah Marshall-Pescini[a,b*+], Akshay Rao[a,b+], Zsófia Virányi[a,b], Friederike Range[a,b]

a: Comparative Cognition, Messerli Research Institute, University of Veterinary Medicine of Vienna, Medical University of Vienna, University of Vienna, Vienna, Austria

b: Wolf Science Center, Dörfles 48, 2115 Ernstbrunn

* Corresponding author

\+ Co-first author

5.3.1 Abstract

A key element thought to have changed during domestication is dogs' propensity to communicate with humans, particularly their inclination to gaze at them. A classic test to measure this is the 'unsolvable task', where after repeated successes in obtaining a reward by object-manipulation, the animal is confronted with an unsolvable version of the task. 'Looking back' at humans has been considered an expression of dogs seeking help. While it occurs more in dogs than in socialized wolves, the level of exposure to human communication also appears to play a role. We tested similarly raised adult wolves and mixed breed dogs, pet dogs and free-ranging dogs. Unlike previous studies, we included 'persistence' in trying to solve the task as a potential explanatory factor in addition to species and levels of socialization. Wolves were more persistent than all dog groups. Regardless of socialization or species, less persistent animals looked back sooner and for longer. Free-ranging dogs, despite little exposure to dog-human communication, behaved similarly to other dogs. Together, these results suggest that basic dog-wolf differences in motivation and exploration may override differences in human-directed behaviour when animals are equally socialized, and that once the human is considered a social partner, looking behaviour occurs easily.

Key words: Persistence, Dog-Wolf comparison, Behavioural variety, Comparative cognition, Problem-solving behaviour, Physical Cognition, Individual Consistency

5.3.2 Introduction

Domestication is thought to have changed dogs' ability to communicate and cooperate with humans[1–4]. One key element of this communication is 'looking back' towards a human when confronted with an unsolvable task; this behaviour is considered to be a communicative act aimed at seeking human assistance. Indeed, in early studies comparing wolves and malamutes, Frank & Frank (1985) presented both with puzzle boxes of increasing complexity and noted how wolf pups would 'attack each puzzle immediately' and persist 'until the problem was solved or time ran out' (pp. 271) in contrast to dog pups who quickly reverted to seeking human attention upon discovering that the food was not immediately available. In a seminal study comparing dogs and wolves, Miklósi and colleagues found that when confronted with an unexpectedly unsolvable task, 4 month-old pet dogs were more likely to "look back" to their owner and did so sooner and for longer than wolves of the same age raised in a 'pet-like' environment[3]. Since this first study, the propensity to look back in dogs has been shown to differ between breed-groups[6,7] and to have a genetic basis[8,9], providing further circumstantial support for a potential effect of domestication on this behaviour.

Additionally, a variety of studies using the same paradigm have also shown that dogs' experience with dog-human communication may affect their looking back behaviour. For example, kennelled Labrador retrievers with reduced exposure to humans from birth (i.e. limited to daily contact with humans cleaning their kennels and putting down a bowl of food) showed a higher latency and shorter duration of looking back in an unsolvable task paradigm compared to breed-matched pet dogs[10]. Conversely, dogs that engaged in activities which required constant intensive coordination with their owners (e.g. agility) showed a higher propensity to look back in such tasks than both, pet dogs with no specific training experiences and dogs trained for more independent tasks (i.e. search and rescue)[11]. Furthermore, in two large-scale studies (175 and 125 dogs tested respectively) using the unsolvable task with a non-trained pet dog population, older dogs spent longer looking back than younger animals, leading authors to conclude this was likely an effect linked to their longer experience with humans in comparable situations[6,7]. Taken together, these results highlight that both the degree and type of interaction with humans has strong effects on dogs' 'looking back' behaviours in such tasks.

To further elucidate the roles of domestication and experience with human interactions in the 'looking back' response, we used the unsolvable task paradigm to test adult wolves (N = 15) and mixed-breed dogs (WSCD, N = 14) at the Wolf Science Center that, having been raised and kept in the same manner from birth, have been equally exposed to human communication (see Table 11 under 5.3.3.2 Subjects on Page 85).

Furthermore, we tested two populations of dogs with very different experiences of dog-human communication i.e. adult mixed breed pet dogs living in Vienna, Austria (PD, N = 19) and free-ranging dogs in India (FRD, N = 11, see Figure 22, below). The tested free-ranging dogs lived on the streets, were mostly dependent on scavenging on human refuse and although friendly with humans, had no known established relationship with any specific person/s. Based on this, we considered them representative of a more independent dog population with noticeably less experience of humans helping them to obtain out-of-reach objects/food compared to pet dogs living in close contact with their owners in a Western, urbanized environment.

Figure 22: A free-ranging dog on the streets of India 'looking back' towards the experimenter during the unsolvable trial.

Like previous studies, the task consisted of three trials in which subjects could overturn a container to obtain food, followed by a single trial in which the container was fixed to a board, thereby making the task unsolvable[11]. We analysed data comparing the groups on their likelihood and latency to look back, the duration and frequency of gazing at a human, and gaze alternation behaviours (i.e. the frequency of looking at the apparatus and then a human or vice versa). Furthermore, since a number of studies using different problem solving tasks have shown that wolves are more persistent than dogs in such tasks[5,12] and that more persistent animals are also those that look back less frequently[13–15], unlike previous studies using the 'unsolvable paradigm', we included persistence (i.e. the time spent interacting with the apparatus) as a potential explanatory factor alongside group (i.e. wolves, equally raised dogs, pet dogs and free-ranging dogs) in all our analyses (see 5.3.3.6 Analyses on Page 88).

We also extended the unsolvable trial to 3 minutes (compared to most studies in which animals had just 1 or 2 minutes to attempt the task[3,6,7]) to potentially allow more persistent animals to also exhibit 'looking back' behaviours. We nevertheless also report results of group comparisons when persistence was not factored into the analyses to allow for greater comparability with previous studies.

5.3.3 Materials and methods

5.3.3.1 Ethics Statement

All procedures and methods were discussed and approved by the institutional ethics committee in accordance with Good Scientific Practice guidelines and national legislation. All methods were performed in accordance with the relevant guidelines and regulations. Informed consent was obtained from all owners. Ethical approval for this study was obtained from the 'Ethik und Tierschutzkommission' of the University of Veterinary Medicine (Protocol number ETK-02/02/16 and ETK-03/02/16).

5.3.3.2 Subjects

5.3.3.2.1 Similarly raised and kept wolves and dogs

15 wolves (3F, 12M; mean age in years: 1.89, range: 1.09 to 3.7) and 14 mixed-breed dogs (4F, 10M: mean age in years: 1.02, range: 0.96 to 1.06) housed at the Wolf Science Center were tested (see Table 11 on Page 85). Wolves and dogs at the WSC (www.wolfscience.at) are raised and kept in the same way and participate in various behavioural tests every week where they are rewarded with food. All wolves and dogs live in conspecific packs but are worked daily in separation from their pack members. Participation in all training and testing sessions is voluntary. For more details about the upbringing and keeping of the animals please see Range & Virányi (2011).

Differently from previous generations of dog and wolf puppies (see Range and Virányi 2014 for a full description), dog pups raised in 2014 were the offspring of females housed at the WSC. Hence the raising procedure for these animals involved both mother- and human-raising. During the day pups spent their time with human caregivers in a hand-raising enclosure separated from their mother but together with a few of their own littermates and pups from a second litter. During this time, they underwent the same treatment as previous pups raised at the WSC, i.e. copious amount of interaction with both familiar and unfamiliar humans as well as regular bottle-feeding by caregivers. At night, the pups were reunited with their mother and other pack mates in their home enclosures. At 2 months of age, 4 pups from each litter were randomly selected to remain at the WSC and the others were given to private owners to be raised as pets. The raising routine described above continued until 5 months of age when, as with previous litters, pups started living on a more permanent basis within their packs.

However, they continued to maintain regular and frequent contact with both familiar and unfamiliar humans and regularly participated in cognitive testing. In all other respects (feeding, medical, testing routines etc.), the raising of the 2014 dog cohort was the same as previous dog and wolf pup litters.

5.3.3.2.2 Free-ranging dogs

Free-ranging dogs were approached on the streets of Mumbai, India and on the campus of the Indian Institute of Science, Bangalore, India. Dogs that visually appeared to be over 2 years of age and appeared solitary when spotted were chosen preferentially to avoid interference from other individuals. A pre-test (see 5.3.3.4.3 Pre-test for free-ranging dogs on Page 87) was conducted to assess whether the dog was willing/comfortable enough to participate in the experiment. The pre-test was carried out with 46 dogs, 16 of which did not eat the food or were too wary to approach. A total of 31 free-ranging dogs proceeded to be tested. 8 dogs could not solve the task even after the experimenter attempted to demonstrate a solution and were hence not tested with the unsolvable version of the task. Six dogs were excluded from analysis because other dogs approached and interfered with the procedure during testing, 1 dog was excluded because a human interfered during testing, 1 dog was excluded because he had an injury on his leg, and 3 dogs, succeeded in breaking the apparatus during the ‘unsolvable’ task, thereby curtailing the duration of the test. Hence, a total of 11 free ranging dogs (1F, 10M) were included in the analyses.

5.3.3.2.3 Pet Dogs

Mixed-breed pet dogs were tested in two dog parks in Vienna. Dog owners were approached and asked whether they would like their dog to participate in a “cognition task” aimed at comparing different populations of dogs to wolves. Owners were asked about their dogs’ age, sex and whether the dogs had previously participated in any cognitive tasks. Only mixed-breed dogs over 1.5 years of age with no prior experience with cognitive testing and no high-level training experience were used to match the group of free-ranging dogs as much as possible. A total of 25 pet dogs were tested. When testing 6 of these, other dogs in the park approached and interfered with the procedure so these individuals were excluded from analyses. The final sample consisted of 19 mixed breed pet dogs (10F, 9M mean age in years: 7; range: 3 to 12).

Table 11: Subjects housed at the Wolf Science Centre participating in the study.
* indicates dogs that were only partly raised as the wolves and the other dogs.

Name	Species	Sex	Age at testing (years)
Amarok	Wolf	Male	3.67
Apache	Wolf	Male	1.09
Aragorn	Wolf	Male	1.40
Cherokee	Wolf	Male	1.09
Chitto	Wolf	Male	3.70
Geronimo	Wolf	Male	1.14
Kaspar	Wolf	Male	1.40
Kenai	Wolf	Male	1.40
Nanuk	Wolf	Male	1.15
Shima	Wolf	Female	1.40
Tala	Wolf	Female	3.70
Tatonga	Wolf	Male	1.17
Wamblee	Wolf	Male	3.62
Wapi	Wolf	Male	1.28
Yukon	Wolf	Female	1.14
Alika	Dog	Female	1.01
Banzai*	Dog	Male	1.03
Enzi*	Dog	Male	1.03
Gombo*	Dog	Male	1.06
Hiari*	Dog	Male	1.06
Imara*	Dog	Female	1.06
Kilio	Dog	Male	0.96
Maisha	Dog	Male	0.96
Nuru	Dog	Male	1.00
Panya*	Dog	Female	1.03
Pepeo*	Dog	Male	1.03
Rafiki	Dog	Male	1.00
Sahibu*	Dog	Male	1.06
Zuri	Dog	Female	1.00

5.3.3.3 Apparatus

A food reward (meat for wolves and WSC dogs, and pieces of sausage for pets and free-ranging dogs) was placed on a wooden board (approximately 60 cm × 30 cm) and covered with an overturned container (a commercial Tupperware box measuring approximately 15 cm^3 for the dogs and a stainless-steel bowl measuring 30 cm in diameter for wolves). The containers had holes punched into them to allow the animals to smell the food. In the unsolvable trial, the same container was screwed onto the board so that it was no longer possible to overturn.

5.3.3.4 Procedure

5.3.3.4.1 WSC Wolves and Dogs

Wolves and pack-living dogs were tested in an indoor testing area at the Wolf Science Center, Austria. An unfamiliar experimenter and a trainer present in the area. In some cases, a cameraperson was filming, whilst in others, the video-camera was set up on a tripod and remote controlled. The animal was brought into the testing room on a collar by a trainer. The apparatus was present in the room, un-baited, before the animal was brought in. The animal could explore the room and the apparatus for a few minutes before testing began. The trainer and experimenter stood approximately 50 to 75 cm away from adjacent sides of the board. While the trainer held the animal by their side, the experimenter held some food in their hand, showed it to the animal and baited the apparatus by placing the food on the wooden board and covering it with the container. The animal was then released, whilst all people present in the room stood silently avoiding direct eye contact with the animal.

Solvable trials were terminated after 3 minutes or after the animal obtained the food. Only animals that could successfully obtain food in all three solvable trials were tested with the unsolvable apparatus. The unsolvable trial, which also lasted 3 minutes, consisted of the same apparatus but with the container fastened to the wooden board with screws. When a solvable trial ended, the trainer/owner called the animal back and held it by the collar while the experimenter re-baited the apparatus.

5.3.3.4.2 Pet dogs and free-ranging dogs

The test procedure was almost identical to that for the Wolf Science Center dogs and wolves apart from some minor adjustments. First, free-ranging dogs and pet dogs were tested outdoors, on sidewalks or streets and in ‘dog zones’/parks respectively. Second, the experimenter stood between 1m and 1.5m from the apparatus (a bit further than for wolves and WSC dogs). Third, for pet dogs, the owner was also present during testing and hence adopted the location of the ‘trainer’ in the dog and wolf testing, but for free-ranging dogs, no owner was present for obvious reasons. A cameraperson was also always present. After each trial, pet dogs were called back by their owners and held by their collars (just as for dogs and wolves at the WSC) whilst the experimenter re-baited the apparatus. However, in the case of free ranging dogs, to bait the apparatus, the experimenter distracted the animal by tossing a small piece of food a few meters away from the apparatus; hence differently from the animals in the other groups, the exact start location of free-ranging dogs could not be standardized.

Just as with WSC dogs and wolves, the pet and free-ranging dogs needed to be successful in all 3 solvable trials before being presented with the unsolvable trial. Four pet dogs were not able to solve the first solvable trial, so the experimenter moved the container off the board in view of the dogs allowing the dogs to eat the food reward, and then each dog was given 3 more solvable trials (which they then solved).

5.3.3.4.3 Pre-test for free-ranging dogs

Once a potential subject was spotted, the experimenter walked in the direction of the dog without making direct eye contact. From 2 to 3 meters away, the experimenter attempted to catch the dog's attention, tossed a piece of sausage in the direction of the dog and took a few steps away (stage 1). If the dog showed signs of fear or stress (back crouching, tail tucked between legs, walking away from the person, rapidly pacing towards the food and away from it, growling or barking at the experimenter) the experimenter walked away from the dog without any further interaction. If the dog consumed the food, the experimenter kneeled and placed a piece of sausage about 20 – 30 cm from his feet (stage 2). If the dog was hesitant to approach, the experimenter slowly took a few steps back, away from the dog. A maximum of three food presentations were carried out at this distance. If, after 3 presentations, the dog still showed signs of fear or stress, it was excluded from further testing. If the dog approached the experimenter and consumed the food at least once, it moved on to stage 3. In stage 3, the experimenter held a piece of sausage in the palm of his extended arm towards the dog offering the food. If the dog did not approach and consume the food from the hand, the experimenter placed it on the ground just in front of him and remained still. Dogs went on to be tested if they consumed the food with no signs of stress at least in stage 2. Out of the 46 dogs that underwent the pre-test, 9 dogs did not pass stage 1, 4 dogs passed only stage 2 and 26 dogs passed stages 2 and 3. Seven dogs approached the experimenter without any signs of fear or stress, sniffed the food but did not consume it. These dogs were not tested. The experimenter also offered all pet dogs a piece of food from his hand prior to starting the test.

5.3.3.5 Behavioural Coding

Following Miklósi et al.[3] and Marshall-Pescini et al.[11], several behaviours were coded from video. The 'latency to success' in solvable trials was calculated as the time that passed from the animal first touching the apparatus to the food being uncovered. This allowed a comparison across groups despite potential differences in the starting location of the animals. In the unsolvable trial, 'Persistence' was measured in terms of the duration the animal spent interacting with the apparatus (i.e. pawing, licking, sniffing, scratching, biting, nibbling, pulling and pushing the container or wooden board). 'Looking back' (i.e. raising or turning the head and looking towards a human) was coded separately for each person present in the testing area. For the analyses, the latency of looking back consisted of the time that passed from the moment the animal started interacting with the apparatus, to the first look to any person (regardless of identity).

The frequency and duration of 'looking back' were measured as the sum of the gazes and time spent looking at people present in the test area. In former studies using the unsolvable task paradigm[18], 'Gaze alternation' (i.e. looking towards the apparatus immediately followed by a look to the person or vice versa) was suggested as a potentially more stringent measure of communicative behaviours towards human. Hence, we also included the frequency of occurrence of this behavioural sequence in our analyses. For analyses on the latency, frequency and duration of looking back, we included only animals that had in fact exhibited the behaviour.

5.3.3.6 Analyses

Inter-observer reliability was carried out with a second observer coding 20% of the video data (Intra-class correlation coefficient: Gaze human: frequency ICC = 0.9, duration ICC = 0.94, latency ICC = 0.95; Latency to success ICC = 0.99; Duration interact apparatus ICC = 0.99; Frequency Gaze alternation ICC = 0.76). Because the number of people in the test area (experimenter, cameraperson, owner/trainer) was not consistent across dog populations (see 5.3.3.4 Procedure on Page 86), we ran a generalized linear model (Poisson distribution) to check whether this may have affected the frequency of the dogs' looking behaviour in the unsolvable trial. We found that the number of individuals in the test area had no effect on the frequency of looking back (GLM: $\chi^2 = 0.439$, $P = 0.508$). To assess potential learning effects across solvable trials, a linear mixed model with the latency to success as response variable, trial and group as explanatory factors and the identity of the individuals as the random factor was used. For the unsolvable trial, we used linear models with (a) the time spent interacting with the apparatus, (b) latency or (c) duration of looking back as the response variable and group, persistence and the interaction between group and persistence as explanatory factors. Generalized linear models (d) with a binomial distribution for the occurrence of looking back and (e) a quasi-Poisson distribution (to correct for over-dispersion) for the frequency of looking and gaze alternation, were also run with the same explanatory factors. Backwards stepwise model reduction based on p-values was carried out. Models (b) to (f) were also run with just group and not persistence (i.e. the time spent interacting with the apparatus) as an explanatory variable to allow for comparison with previous studies that had not taken persistence into account. All models were run in R (version 3.2)[19], using the package lme4[20] followed, where necessary, by corrected multiple comparisons using the package multcomp[21].

5.3.4 Results

Results showed that across solvable trials, animals in all groups improved significantly in the latency to obtain the reward (mean: Trial 1 = 19.5; Trial 2 = 6.6; Trial 3 = 4.9 seconds; LMM: $\chi^2 = 11.72$, $P < 0.001$). However, in all trials, wolves were faster at accessing the food than all dog groups [LMM: $\chi^2 = 53.9$, $P < 0.001$; mean: Wolves = 4 seconds vs. WSC Dogs (WSCD) = 12.2 seconds, $\chi^2 = 5.1$; vs. Pet Dogs (PD) = 6.4 seconds, $\chi^2 = 5.6$; vs. Free-Ranging Dogs (FRD) = 20.8 seconds, $\chi^2 = 7.7$; all $P < 0.001$] and free-ranging dogs tended to be significantly slower than pets ($\chi^2 = 2.5$, $P = 0.057$; see Table S1 and Table S2 on Page 182 of the Appendix for full results).

In the unsolvable trial, while wolves spent more time interacting with the apparatus than all dog groups, dog groups did not differ from one another (LM: df = 3, F = 9.08, $P < 0.0001$; Wolves vs. WSCD, t = 4.32; Wolves vs. PD, t = 4.73, both $P < 0.001$; Wolves vs. FRD, t = 3.12, $P = 0.015$; Figure 23 below and Table S3 on Page 182 of the Appendix). These results support studies showing that wolves are more persistent than dogs in manipulative tasks[5,12].

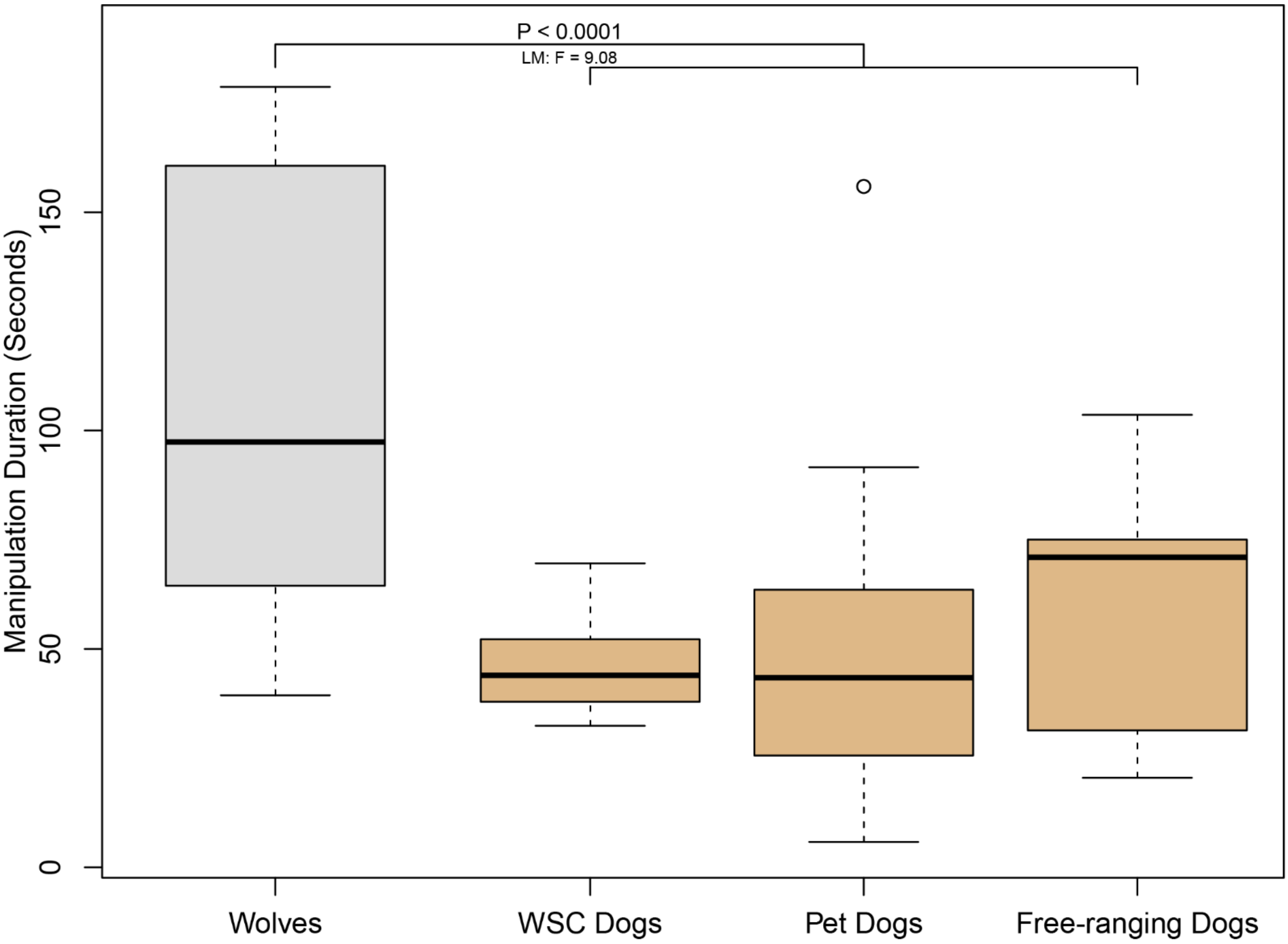

Figure 23: Animals' persistence with the apparatus during the unsolvable trial

In the unsolvable trial, 11/15 wolves, all 14 WSC dogs, all 19 pets and all 11 free-ranging dogs looked back towards a human. The group difference was significant (GLM: $\chi^2 = 11.8$, $P = 0.008$) and persistence ($\chi^2 = 21.7$, $P < 0.001$) significantly affected the likelihood of looking back (Table S4 on Page 182 of the Appendix). Interestingly, 3 of the 4 wolves that did not look back at all spent more than 170 seconds (94% of the total trial duration) interacting with the apparatus. It is possible that had we extended the testing time further these animals would also have eventually looked towards a person.

Considering only the animals that looked at a human in the unsolvable trial (Wolves N = 11, WSCD N = 14; PD N = 19; FRD N = 11): no group difference emerged in the latency to look back (Table S5 on Page 183 of the Appendix); rather, regardless of group, the longer an individual spent interacting with the apparatus, the longer it took for them to look back at a person (LM: $F = 11.9$, $P = 0.001$; Figure 24 on Page 91). No group difference emerged (LM: $F = 2.62$, $P = 0.06$) even when persistence was not considered. Furthermore, no group difference emerged in the duration of looking back; rather, regardless of group, the more time animals spent interacting with the apparatus the less time they spent looking at a person (LM: $F = 33.4$, $P < 0.001$; Table S6 on Page 183 of the Appendix). Analogous results emerged for the frequency of looking back: regardless of group, the more time an animal spent interacting with the apparatus the less frequently it looked back (GLM: $\chi^2 = 11.39$, $P < 0.001$; Table S7 on Page 183 of the Appendix). Without persistence as an explanatory factor, a group effect emerged on the duration of looking (LM: $F = 8.4$, $P < 0.001$): wolves looked towards humans for shorter periods than dogs in all groups, but no difference emerged between dog groups (Table S8 on Page 183 of the Appendix). Similarly, when persistence was not included in the model, a group effect emerged on the frequency of looking back (GLM: $\chi^2 = 16.09$, $P = 0.001$): wolves looked towards humans less often than dogs in all groups while dog groups did not differ from each other (Table S9 on Page 183 of the Appendix).

Finally, for frequency of 'gaze alternations' (i.e. looks to the apparatus immediately followed or preceded by a look to a person), a behaviour that has been considered a more stringent measure of communicative behaviour between dogs and humans in such tasks[18], a group effect emerged (GLM: $\chi^2 = 8.75$, $P = 0.034$; Table S10 on Page 184 of the Appendix). However, corrected post-hoc comparisons showed only a marginally significant difference between pet and WSC dogs ($z = 2.55$, $P = 0.05$; Table S11 on Page 184 of the Appendix). Again, regardless of group, the more time spent interacting with the apparatus, the fewer gaze alternation behaviours were exhibited (GLM: $\chi^2 = 11.39$, $P < 0.001$; Table S12 on Page 184 of the Appendix).

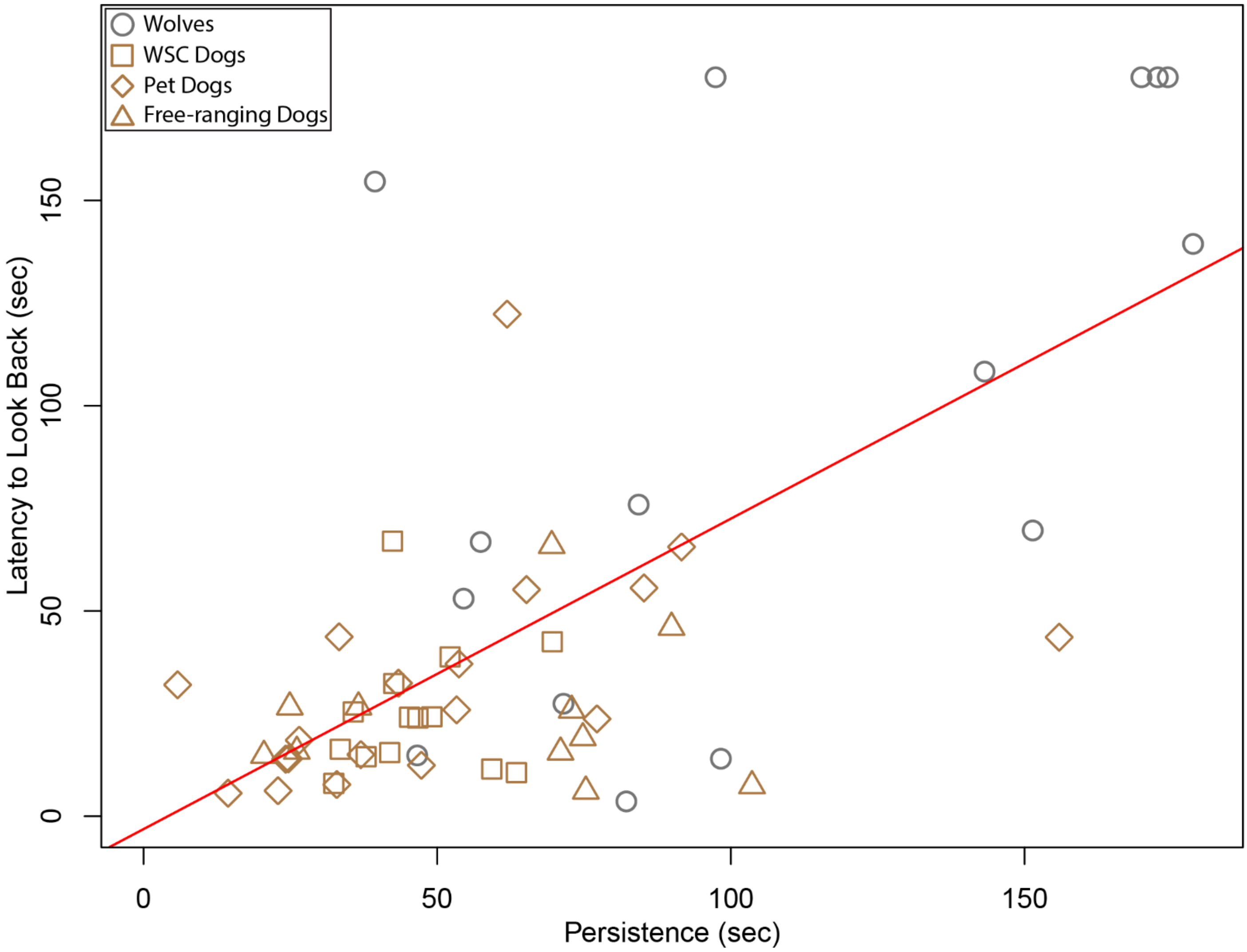

Figure 24: Linear positive relationship between persistence and the latency to look back at the person. Regardless of group, the more animals spent interacting with the apparatus the longer they took to look back at the person.

5.3.5 Discussion

Overall, these results highlight the strong link between persistence in attempting to solve the task and different measures of looking back towards humans. In fact, when persistence is factored into the analyses, group differences in human-directed gazing behaviours do not emerge in our study populations. Rather, regardless of group, the less persistent an animal, the sooner, longer and more frequently it will look back.

Since the current study was the first to include persistence as a potential explanatory factor (but see Udell (2015) for a similar suggestion), we also ran analyses without this variable to allow us to compare results to previous studies using this paradigm. Indeed, without including persistence in the analyses, the results replicate (with adults) the dog-wolf differences shown in 4-month old juveniles by Miklósi et al. (2003). However, when taking persistence into account, it emerged as the better explanatory variable in our sample, indicating that in this task, species differences occur in dogs' and wolves' tendencies to persist rather than in their readiness to look at humans (as suggested by Udell (2015)).

One interesting possibility is that due to their stronger physical capabilities, wolves may have a different perception from dogs of what 'unsolvable' is, and hence be more tenacious in their attempt to obtain a hidden food reward. We partially took this into account by presenting wolves with a stainless-steel apparatus. Yet, this possibility cannot be completely excluded. Nevertheless, it is interesting to note that not only have wolves been shown to be more persistent than pet dogs in manipulative tasks involving food[12], but they have also been shown to be more explorative than similarly raised dogs both as adults[22] and as pups[23], even when confronted with novel objects and environments with no food involved. Together, these results raise the hypothesis that more basic dog-wolf differences linked to their explorative and independent problem-solving behaviours may have 'knock-on' effects on their interaction with people in such tests. Indeed, in studies in which human-directed gazing behaviour is measured without the potentially confounding variable of persistence (e.g. in a 'showing' task where animals need to indicate the location of hidden/unavailable food to an 'ignorant' human) equally raised wolves and dogs show the same capacity to communicate with their human partner[24]. Further support also comes from studies showing that wolves, when exposed from puppyhood to similar experiences as dogs, are equal, if not better, at following human gazing cues into distant space and around barriers[16,25], and do not differ in their capacity to learn from human partners[26].

These results suggest that, while dogs may have a genetic predisposition enabling them to form close relationships with humans with relatively little exposure[27], when wolves are intensively socialized, their communication with humans resembles that of similar socialized and kept pack dogs. A further question is whether with even more intensive (e.g. pet-like) socialization, wolves would equal the performance of pet dogs that, in some studies, show even more sophisticated communicative interactions with humans than pack dogs[24]. Nevertheless, current results suggest that gazing behaviours towards humans are not necessarily a direct effect of domestication[28], but potentially a behaviour that emerges because of animals' acceptance of humans as social partners[29]. Interestingly, very few behavioural differences emerged between the studied dog populations. While free-ranging dogs were slightly slower at solving the task in the 'solvable' trials than other dog groups – perhaps due to their limited experience with these kinds of objects and situations – looking back did not vary across groups. This is surprising to some extent, since if 'looking back' is to be interpreted as a communicative act by which a dog 'looks for help' from its human partner, we would expect dogs with a vastly greater experience of humans helping them (i.e. pet dogs) to be much more inclined to exhibit such a behaviour compared to free-ranging dogs living as independent scavengers.

So why did our study populations, particularly pet and free-ranging dogs, show such similar behavioural patterns in the current task? The most likely possibility is that the populations were more homogenous in the crucial aspects affecting looking (i.e. in their persistence on the task and their level of socialization to humans as social companions and potential food-providers) than we expected back. There was, in fact, no difference between groups in terms of persistence, with the mean time spent interacting with the apparatus ranging between 46 and 61 seconds out of the 3 minutes provided. This appears quite comparable overall to Passalacqua et al.[6] and Konno et al.[7] who both found the mean duration of interaction to be approx. 30 seconds with a test duration of 1 minute. Furthermore, dog groups did not differ in the time spent interacting with the human during testing (see Table S12 on Page 184 of the Appendix), which provides some evidence that they showed equal levels of 'friendliness' towards people in this kind of situation. It has been suggested that the ability to gain 'human favour' may be a crucial element affecting survival of free-ranging dogs[30] and looking at people may be a crucial behaviour to obtain such 'favour'. It is thus possible that the natural socioecology of the free-ranging dogs we tested (in terms of their reliance on human refuse and hand-outs, and early exposure to the human social environment) provided the necessary and sufficient conditions for them to show similar levels of persistence and social behaviour towards humans as the other dog populations we tested.

In sum, 'looking back behaviour' is strongly linked to when an animal gives up trying to solve the unsolvable task. While we found no effect of the dogs' prior experience to humans helping them, more persistent dogs were less inclined to look back towards a human. Furthermore, wolves were more persistent in the task than dogs and this largely explains why they took longer and looked less frequently and for a shorter time towards humans than dogs. Given the confounding effect of persistence on looking behaviour in the unsolvable task, future studies should aim at designing tasks allowing an independent assessment of these two variables and a better understanding of the causal link between them.

5.3.6 Acknowledgments

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6 Discussion

My dissertation aimed at investigating motivation and persistence in dogs and wolves to better understand whether differences in their problem-solving success are contingent to their feeding ecology. We conducted three experiments with similarly raised and kept dogs and wolves at the Wolf Science Center, Ernstbrunn, Austria, one of which was also performed with pet dogs in Vienna, Austria and free-ranging dogs in Bombay and Bangalore, India. We investigated food preferences (which may directly affect animals' motivation) and used two variants of the classic "unsolvable task" paradigm to evaluate persistence.

The main aim of our first study was to assess if dogs' and wolves' food preferences may have changed during domestication, potentially due to changes in their foraging styles. We predicted that due to their adaptations to a more opportunistic, scavenging style during domestication and their genetic adaptions to starch digestion[1,2], dogs may have a less strict preference for a single food type and show a weaker preference for meat over starch-rich food compared to wolves. We used two experimental paradigms (a two-choice and a multiple-choice task) and overall, found only minor differences in dogs' and wolves' food preferences. Contrary to our prediction, the two species did not differ in their preference for meat in either testing paradigm. This finding has implications for our understanding of the domestication process. Despite dogs having evolved a more scavenging feeding style, we found no evidence that their food preferences have changed compared to wolves. Dogs also show adaptations that allow them to digest starch[1] (but see 2), and though protein is an inefficient source of energy[3], dogs still prefer high-protein food.

It is possible that while the domestication process has resulted in dogs adopting a foraging style different from wolves, it has not completely replaced their ability to hunt. Indeed, dogs are known to be capable of hunting[4–6], and this may contribute to the lack of difference in food preferences between the two species. In fact, free-ranging dogs in India have also been found to prefer protein rich foods (but this preference is not innate)[7]. Another possibility is that while food preference and foraging styles are generally connected in many birds and mammals[8,9], this may not be the case in dogs and wolves. Similarities in our populations' raising and upkeep may also have buffered potential differences in food preferences. Though studies have tested food preferences in animals[10–20] (including domesticated species[11,13–15,20]), there is little information about whether and how food preferences differ between domesticated species and their wild counterparts. Further, there are subtle methodological differences between these studies (which affect the outcomes of such experiments as evidenced by our study) making generalized conclusions difficult. More comparative research is required before we can make broad, generalisable claims about how domestication processes influence food preferences.

An animal's food preferences can affect its task-directed motivation. For example, Bentosela et al. (2009) showed that when rewarded with highly preferred food, dogs maintained a gaze towards an experimenter longer than when rewarded with food the dogs did not prefer as much. A study by Fontenot et al. (2007) showed that Capuchin monkeys were faster at performing a token exchange task when given a more preferred food reward than when given a less preferred one. Studies on Corvids by Wascher et al. (2012) and Hillemann et al. (2014), and a study on cockatoos by Auersperg et al (2013) demonstrated similar findings. Hunger is also an important motivator that drives behaviour[26]. For instance, Hovland et al. (2006) showed that in an operant task, farmed silver foxes often "over-paid" the set price for food. Hence, it was important to establish if and how our subjects' hunger states and preferences for rewards used in experiments affected the experiments' outcomes. We observed only a slight effect of satiation on choice diversity where when "fed", wolves were more "selective" than dogs and found that our subjects' preferences were determined mostly by the rarity of foods in their daily diet. This implies that feeding motivation is driven more by rarity and food preferences than by hunger. Considering studies with several other species, [16,23–25,27] this pattern is certainly not restricted to dogs and wolves.

Establishing that dogs and wolves at the Wolf Science Center do not differ in their preferences has significant implications for behavioural studies conducted at the facility. These animals have participated in several cognitive and behavioural experiments over their lifetime. Most, if not all of these experiments involve food rewards [28–34]. Results from this study imply that dogs and wolves were not affected differently by the type of foods used as rewards in experiments. The differences that have been observed in the two species are more likely due to differences in the species' motivational states (independent of the type of food reward) and differences in their correlates of problem-solving success, such as persistence.

Persistence is one of the most important correlates of problem-solving success[35–45] (along with motor diversity, neophobia, etc[42]). Persistence predicted success in a problem-solving task requiring innovation in carnivores such as lions, leopards and tigers[46]. Several studies with species such as the spotted hyena[46–48], red fronted lemur[38], meerkat[44] and various species of birds[40–42] have mirrored this pattern. Broadly, persistence is influenced by a species' ecology, social structure and living conditions[43,49–51]. For instance Benson-Amran et al. (2013) found that captive hyenas were more persistent than wild conspecifics in a problem solving task and Borrego & Gaines (2016) found that social carnivores were more persistent than non-social ones in a puzzle-box task. Dogs and wolves have consistently been shown to differ in their problem-solving success[29,31–33,35,37,52–58]. Having established that differences in food preferences do not affect their performance, it is likely that performance differences may be influenced by differences in their persistence, which in turn may tie back to differences in their feeding and/or socioecologies.

Our second study aimed at having a clearer understanding of dogs' and wolves' persistence in an independent problem-solving task without a major confounding factor that studies so far have had[37,54,56,59–64]: human presence in the test setting. Human presence is a confounding factor as dogs and wolves react differently to humans during cognitive testing[37,54,56,61]. Dogs show more human-directed behaviour (such as gazing or 'looking back') than wolves. It is hence possible that dogs persist less at a task because they are more focussed on the human. Results from the only other study that tested dog-wolf differences in persistence in the absence of humans compared pet dogs to wolves. Differences in the subjects' life experience was a confounding factor: results could have been explained by dogs (but not wolves) having been inhibited from interacting with objects in their daily lives or by dogs preferring to use a social problem-solving strategy in the presence of a human.

We found wolves to be more persistent than dogs in object manipulation, in line with previous studies[31–35,37,65]. Further, (though we could not test whether dogs and wolves differed statistically), wolves showed three times the median motor diversity than dogs with both objects. Importantly these differences held even in the absence of humans and with dogs and wolves that have the same level of experience with both, humans and with interacting with different objects. Based on these results, neither differences in subjects' experience with humans (e.g. humans inhibiting subjects from interacting with objects) nor "social problem-solving strategies" appeared to affect dogs' and wolves' persistence.

However, it was still unclear why human presence affects dogs and wolves so differently. One possibility was that the difference in reaction towards humans may be due to dogs' human reliance and their expectations that humans would solve problems for them, which causes them to turn to humans "for help" instead of persisting at a given task. Study 3 aimed to tackle this possibility. We found that three populations of dogs with different levels of experience with (and therefore, potentially also different expectations from) humans, did not differ from each other either in their persistence or in their human-directed behaviour. Again, wolves were more persistent and showed less human-directed behaviour than all three groups of dogs.

Taken together, results from our studies point in the direction of the socioecological hypothesis. Dogs and wolves have evolved different feeding and socioecologies[66] since their divergence[2]. Wolves are cooperative breeders that live in packs[32] (with hierarchies less steeper than dogs[67]) and are hunters[66] with very varied success rates[68]. In the face of constant failure in hunts, persistence is essential to wolves' survival[68]. Further, complex social hierarchies are known to affect problem-solving performance in several animals. While results vary between species (innovation, greater persistence, exploration, etc. were found to be higher in subdominant individuals in some cases, but higher in dominant individuals in others; see Griffin et al. 2014 for a complete review of this literature), wolves' social structure may well factor into their increased persistence. Further studies are, however, required to better understand if and how wolves' hierarchies can affect their persistence and other correlates of problem-solving success.

Dogs, living in a human dominated niche[32] and being primarily scavengers[32,66] dependant on human refuse[32,66,69–71], do not need to be as persistent. In fact, dogs' persistence may even have been selected against[35]. Finally, human-directed communicative gestures, such as gaze alternation or gazing at a human when confronted with an unsolvable problem are not exclusive to dogs. A recent study with goats[72] and with horses[73] found that when confronted with an unsolvable task, subjects would turn towards a human, presumably to seek help. Regardless of species, being very persistent, being difficult to control, being very independent and avoidant of humans are unfavourable traits in the domestication process[74]; so dogs' behaviour in these tasks is far from surprising.

Overall, while this dissertation has helped gain important insights into dogs' and wolves' persistence, a psychological propensity that seems to be influenced by differences in their feeding and socioecology, there are more factors that play a role in the two species' problem-solving performance. Neophobia, exploration, motor diversity, behavioural flexibility and motivation to work are all known to be predictors of problem-solving performance and, like persistence, are influenced by a species' ecology, social structure and living conditions[43,49–51].

A higher level of motivation (or willingness to engage in a task) than dogs may be a potential reason for wolves' greater persistence (or willingness to continue engaging in a task). Future studies could aim to test this factor directly by analysing how dogs and wolves differ in their motivation to engage in a task that becomes increasingly taxing. The "maximum price paid" approach has been used with ciclids[75], rats[76], chicks[77,78], mink[79] and foxes[27] to quantify how motivated animals are to access resources (such as nest boxes, social contact, mates, food, etc). If wolves' persistence is tied to a stronger motivation to work compared to dogs, wolves will be more likely than dogs to attempt a high-investment task. Apart from differences in persistence, differences in behavioural flexibility may also influence dogs' and wolves' success in problem-solving tasks. Behavioural flexibility is correlated with persistence[38,40,42,46,47], so it is likely that wolves may be more flexible in their approach to a problem. However, though dogs do not need high levels of persistence to survive, they likely encounter various types of puzzle-box like problems when foraging through human refuse. It is plausible that dogs may be able to show some amount of behavioural flexibility, but due to the vast availability of resources, may not necessarily persist long enough to try different problem-solving strategies. A task designed specifically to test dogs' and wolves' motor diversity and behavioural flexibility such as a multiple access box[80] could provide better insights into this aspect of their behaviour. Together, these studies could help build a better understanding of how ecological differences shape cognitive abilities.

6.1 Conclusions

Since their divergence, wolves and dogs have evolved different skill sets to tackle different sets of problems. Wolves are more persistent, show more motor diversity and less human-directed behaviour in independent physical problem-solving tasks compared to dogs. However, dogs, regardless of their experience with humans, are more likely to show human-directed behaviour and show greater amounts of human-directed behaviour than their wild counterparts, wolves. Differences in the correlates of problem-solving success in dogs and wolves (and not in their preferences for rewards) may be the reason for their greater success in such tasks. These differences are likely to have evolved due to differences in their feeding and socioecologies over the course of domestication. It is likely that these differences may not be restricted to just dogs and wolves but may generalize to other domesticated species and their wild counterparts. However, our sample obviously cannot provide evidence for all species (or even for all dogs and all wolves) and more research is needed to understand how far our findings can be generalized.

6.2 References (Discussion)

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7 Appendix

7.1 Article 1

Rao A, Range F, Kadletz K, Kotrschal K, Marshall-Pescini S.; Food preferences of similarly raised and kept captive dogs and wolves. *PLoS ONE 13(9): e0203165* (DOI: 10.1371/journal.pone.0203165).

7.1.1 Supplementary Video

The video highlights the procedures for the two-choice task and the cafeteria paradigm.

To view the video, please scan the QR code on the right, or visit http://bit.do/FP-Video.

7.1.2 Complete GEE model information for Choice 1

7.1.2.1 Factors affecting Choice 1, Overall model

Model Information

Dependent Variable		Choice.Food[a]
Probability Distribution		Multinomial
Link Function		Cumulative logit
Subject Effect	1	Animal
Within-Subject Effect	1	Trial
Working Correlation Matrix Structure		Independent

a. The procedure applies the cumulative link function to the dependent variable values in ascending order.

Tests of Model Effects

Source	Type III		
	Wald χ^2	**df**	**Sig.**
Species	1.091	1	0.296
Condition	4.700	1	0.030
Species * Condition	0.721	1	0.396

Dependent Variable: Choice.Food
Model: (Threshold), Species, Condition, Species * Condition

Parameter Estimates

Parameter		B	Std. Error	95% Wald Confidence Interval		Hypothesis Test			Exp(B)	95% Wald Confidence Interval for Exp(B)	
				Lower	Upper	Wald χ^2	df	Sig.		Lower	Upper
Threshold	[Choice.Food=Chick]	-1.130	0.3058	-1.729	-0.530	13.642	1	0.000	0.323	0.177	0.588
	[Choice.Food=Control]	-1.034	0.2918	-1.606	-0.462	12.559	1	0.000	0.356	0.201	0.630
	[Choice.Food=DryFood]	-0.737	0.2712	-1.269	-0.206	7.393	1	0.007	0.478	0.281	0.814
	[Choice.Food=Meat]	0.731	0.2756	0.191	1.271	7.031	1	0.008	2.077	1.210	3.564
	[Choice.Food=Sausage]	2.138	0.3210	1.509	2.767	44.377	1	0.000	8.483	4.522	15.914
[Species=Dog]		0.458	0.3209	-0.171	1.087	2.035	1	0.154	1.581	0.843	2.964
[Species=Wolf]		0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed]		-0.265	0.2976	-0.848	0.318	0.792	1	0.374	0.767	0.428	1.375
[Condition=Unfed]		0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Condition=Fed]		-0.353	0.4159	-1.168	0.462	0.721	1	0.396	0.702	0.311	1.587
[Species=Dog] * [Condition=Unfed]		0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Fed]		0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Unfed]		0[a]	.	.	.	.	.	.	1	.	.
(Scale)		1									

Dependent Variable: Choice.Food

Model: (Threshold), Species, Condition, Species * Condition

a. Set to zero because this parameter is redundant.

7.1.2.2 Analysis for Chicks, Choice 1

Model Information

Dependent Variable		Chick.or.Not[a]
Probability Distribution		Binomial
Link Function		Logit
Subject Effect	1	Animal
Within-Subject Effect	1	Trial
Working Correlation Matrix Structure		Independent

a. The procedure models 0 as the response, treating 1 as the reference category.

Tests of Model Effects

Source	Type III		
	Wald χ^2	df	Sig.
(Intercept)	32.814	1	0.000
Species	0.768	1	0.381
Condition	4.627	1	0.031
Species * Condition	1.683	1	0.194

Dependent Variable: Chick.or.Not

Model: (Intercept), Species, Condition, Species * Condition

Goodness of Fit[a]

	Value
Quasi Likelihood under Independence Model Criterion (QIC)[b]	636.012
Corrected Quasi Likelihood under Independence Model Criterion (QICC)[b]	619.407

Dependent Variable: Chick.or.Not

Model: (Intercept), Species, Condition, Species * Condition[a]

a. Information criteria are in smaller-is-better form.

b. Computed using the full log quasi-likelihood function.

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test			Exp(B)	95% Wald Confidence Interval for Exp(B)	
			Lower	Upper	Wald χ^2	df	Sig.		Lower	Upper
(Intercept)	1.122	0.4063	0.326	1.919	7.626	1	0.006	3.071	1.385	6.811
[Species=Dog]	0.750	0.5575	-0.343	1.842	1.808	1	0.179	2.116	0.710	6.311
[Species=Wolf]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed]	-0.257	0.3987	-1.039	0.524	0.416	1	0.519	0.773	0.354	1.689
[Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Condition=Fed]	-0.782	0.6025	-1.963	0.399	1.683	1	0.194	0.458	0.140	1.491
[Species=Dog] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Fed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
(Scale)	1									

Dependent Variable: Chick.or.Not
Model: (Intercept), Species, Condition, Species * Condition
a. Set to zero because this parameter is redundant.

7.1.2.3 Analysis for Meat, Choice 1

Model Information

Dependent Variable		Meat.or.Not[a]
Probability Distribution		Binomial
Link Function		Logit
Subject Effect	1	Animal
Within-Subject Effect	1	Trial
Working Correlation Matrix Structure		Independent

a. The procedure models 0 as the response, treating 1 as the reference category.

Tests of Model Effects

Source	Type III		
	Wald χ^2	df	Sig.
(Intercept)	21.037	1	0.000
Species	0.002	1	0.969
Condition	1.025	1	0.311
Species * Condition	5.126	1	0.024

Dependent Variable: Meat.or.Not
Model: (Intercept), Species, Condition, Species * Condition

Goodness of Fit[a]

	Value
Quasi Likelihood under Independence Model Criterion (QIC)[b]	733.329
Corrected Quasi Likelihood under Independence Model Criterion (QICC)[b]	722.226

Dependent Variable: Meat.or.Not
Model: (Intercept), Species, Condition, Species * Condition[a]
a. Information criteria are in smaller-is-better form.
b. Computed using the full log quasi-likelihood function.

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test			Exp(B)	95% Wald Confidence Interval for Exp(B)	
			Lower	Upper	Wald χ^2	df	Sig.		Lower	Upper
(Intercept)	1.122	0.3335	0.468	1.776	11.320	1	0.001	3.071	1.597	5.905
[Species=Dog]	-0.633	0.4192	-1.454	0.189	2.277	1	0.131	0.531	0.234	1.208
[Species=Wolf]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed]	-0.899	0.2900	-1.467	-0.331	9.612	1	0.002	0.407	0.231	0.718
[Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Condition=Fed]	1.242	0.5487	0.167	2.318	5.126	1	0.024	3.464	1.182	10.153
[Species=Dog] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Fed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
(Scale)	1									

Dependent Variable: Meat.or.Not

Model: (Intercept), Species, Condition, Species * Condition

a. Set to zero because this parameter is redundant.

7.1.2.3.1 Estimated Marginal Means: Species * Condition

Estimates

Species	Condition	Mean	Std. Error	95% Wald Confidence Interval	
				Lower	Upper
Dog	Fed	0.70	0.060	0.57	0.80
	Unfed	0.62	0.060	0.50	0.73
Wolf	Fed	0.56	0.062	0.43	0.67
	Unfed	0.75	0.062	0.62	0.86

Pairwise Comparisons

(I) Species*Condition	(J) Species*Condition	Mean Difference (I-J)	Std. Error	df	Sequential Bonferroni Sig.	95% Wald Confidence Interval for Difference[a]	
						Lower	Upper
[Species=Dog] * [Condition=Fed]	[Species=Dog] * [Condition=Unfed]	0.08	0.104	1	1.000	-0.16	0.31
	[Species=Wolf] * [Condition=Fed]	0.14	0.086	1	0.505	-0.08	0.36
	[Species=Wolf] * [Condition=Unfed]	-0.06	0.086	1	1.000	-0.25	0.14
[Species=Dog] * [Condition=Unfed]	[Species=Dog] * [Condition=Fed]	-0.08	0.104	1	1.000	-0.31	0.16
	[Species=Wolf] * [Condition=Fed]	0.06	0.086	1	1.000	-0.14	0.27
	[Species=Wolf] * [Condition=Unfed]	-0.13	0.086	1	0.505	-0.35	0.08
[Species=Wolf] * [Condition=Fed]	[Species=Dog] * [Condition=Fed]	-0.14	0.086	1	0.505	-0.36	0.08
	[Species=Dog] * [Condition=Unfed]	-0.06	0.086	1	1.000	-0.27	0.14
	[Species=Wolf] * [Condition=Unfed]	-0.20[b]	0.059	1	0.005	-0.36	-0.04
[Species=Wolf] * [Condition=Unfed]	[Species=Dog] * [Condition=Fed]	0.06	0.086	1	1.000	-0.14	0.25
	[Species=Dog] * [Condition=Unfed]	0.13	0.086	1	0.505	-0.08	0.35
	[Species=Wolf] * [Condition=Fed]	0.20[b]	0.059	1	0.005	0.04	0.36

Pairwise comparisons of estimated marginal means based on the original scale of dependent variable Meat.or.Not

a. Confidence interval bounds are approximate.

b. The mean difference is significant at the .05 level.

Overall Test Results

Wald χ^2	df	Sig.
11.777	3	0.008

The Wald chi-square tests the effect of Species*Condition. This test is based on the linearly independent pairwise comparisons among the estimated marginal means.

7.1.2.4 Analysis for Sausage, Choice 1

Model Information

Dependent Variable		Sausage.or.Not[a]
Probability Distribution		Binomial
Link Function		Logit
Subject Effect	1	Animal
Within-Subject Effect	1	Trial
Working Correlation Matrix Structure		Independent

a. The procedure models 0 as the response, treating 1 as the reference category.

Tests of Model Effects

Source	Type III		
	Wald χ^2	df	Sig.
(Intercept)	51.400	1	0.000
Species	0.241	1	0.623
Condition	2.961	1	0.085
Species * Condition	0.073	1	0.787

Dependent Variable: Sausage.or.Not
Model: (Intercept), Species, Condition, Species * Condition

Goodness of Fit[a]

	Value
Quasi Likelihood under Independence Model Criterion (QIC)[b]	609.442
Corrected Quasi Likelihood under Independence Model Criterion (QICC)[b]	598.425

Dependent Variable: Sausage.or.Not
Model: (Intercept), Species, Condition, Species * Condition[a]
a. Information criteria are in smaller-is-better form.
b. Computed using the full log quasi-likelihood function.

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test			Exp(B)	95% Wald Confidence Interval for Exp(B)	
			Lower	Upper	Wald χ^2	df	Sig.		Lower	Upper
(Intercept)	1.075	0.3112	0.465	1.685	11.942	1	0.001	2.931	1.593	5.394
[Species=Dog]	-0.098	0.4077	-0.897	0.702	0.057	1	0.811	0.907	0.408	2.017
[Species=Wolf]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed]	0.561	0.3846	-0.193	1.315	2.127	1	0.145	1.752	0.825	3.724
[Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Condition=Fed]	-0.152	0.5634	-1.257	0.952	0.073	1	0.787	0.859	0.285	2.590
[Species=Dog] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Fed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
(Scale)	1									

Dependent Variable: Sausage.or.Not
Model: (Intercept), Species, Condition, Species * Condition
a. Set to zero because this parameter is redundant.

7.1.2.5 Analysis for Dry Food, Choice 1

Model Information

Dependent Variable	DryFood.or.Not[a]
Probability Distribution	Binomial
Link Function	Logit
Subject Effect 1	Animal
Within-Subject Effect 1	Trial
Working Correlation Matrix Structure	Independent

a. The procedure models 0 as the response, treating 1 as the reference category.

Tests of Model Effects

Source	Type III		
	Wald χ^2	df	Sig.
(Intercept)	140.193	1	0.000
Species	0.001	1	0.979
Condition	2.573	1	0.109
Species * Condition	1.905	1	0.168

Dependent Variable: DryFood.or.Not
Model: (Intercept), Species, Condition, Species * Condition

Goodness of Fit[a]

	Value
Quasi Likelihood under Independence Model Criterion (QIC)[b]	265.105
Corrected Quasi Likelihood under Independence Model Criterion (QICC)[b]	258.700

Dependent Variable: DryFood.or.Not
Model: (Intercept), Species, Condition, Species * Condition[a]
a. Information criteria are in smaller-is-better form.
b. Computed using the full log quasi-likelihood function.

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test			Exp(B)	95% Wald Confidence Interval for Exp(B)	
			Lower	Upper	Wald χ^2	df	Sig.		Lower	Upper
(Intercept)	2.140	0.5015	1.157	3.123	18.211	1	0.000	8.500	3.181	22.714
[Species=Dog]	0.611	0.7035	-0.767	1.990	0.756	1	0.385	1.843	0.464	7.317
[Species=Wolf]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed]	1.349	0.5142	0.341	2.357	6.882	1	0.009	3.853	1.406	10.555
[Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Condition=Fed]	-1.248	0.9040	-3.020	0.524	1.905	1	0.168	0.287	0.049	1.689
[Species=Dog] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Fed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
(Scale)	1									

Dependent Variable: DryFood.or.Not
Model: (Intercept), Species, Condition, Species * Condition
a. Set to zero because this parameter is redundant.

7.1.2.6 Analysis for Tofu, Choice 1

Model Information

Dependent Variable		Tofu.or.Not[a]
Probability Distribution		Binomial
Link Function		Logit
Subject Effect	1	Animal
Within-Subject Effect	1	Trial
Working Correlation Matrix Structure		Independent

a. The procedure models 0 as the response, treating 1 as the reference category.

Tests of Model Effects

Source	Type III		
	Wald χ^2	df	Sig.
(Intercept)	116.726	1	0.000
Species	1.114	1	0.291
Condition	0.949	1	0.330
Species * Condition	0.191	1	0.662

Dependent Variable: Tofu.or.Not
Model: (Intercept), Species, Condition, Species * Condition

Goodness of Fit[a]

	Value
Quasi Likelihood under Independence Model Criterion (QIC)[b]	403.218
Corrected Quasi Likelihood under Independence Model Criterion (QICC)[b]	394.391

Dependent Variable: Tofu.or.Not
Model: (Intercept), Species, Condition, Species * Condition[a]
a. Information criteria are in smaller-is-better form.
b. Computed using the full log quasi-likelihood function.

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test			Exp(B)	95% Wald Confidence Interval for Exp(B)	
			Lower	Upper	Wald χ^2	df	Sig.		Lower	Upper
(Intercept)	2.050	0.4734	1.122	2.978	18.752	1	0.000	7.769	3.072	19.650
[Species=Dog]	-0.235	0.5957	-1.402	0.933	0.155	1	0.693	0.791	0.246	2.541
[Species=Wolf]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed]	0.589	0.6171	-0.621	1.798	0.911	1	0.340	1.802	0.538	6.040
[Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Condition=Fed]	-0.365	0.8342	-2.000	1.270	0.191	1	0.662	0.694	0.135	3.561
[Species=Dog] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Fed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
(Scale)	1									

Dependent Variable: Tofu.or.Not
Model: (Intercept), Species, Condition, Species * Condition
a. Set to zero because this parameter is redundant.

7.1.3 Complete GEE model information for Choice 2

7.1.3.1 Factors affecting Choice 2, Overall model

Model Information

Dependent Variable		Choice.2[a]
Probability Distribution		Multinomial
Link Function		Cumulative logit
Subject Effect	1	Animal
Within-Subject Effect	1	Trial
Working Correlation Matrix Structure		Independent

a. The procedure applies the cumulative link function to the dependent variable values in ascending order.

Tests of Model Effects

Source	Type III		
	Wald χ^2	df	Sig.
Species	0.231	1	0.631
Condition	3.094	1	0.079
Proximity.to.Choice.1	2.254	1	0.133
Species * Condition	1.926	1	0.165
Species * Proximity.to.Choice.1	2.001	1	0.157
Condition * Proximity.to.Choice.1	0.006	1	0.936
C1.Chick.or.Not	2.557	1	0.110
C1.Meat.or.Not	2.920	1	0.087
C1.Sausage.or.Not	5.486	1	0.019
C1.DryFood.or.Not	1.892	1	0.169
C1.Tofu.or.Not	3.762	1	0.052

Dependent Variable: Choice.2

Model: (Threshold), Species, Condition, Proximity.to.Choice.1, Species * Condition, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.Chick.or.Not, C1.Meat.or.Not, C1.Sausage.or.Not, C1.DryFood.or.Not, C1.Tofu.or.Not

Parameter Estimates

Parameter		B	Std. Error	95% Wald Confidence Interval		Hypothesis Test			Exp(B)	95% Wald Confidence Interval for Exp(B)	
				Lower	Upper	Wald χ^2	df	Sig.		Lower	Upper
Threshold	[Choice.2=Chick]	-2.014	0.6308	-3.250	-0.778	10.193	1	0.001	0.133	0.039	0.460
	[Choice.2=Control]	-1.776	0.6456	-3.041	-0.510	7.564	1	0.006	0.169	0.048	0.600
	[Choice.2=DryFood]	-1.165	0.6463	-2.432	0.102	3.250	1	0.071	0.312	0.088	1.107
	[Choice.2=Meat]	-0.262	0.6650	-1.565	1.041	0.155	1	0.694	0.770	0.209	2.833
	[Choice.2=Nil]	-0.170	0.6611	-1.466	1.125	0.066	1	0.797	0.843	0.231	3.082
	[Choice.2=Sausage]	1.125	0.6880	-0.223	2.474	2.674	1	0.102	3.080	0.800	11.864
[Species=Dog]		0.782	0.4220	-0.046	1.609	3.430	1	0.064	2.185	0.955	4.997
[Species=Wolf]		0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed]		0.822	0.3867	0.064	1.580	4.522	1	0.033	2.276	1.067	4.856
[Condition=Unfed]		0[a]	.	.	.	.	.	.	1	.	.
[Proximity.to.Choice.1=No]		0.003	0.2995	-0.584	0.590	0.000	1	0.992	1.003	0.558	1.804
[Proximity.to.Choice.1=Yes]		0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Condition=Fed]		-0.708	0.5098	-1.707	0.292	1.926	1	0.165	0.493	0.181	1.339
[Species=Dog] * [Condition=Unfed]		0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Fed]		0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Unfed]		0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Proximity.to.Choice.1=No]		-0.639	0.4518	-1.525	0.246	2.001	1	0.157	0.528	0.218	1.279
[Species=Dog] * [Proximity.to.Choice.1=Yes]		0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Proximity.to.Choice.1=No]		0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Proximity.to.Choice.1=Yes]		0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed] * [Proximity.to.Choice.1=No]		-0.033	0.4085	-0.833	0.768	0.006	1	0.936	0.968	0.435	2.155
[Condition=Fed] * [Proximity.to.Choice.1=Yes]		0[a]	.	.	.	.	.	.	1	.	.
[Condition=Unfed] * [Proximity.to.Choice.1=No]		0[a]	.	.	.	.	.	.	1	.	.
[Condition=Unfed] * [Proximity.to.Choice.1=Yes]		0[a]	.	.	.	.	.	.	1	.	.
C1.Chick.or.Not		-1.044	0.6529	-2.324	0.236	2.557	1	0.110	0.352	0.098	1.266
C1.Meat.or.Not		-1.147	0.6715	-2.464	0.169	2.920	1	0.087	0.317	0.085	1.184
C1.Sausage.or.Not		-1.526	0.6513	-2.802	-0.249	5.486	1	0.019	0.218	0.061	0.780
C1.DryFood.or.Not		-0.906	0.6587	-2.197	0.385	1.892	1	0.169	0.404	0.111	1.469
C1.Tofu.or.Not		-1.026	0.5288	-2.062	0.011	3.762	1	0.052	0.359	0.127	1.011
(Scale)		1									

Dependent Variable: Choice.2
Model: (Threshold), Species, Condition, Proximity.to.Choice.1, Species * Condition, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.Chick.or.Not, C1.Meat.or.Not, C1.Sausage.or.Not, C1.DryFood.or.Not, C1.Tofu.or.Not
a. Set to zero because this parameter is redundant.

7.1.3.2 Analysis for Chicks, Choice 2

Model Information

Dependent Variable		C2.Chick.or.Not[a]
Probability Distribution		Binomial
Link Function		Logit
Subject Effect	1	Animal
Within-Subject Effect	1	Trial
Working Correlation Matrix Structure		Independent

a. The procedure models 0 as the response, treating 1 as the reference category.

Tests of Model Effects

Source	Type III		
	Wald χ^2	df	Sig.
(Intercept)	25.373	1	0.000
Species	0.024	1	0.877
Condition	4.775	1	0.029
Species * Condition	2.019	1	0.155
Proximity.to.Choice.1	6.066	1	0.014
Species * Proximity.to.Choice.1	1.799	1	0.180
Condition * Proximity.to.Choice.1	0.755	1	0.385
C1.Meat.or.Not	1.053	1	0.305
C1.Sausage.or.Not	6.517	1	0.011
C1.DryFood.or.Not	0.100	1	0.752
C1.Tofu.or.Not	0.083	1	0.773

Dependent Variable: C2.Chick.or.Not
Model: (Intercept), Species, Condition, Species * Condition, Proximity.to.Choice.1, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.Meat.or.Not, C1.Sausage.or.Not, C1.DryFood.or.Not, C1.Tofu.or.Not

Goodness of Fit[a]

	Value
Quasi Likelihood under Independence Model Criterion (QIC)[b]	588.161
Corrected Quasi Likelihood under Independence Model Criterion (QICC)[b]	571.113

Dependent Variable: C2.Chick.or.Not
Model: (Intercept), Species, Condition, Species * Condition, Proximity.to.Choice.1, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.Meat.or.Not, C1.Sausage.or.Not, C1.DryFood.or.Not, C1.Tofu.or.Not[a]

a. Information criteria are in smaller-is-better form.

b. Computed using the full log quasi-likelihood function.

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test			Exp(B)	95% Wald Confidence Interval for Exp(B)	
			Lower	Upper	Wald χ^2	df	Sig.		Lower	Upper
(Intercept)	1.201	0.3648	0.486	1.916	10.839	1	0.001	3.324	1.626	6.794
[Species=Dog]	0.787	0.5209	-0.234	1.808	2.283	1	0.131	2.197	0.792	6.099
[Species=Wolf]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed]	1.324	0.4901	0.364	2.285	7.300	1	0.007	3.759	1.439	9.824
[Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Condition=Fed]	-0.788	0.5545	-1.875	0.299	2.019	1	0.155	0.455	0.153	1.348
[Species=Dog] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Fed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Proximity.to.Choice.1=No]	0.009	0.3596	-0.696	0.713	0.001	1	0.981	1.009	0.498	2.041
[Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Proximity.to.Choice.1=No]	-0.671	0.4999	-1.650	0.309	1.799	1	0.180	0.511	0.192	1.362
[Species=Dog] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Proximity.to.Choice.1=No]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed] * [Proximity.to.Choice.1=No]	-0.556	.6404	-1.811	0.699	0.755	1	0.385	0.573	0.163	2.011
[Condition=Fed] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Unfed] * [Proximity.to.Choice.1=No]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Unfed] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
C1.Meat.or.Not	-0.388	0.3780	-1.129	0.353	1.053	1	0.305	0.678	0.323	1.423
C1.Sausage.or.Not	-0.970	0.3799	-1.714	-0.225	6.517	1	0.011	0.379	0.180	0.798
C1.DryFood.or.Not	-0.157	0.4963	-1.129	0.816	0.100	1	0.752	0.855	0.323	2.261
C1.Tofu.or.Not	-0.157	0.5449	-1.225	0.911	0.083	1	0.773	0.854	0.294	2.486
(Scale)	1									

Dependent Variable: C2.Chick.or.Not

Model: (Intercept), Species, Condition, Species * Condition, Proximity.to.Choice.1, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.Meat.or.Not, C1.Sausage.or.Not, C1.DryFood.or.Not, C1.Tofu.or.Not

a. Set to zero because this parameter is redundant.

7.1.3.2.1 Estimated Marginal Means 1: Condition

Estimates

Condition	Mean	Std. Error	95% Wald Confidence Interval	
			Lower	Upper
Fed	0.85	0.031	0.77	0.90
Unfed	0.74	0.046	0.64	0.82

Covariates appearing in the model are fixed at the following values: C1.Meat.or.Not = 0.35; C1.Sausage.or.Not = 0.22; C1.DryFood.or.Not = 0.06; C1.Tofu.or.Not = 0.11

Pairwise Comparisons

(I) Condition	(J) Condition	Mean Difference (I-J)	Std. Error	df	Sequential Bonferroni Sig.	95% Wald Confidence Interval for Difference[b]	
						Lower	Upper
Fed	Unfed	0.10[a]	0.049	1	0.033	0.01	0.20
Unfed	Fed	-0.10[a]	0.049	1	0.033	-0.20	-0.01

Pairwise comparisons of estimated marginal means based on the original scale of dependent variable C2.Chick.or.Not

a. The mean difference is significant at the .05 level.

b. Confidence interval bounds are approximate.

Overall Test Results

Wald χ^2	df	Sig.
4.525	1	0.033

The Wald chi-square tests the effect of Condition. This test is based on the linearly independent pairwise comparisons among the estimated marginal means.

7.1.3.2.2 Estimated Marginal Means 2: Proximity to Choice 1

Estimates

Proximity.to.Choice.1	Mean	Std. Error	95% Wald Confidence Interval	
			Lower	Upper
No	0.75	0.038	0.66	0.81
Yes	0.84	0.033	0.77	0.90

Covariates appearing in the model are fixed at the following values: C1.Meat.or.Not = 0.35; C1.Sausage.or.Not = 0.22; C1.DryFood.or.Not = 0.06; C1.Tofu.or.Not = 0.11

Overall Test Results

Wald χ^2	df	Sig.
6.327	1	0.012

The Wald chi-square tests the effect of Proximity.to.Choice.1. This test is based on the linearly independent pairwise comparisons among the estimated marginal means.

7.1.3.3 Analysis for Meat, Choice 2

Model Information

Dependent Variable		C2.Meat.or.Not[a]
Probability Distribution		Binomial
Link Function		Logit
Subject Effect	1	Animal
Within-Subject Effect	1	Trial
Working Correlation Matrix Structure		Independent

a. The procedure models 0 as the response, treating 1 as the reference category.

Tests of Model Effects

Source	Type III		
	Wald χ^2	df	Sig.
(Intercept)	33.683	1	0.000
Species	3.590	1	0.058
Condition	0.300	1	0.584
Proximity.to.Choice.1	1.913	1	0.167
Species * Condition	0.005	1	0.944
Species * Proximity.to.Choice.1	1.609	1	0.205
Condition * Proximity.to.Choice.1	11.934	1	0.001
C1.Sausage.or.Not	0.077	1	0.781
C1.DryFood.or.Not	0.866	1	0.352
C1.Tofu.or.Not	3.499	1	0.061
C1.Chick.or.Not	0.253	1	0.615

Dependent Variable: C2.Meat.or.Not

Model: (Intercept), Species, Condition, Proximity.to.Choice.1, Species * Condition, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.Sausage.or.Not, C1.DryFood.or.Not, C1.Tofu.or.Not, C1.Chick.or.Not

Goodness of Fit[a]

	Value
Quasi Likelihood under Independence Model Criterion (QIC)[b]	597.276
Corrected Quasi Likelihood under Independence Model Criterion (QICC)[b]	580.427

Dependent Variable: C2.Meat.or.Not

Model: (Intercept), Species, Condition, Proximity.to.Choice.1, Species * Condition, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.Sausage.or.Not, C1.DryFood.or.Not, C1.Tofu.or.Not, C1.Chick.or.Not[a]

a. Information criteria are in smaller-is-better form.

b. Computed using the full log quasi-likelihood function.

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test			Exp(B)	95% Wald Confidence Interval for Exp(B)	
			Lower	Upper	Wald χ^2	df	Sig.		Lower	Upper
(Intercept)	1.709	0.4281	0.870	2.548	15.945	1	0.000	5.525	2.388	12.786
[Species=Dog]	0.916	0.6380	-0.334	2.167	2.063	1	0.151	2.500	0.0716	8.732
[Species=Wolf]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed]	-1.068	0.5440	-2.134	-0.002	3.855	1	0.050	0.344	0.118	0.998
[Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Proximity.to.Choice.1=No]	-0.946	0.5095	-1.945	0.052	3.448	1	0.063	0.388	0.143	1.054
[Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Condition=Fed]	-0.052	0.7312	-1.485	1.381	0.005	1	0.944	0.950	0.227	3.981
[Species=Dog] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Fed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Proximity.to.Choice.1=No]	-0.800	0.6304	-2.035	0.436	1.609	1	0.205	0.449	0.131	1.546
[Species=Dog] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Proximity.to.Choice.1=No]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed] * [Proximity.to.Choice.1=No]	1.808	0.5233	0.782	2.834	11.934	1	0.001	6.097	2.186	17.005
[Condition=Fed] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Unfed] * [Proximity.to.Choice.1=No]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Unfed] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
C1.Sausage.or.Not	-0.104	0.3764	-0.842	0.633	0.077	1	0.781	0.901	0.431	1.884
C1.DryFood.or.Not	0.421	0.4520	-0.465	1.307	0.866	1	0.352	1.523	0.628	3.693
C1.Tofu.or.Not	-0.911	0.4869	-1.865	0.043	3.499	1	0.061	0.402	0.155	1.044
C1.Chick.or.Not	0.168	0.3329	-0.485	0.820	0.253	1	0.615	1.182	0.616	2.270
(Scale)	1									

Dependent Variable: C2.Meat.or.Not

Model: (Intercept), Species, Condition, Proximity.to.Choice.1, Species * Condition, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.Sausage.or.Not, C1.DryFood.or.Not, C1.Tofu.or.Not, C1.Chick.or.Not

a. Set to zero because this parameter is redundant.

7.1.3.3.1 Estimated Marginal Means: Condition * Proximity to Choice 1

Estimates

Condition	Proximity.to.Choice.1	Mean	Std. Error	95% Wald Confidence Interval	
				Lower	Upper
Fed	No	0.81	0.041	0.72	0.88
	Yes	0.73	0.057	0.61	0.83
Unfed	No	0.68	0.053	0.57	0.78
	Yes	0.89	0.037	0.79	0.95

Covariates appearing in the model are fixed at the following values: C1.Sausage.or.Not = 0.22; C1.DryFood.or.Not = 0.06; C1.Tofu.or.Not = 0.11; C1.Chick.or.Not = 0.24

Pairwise Comparisons

(I) Condition * Proximity.to.Choice.1	(J) Condition * Proximity.to.Choice.1	Mean Difference (I-J)	Std. Error	df	Sequential Bonferroni Sig.	95% Wald Confidence Interval for Difference[a]	
						Lower	Upper
[Condition=Fed] * [Proximity.to.Choice.1=No]	[Condition=Fed] * [Proximity.to.Choice.1=Yes]	0.08	0.063	1	0.489	-0.07	0.23
	[Condition=Unfed] * [Proximity.to.Choice.1=No]	0.13	0.080	1	0.396	-0.07	0.33
	[Condition=Unfed] * [Proximity.to.Choice.1=Yes]	-0.08	0.056	1	0.489	-0.21	0.06
[Condition=Fed] * [Proximity.to.Choice.1=Yes]	[Condition=Fed] * [Proximity.to.Choice.1=No]	-0.08	0.063	1	0.489	-0.23	0.07
	[Condition=Unfed] * [Proximity.to.Choice.1=No]	0.05	0.096	1	0.588	-0.14	0.24
	[Condition=Unfed] * [Proximity.to.Choice.1=Yes]	-0.16[b]	0.061	1	0.048	-0.31	0.00
[Condition=Unfed] * [Proximity.to.Choice.1=No]	[Condition=Fed] * [Proximity.to.Choice.1=No]	-0.13	0.080	1	0.396	-0.33	0.07
	[Condition=Fed] * [Proximity.to.Choice.1=Yes]	-0.05	0.096	1	0.588	-0.24	0.14
	[Condition=Unfed] * [Proximity.to.Choice.1=Yes]	-0.21[b]	0.065	1	0.008	-0.38	-0.04
[Condition=Unfed] * [Proximity.to.Choice.1=Yes]	[Condition=Fed] * [Proximity.to.Choice.1=No]	0.08	0.056	1	0.489	-0.06	0.21
	[Condition=Fed] * [Proximity.to.Choice.1=Yes]	0.16[b]	0.061	1	0.048	0.00	0.31
	[Condition=Unfed] * [Proximity.to.Choice.1=No]	0.21[b]	0.065	1	0.008	0.04	0.38

Pairwise comparisons of estimated marginal means based on the original scale of dependent variable C2.Meat.or.Not

a. Confidence interval bounds are approximate.

b. The mean difference is significant at the .05 level.

Overall Test Results

Wald χ^2	df	Sig.
20.173	3	0.000

The Wald chi-square tests the effect of Condition*Proximity.to.Choice.1. This test is based on the linearly independent pairwise comparisons among the estimated marginal means.

7.1.3.4 Analysis for Sausage, Choice 2

Model Information

Dependent Variable		C2.Sausage.or.Not[a]
Probability Distribution		Binomial
Link Function		Logit
Subject Effect	1	Animal
Within-Subject Effect	1	Trial
Working Correlation Matrix Structure		Independent

a. The procedure models 0 as the response, treating 1 as the reference category.

Tests of Model Effects

Source	Type III		
	Wald χ^2	df	Sig.
(Intercept)	57.144	1	0.000
Species	0.559	1	0.455
Condition	1.322	1	0.250
Proximity.to.Choice.1	10.714	1	0.001
Species * Condition	0.291	1	0.589
Species * Proximity.to.Choice.1	1.999	1	0.157
Condition * Proximity.to.Choice.1	1.393	1	0.238
C1.DryFood.or.Not	11.024	1	0.001
C1.Tofu.or.Not	2.348	1	0.125
C1.Chick.or.Not	9.731	1	0.002
C1.Meat.or.Not	7.699	1	0.006

Dependent Variable: C2.Sausage.or.Not
Model: (Intercept), Species, Condition, Proximity.to.Choice.1, Species * Condition, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.DryFood.or.Not, C1.Tofu.or.Not, C1.Chick.or.Not, C1.Meat.or.Not

Goodness of Fit[a]

	Value
Quasi Likelihood under Independence Model Criterion (QIC)[b]	591.670
Corrected Quasi Likelihood under Independence Model Criterion (QICC)[b]	579.601

Dependent Variable: C2.Sausage.or.Not
Model: (Intercept), Species, Condition, Proximity.to.Choice.1, Species * Condition, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.DryFood.or.Not, C1.Tofu.or.Not, C1.Chick.or.Not, C1.Meat.or.Not[a]
a. Information criteria are in smaller-is-better form.
b. Computed using the full log quasi-likelihood function.

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test			Exp(B)	95% Wald Confidence Interval for Exp(B)	
			Lower	Upper	Wald χ^2	df	Sig.		Lower	Upper
(Intercept)	2.485	0.4791	1.546	3.424	26.904	1	0.000	12.000	4.692	30.688
[Species=Dog]	-0.074	0.5750	-1.201	1.053	0.016	1	0.898	0.929	0.301	2.867
[Species=Wolf]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed]	0.208	0.4038	-0.583	1.000	0.266	1	0.606	1.231	0.558	2.717
[Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Proximity.to.Choice.1=No]	-1.144	0.5260	-2.175	-0.113	4.729	1	0.030	0.319	0.114	0.893
[Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Condition=Fed]	-0.250	0.4627	-1.157	0.657	0.291	1	0.589	0.779	0.315	1.929
[Species=Dog] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Fed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Proximity.to.Choice.1=No]	0.886	0.6266	-0.342	2.114	1.999	1	0.157	2.425	0.710	8.281
[Species=Dog] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Proximity.to.Choice.1=No]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed] * [Proximity.to.Choice.1=No]	-0.668	0.5659	-1.777	0.441	1.393	1	0.238	0.513	0.169	1.555
[Condition=Fed] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Unfed] * [Proximity.to.Choice.1=No]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Unfed] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
C1.DryFood.or.Not	-1.404	0.4228	-2.232	-0.575	11.024	1	0.001	0.246	0.107	0.563
C1.Tofu.or.Not	-0.642	0.4188	-1.463	0.179	2.348	1	0.125	0.526	0.232	1.196
C1.Chick.or.Not	-1.021	0.3271	-1.662	-0.379	9.731	1	0.002	0.360	0.190	0.684
C1.Meat.or.Not	-0.785	0.2830	-1.340	-0.231	7.699	1	0.006	0.456	0.262	0.794
(Scale)	1									

Dependent Variable: C2.Sausage.or.Not

Model: (Intercept), Species, Condition, Proximity.to.Choice.1, Species * Condition, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.DryFood.or.Not, C1.Tofu.or.Not, C1.Chick.or.Not, C1.Meat.or.Not

a. Set to zero because this parameter is redundant.

7.1.3.5 Analysis for Dry Food, Choice 2

Model Information

Dependent Variable		C2.DryFood.or.Not[a]
Probability Distribution		Binomial
Link Function		Logit
Subject Effect	1	Animal
Within-Subject Effect	1	Trial
Working Correlation Matrix Structure		Independent

a. The procedure models 0 as the response, treating 1 as the reference category.

Tests of Model Effects

Source	Type III		
	Wald χ^2	df	Sig.
(Intercept)	22.408	1	0.000
Species	0.971	1	0.324
Condition	0.017	1	0.897
Proximity.to.Choice.1	3.858	1	0.050
Species * Condition	0.056	1	0.813
Species * Proximity.to.Choice.1	0.092	1	0.761
Condition * Proximity.to.Choice.1	0.402	1	0.526
C1.Tofu.or.Not	0.042	1	0.837
C1.Chick.or.Not	2.290	1	0.130
C1.Meat.or.Not	2.109	1	0.146
C1.Sausage.or.Not	0.419	1	0.517

Dependent Variable: C2.DryFood.or.Not

Model: (Intercept), Species, Condition, Proximity.to.Choice.1, Species * Condition, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.Tofu.or.Not, C1.Chick.or.Not, C1.Meat.or.Not, C1.Sausage.or.Not

Goodness of Fit[a]

	Value
Quasi Likelihood under Independence Model Criterion (QIC)[b]	447.317
Corrected Quasi Likelihood under Independence Model Criterion (QICC)[b]	436.037

Dependent Variable: C2.DryFood.or.Not

Model: (Intercept), Species, Condition, Proximity.to.Choice.1, Species * Condition, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.Tofu.or.Not, C1.Chick.or.Not, C1.Meat.or.Not, C1.Sausage.or.Not[a]

a. Information criteria are in smaller-is-better form.

b. Computed using the full log quasi-likelihood function.

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test			Exp(B)	95% Wald Confidence Interval for Exp(B)	
			Lower	Upper	Wald χ^2	df	Sig.		Lower	Upper
(Intercept)	2.418	0.6222	1.198	3.637	15.100	1	0.0000	11.221	3.314	37.987
[Species=Dog]	-0.487	0.5638	-1.592	0.619	0.745	1	0.388	0.615	0.204	1.856
[Species=Wolf]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed]	0.228	0.4404	-0.635	1.091	0.269	1	0.604	1.256	0.530	2.978
[Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Proximity.to.Choice.1=No]	0.881	0.7941	-0.675	2.438	1.232	1	0.267	2.414	0.509	11.448
[Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Condition=Fed]	-0.141	0.5960	-1.309	1.027	0.056	1	0.813	0.868	0.270	2.792
[Species=Dog] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Fed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Proximity.to.Choice.1=No]	0.252	0.8311	-1.376	1.881	0.092	1	0.761	1.287	0.252	6.562
[Species=Dog] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Proximity.to.Choice.1=No]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed] * [Proximity.to.Choice.1=No]	-0.389	0.6134	-1.591	0.813	0.402	1	0.526	0.678	0.204	2.255
[Condition=Fed] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Unfed] * [Proximity.to.Choice.1=No]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Unfed] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
C1.Tofu.or.Not	-0.133	0.6451	-1.397	1.131	0.042	1	0.837	0.876	0.247	3.100
C1.Chick.or.Not	-0.776	0.5129	-1.782	0.229	2.290	1	0.130	0.460	0.168	1.257
C1.Meat.or.Not	-0.836	0.5755	-1.964	0.292	2.109	1	0.146	0.434	0.140	1.339
C1.Sausage.or.Not	-0.389	0.6011	-1.567	0.789	0.419	1	0.517	0.678	0.209	2.201
(Scale)	1									

Dependent Variable: C2.DryFood.or.Not

Model: (Intercept), Species, Condition, Proximity.to.Choice.1, Species * Condition, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.Tofu.or.Not, C1.Chick.or.Not, C1.Meat.or.Not, C1.Sausage.or.Not

a. Set to zero because this parameter is redundant.

7.1.3.6 Analysis for Tofu, Choice 2

Model Information

Dependent Variable		C2.Tofu.or.Not[a]
Probability Distribution		Binomial
Link Function		Logit
Subject Effect	1	Animal
Within-Subject Effect	1	Trial
Working Correlation Matrix Structure		Independent

a. The procedure models 0 as the response, treating 1 as the reference category.

Tests of Model Effects

Source	Type III		
	Wald χ^2	df	Sig.
(Intercept)	23.398	1	0.000
Species	6.041	1	0.014
Condition	5.318	1	0.021
Proximity.to.Choice.1	19.681	1	0.000
Species * Condition	4.523	1	0.033
Species * Proximity.to.Choice.1	1.243	1	0.265
Condition * Proximity.to.Choice.1	2.792	1	0.095
C1.Chick.or.Not	0.540	1	0.463
C1.Meat.or.Not	0.258	1	0.611
C1.Sausage.or.Not	0.108	1	0.742
C1.DryFood.or.Not	0.584	1	0.445

Dependent Variable: C2.Tofu.or.Not
Model: (Intercept), Species, Condition, Proximity.to.Choice.1, Species * Condition, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.Chick.or.Not, C1.Meat.or.Not, C1.Sausage.or.Not, C1.DryFood.or.Not

Goodness of Fit[a]

	Value
Quasi Likelihood under Independence Model Criterion (QIC)[b]	434.706
Corrected Quasi Likelihood under Independence Model Criterion (QICC)[b]	418.394

Dependent Variable: C2.Tofu.or.Not
Model: (Intercept), Species, Condition, Proximity.to.Choice.1, Species * Condition, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.Chick.or.Not, C1.Meat.or.Not, C1.Sausage.or.Not, C1.DryFood.or.Not[a]

a. Information criteria are in smaller-is-better form.

b. Computed using the full log quasi-likelihood function.

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test			Exp(B)	95% Wald Confidence Interval for Exp(B)	
			Lower	Upper	Wald χ^2	df	Sig.		Lower	Upper
(Intercept)	1.868	0.4561	.974	2.762	16.779	1	0.000	6.476	2.649	15.831
[Species=Dog]	-1.500	0.5674	-2.612	-0.388	6.990	1	0.008	0.223	0.073	0.678
[Species=Wolf]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed]	-1.305	0.6396	-2.558	-0.051	4.162	1	0.041	0.271	0.077	0.950
[Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Proximity.to.Choice.1=No]	4.314	1.3367	1.694	6.934	10.417	1	0.001	74.747	5.443	1026.537
[Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Condition=Fed]	1.826	0.8586	0.143	3.509	4.523	1	0.033	6.209	1.154	33.413
[Species=Dog] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Fed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Condition=Unfed]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Dog] * [Proximity.to.Choice.1=No]	-1.290	1.1572	-3.558	0.978	1.243	1	0.265	0.275	0.028	2.659
[Species=Dog] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Proximity.to.Choice.1=No]	0[a]	.	.	.	.	.	.	1	.	.
[Species=Wolf] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Fed] * [Proximity.to.Choice.1=No]	-1.578	0.9445	-3.430	0.273	2.792	1	0.095	0.206	0.032	1.314
[Condition=Fed] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Unfed] * [Proximity.to.Choice.1=No]	0[a]	.	.	.	.	.	.	1	.	.
[Condition=Unfed] * [Proximity.to.Choice.1=Yes]	0[a]	.	.	.	.	.	.	1	.	.
C1.Chick.or.Not	0.373	0.5083	-0.623	1.370	0.540	1	0.463	1.453	0.536	3.934
C1.Meat.or.Not	0.295	0.5808	-0.843	1.434	0.258	1	0.611	1.343	0.430	4.194
C1.Sausage.or.Not	0.159	0.4835	-0.789	1.106	0.108	1	0.742	1.172	0.454	3.024
C1.DryFood.or.Not	0.657	0.8593	-1.027	2.341	0.584	1	0.445	1.929	0.358	10.391
(Scale)	1									

Dependent Variable: C2.Tofu.or.Not

Model: (Intercept), Species, Condition, Proximity.to.Choice.1, Species * Condition, Species * Proximity.to.Choice.1, Condition * Proximity.to.Choice.1, C1.Chick.or.Not, C1.Meat.or.Not, C1.Sausage.or.Not, C1.DryFood.or.Not

a. Set to zero because this parameter is redundant.

7.1.3.6.1 Estimated Marginal Means: Species* Condition

Estimates

Species	Condition	Mean	Std. Error	95% Wald Confidence Interval	
				Lower	Upper
Dog	Fed	0.87	0.037	0.78	0.93
	Unfed	0.90	0.035	0.80	0.95
Wolf	Fed	0.90	0.051	0.75	0.97
	Unfed	0.99	0.010	0.95	1.00

Covariates appearing in the model are fixed at the following values: C1.Chick.or.Not = 0.24; C1.Meat.or.Not = 0.35; C1.Sausage.or.Not = 0.22; C1.DryFood.or.Not = 0.06

Pairwise Comparisons

Species*Condition (I)	Species*Condition (J)	Mean Difference (I-J)	Std. Error	df	Sequential Bonferroni Sig.	95% Wald Confidence Interval for Difference[a]	
						Lower	Upper
[Species=Dog] * [Condition=Fed]	[Species=Dog] * [Condition=Unfed]	-0.03	0.056	1	1.000	-0.15	0.09
	[Species=Wolf] * [Condition=Fed]	-0.03	0.057	1	1.000	-0.17	0.10
	[Species=Wolf] * [Condition=Unfed]	-0.12[b]	0.037	1	0.009	-0.22	-0.02
[Species=Dog] * [Condition=Unfed]	[Species=Dog] * [Condition=Fed]	0.03	0.056	1	1.000	-0.09	0.15
	[Species=Wolf] * [Condition=Fed]	0.00	0.061	1	1.000	-0.13	0.12
	[Species=Wolf] * [Condition=Unfed]	-0.09[b]	0.034	1	0.035	-0.18	0.00
[Species=Wolf] * [Condition=Fed]	[Species=Dog] * [Condition=Fed]	0.03	0.057	1	1.000	-0.10	0.17
	[Species=Dog] * [Condition=Unfed]	0.00	0.061	1	1.000	-0.12	0.13
	[Species=Wolf] * [Condition=Unfed]	-0.09	0.049	1	0.316	-0.21	0.04
[Species=Wolf] * [Condition=Unfed]	[Species=Dog] * [Condition=Fed]	0.12[b]	0.037	1	0.009	0.02	0.22
	[Species=Dog] * [Condition=Unfed]	0.09[b]	0.034	1	0.035	0.00	0.18
	[Species=Wolf] * [Condition=Fed]	0.09	0.049	1	0.316	-0.04	0.21

Pairwise comparisons of estimated marginal means based on the original scale of dependent variable C2.Tofu.or.Not

a. Confidence interval bounds are approximate.

b. The mean difference is significant at the 0.05 level.

Overall Test Results

Wald χ^2	df	Sig.
24.174	3	0.000

The Wald chi-square tests the effect of Species*Condition. This test is based on the linearly independent pairwise comparisons among the estimated marginal means.

7.2 Article 2

Rao A[+*], Bernasconi L[+], Lazzaroni M, Marshall-Pescini S, Range F.; Differences in persistence between dogs and wolves in an unsolvable task in the absence of humans. *PeerJ 6:e5944* (DOI: 10.7717/peerj.5944).

7.2.1 Supplementary Video

The video shows examples of the manipulative behaviours that were coded for each object.

To view the video, please scan the QR code on the right, or visit http://bit.do/UT-Video.

7.2.2 Descriptive statistics of each correlate in dogs and wolves.

Variable	Statistic	Ball		Pipe	
		Dogs	**Wolves**	**Dogs**	**Wolves**
Contact Latency (Seconds)	Min	0.6	0.4	0.6	0.2
	Max	2.0	2.0	2.4	3.2
	Mean	1.0	1.2	1.1	1.3
	Median	0.9	1.2	1.0	1.0
	Std. Dev	0.4	0.7	0.5	0.9
Persistence (Seconds)	Min	0.0	14.6	0.0	0.2
	Max	282.8	940.8	821.4	950.6
	Mean	29.4	319.0	97.3	239.9
	Median	4.1	169.2	2.4	45.7
	Std. Dev	73.3	299.2	244.2	356.8
Motor Diversity	Min	0	6	0	1
	Max	13	17	14	14
	Mean	3	10	3	7
	Median	3	9	2	6
	Std. Dev	3	3	4	5

7.2.3 Results for analyses for persistence including outliers

The results from the model built using the Gamma distribution (AIC = 500.6998) differed from the results from models built using the Box-Cox T Original (AIC = 505.0368), Weibull (AIC = 509.0868) and Log-Normal (AIC = 826.7205) distributions (results from these three distributions were the same). This implies that these models may not be robust and that the following results should be interpreted with caution.

When modelled using the Box-Cox T Original distribution, wolves were more persistent than dogs (GAMLSS: t = 2.21, P = 0.032) in their manipulation of both objects (i.e. the interaction between species and object was not significant, GAMLSS: t = -1.65, P = 0.10). Subjects' persistence did not differ between objects (GAMLSS: t = -0.36, P = 0.72) and was not affected by age (GAMLSS: t = 1.07, P = 0.29).

When modelled using the Gamma distribution, dogs and wolves did not differ significantly in their persistence in manipulating either object (GAMLSS: t = 1.34, P = 0.19) (i.e., the interaction between species and object was not significant, GAMLSS: t = -1.81, P = 0.08). Subjects' persistence did not differ between objects (GAMLSS: t = 1.46, P – 0.15) and was not affected by age (GAMLSS: t = 0.92, P = 0.36).

7.2.4 Complete GAMLSS Model Information

7.2.4.1 Persistence Models

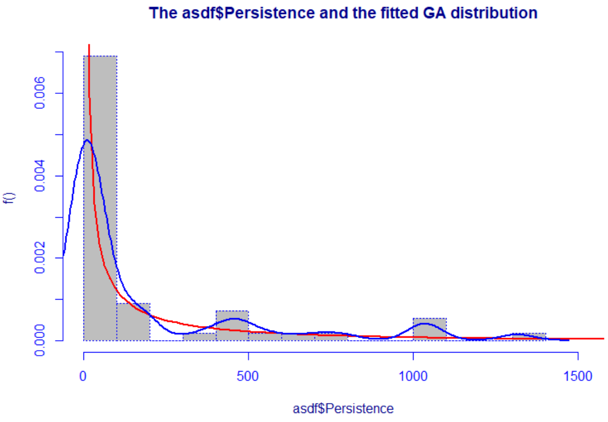
7.2.4.1.1 Response Variable Distribution Checks

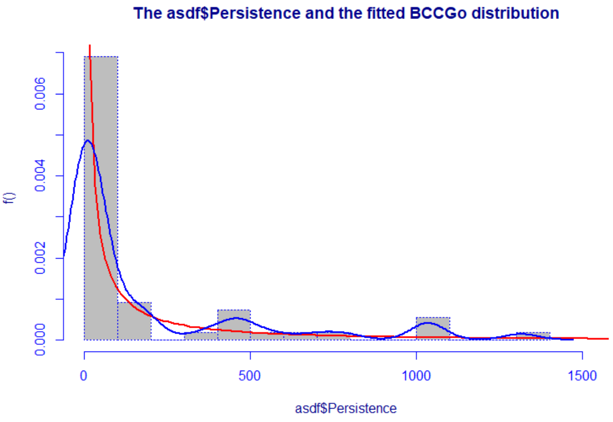
```
Persistence.Distribution$fit
```

Distribution	AIC	Errors in Plot?
BCPEo	444.935388	Yes
GG	455.096973	Yes
GB2	457.614243	Yes
GIG	457.950489	Yes
IGAMMA	547.4639	No
GA	458.178068	No
BCCGo	463.276357	No

Distribution	AIC	Errors in Plot?
BCTo	465.276357	No
WEI2	469.313586	No
WEI	469.313586	No
WEI3	469.313586	No
LOGNO2	494.746702	No
LOGNO	494.746702	No

7.2.4.1.2 Density plots of examples of distributions used in final models





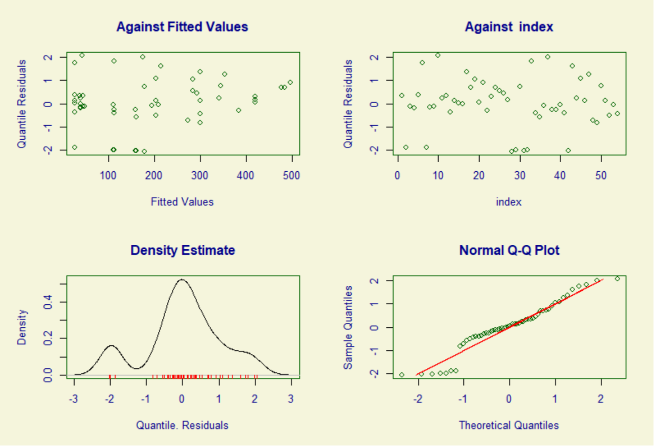
7.2.4.1.3 Model Distribution Selection

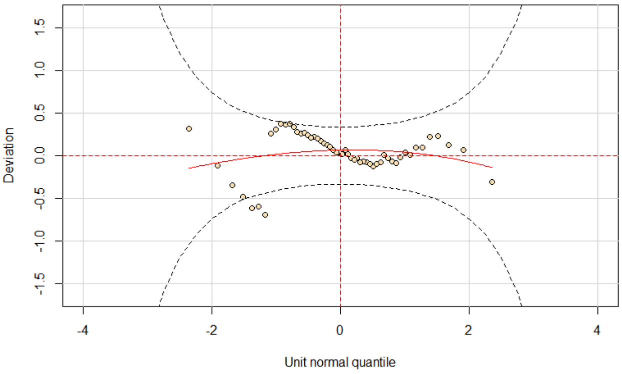
```
Persistence.DISTRIBUTION <- gamlss(Persistence ~ Species*Object + Age,
                                   random = ~1|Individual, family = "DISTRIBUTION",
                                   data = asdf)
```

Model	df	AIC	Residuals outside CI
Persistence.GA	6	471.144609	3
Persistence.BCTo	8	472.382229	4
Persistence.WEI	6	478.48115	14
Persistence.WEI3	6	478.481189	14
Persistence.WEI2	6	478.481915	13
Persistence.LOGNO2	6	780.468216	23
Persistence.LOGNO	6	780.468216	23
Persistence.BCCGo	7	9375.03115	-

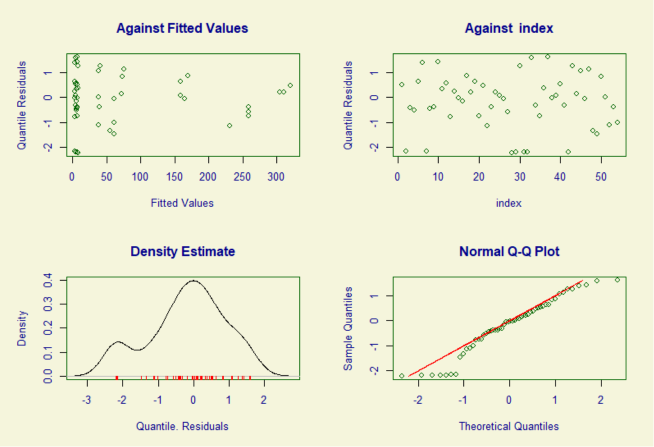
7.2.4.1.4 Model Diagnostics Plots

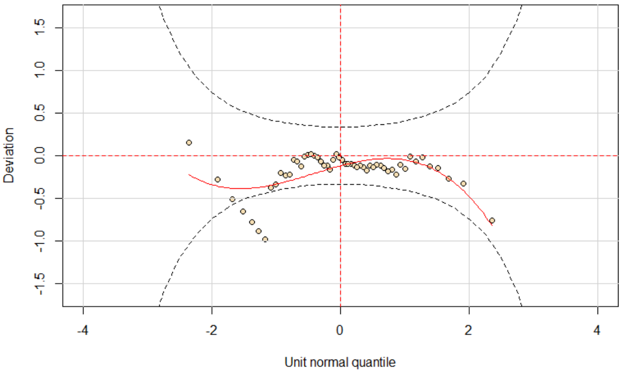
`plot(Persistence.GA) & wp(Persistence.GA)`



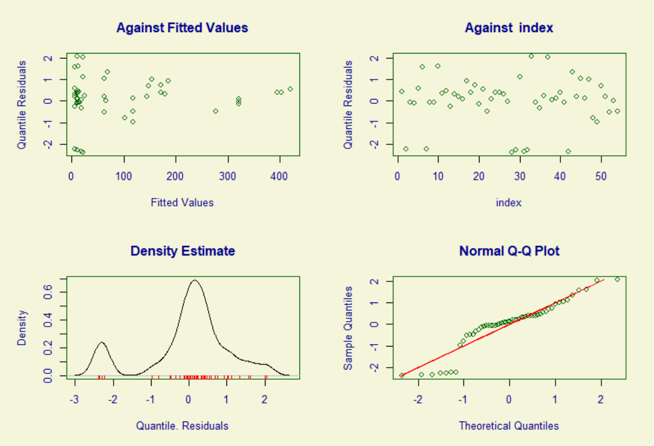


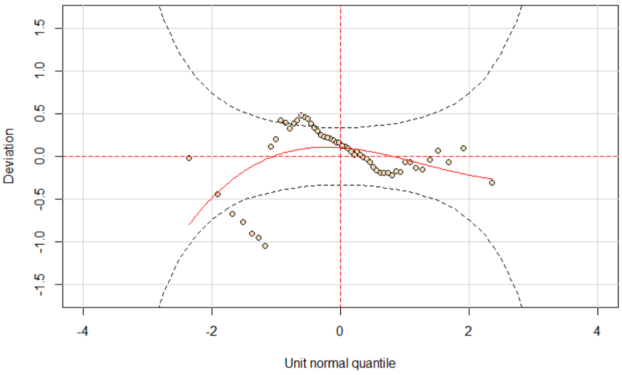
`plot(Persistence.BCTo) & wp(Persistence.BCTo)`



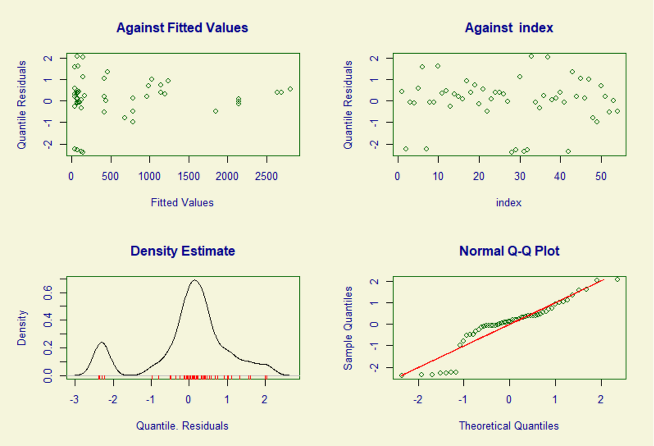


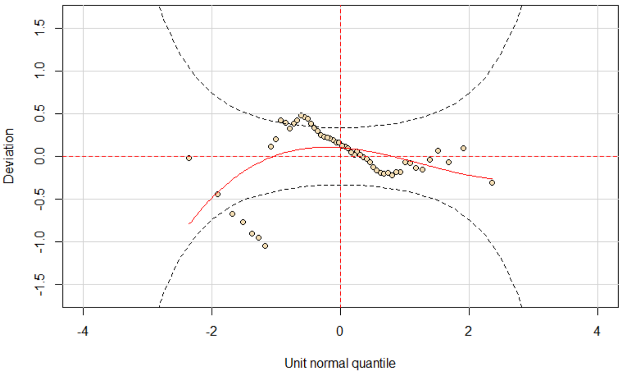
`plot(Persistence.WEI) & wp(Persistence.WEI)`



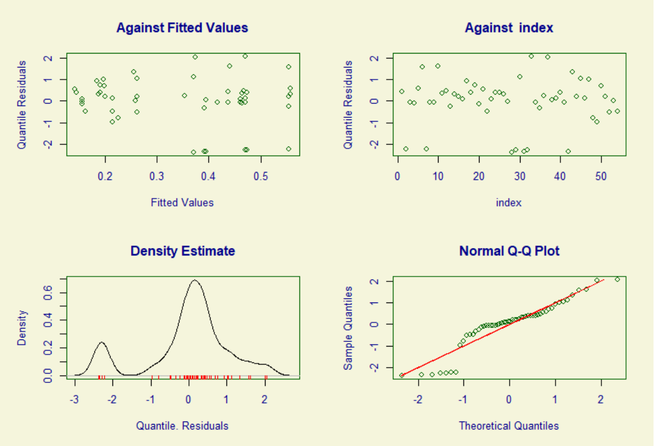


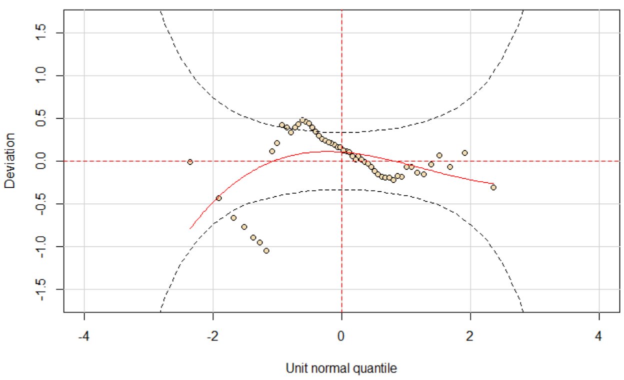
`plot(Persistence.WEI3) & wp(Persistence.WEI3)`



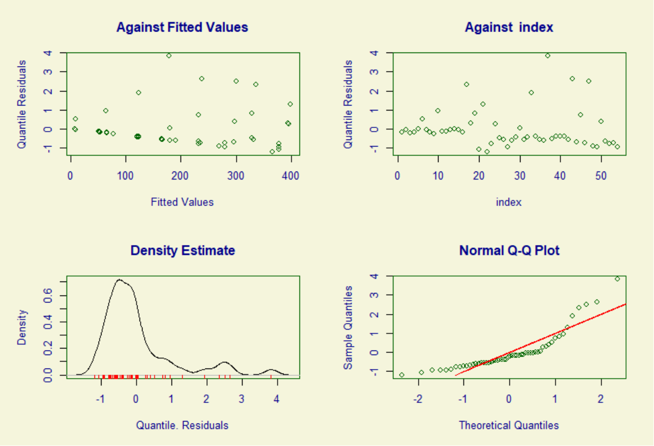


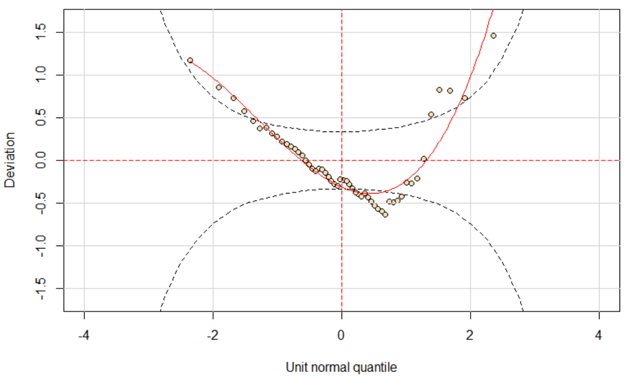
plot(Persistence.WEI2) & wp(Persistence.WEI2)



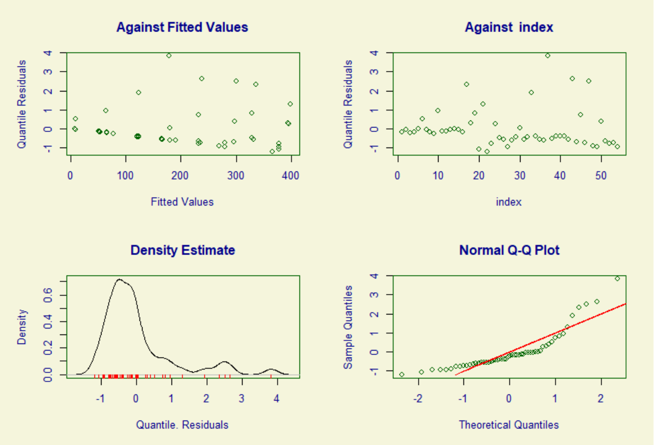


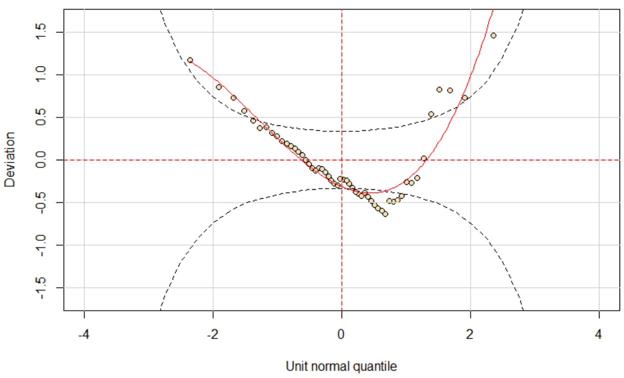
plot(Persistence.LOGNO2) & wp(Persistence.LOGNO2)





plot(Persistence.LOGNO) & wp(Persistence.LOGNO)





7.2.4.1.5 Model Reduction & Validation

7.2.4.1.5.1 Gamma Models

```
summary(Persistence.GA)
******************************************************************
Family:  c("GA", "Gamma") 

Call:  gamlss(formula = Persistence ~ Species * Object + Age,  
       family = "GA", data = na.omit(asdf), control = con, random = ~1 | Individual) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                       Estimate Std. Error t value Pr(>|t|)   
(Intercept)              3.0281     0.8996   3.366  0.00151 **
SpeciesWolf              2.0694     0.8809   2.349  0.02297 * 
ObjectPipe               1.3928     0.7705   1.808  0.07692 . 
Age                      0.1292     0.1653   0.782  0.43815   
SpeciesWolf:ObjectPipe  -1.7297     1.1809  -1.465  0.14950   
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  0.76252    0.07419   10.28 1.02e-13 ***
------------------------------------------------------------------
No. of observations in the fit:  54 
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  48 
                      at cycle:  2 
 
Global Deviance:     459.1446 
            AIC:     471.1446 
            SBC:     483.0785 
******************************************************************
```

```
dropterm(Persistence.GA, test = "Chisq")
Single term deletions for mu
Model: Persistence ~ Species * Object + Age
               Df    AIC     LRT Pr(Chi)
<none>            471.14                
Age             1 469.75 0.60761  0.4357
Species:Object  1 471.22 2.07727  0.1495
```

```
summary(Persistence.GA.2)
******************************************************************
Family:  c("GA", "Gamma") 

Call:  gamlss(formula = Persistence ~ Species + Object + Age,  
       family = "GA", data = na.omit(asdf), control = con, random = ~1 | Individual) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)   3.4547     0.9266   3.728   0.0005 ***
SpeciesWolf   1.2552     0.6993   1.795   0.0788 .  
ObjectPipe    0.6699     0.6352   1.055   0.2968    
Age           0.1266     0.1674   0.756   0.4533    
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  0.77393    0.07407   10.45  4.6e-14 ***
------------------------------------------------------------------
No. of observations in the fit:  54 
Degrees of Freedom for the fit:  5
      Residual Deg. of Freedom:  49 
                      at cycle:  2 
 
Global Deviance:     461.2219 
            AIC:     471.2219 
            SBC:     481.1668 
******************************************************************
```

7.2.4.1.5.2 Box-Cox T Original Models

```
summary(Persistence.BCTo)
******************************************************************
Family: c("BCTo", "Box-Cox-t-orig.")

Call: gamlss(formula = Persistence ~ Species * Object + Age, 
       family = "BCTo", data = na.omit(asdf), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                       Estimate Std. Error t value Pr(>|t|)
(Intercept)              0.9022     0.7954   1.134    0.263
SpeciesWolf              3.4660     0.7307   4.744 2.07e-05 ***
ObjectPipe               0.1557     0.7024   0.222    0.826
Age                      0.1630     0.1487   1.096    0.279
SpeciesWolf:ObjectPipe  -1.5952     1.0694  -1.492    0.143
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   0.3788     0.3357   1.128    0.265
------------------------------------------------------------------
Nu link function:  identity
Nu Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  0.10731    0.07888    1.36     0.18
------------------------------------------------------------------
Tau link function:  log
Tau Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   0.1502     0.4464   0.337    0.738
------------------------------------------------------------------
No. of observations in the fit:  54 
Degrees of Freedom for the fit:  8
      Residual Deg. of Freedom:  46 
                      at cycle:  20 

Global Deviance:     456.3822 
            AIC:     472.3822 
            SBC:     488.2941 
******************************************************************
```

```
dropterm(Persistence.BCTo, test = "Chisq")
Single term deletions for mu
Model: Persistence ~ Species * Object + Age
               Df    AIC    LRT Pr(Chi)
<none>            472.38               
Age             1 471.51 1.1258  0.2887
Species:Object  1 472.26 1.8732  0.1711
```

```
summary(Persistence.BCTo2)
******************************************************************
Family: c("BCTo", "Box-Cox-t-orig.")

Call: gamlss(formula = Persistence ~ Species + Object + Age,
      family = "BCTo", data = na.omit(asdf), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   1.1990     0.9015   1.330 0.189943
SpeciesWolf   2.9267     0.7718   3.792 0.000426 ***
ObjectPipe   -0.4757     0.6160  -0.772 0.443868
Age           0.1361     0.1760   0.774 0.443078
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   0.5673     0.3778   1.502     0.14
------------------------------------------------------------------
Nu link function:  identity
Nu Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  0.13653    0.08641    1.58    0.121
------------------------------------------------------------------
Tau link function:  log
Tau Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   0.3865     0.5790   0.667    0.508
------------------------------------------------------------------
No. of observations in the fit:  54
Degrees of Freedom for the fit:  7
      Residual Deg. of Freedom:  47
                      at cycle:  21

Global Deviance:     458.2554
            AIC:     472.2554
            SBC:     486.1783
******************************************************************
```

7.2.4.1.5.3 Weibull Models

```
summary(Persistence.WEI)
******************************************************************
Family: c("WEI", "Weibull")

Call: gamlss(formula = Persistence ~ Species * Object + Age,
      family = "WEI", data = na.omit(asdf), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                       Estimate Std. Error t value Pr(>|t|)
(Intercept)              1.3296     1.2897   1.031   0.3078
SpeciesWolf              2.9151     1.3044   2.235   0.0301 *
ObjectPipe               0.5124     1.1156   0.459   0.6480
Age                      0.2089     0.2417   0.864   0.3917
SpeciesWolf:ObjectPipe  -1.5139     1.6988  -0.891   0.3773
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  -1.1253     0.1144  -9.836 4.33e-13 ***
------------------------------------------------------------------
No. of observations in the fit:  54
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  48
                      at cycle:  4

Global Deviance:     466.4812
            AIC:     478.4812
            SBC:     490.4151
******************************************************************
```

```
dropterm(Persistence.WEI, test = "Chisq")
Single term deletions for mu
Model: Persistence ~ Species * Object + Age
               Df    AIC     LRT Pr(Chi)
<none>            478.48
Age             1 477.22 0.74338  0.3886
Species:Object  1 477.26 0.78022  0.3771
```

```
summary(Persistence.WEI2)
******************************************************************
Family: c("WEI", "Weibull")

Call: gamlss(formula = Persistence ~ Species + Object + Age,
       family = "WEI", data = na.omit(asdf), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   1.6360     1.2767   1.281   0.2061
SpeciesWolf   2.1743     1.0010   2.172   0.0347 *
ObjectPipe   -0.1444     0.8599  -0.168   0.8673
Age           0.2104     0.2451   0.858   0.3948
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  -1.1399     0.1135  -10.04 1.77e-13 ***
------------------------------------------------------------------
No. of observations in the fit:  54
Degrees of Freedom for the fit:  5
      Residual Deg. of Freedom:  49
                      at cycle:  4

Global Deviance:     467.2614
            AIC:     477.2614
            SBC:     487.2063
******************************************************************
```

7.2.4.1.5.4 Log-Normal Models

```
summary(Persistence.LOGNO)
******************************************************************
Family: c("NO", "Normal")

Call: gamlss(formula = Persistence ~ Species * Object + Age,
       data = na.omit(asdf), control = con, random = ~1 | Individual, Family = "LOGNO")

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
                       Estimate Std. Error t value Pr(>|t|)
(Intercept)              -29.64     125.99  -0.235   0.8150
SpeciesWolf              289.25     130.70   2.213   0.0317 *
ObjectPipe               113.49     107.04   1.060   0.2943
Age                       16.22      24.68   0.657   0.5143
SpeciesWolf:ObjectPipe  -211.17     164.07  -1.287   0.2042
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  5.69651    0.09622    59.2   <2e-16 ***
------------------------------------------------------------------
No. of observations in the fit:  54
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  48
                      at cycle:  2

Global Deviance:     768.4682
            AIC:     780.4682
            SBC:     792.4021
******************************************************************
```

```
dropterm(Persistence.LOGNO, test = "Chisq")
Single term deletions for mu
Model: Persistence ~ Species * Object + Age
               Df    AIC     LRT Pr(Chi)
<none>            780.47
Age             1 778.90 0.43004  0.5120
Species:Object  1 780.10 1.63146  0.2015
```

`summary(Persistence.LOGNO2)`

```
******************************************************************
Family:  c("LOGNO", "Log Normal") 

Call:  gamlss(formula = Persistence ~ Species + Object + Age,  
      family = "LOGNO", data = na.omit(asdf), control = con, random = ~1 | Individual) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
            Estimate Std. Error t value Pr(>|t|)   
(Intercept)  -1.3138     1.9207  -0.684  0.49717   
SpeciesWolf   4.2744     1.5764   2.712  0.00921 **
ObjectPipe   -1.9848     1.2785  -1.552  0.12698   
Age           0.3988     0.3887   1.026  0.30989   
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  1.54578    0.09622   16.06   <2e-16 ***
------------------------------------------------------------------
No. of observations in the fit:  54 
Degrees of Freedom for the fit:  5
      Residual Deg. of Freedom:  49 
                      at cycle:  2 
 
Global Deviance:     486.6034 
            AIC:     496.6034 
            SBC:     506.5483 
******************************************************************
```

7.2.4.1.5.5 Model Comparison

`AIC(All Previous Models)`

Model	df	AIC
Persistence.GA.2	4	469.786522
Persistence.GA	6	471.144609
Persistence.BCTo.2	7	472.255443
Persistence.BCTo	8	472.382229
Persistence.WEI.2	5	477.261367
Persistence.WEI	6	478.48115
Persistence.LOGNO.2	5	496.603369
Persistence.LOGNO	6	780.468216

7.2.4.2 Contact Latency Models

7.2.4.2.1 Dogs

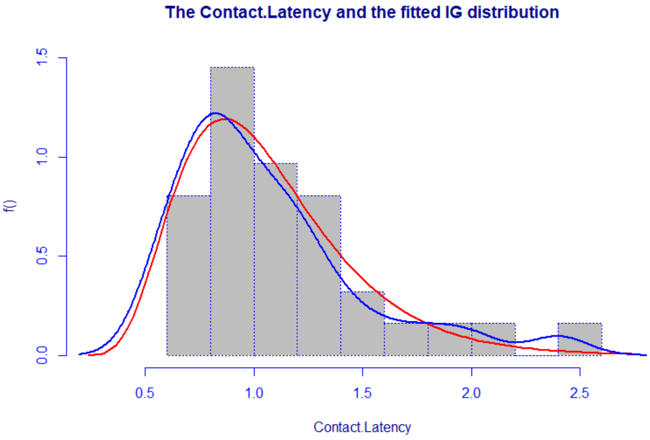
7.2.4.2.1.1 Response Variable Distribution Checks

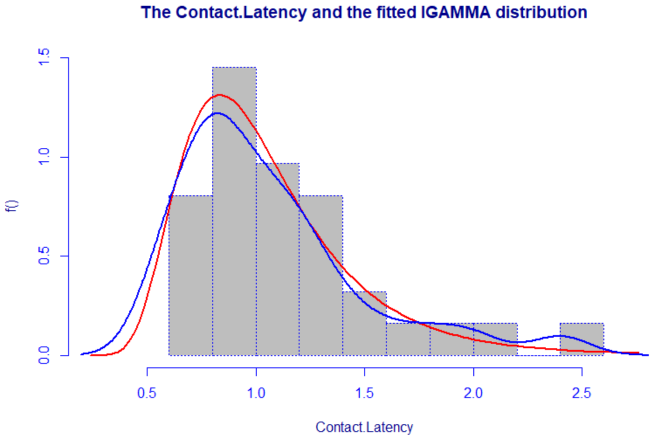
`Dogs.Latency.Distribution$fit`

Distribution	AIC	Errors in Plot?
IGAMMA	25.89524136	No
exGAUS	27.12539013	No
GG	27.14205944	No
IG	27.26266424	No
BCCGo	27.42606623	No
BCCG	27.42606623	No

Distribution	AIC	Errors in Plot?
LOGNO2	27.44045258	No
LOGNO	27.44045258	No
GIG	27.89524136	No
GB2	29.14238404	Yes
BCT	29.42606623	No
BCTo	29.42610463	Yes
GA	30.01443782	No

7.2.4.2.1.2 Density plots of examples of distributions used in final models





7.2.4.2.1.3 Model Distribution Selection

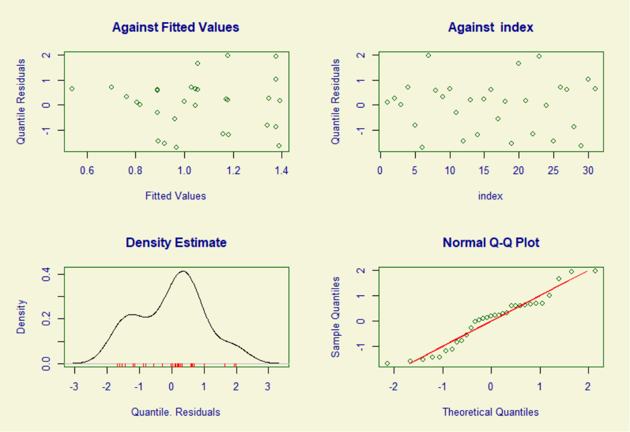
```
Latency.Dogs.DISTRIBUTION <- gamlss(Contact.Latency ~ Object*Approach.Posture +
                              Object*Persistence + Age, random = ~1|Individual,
                              family = "DISTRIBUTION", data = dogs)
```

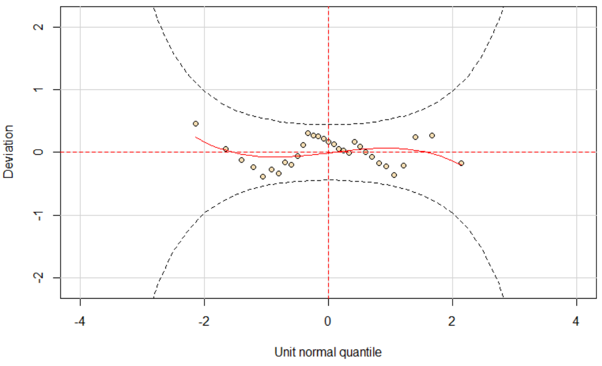
Model	df	AIC
Latency.Dogs.IG	8	22.2139762
Latency.Dogs.IGAMMA	8	23.9994415
Latency.Dogs.LOGNO	8	24.452884
Latency.Dogs.GA	8	25.0946606
Latency.Dogs.GG	9	25.7231161

Model	df	AIC
Latency.Dogs.BCCGo	9	25.8781709
Latency.Dogs.GIG	9	26.0003484
Latency.Dogs.BCCG	9	27.2859465
Latency.Dogs.BCT	10	29.2858833

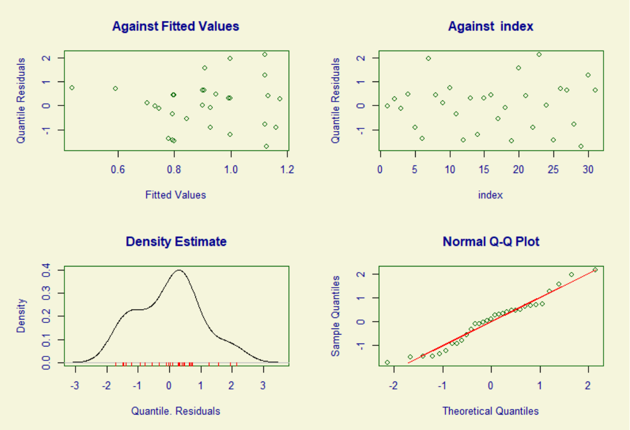
7.2.4.2.1.4 Model Diagnostics Plots

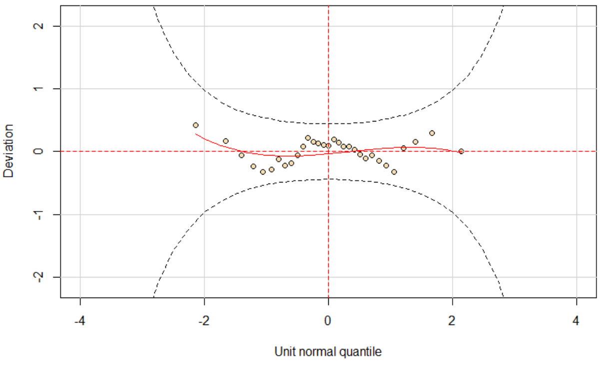
`plot(Latency.Dogs.IG) & wp(Latency.Dogs.IG)`



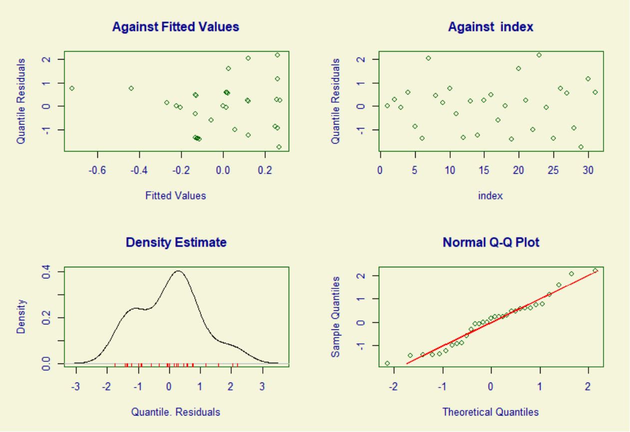


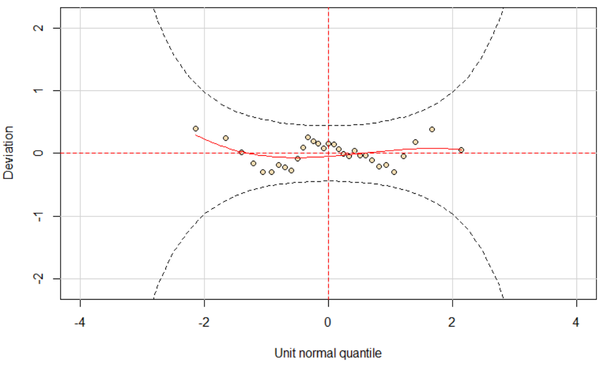
`plot(Latency.Dogs.IGAMMA) & wp(Latency.Dogs.IGAMMA)`



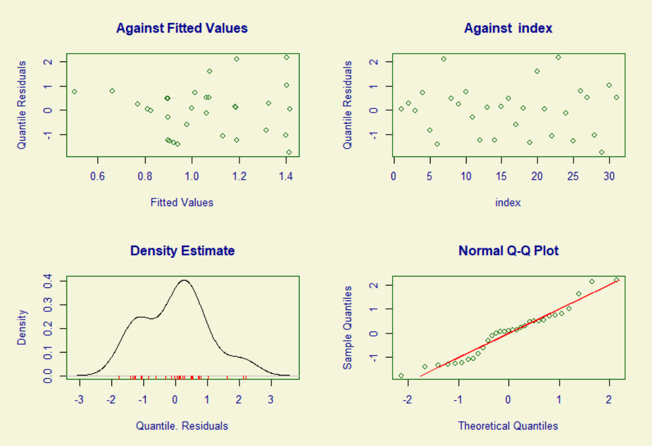


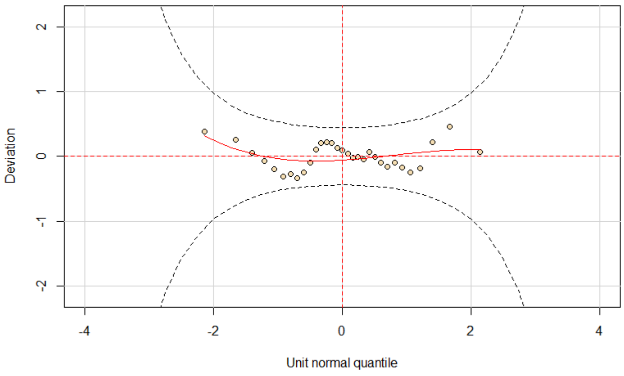
plot(Latency.Dogs.LOGNO) & wp(Latency.Dogs.LOGNO)



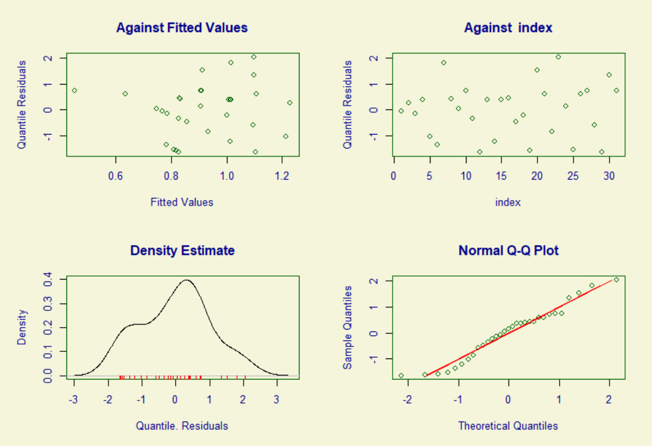


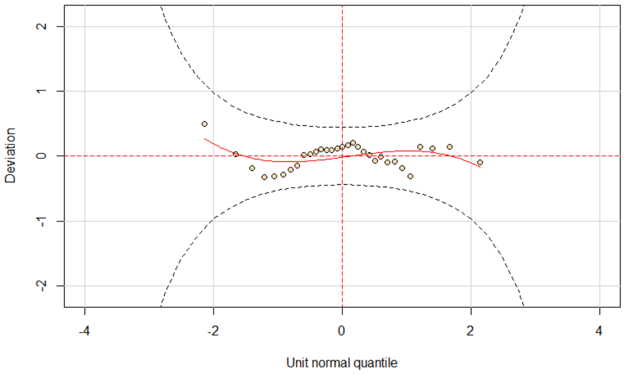
plot(Latency.Dogs.GA) & wp(Latency.Dogs.GA)



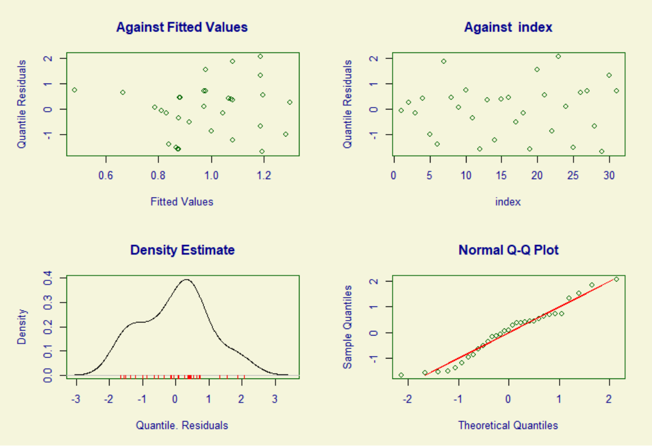


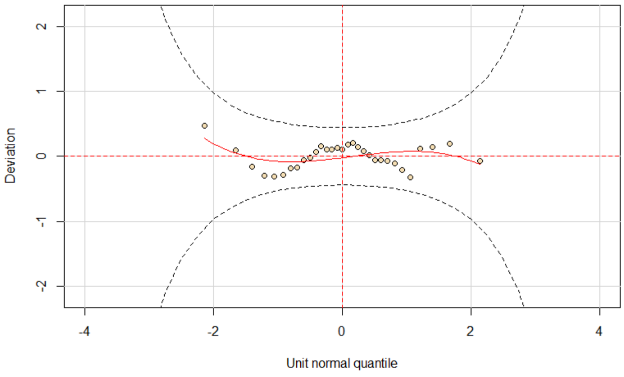
plot(Latency.Dogs.GG) & wp(Latency.Dogs.GG)



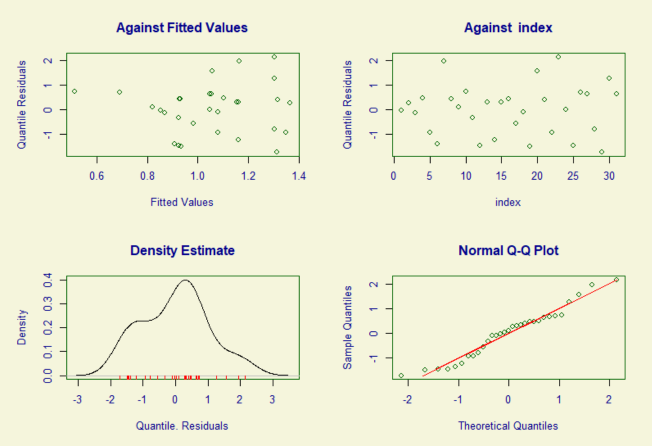


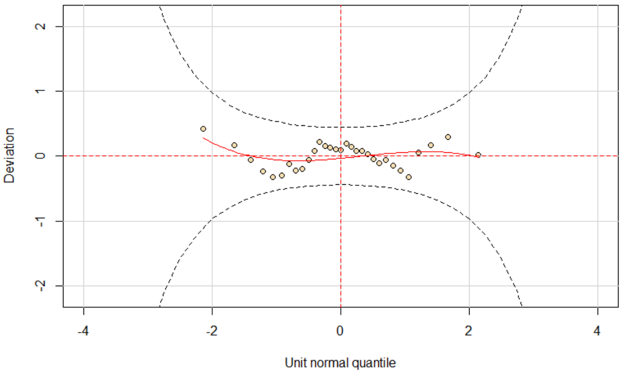
plot(Latency.Dogs.BCCGo) & wp(Latency.Dogs.BCCGo)



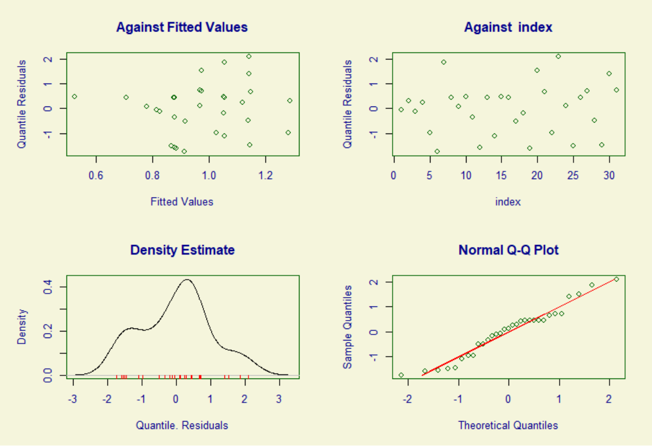


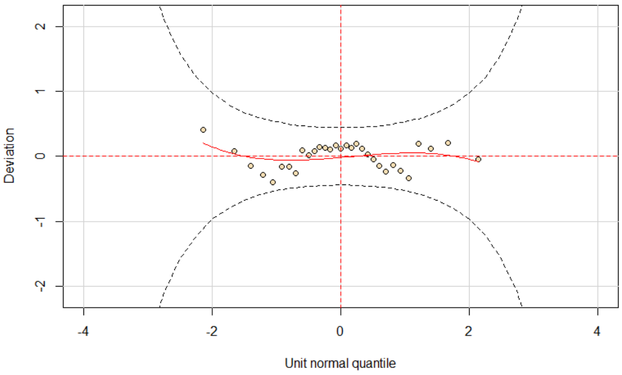
plot(Latency.Dogs.GIG) & wp(Latency.Dogs.GIG)



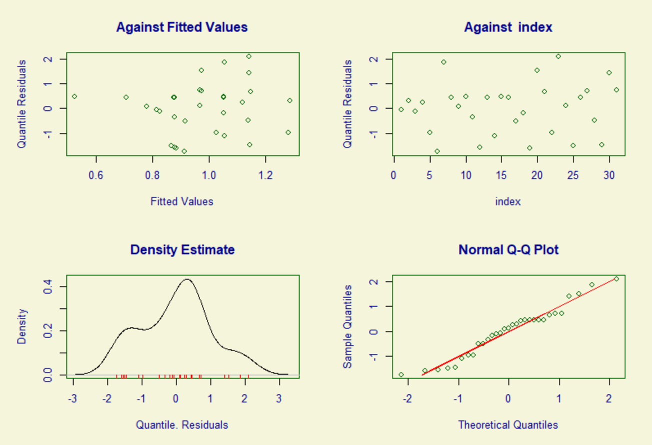


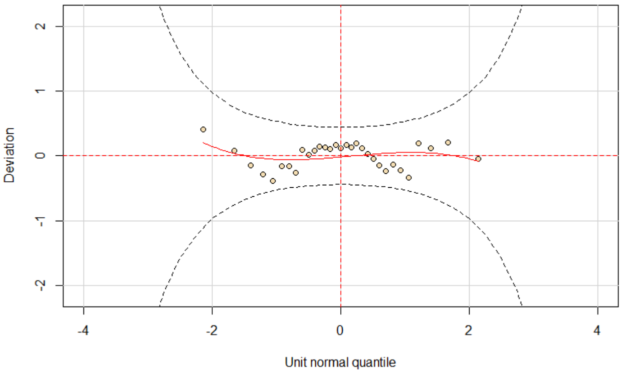
plot(Latency.Dogs.BCCG) & wp(Latency.Dogs.BCCG)





plot(Latency.Dogs.BCT) & wp(Latency.Dogs.BCT)





7.2.4.2.1.5 Model Reduction and Validation

7.2.4.2.1.5.1 Inverse Gaussian

```
summary(Latency.Dogs.IG)
******************************************************************
Family:  c("IG", "Inverse Gaussian")

Call:  gamlss(formula = Contact.Latency ~ Object * Approach.Posture + Object * Persistence + Age,
      family = "IG", data = na.omit(dogs), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                                   Estimate Std. Error t value Pr(>|t|)
(Intercept)                       0.4102365  0.1781549   2.303  0.03068 *
ObjectPipe                        0.1569040  0.1185724   1.323  0.19875
Approach.PostureUnsure            0.1349085  0.1920899   0.702  0.48953
Persistence                      -0.0012333  0.0005199  -2.372  0.02641 *
Age                              -0.1026588  0.0360592  -2.847  0.00913 **
ObjectPipe:Approach.PostureUnsure -0.4556678  0.3444472  -1.323  0.19887
ObjectPipe:Persistence            0.0009844  0.0005155   1.910  0.06872 .
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  -1.3017     0.1529  -8.515 1.45e-08 ***
------------------------------------------------------------------
No. of observations in the fit:  31
Degrees of Freedom for the fit:  8
      Residual Deg. of Freedom:  23
                      at cycle:  2

Global Deviance:     6.213976
            AIC:     22.21398
            SBC:     33.68587
******************************************************************
```

```
dropterm(Latency.Dogs.IG, test = "Chisq")
Single term deletions for mu
Model: Contact.Latency ~ Object * Approach.Posture + Object * Persistence + Age
                        Df    AIC    LRT   Pr(Chi)
<none>                     22.214
Age                      1 27.960 7.7464 0.005382 **
Object:Approach.Posture  1 21.622 1.4077 0.235436
Object:Persistence       1 22.384 2.1705 0.140683
```

```
summary(Latency.Dogs.IG.2)
******************************************************************
Family:  c("IG", "Inverse Gaussian")

Call:  gamlss(formula = Contact.Latency ~ Object * Persistence + Age + Approach.Posture,
      family = "IG", data = na.omit(dogs), control = con, random = ~1 | Individual)

Fitting method: RS()

------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                        Estimate Std. Error t value Pr(>|t|)
(Intercept)            0.4136302  0.1807401   2.289   0.0312 *
ObjectPipe             0.1216014  0.1180047   1.030   0.3131
Persistence           -0.0012998  0.0005321  -2.443   0.0223 *
Age                   -0.0993958  0.0364335  -2.728   0.0117 *
Approach.PostureUnsure 0.0448015  0.1716762   0.261   0.7963
ObjectPipe:Persistence 0.0010621  0.0005275   2.013   0.0554 .
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   -1.279      0.151   -8.47 1.13e-08 ***
------------------------------------------------------------------
No. of observations in the fit:  31
Degrees of Freedom for the fit:  7
      Residual Deg. of Freedom:  24
                      at cycle:  2

Global Deviance:     7.621691
            AIC:     21.62169
            SBC:     31.6596
******************************************************************
```

```
dropterm(Latency.Dogs.IG.2, test = "Chisq")
Single term deletions for mu
Model: Contact.Latency ~ Object * Persistence + Age + Approach.Posture
                   Df    AIC    LRT Pr(Chi)
<none>                21.622
Age                 1 26.747 7.1255  0.0076 **
Approach.Posture    1 19.692 0.0700  0.7914
Object:Persistence  1 21.992 2.3701  0.1237
```

```
summary(Latency.Dogs.IG.3)
******************************************************************
Family:  c("IG", "Inverse Gaussian") 

Call:  gamlss(formula = Contact.Latency ~ Object + Persistence + Age + Approach.Posture,  
      family = "IG", data = na.omit(dogs), control = con, random = ~1 | Individual) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                        Estimate Std. Error t value Pr(>|t|)    
(Intercept)            3.989e-01  1.866e-01   2.138 0.042479 *  
ObjectPipe             1.729e-01  1.200e-01   1.441 0.162116    
Persistence           -2.827e-04  6.492e-05  -4.354 0.000199 ***
Age                   -1.058e-01  3.708e-02  -2.853 0.008580 ** 
Approach.PostureUnsure  7.570e-02  1.773e-01   0.427 0.673021    
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  -1.2408     0.1529  -8.114 1.81e-08 ***
------------------------------------------------------------------
No. of observations in the fit:  31 
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  25 
                      at cycle:  2 
 
Global Deviance:     9.991834 
            AIC:     21.99183 
            SBC:     30.59576 
******************************************************************
```

7.2.4.2.1.5.2 Inverse Gamma

```
summary(Latency.Dogs.IGAMMA)
******************************************************************
Family:  c("IGAMMA", "Inverse Gamma") 

Call:  gamlss(formula = Contact.Latency ~ Object * Approach.Posture + Object * Persistence + Age,  
      family = "IGAMMA", data = na.omit(dogs), control = con, random = ~1 | Individual) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                                    Estimate Std. Error t value Pr(>|t|)  
(Intercept)                        0.1943433  0.1590614   1.222   0.2342  
ObjectPipe                         0.1157691  0.1168878   0.990   0.3323  
Approach.PostureUnsure             0.1614497  0.1827590   0.883   0.3862  
Persistence                       -0.0015549  0.0008241  -1.887   0.0719 .
Age                               -0.0813011  0.0313085  -2.597   0.0161 *
ObjectPipe:Approach.PostureUnsure -0.3494135  0.3383956  -1.033   0.3125  
ObjectPipe:Persistence             0.0012806  0.0008414   1.522   0.1416  
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  -1.2911     0.1288  -10.02 7.32e-10 ***
------------------------------------------------------------------
No. of observations in the fit:  31 
Degrees of Freedom for the fit:  8
      Residual Deg. of Freedom:  23 
                      at cycle:  9 
 
Global Deviance:     7.999442 
            AIC:     23.99944 
            SBC:     35.47134 
******************************************************************
```

```
dropterm(Latency.Dogs.IGAMMA, test = "Chisq")
Single term deletions for mu
Model: Contact.Latency ~ Object * Approach.Posture + Object * Persistence + Age
                        Df    AIC    LRT Pr(Chi)  
<none>                     23.999                 
Age                      1 28.092 6.0927 0.01357 *
Object:Approach.Posture  1 23.092 1.0925 0.29591  
Object:Persistence       1 24.297 2.2973 0.12960  
```

```
summary(Latency.Dogs.IGAMMA.2)
******************************************************************
Family:  c("IGAMMA", "Inverse Gamma") 

Call:  gamlss(formula = Contact.Latency ~ Object * Persistence + Age + Approach.Posture,  
       family = "IGAMMA", data = na.omit(dogs), control = con, random = ~1 | Individual) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)  
(Intercept)             0.2058006  0.1613666   1.275   0.2144  
ObjectPipe              0.0718711  0.1108730   0.648   0.5230  
Persistence            -0.0016423  0.0008340  -1.969   0.0606 .
Age                    -0.0792909  0.0318927  -2.486   0.0203 *
Approach.PostureUnsure  0.0565357  0.1593793   0.355   0.7259  
ObjectPipe:Persistence  0.0013911  0.0008498   1.637   0.1147  
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  -1.2739     0.1287  -9.902 5.96e-10 ***
---
No. of observations in the fit:  31 
Degrees of Freedom for the fit:  7
      Residual Deg. of Freedom:  24 
                      at cycle:  9 

Global Deviance:     9.091991 
            AIC:     23.09199 
            SBC:     33.1299 
******************************************************************
```

```
dropterm(Latency.Dogs.IGAMMA.2, test = "Chisq")
Single term deletions for mu
Model: Contact.Latency ~ Object * Persistence + Age + Approach.Posture
                   Df    AIC    LRT Pr(Chi)  
<none>                23.092                 
Age                 1 26.725 5.6327 0.01763 *
Approach.Posture    1 21.216 0.1242 0.72456  
Object:Persistence  1 23.766 2.6737 0.10202  
```

```
summary(Latency.Dogs.IGAMMA.3)
******************************************************************
Family:  c("IGAMMA", "Inverse Gamma") 

Call:  gamlss(formula = Contact.Latency ~ Object + Persistence + Age +  
       Approach.Posture, family = "IGAMMA",  
       data = na.omit(dogs), control = con, random = ~1 | Individual) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)  
(Intercept)             0.1415034  0.1646664   0.859   0.3983  
ObjectPipe              0.1429034  0.1076359   1.328   0.1963  
Persistence            -0.0003477  0.0001859  -1.871   0.0732 .
Age                    -0.0797352  0.0332547  -2.398   0.0243 *
Approach.PostureUnsure  0.0879124  0.1650867   0.533   0.5991  
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  -1.2319     0.1279  -9.635 6.76e-10 ***
------------------------------------------------------------------
No. of observations in the fit:  31 
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  25 
                    at cycle:  9 
 
Global Deviance:     11.76571 
            AIC:     23.76571 
            SBC:     32.36963 
******************************************************************
```

7.2.4.2.1.5.3 Log-Normal

```
summary(Latency.Dogs.LOGNO)
******************************************************************
Family:  c("LOGNO", "Log Normal") 

Call:  gamlss(formula = Contact.Latency ~ Object * Approach.Posture + Object * Persistence + Age,  
       family = "LOGNO", data = na.omit(dogs), control = con, random = ~1 | Individual) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
                                    Estimate Std. Error t value Pr(>|t|)  
(Intercept)                        0.3378984  0.1625735   2.078   0.0490 *
ObjectPipe                         0.1412920  0.1184929   1.192   0.2453  
Approach.PostureUnsure             0.1363869  0.1853760   0.736   0.4693  
Persistence                       -0.0015129  0.0008023  -1.886   0.0720 .
Age                               -0.0908627  0.0326460  -2.783   0.0106 *
ObjectPipe:Approach.PostureUnsure -0.3975069  0.3451327  -1.152   0.2613  
ObjectPipe:Persistence             0.0012175  0.0008265   1.473   0.1543  
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)   -1.271      0.127  -10.01  7.5e-10 ***
------------------------------------------------------------------
No. of observations in the fit:  31 
Degrees of Freedom for the fit:  8
      Residual Deg. of Freedom:  23 
                    at cycle:  2 
 
Global Deviance:     8.452884 
            AIC:     24.45288 
            SBC:     35.92478 
******************************************************************
```

```
dropterm(Latency.Dogs.LOGNO, test = "Chisq")
Single term deletions for mu
Model: Contact.Latency ~ Object * Approach.Posture + Object * Persistence + Age
                        Df    AIC    LRT Pr(Chi)
<none>                     24.453
Age                      1 29.368 6.9147 0.008549 **
Object:Approach.Posture  1 23.752 1.2989 0.254408
Object:Persistence       1 24.550 2.0970 0.147588
```

```
summary(Latency.Dogs.LOGNO.2)
******************************************************************
Family:  c("LOGNO", "Log Normal")

Call:  gamlss(formula = Contact.Latency ~ Object * Persistence + Age + Approach.Posture,
       family = "LOGNO", data = na.omit(dogs), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)
(Intercept)             0.3517489  0.1655606   2.125   0.0441 *
ObjectPipe              0.0953582  0.1139420   0.837   0.4109
Persistence            -0.0016021  0.0008155  -1.965   0.0611 .
Age                    -0.0884757  0.0332699  -2.659   0.0137 *
Approach.PostureUnsure  0.0277571  0.1629674   0.170   0.8662
ObjectPipe:Persistence  0.0013275  0.0008384   1.583   0.1264
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   -1.250      0.127  -9.845 6.66e-10 ***
------------------------------------------------------------------
No. of observations in the fit:  31
Degrees of Freedom for the fit:  7
      Residual Deg. of Freedom:  24
                      at cycle:  2

Global Deviance:     9.751817
            AIC:     23.75182
            SBC:     33.78973
******************************************************************
```

```
dropterm(Latency.Dogs.LOGNO.2, test = "Chisq")
Single term deletions for mu
Model: Contact.Latency ~ Object * Persistence + Age + Approach.Posture
                   Df    AIC    LRT Pr(Chi)
<none>                23.752
Age                 1 28.122 6.3703  0.0116 *
Approach.Posture    1 21.781 0.0290  0.8648
Object:Persistence  1 24.163 2.4108  0.1205
```

```
summary(Latency.Dogs.LOGNO.3)
******************************************************************
Family:  c("LOGNO", "Log Normal")

Call:  gamlss(formula = Contact.Latency ~ Object + Persistence + Age +
       Approach.Posture, family = "LOGNO", data = na.omit(dogs),
       control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)
(Intercept)             0.3098394  0.1699111   1.824   0.0802 .
ObjectPipe              0.1567504  0.1113900   1.407   0.1717
Persistence            -0.0003516  0.0002112  -1.665   0.1085
Age                    -0.0909106  0.0345520  -2.631   0.0144 *
Approach.PostureUnsure  0.0569946  0.1683378   0.339   0.7378
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   -1.211      0.127  -9.539 8.24e-10 ***
------------------------------------------------------------------
No. of observations in the fit:  31
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  25
                      at cycle:  2

Global Deviance:     12.1626
            AIC:     24.1626
            SBC:     32.76652
```

7.2.4.2.1.5.4 Gamma

```
summary(Latency.Dogs.GA)
******************************************************************
Family:  c("GA", "Gamma") 

Call:  gamlss(formula = Contact.Latency ~ Object * Approach.Posture + Object * Persistence + Age,  
      family = "GA", data = na.omit(dogs), control = con, random = ~1 | Individual) 

Fitting method: RS() 

------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                                    Estimate Std. Error t value Pr(>|t|)  
(Intercept)                        0.4196806  0.1644667   2.552  0.01783 *
ObjectPipe                         0.1643692  0.1172481   1.402  0.17430  
Approach.PostureUnsure             0.1094975  0.1837670   0.596  0.55709  
Persistence                       -0.0014680  0.0007488  -1.960  0.06217 .
Age                               -0.1026352  0.0336409  -3.051  0.00567 **
ObjectPipe:Approach.PostureUnsure -0.4472226  0.3441880  -1.299  0.20670  
ObjectPipe:Persistence             0.0011600  0.0007603   1.526  0.14071  
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  -1.2739     0.1301  -9.796 1.13e-09 ***
------------------------------------------------------------------
No. of observations in the fit:  31 
Degrees of Freedom for the fit:  8
      Residual Deg. of Freedom:  23 
                      at cycle:  2 
 
Global Deviance:     9.094661 
            AIC:     25.09466 
            SBC:     36.56656 
******************************************************************
```

```
dropterm(Latency.Dogs.GA, test = "Chisq")
Single term deletions for mu
Model: Contact.Latency ~ Object * Approach.Posture + Object * Persistence + Age
                        Df    AIC    LRT Pr(Chi)  
<none>                     23.999                 
Age                      1 28.092 6.0927 0.01357 *
Object:Approach.Posture  1 23.092 1.0925 0.29591  
Object:Persistence       1 24.297 2.2973 0.12960  
```

```
summary(Latency.Dogs.GA.2)
******************************************************************
Family:  c("GA", "Gamma") 

Call:  gamlss(formula = Contact.Latency ~ Object * Persistence + Age + Approach.Posture,  
      family = "GA", data = na.omit(dogs), control = con, random = ~1 | Individual) 

Fitting method: RS() 

------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)   
(Intercept)             0.4317947  0.1681393   2.568  0.01688 * 
ObjectPipe              0.1182663  0.1147076   1.031  0.31281   
Persistence            -0.0015582  0.0007647  -2.038  0.05277 . 
Age                    -0.0996764  0.0342883  -2.907  0.00773 **
Approach.PostureUnsure  0.0019261  0.1633738   0.012  0.99069   
ObjectPipe:Persistence  0.0012676  0.0007755   1.635  0.11518   
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  -1.2496     0.1297  -9.636 1.01e-09 ***
------------------------------------------------------------------
No. of observations in the fit:  31 
Degrees of Freedom for the fit:  7
      Residual Deg. of Freedom:  24 
                      at cycle:  2 
 
Global Deviance:     10.64324 
            AIC:     24.64324 
            SBC:     34.68115 
******************************************************************
```

```
dropterm(Latency.Dogs.GA.2, test = "Chisq")
Single term deletions for mu
Model: Contact.Latency ~ Object * Persistence + Age + Approach.Posture
                   Df    AIC    LRT Pr(Chi)
<none>                24.643
Age                 1 30.183 7.5400 0.006034 **
Approach.Posture    1 22.643 0.0001 0.990230
Object:Persistence  1 24.863 2.2196 0.136270
```

```
summary(Latency.Dogs.GA.3)
******************************************************************
Family:  c("GA", "Gamma")

Call:  gamlss(formula = Contact.Latency ~ Object + Persistence + Age + Approach.Posture,
      family = "GA", data = na.omit(dogs), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)
(Intercept)             0.4038062  0.1724769   2.341  0.02749 *
ObjectPipe              0.1706946  0.1134002   1.505  0.14479
Persistence            -0.0003501  0.0001603  -2.185  0.03851 *
Age                    -0.1037697  0.0352672  -2.942  0.00693 **
Approach.PostureUnsure  0.0296296  0.1678586   0.177  0.86131
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  -1.2148     0.1296  -9.375 1.16e-09 ***
------------------------------------------------------------------
No. of observations in the fit:  31
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  25
                      at cycle:  2

Global Deviance:     12.86282
            AIC:     24.86282
            SBC:     33.46674
******************************************************************
```

7.2.4.2.1.5.5 Model AIC Values & Plots

Model	df	AIC
Latency.Dogs.IG.2	7	21.6216907
Latency.Dogs.IG.3	6	21.991834
Latency.Dogs.IG	8	22.2139762
Latency.Dogs.IGAMMA.2	7	23.0919912
Latency.Dogs.IGAMMA.3	6	23.7657082
Latency.Dogs.IGAMMA	8	23.9994415

Model	df	AIC
Latency.Dogs.LOGNO.2	7	23.751817
Latency.Dogs.LOGNO.3	6	24.162601
Latency.Dogs.LOGNO	8	24.452884
Latency.Dogs.GA.2	7	24.6432376
Latency.Dogs.GA.3	6	24.8628194
Latency.Dogs.GA	8	25.0946606

7.2.4.2.2 Wolves

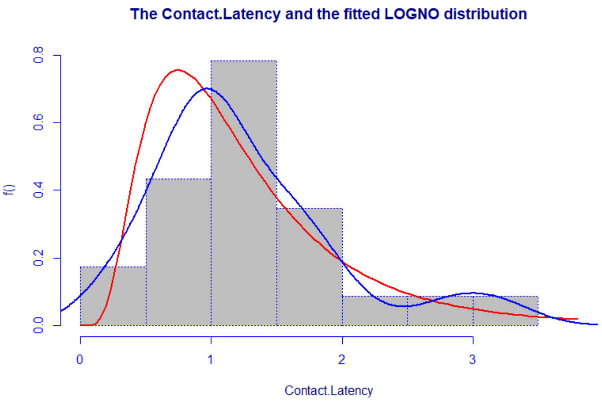
7.2.4.2.2.1 Response Variable Distribution Checks

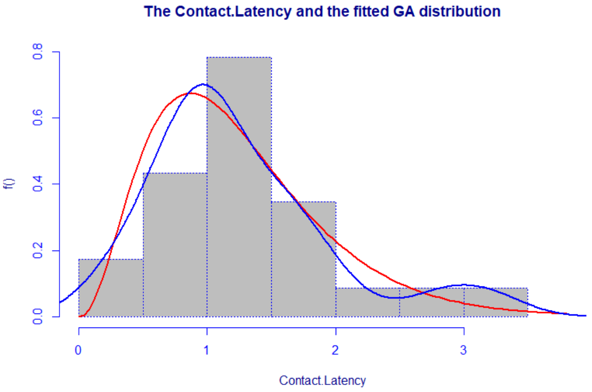
```
Wolves.Latency.Distribution$fit
```

Distribution	AIC	Errors in Plot?
BCPEo	42.5956468	No
GA	46.7551277	No
WEI	47.8204512	No
WEI3	47.8204512	No
WEI2	47.8204512	No
LOGNO2	48.007022	No
LOGNO	48.007022	No
exGAUS	48.1292579	No
BCCGo	48.6930046	No

Distribution	AIC	Errors in Plot?
BCCG	48.6930046	No
GG	48.7442016	No
GIG	48.7551277	No
IG	49.2806389	No
GB2	50.2402167	Yes
BCT	50.3641552	No
BCTo	50.3641552	No
IGAMMA	52.8433712	Yes
EXP	58.0239751	No

7.2.4.2.2.2 Density plots of examples of distributions used in final models





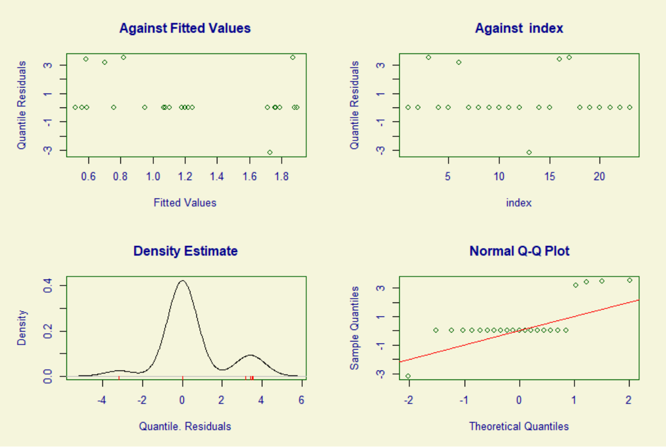
7.2.4.2.2.3 Model Distribution Selection

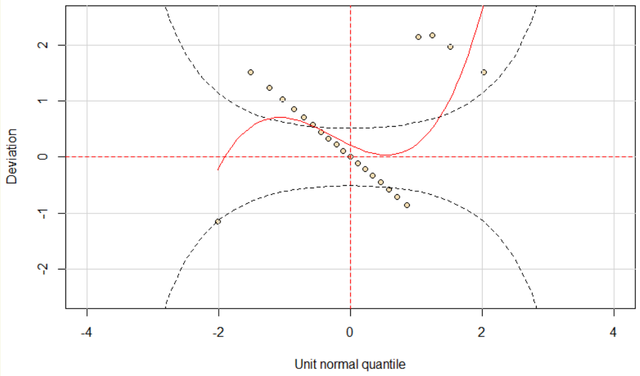
```
Latency.Wolves.DISTRIBUTION <- gamlss(Contact.Latency ~ Object*Approach.Posture +
                               Object*Persistence + Age, random = ~1|Individual,
                               family = "DISTRIBUTION", data = wolves)
```

Model	df	AIC	Residuals outside CI
Latency.Wolves.BCPEo	9	37.4157307	14
Latency.Wolves.LOGNO	7	46.3634629	0
Latency.Wolves.GA	7	46.5175795	0
Latency.Wolves.WEI	7	46.9785802	0
Latency.Wolves.BCCG	8	47.1128132	0
Latency.Wolves.GIG	8	48.0492091	0
Latency.Wolves.BCCGo	8	48.3522457	0
Latency.Wolves.BCT	9	49.1125839	0
Latency.Wolves.BCTo	9	50.3524066	-
Latency.Wolves.IG	7	50.4243689	0

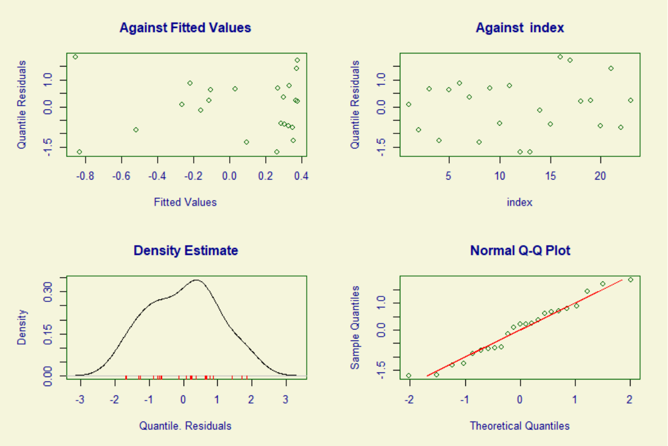
7.2.4.2.2.4 Model Diagnostics Plots

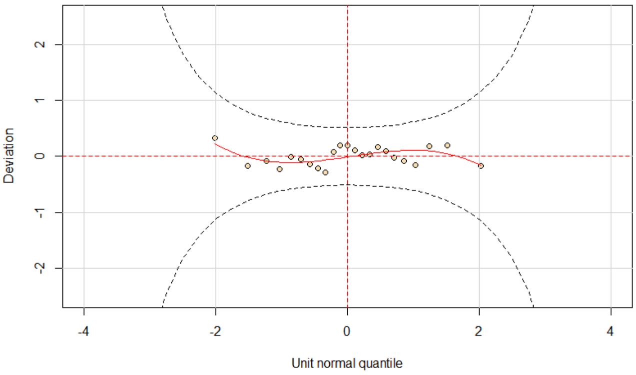
`plot(Latency.Wolves.BCPEo) & wp(Latency.Wolves.BCPEo)`



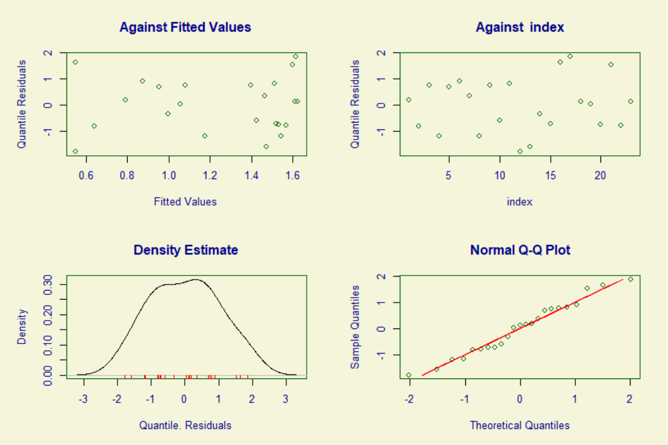


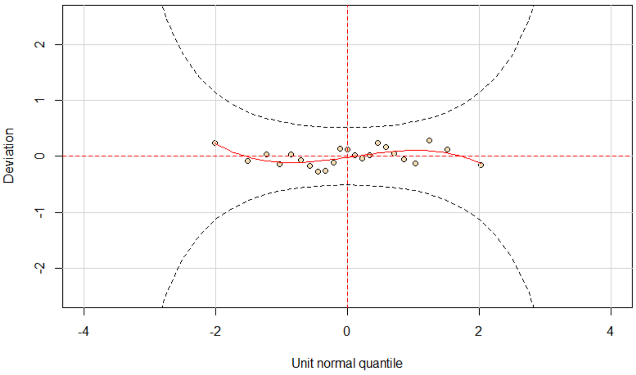
`plot(Latency.Wolves.LOGNO) & wp(Latency.Wolves.LOGNO)`



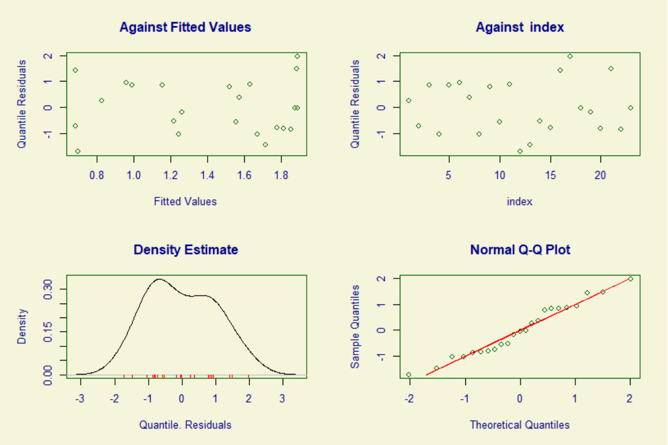


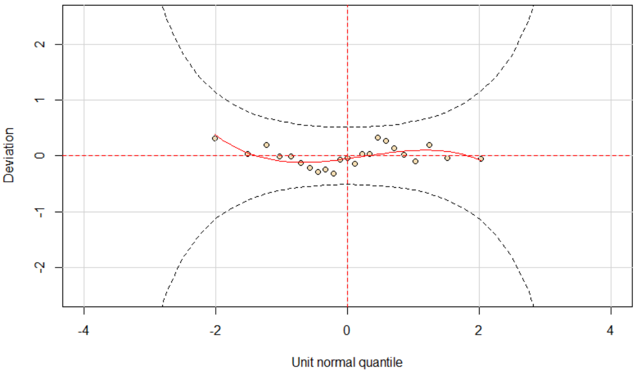
`plot(Latency.Wolves.GA) & wp(Latency.Wolves.GA)`



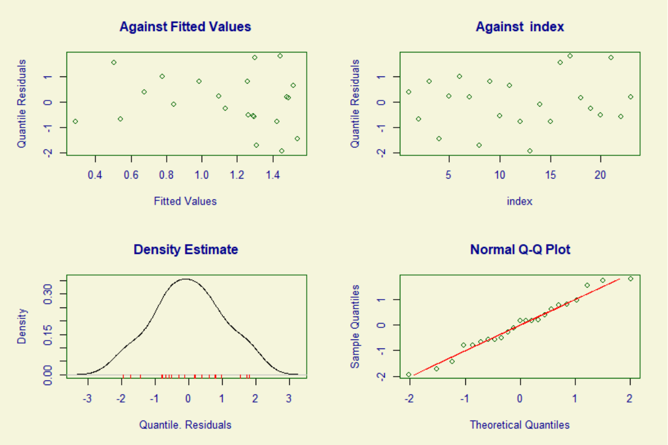


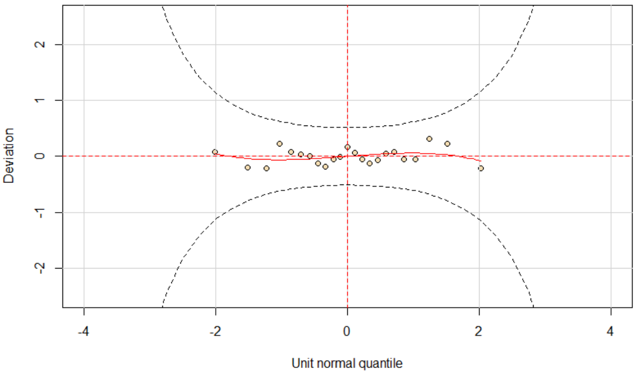
`plot(Latency.Wolves.WEI) & wp(Latency.Wolves.WEI)`



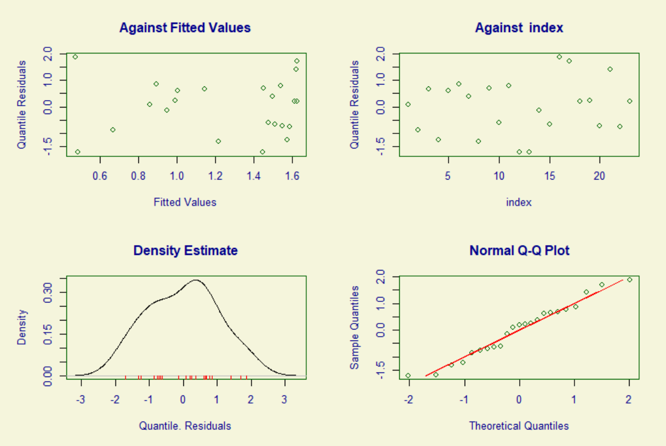


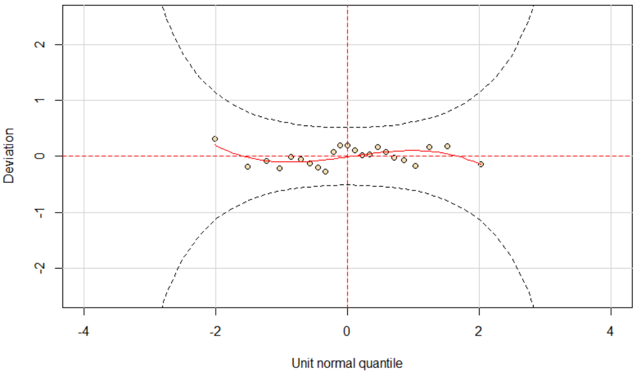
`plot(Latency.Wolves.BCCG) & wp(Latency.Wolves.BCCG)`



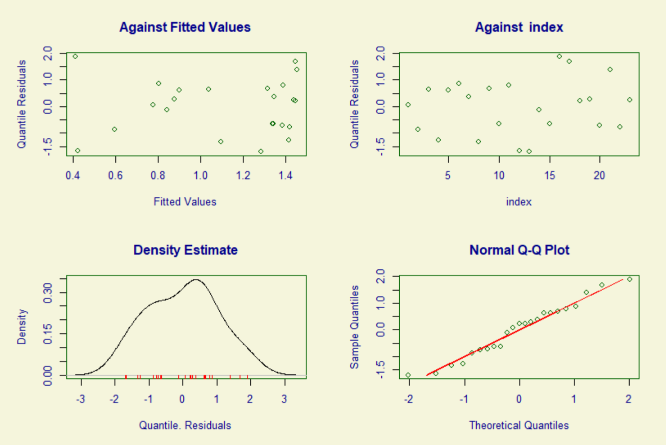


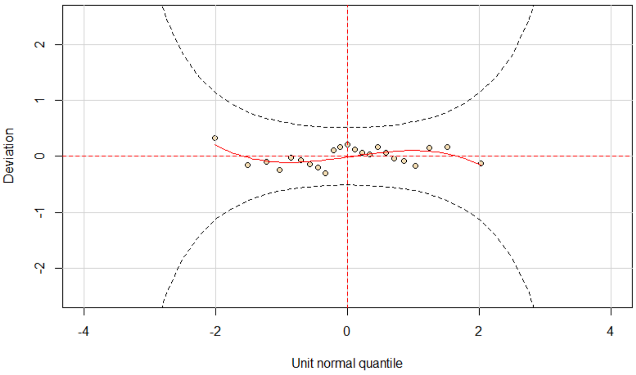
plot(Latency.Wolves.GIG) & wp(Latency.Wolves.GIG)



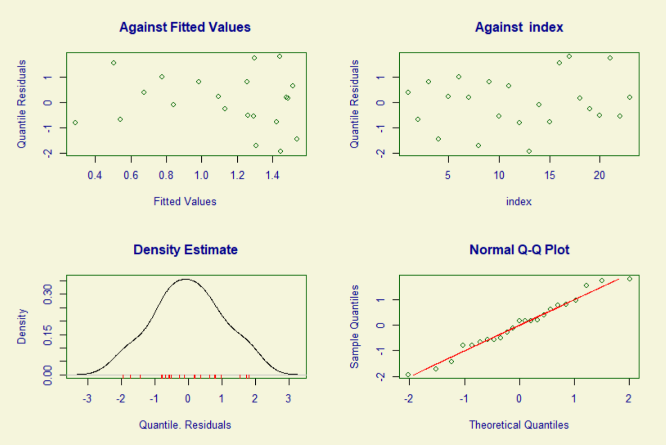


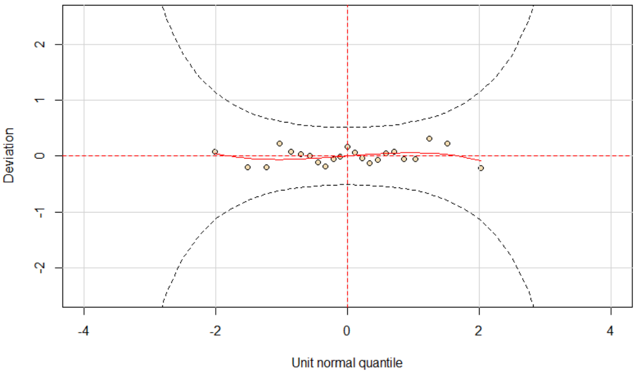
plot(Latency.Wolves.BCCGo) & wp(Latency.Wolves.BCCGo)



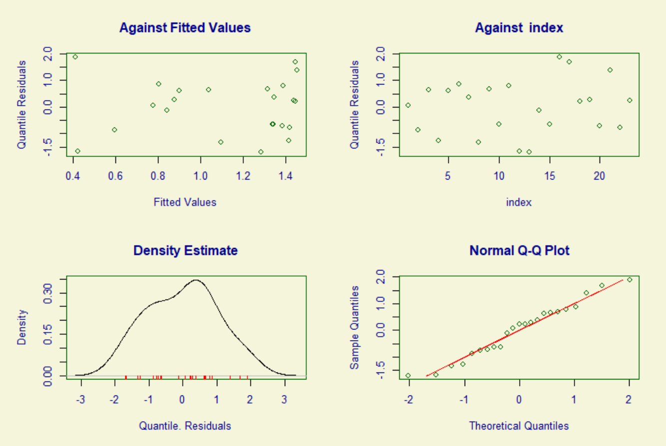


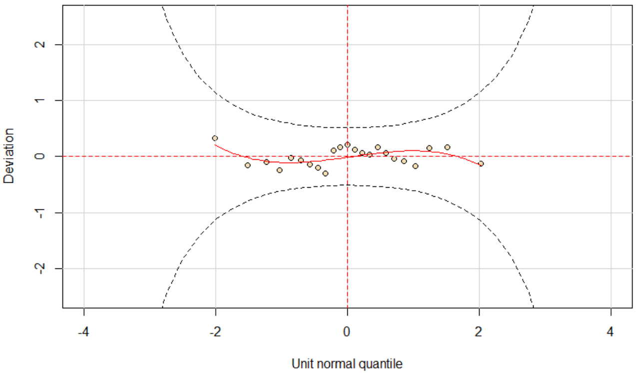
plot(Latency.Wolves.BCT) & wp(Latency.Wolves.BCT)



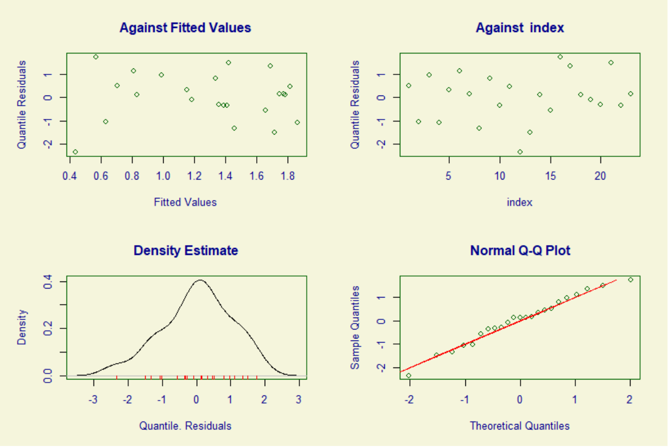


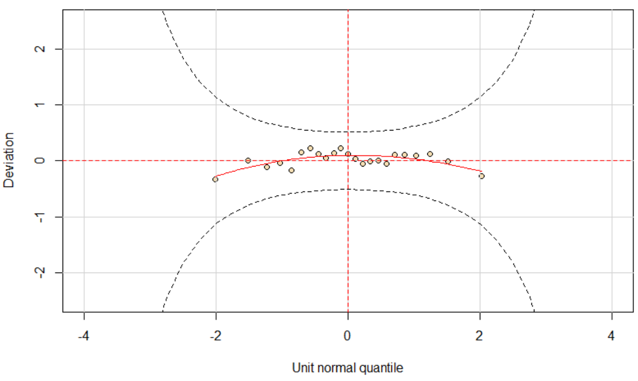
plot(Latency.Wolves.BCTo) & wp(Latency.Wolves.BCTo)





```
plot(Latency.Wolves.IG) & wp(Latency.Wolves.IG)
```





7.2.4.2.2.5 Model Reduction and Validation

7.2.4.2.2.5.1 Log-Normal

```
summary(Latency.Wolves.LOGNO)
******************************************************************
Family:  c("LOGNO", "Log Normal") 

Call:  gamlss(formula = Contact.Latency ~ Object * Approach.Posture + Object * Persistence + Age,  
      family = "LOGNO", data = na.omit(wolves), control = con, random = ~1 | Individual) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)
(Intercept)             3.934e-01  4.354e-01   0.904    0.380
ObjectPipe             -1.605e-02  2.839e-01  -0.057    0.956
Approach.PostureUnsure -6.026e-01  3.719e-01  -1.621    0.125
Persistence            -6.340e-04  4.472e-04  -1.418    0.176
Age                     3.605e-05  5.844e-02   0.001    1.000
ObjectPipe:Persistence -5.450e-04  5.707e-04  -0.955    0.354
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  -0.7749     0.1474  -5.255 7.85e-05 ***
------------------------------------------------------------------
No. of observations in the fit:  23 
Degrees of Freedom for the fit:  7
      Residual Deg. of Freedom:  16 
                      at cycle:  2 
 
Global Deviance:     32.36346 
            AIC:     46.36346 
            SBC:     54.31192 
******************************************************************

dropterm(Latency.Wolves.LOGNO, test = "Chisq")
Single term deletions for mu
Model: Contact.Latency ~ Object * Approach.Posture + Object * Persistence + Age
                        Df    AIC     LRT Pr(Chi)
<none>                     46.363                
Age                      1 44.363 0.00000  0.9995
Object:Approach.Posture  0 46.363 0.00000        
Object:Persistence       1 45.258 0.89422  0.3443
```

```
summary(Latency.Wolves.LOGNO.2)
******************************************************************
Family:  c("LOGNO", "Log Normal") 

Call:  gamlss(formula = Contact.Latency ~ Object * Persistence + Approach.Posture + Age,  
       family = "LOGNO", data = na.omit(wolves), control = con, random = ~1 | Individual) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)
(Intercept)             3.934e-01  4.354e-01   0.904    0.380
ObjectPipe             -1.605e-02  2.839e-01  -0.057    0.956
Persistence            -6.340e-04  4.472e-04  -1.418    0.176
Approach.PostureUnsure -6.026e-01  3.719e-01  -1.621    0.125
Age                     3.605e-05  5.844e-02   0.001    1.000
ObjectPipe:Persistence -5.450e-04  5.707e-04  -0.955    0.354
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  -0.7749     0.1474  -5.255 7.85e-05 ***
------------------------------------------------------------------
No. of observations in the fit:  23 
Degrees of Freedom for the fit:  7
      Residual Deg. of Freedom:  16 
                      at cycle:  2 
 
Global Deviance:     32.36346 
            AIC:     46.36346 
            SBC:     54.31192 
******************************************************************
```

```
dropterm(Latency.Wolves.LOGNO.2, test = "Chisq")
Single term deletions for mu
Model: Contact.Latency ~ Object * Persistence + Approach.Posture + Age
                   Df    AIC     LRT Pr(Chi)
<none>                46.363                
Approach.Posture    1 46.850 2.48703  0.1148
Age                 1 44.363 0.00000  0.9995
Object:Persistence  1 45.258 0.89422  0.3443
```

```
summary(Latency.Wolves.LOGNO.3)
******************************************************************
Family:  c("LOGNO", "Log Normal") 

Call:  gamlss(formula = Contact.Latency ~ Persistence + Object + Approach.Posture + Age,  
       family = "LOGNO", data = na.omit(wolves), control = con, random = ~1 | Individual) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)   
(Intercept)             0.5406153  0.4152015   1.302  0.21026   
Persistence            -0.0009686  0.0002833  -3.418  0.00327 **
ObjectPipe             -0.2024413  0.2102612  -0.963  0.34914   
Approach.PostureUnsure -0.6470474  0.3761826  -1.720  0.10358   
Age                    -0.0025617  0.0595226  -0.043  0.96617   
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  -0.7554     0.1474  -5.124 8.47e-05 ***
------------------------------------------------------------------
No. of observations in the fit:  23 
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  17 
                      at cycle:  2 
 
Global Deviance:     33.25768 
            AIC:     45.25768 
            SBC:     52.07065 
******************************************************************
```

7.2.4.2.2.5.2 Gamma

```
summary(Latency.Wolves.GA)
******************************************************************
Family:  c("GA", "Gamma") 

Call:  gamlss(formula = Contact.Latency ~ Object * Approach.Posture + Object * Persistence + Age,  
      family = "GA", data = na.omit(wolves), control = con, random = ~1 | Individual) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)  
(Intercept)             0.4483751  0.4331479   1.035   0.3160  
ObjectPipe              0.0058086  0.2723396   0.021   0.9832  
Approach.PostureUnsure -0.6013323  0.3701945  -1.624   0.1238  
Persistence            -0.0006806  0.0003790  -1.796   0.0914 .
Age                     0.0041454  0.0600371   0.069   0.9458  
ObjectPipe:Persistence -0.0003632  0.0004724  -0.769   0.4532  
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  -0.8048     0.1484  -5.425 5.62e-05 ***
------------------------------------------------------------------
No. of observations in the fit:  23 
Degrees of Freedom for the fit:  7
      Residual Deg. of Freedom:  16 
                      at cycle:  2 

Global Deviance:     32.51758 
            AIC:     46.51758 
            SBC:     54.46604 
******************************************************************
```

```
dropterm(Latency.Wolves.GA, test = "Chisq")
Single term deletions for mu
Model: Contact.Latency ~ Object * Approach.Posture + Object * Persistence + Age
                        Df    AIC    LRT Pr(Chi)
<none>                     46.518               
Age                      1 44.523 0.0051  0.9431
Object:Approach.Posture  0 46.518 0.0000        
Object:Persistence       1 44.950 0.4321  0.5110
```

```
summary(Latency.Wolves.GA.2)
******************************************************************
Family:  c("GA", "Gamma") 

Call:  gamlss(formula = Contact.Latency ~ Object * Persistence + Approach.Posture + Age,  
      family = "GA", data = na.omit(wolves), control = con, random = ~1 | Individual) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)  
(Intercept)             0.4483751  0.4331479   1.035   0.3160  
ObjectPipe              0.0058086  0.2723396   0.021   0.9832  
Persistence            -0.0006806  0.0003790  -1.796   0.0914 .
Approach.PostureUnsure -0.6013323  0.3701945  -1.624   0.1238  
Age                     0.0041454  0.0600371   0.069   0.9458  
ObjectPipe:Persistence -0.0003632  0.0004724  -0.769   0.4532  
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  -0.8048     0.1484  -5.425 5.62e-05 ***
------------------------------------------------------------------
No. of observations in the fit:  23 
Degrees of Freedom for the fit:  7
      Residual Deg. of Freedom:  16 
                      at cycle:  2 

Global Deviance:     32.51758 
            AIC:     46.51758 
            SBC:     54.46604 
******************************************************************
```

```
dropterm(Latency.Wolves.GA.2, test = "Chisq")
Single term deletions for mu
Model: Contact.Latency ~ Object * Persistence + Approach.Posture + Age
                   Df    AIC    LRT Pr(Chi)
<none>                46.518
Approach.Posture    1 46.790 2.2726  0.1317
Age                 1 44.523 0.0051  0.9431
Object:Persistence  1 44.950 0.4321  0.5110
```

```
summary(Latency.Wolves.GA.3)
******************************************************************
Family:  c("GA", "Gamma") 

Call:  gamlss(formula = Contact.Latency ~ Persistence + Object + Approach.Posture + Age,  
      family = "GA", data = na.omit(wolves), control = con, random = ~1 | Individual) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
                        Estimate Std. Error t value Pr(>|t|)   
(Intercept)            0.5869804  0.3865818   1.518  0.14729   
Persistence           -0.0008988  0.0002418  -3.717  0.00171 **
ObjectPipe            -0.1210280  0.2061554  -0.587  0.56487   
Approach.PostureUnsure -0.6493395  0.3675023  -1.767  0.09519 . 
Age                   -0.0033821  0.0592149  -0.057  0.95512   
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  -0.7960     0.1481  -5.374 5.05e-05 ***
------------------------------------------------------------------
No. of observations in the fit:  23 
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  17 
                      at cycle:  2 
 
Global Deviance:     32.94968 
            AIC:     44.94968 
            SBC:     51.76264 
******************************************************************
```

7.2.4.2.2.5.3 Weibull

```
summary(Latency.Wolves.WEI)
******************************************************************
Family:  c("WEI", "Weibull") 

Call:  gamlss(formula = Contact.Latency ~ Object * Approach.Posture + Object * Persistence + Age,  
      family = "WEI", data = na.omit(wolves), control = con, random = ~1 | Individual) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
                        Estimate Std. Error t value Pr(>|t|)  
(Intercept)            0.5621230  0.4213164   1.334   0.2008  
ObjectPipe             0.0774597  0.2578471   0.300   0.7677  
Approach.PostureUnsure -0.5876850  0.3490992  -1.683   0.1117  
Persistence           -0.0007229  0.0004001  -1.807   0.0896 .
Age                   -0.0005306  0.0611897  -0.009   0.9932  
ObjectPipe:Persistence -0.0002476  0.0004970  -0.498   0.6252  
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)   0.9101     0.1662   5.476 5.08e-05 ***
------------------------------------------------------------------
No. of observations in the fit:  23 
Degrees of Freedom for the fit:  7
      Residual Deg. of Freedom:  16 
                      at cycle:  4 
 
Global Deviance:     32.97858 
            AIC:     46.97858 
            SBC:     54.92704 
******************************************************************
```

```
dropterm(Latency.Wolves.WEI, test = "Chisq")
Single term deletions for mu
Model: Contact.Latency ~ Object * Approach.Posture + Object * Persistence + Age
                        Df    AIC      LRT Pr(Chi)
<none>                     46.979                 
Age                      1 44.979 0.000081   0.9928
Object:Approach.Posture  0 46.979 0.000000        
Object:Persistence       1 45.221 0.241950   0.6228
```

```
summary(Latency.Wolves.WEI.2)
******************************************************************
Family:  c("WEI", "Weibull") 

Call:  gamlss(formula = Contact.Latency ~ Object * Persistence + Approach.Posture + Age,  
      family = "WEI", data = na.omit(wolves), control = con, random = ~1 | Individual) 

Fitting method: RS() 

------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)  
(Intercept)             0.5621230  0.3274350   1.717   0.1053  
ObjectPipe              0.0774597  0.2576337   0.301   0.7675  
Persistence            -0.0007229  0.0003989  -1.812   0.0887 .
Approach.PostureUnsure -0.5876850  0.3457811  -1.700   0.1086  
Age                    -0.0005306  0.0402149  -0.013   0.9896  
ObjectPipe:Persistence -0.0002476  0.0004906  -0.505   0.6207  
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)   0.9101     0.1662   5.477 5.07e-05 ***
------------------------------------------------------------------
No. of observations in the fit:  23 
Degrees of Freedom for the fit:  7
      Residual Deg. of Freedom:  16 
                      at cycle:  4 
 
Global Deviance:     32.97858 
            AIC:     46.97858 
            SBC:     54.92704 
******************************************************************
```

```
dropterm(Latency.Wolves.WEI.2, test = "Chisq")
Single term deletions for mu
Model: Contact.Latency ~ Object * Persistence + Approach.Posture + Age
                   Df   AIC     LRT Pr(Chi)
<none>                46.979               
Approach.Posture    1 47.177 2.19812  0.1382
Age                 1 44.979 0.00008  0.9928
Object:Persistence  1 45.221 0.24195  0.6228
```

```
summary(Latency.Wolves.WEI.3)
******************************************************************
Family:  c("WEI", "Weibull") 

Call:  gamlss(formula = Contact.Latency ~ Persistence + Object + Approach.Posture + Age,  
      family = "WEI", data = na.omit(wolves), control = con, random = ~1 | Individual) 

Fitting method: RS() 

------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)   
(Intercept)             0.6782045  0.3522054   1.926  0.07105 . 
Persistence            -0.0008737  0.0002496  -3.500  0.00274 **
ObjectPipe             -0.0122778  0.1901729  -0.065  0.94928   
Approach.PostureUnsure -0.6379362  0.3354641  -1.902  0.07430 . 
Age                    -0.0084118  0.0562303  -0.150  0.88284   
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)   0.9057     0.1658   5.464  4.2e-05 ***
------------------------------------------------------------------
No. of observations in the fit:  23 
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  17 
                      at cycle:  4 
 
Global Deviance:     33.22053 
            AIC:     45.22053 
            SBC:     52.0335 
```

7.2.4.2.3 Generalised Inverse Gaussian

```
summary(Latency.Wolves.GIG)
******************************************************************
Family: c("GIG", "Generalised Inverse Gaussian")

Call: gamlss(formula = Contact.Latency ~ Object * Approach.Posture + Object * Persistence + Age,
      family = "GIG", data = na.omit(wolves), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)
(Intercept)             0.4965731  0.4308583   1.153    0.265
ObjectPipe             -0.0069290  0.2809814  -0.025    0.981
Approach.PostureUnsure -0.5969354  0.3679807  -1.622    0.123
Persistence            -0.0006269  0.0004426  -1.417    0.175
Age                    -0.0004834  0.0578306  -0.008    0.993
ObjectPipe:Persistence -0.0005623  0.0005648  -0.996    0.333
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   -0.729      0.188  -3.878 0.000811 ***
------------------------------------------------------------------
Nu link function:  identity
Nu Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  -0.4295    10.5923  -0.041    0.968
------------------------------------------------------------------
No. of observations in the fit:  23
Degrees of Freedom for the fit:  8
      Residual Deg. of Freedom:  15
                      at cycle:  4

Global Deviance:     32.04921
            AIC:     48.04921
            SBC:     57.13316
******************************************************************
```

```
dropterm(Latency.Wolves.GIG, test = "Chisq")
Single term deletions for mu
Model: Contact.Latency ~ Object * Approach.Posture + Object * Persistence + Age
                        Df    AIC     LRT Pr(Chi)
<none>                     48.049
Age                      1 46.049 0.00002  0.9962
Object:Approach.Posture  0 48.049 0.00000
Object:Persistence       1 46.810 0.76050  0.3832
```

```
summary(Latency.Wolves.GIG.2)
******************************************************************
Family:  c("GIG", "Generalised Inverse Gaussian") 

Call:  gamlss(formula = Contact.Latency ~ Object * Persistence + Approach.Posture + Age,  
       family = "GIG", data = na.omit(wolves), control = con, random = ~1 | Individual) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)
(Intercept)             0.4965731  0.4308583   1.153    0.265
ObjectPipe             -0.0069290  0.2809814  -0.025    0.981
Persistence            -0.0006269  0.0004426  -1.417    0.175
Approach.PostureUnsure -0.5969354  0.3679807  -1.622    0.123
Age                    -0.0004834  0.0578306  -0.008    0.993
ObjectPipe:Persistence -0.0005623  0.0005648  -0.996    0.333
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)   -0.729      0.188  -3.878 0.000811 ***
------------------------------------------------------------------
Nu link function:  identity 
Nu Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  -0.4295    10.5923  -0.041    0.968
------------------------------------------------------------------
No. of observations in the fit:  23 
Degrees of Freedom for the fit:  8
      Residual Deg. of Freedom:  15 
                      at cycle:  4 
 
Global Deviance:     32.04921 
            AIC:     48.04921 
            SBC:     57.13316 
******************************************************************
dropterm(Latency.Wolves.GIG.2, test = "Chisq")
Single term deletions for mu
Model: Contact.Latency ~ Object * Persistence + Approach.Posture + Age
                   Df    AIC     LRT Pr(Chi)
<none>                48.049                
Approach.Posture    1 48.475 2.42612  0.1193
Age                 1 46.049 0.00002  0.9962
Object:Persistence  1 46.810 0.76050  0.3832
```

```
summary(Latency.Wolves.GIG.3)
******************************************************************
Family: c("GIG", "Generalised Inverse Gaussian")

Call: gamlss(formula = Contact.Latency ~ Persistence + Object + Approach.Posture + Age,
      family = "GIG", data = na.omit(wolves), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  identity
Mu Coefficients:
                       Estimate Std. Error t value Pr(>|t|)
(Intercept)           0.6065597  0.6188065   0.980  0.34157
Persistence          -0.0009467  0.0002995  -3.161  0.00606 **
ObjectPipe           -0.1609172  0.2296859  -0.701  0.49362
Approach.PostureUnsure -0.6530659  0.3897705  -1.676  0.11326
Age                  -0.0007817  0.0995881  -0.008  0.99383
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  -0.6378     0.4539  -1.405    0.179
------------------------------------------------------------------
Nu link function:  identity
Nu Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)    2.542      6.060   0.419     0.68
------------------------------------------------------------------
No. of observations in the fit:  23
Degrees of Freedom for the fit:  7
      Residual Deg. of Freedom:  16
                      at cycle:  10

Global Deviance:     32.80971
            AIC:     46.80971
            SBC:     54.75817
******************************************************************
```

7.2.4.2.3.1.1 Model AIC Values & Plots

Model	df	AIC
Latency.Wolves.LOGNO.3	6	45.2576836
Latency.Wolves.LOGNO.2	7	46.3634629
Latency.Wolves.LOGNO	7	46.3634629
Latency.Wolves.GA.3	6	44.94967512
Latency.Wolves.GA.2	7	46.51757949
Latency.Wolves.GA	7	46.51757949

Model	df	AIC
Latency.Wolves.WEI.3	6	45.22053018
Latency.Wolves.WEI	7	46.97858022
Latency.Wolves.WEI.2	7	46.97858022
Latency.Wolves.GIG.3	7	46.80970824
Latency.Wolves.GIG.2	8	48.04920909
Latency.Wolves.GIG	8	48.04920909

7.2.4.3 Motor Diversity Models

7.2.4.3.1 Dogs

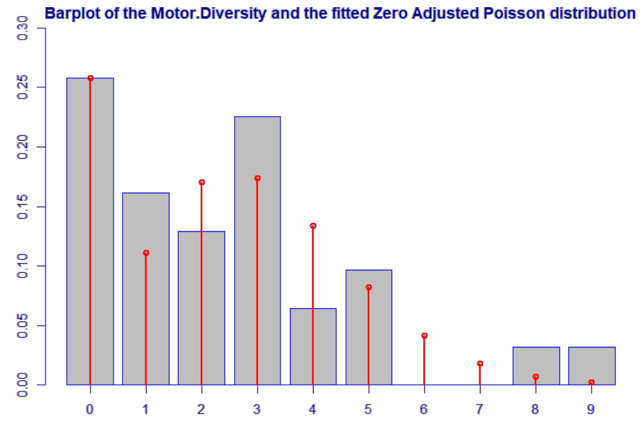
7.2.4.3.1.1 Response Variable Distribution

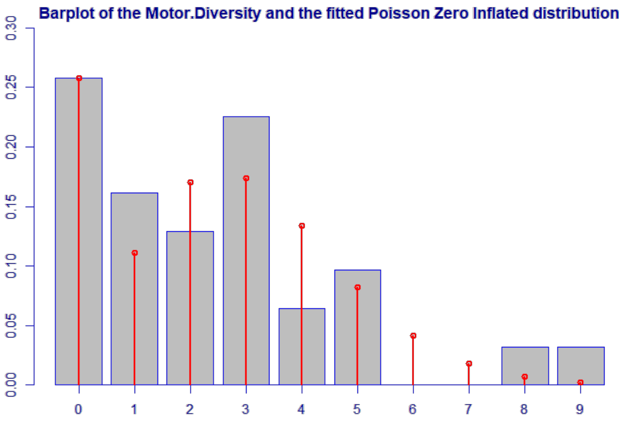
`Dogs.Diversity.Distribution$fit`

Distribution	AIC
GEOM	131.840356
GEOMo	131.840356
DPO	131.926183
NBI	132.9925
GPO	133.39636
ZAPIG	133.454585
ZIPIG	133.454585

Distribution	AIC
ZINBI	133.50528
ZANBI	133.50528
WARING	133.840359
ZIP	133.929318
ZAP	133.929318
PIG	133.929318
NBF	134.143332

7.2.4.3.1.2 Density plots of examples of distributions used in final models


Barplot of the Motor.Diversity and the fitted Zero Adjusted Poisson distribution


Barplot of the Motor.Diversity and the fitted Poisson Zero Inflated distribution

7.2.4.3.1.3 Model Distribution Selection

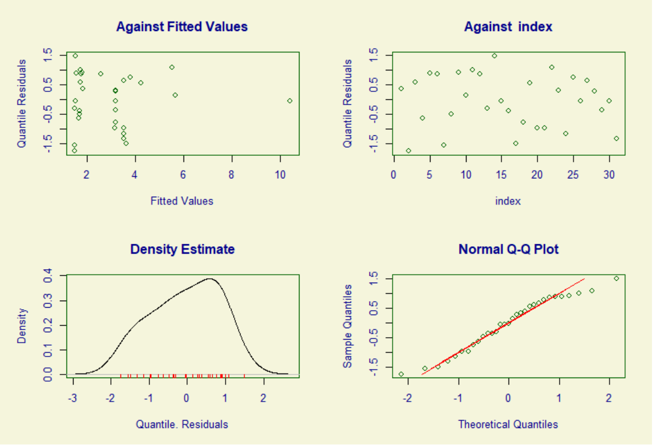
```
Diversity.Dogs.DISTRIBUTION <- gamlss(Motor.Diversity ~ Object*Persistence + Age,
                                      random = ~1|Individual,
                                      family = "DISTRIBUTION", data = dogs)
```

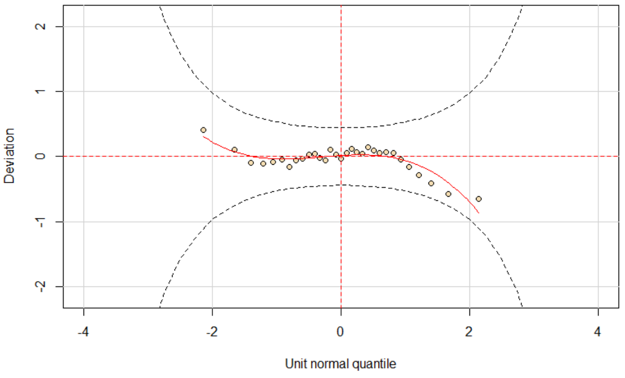
Model	df	AIC
Diversity.Dogs.ZAP	6	117.2878
Diversity.Dogs.ZIP	6	118.941638
Diversity.Dogs.ZANBI	7	119.287843
Diversity.Dogs.ZINBI	7	120.941578
Diversity.Dogs.ZIPIG	7	121.123295
Diversity.Dogs.DPO	6	122.587648

Model	df	AIC
Diversity.Dogs.ZAPIG	7	123.594596
Diversity.Dogs.NBI	6	123.977027
Diversity.Dogs.PIG	6	123.986116
Diversity.Dogs.GPO	6	123.989319
Diversity.Dogs.NBF	7	125.232948
Diversity.Dogs.GEOM	5	130.605775

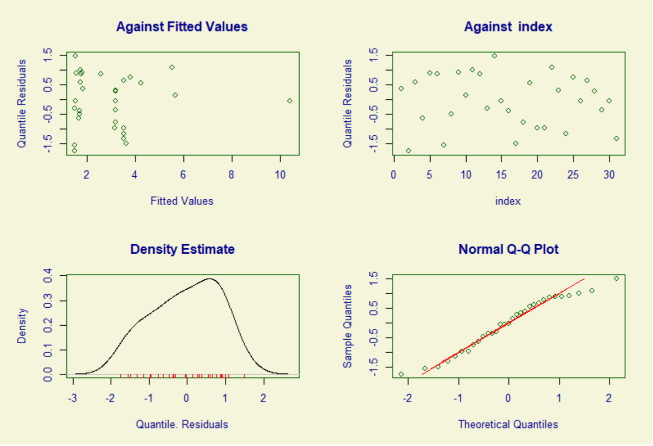
7.2.4.3.1.4 Model Diagnostics Plots

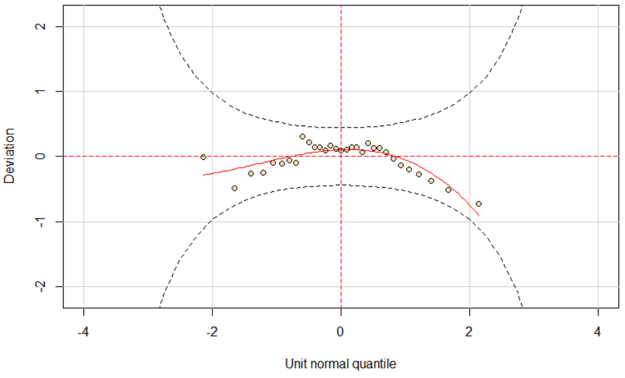
`plot(Diversity.Dogs.ZAP) & wp(Diversity.Dogs.ZAP)`



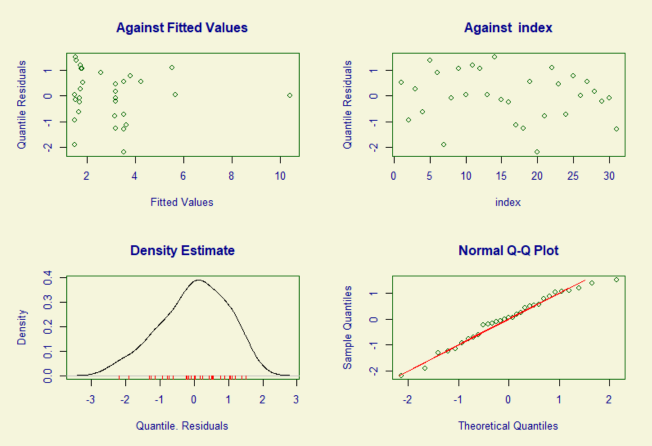


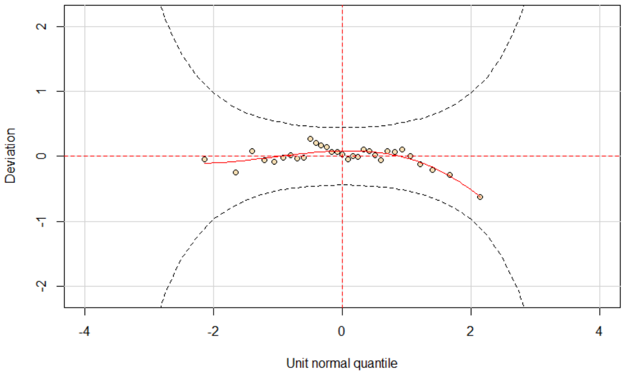
`plot(Diversity.Dogs.ZIP) & wp(Diversity.Dogs.ZIP)`



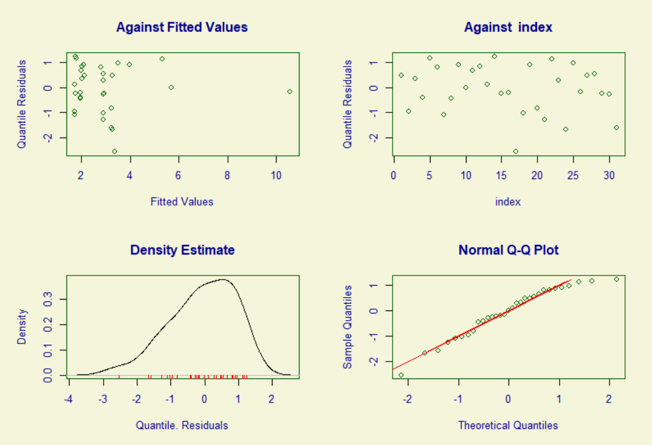


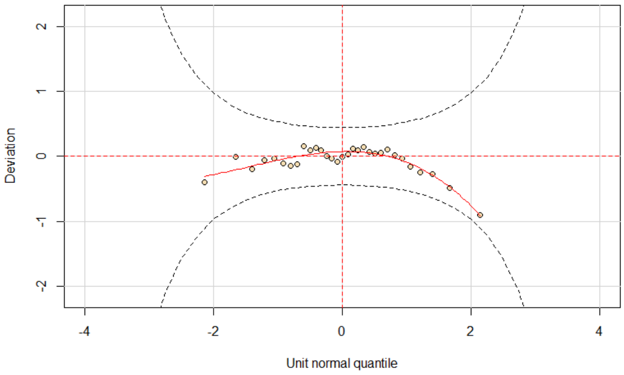
plot(Diversity.Dogs.ZANBI) & wp(Diversity.Dogs.ZANBI)



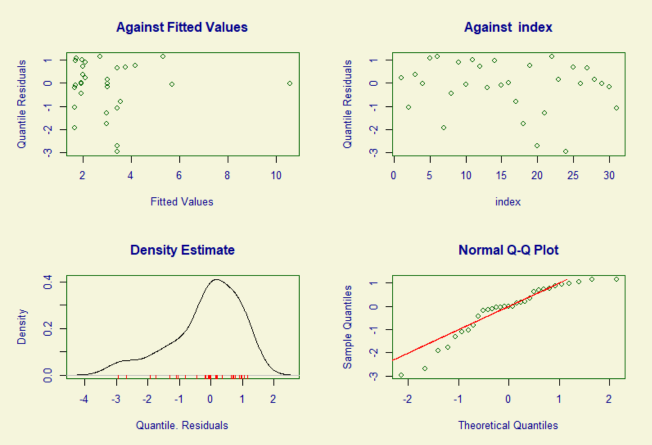


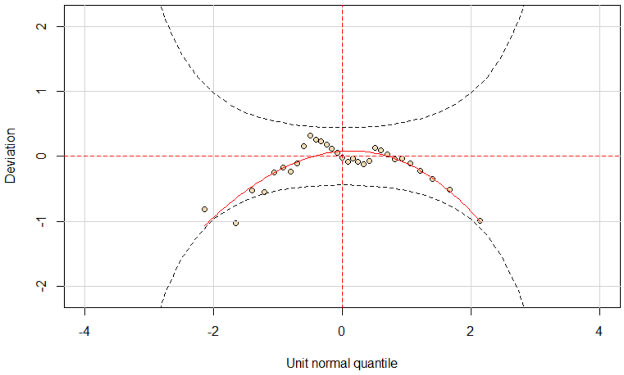
plot(Diversity.Dogs.ZINBI) & wp(Diversity.Dogs.ZINBI)



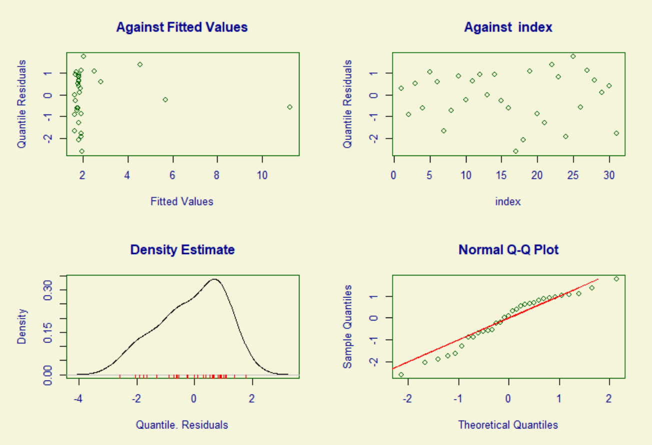


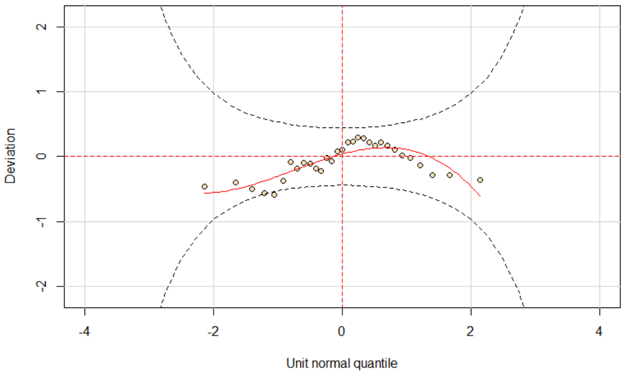
plot(Diversity.Dogs.ZIPIG) & wp(Diversity.Dogs.ZIPIG)



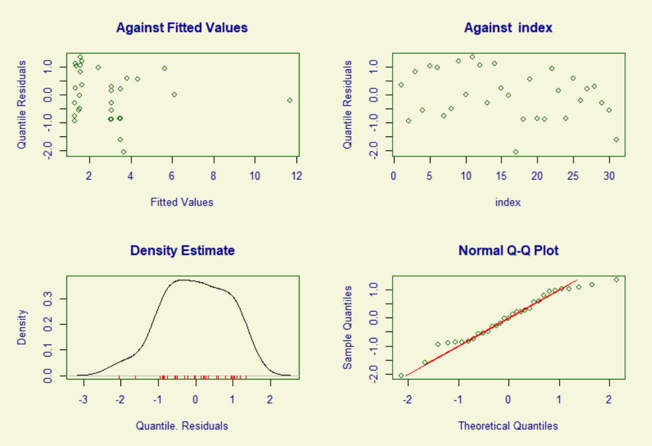


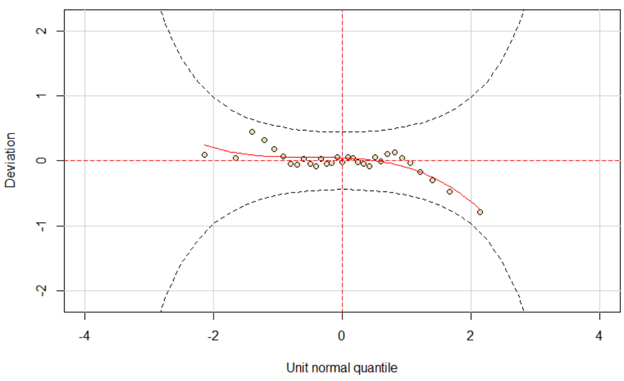
plot(Diversity.Dogs.DPO) & wp(Diversity.Dogs.DPO)



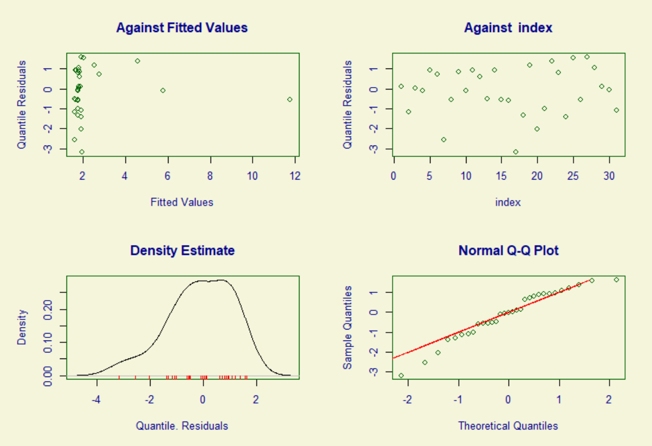


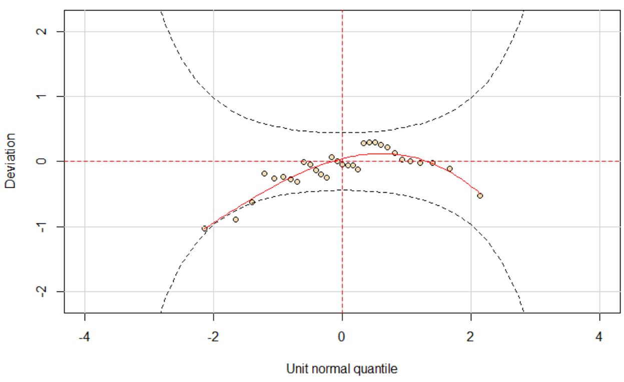
plot(Diversity.Dogs.ZAPIG) & wp(Diversity.Dogs.ZAPIG)



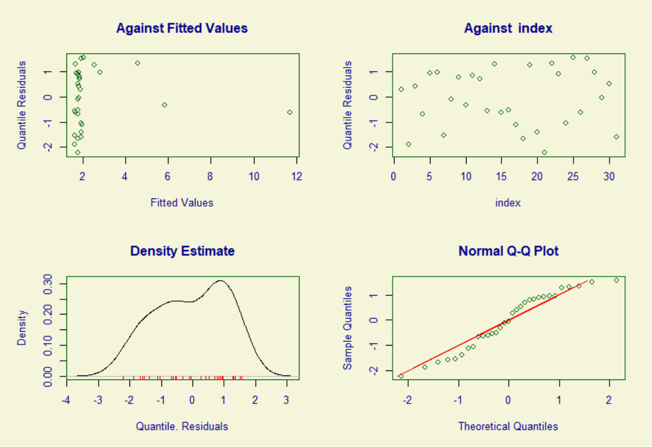


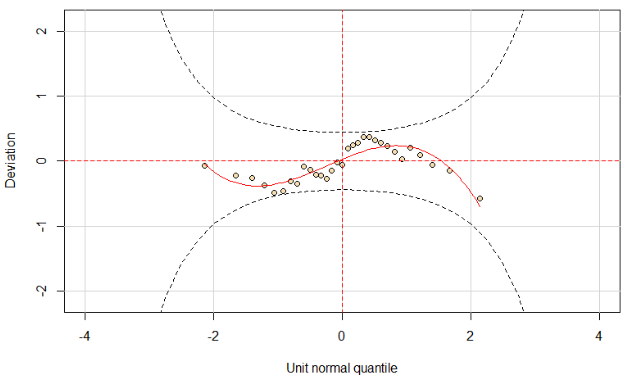
plot(Diversity.Dogs.NBI) & wp(Diversity.Dogs.NBI)



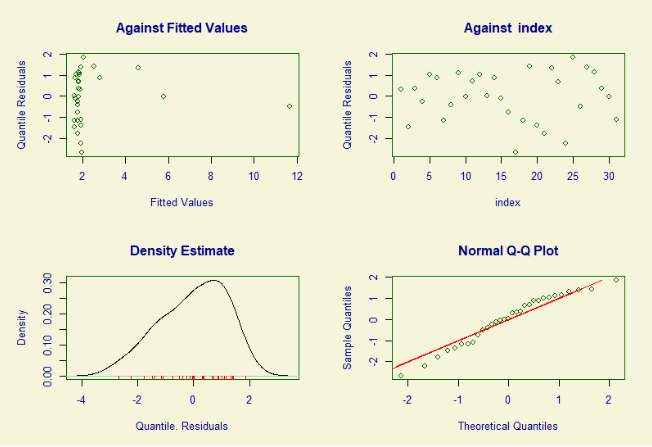


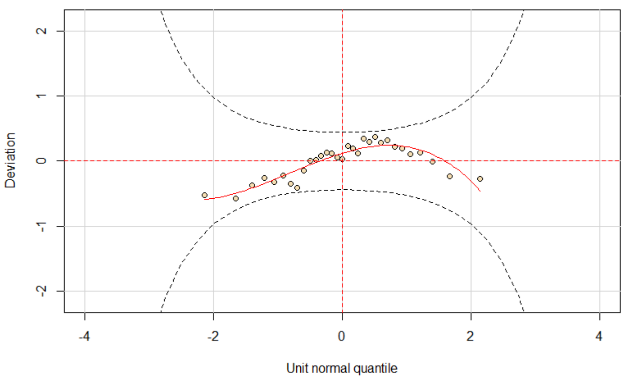
plot(Diversity.Dogs.PIG) & wp(Diversity.Dogs.PIG)



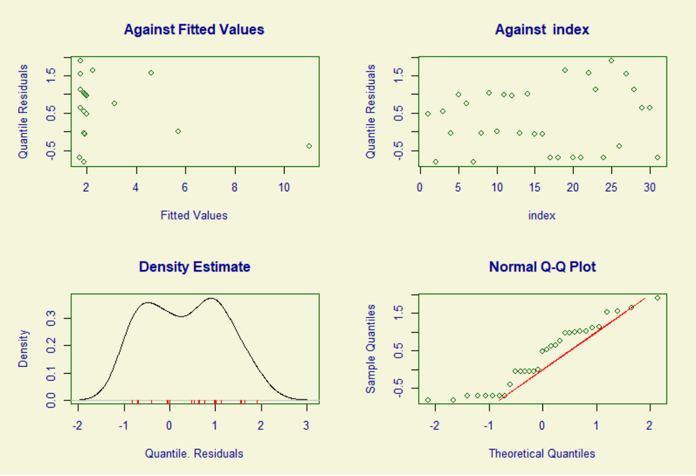


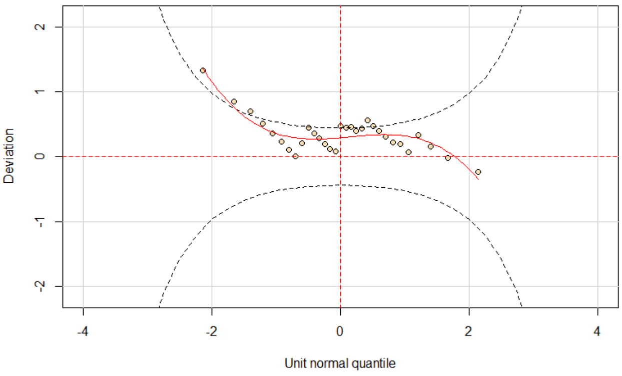
plot(Diversity.Dogs.GPO) & wp(Diversity.Dogs.GPO)



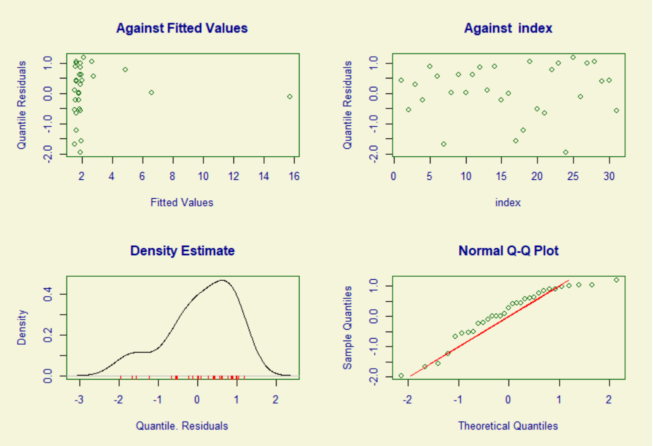


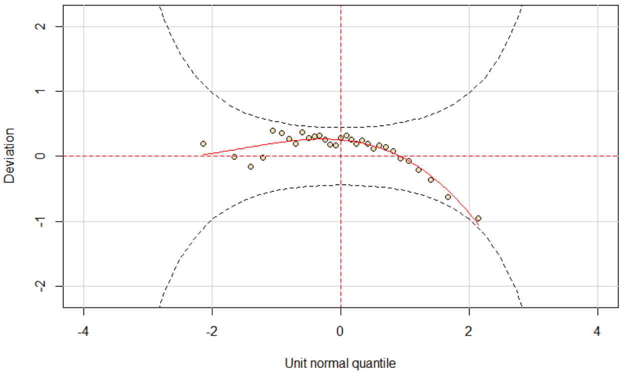
```
plot(Diversity.Dogs.NBF) & wp(Diversity.Dogs.NBF)
```





```
plot(Diversity.Dogs.GEOM) & wp(Diversity.Dogs.GEOM)
```





7.2.4.3.1.5 Model Reduction and Validation

7.2.4.3.1.5.1 Zero Adjusted Poisson

```
summary(Diversity.Dogs.ZAP)
******************************************************************
Family: c("ZAP", "Zero Adjusted Poisson")

Call: gamlss(formula = Motor.Diversity ~ Object * Persistence + Age,
      family = "ZAP", data = na.omit(dogs), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                        Estimate Std. Error t value Pr(>|t|)
(Intercept)             0.316935   0.443544   0.715   0.4815
ObjectPipe              0.748283   0.337201   2.219   0.0358 *
Persistence             0.003257   0.001465   2.223   0.0355 *
Age                     0.037068   0.083626   0.443   0.6614
ObjectPipe:Persistence -0.002452   0.001470  -1.668   0.1077
------------------------------------------------------------------
Sigma link function:  logit
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  -1.0561     0.4105  -2.573   0.0164 *
------------------------------------------------------------------
No. of observations in the fit:  31
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  25
                      at cycle:  2

Global Deviance:     105.2878
            AIC:     117.2878
            SBC:     125.8917
******************************************************************
```

```
dropterm(Diversity.Dogs.ZAP, test = "Chisq")
Single term deletions for mu
Model: Motor.Diversity ~ Object * Persistence + Age
                   Df    AIC     LRT Pr(Chi)
<none>                117.29
Age                 1 115.51 0.21849 0.64019
Object:Persistence  1 118.01 2.71956 0.09913 .
summary(Diversity.Dogs.ZAP.2)
******************************************************************
Family: c(“ZAP”, “Zero Adjusted Poisson”)

Call: gamlss(formula = Motor.Diversity ~ Object + Persistence + Age,
       family = "ZAP", data = na.omit(dogs), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) 0.4659100  0.4244754   1.098 0.282435
ObjectPipe  0.5208601  0.2992994   1.740 0.093638 .
Persistence 0.0008714  0.0002328   3.744 0.000908 ***
Age         0.0477883  0.0825917   0.579 0.567832
------------------------------------------------------------------
Sigma link function:  logit
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  -1.0561     0.4105  -2.573   0.0161 *
------------------------------------------------------------------
No. of observations in the fit:  31
Degrees of Freedom for the fit:  5
      Residual Deg. of Freedom:  26
                      at cycle:  2

Global Deviance:     108.0074
            AIC:     118.0074
            SBC:     125.1773
******************************************************************
```

7.2.4.3.1.5.2 Poisson Zero Inflated

```
summary(Diversity.Dogs.ZIP)
******************************************************************
Family: c(“ZIP”, “Poisson Zero Inflated”)

Call: gamlss(formula = Motor.Diversity ~ Object * Persistence + Age,
       family = "ZIP", data = na.omit(dogs), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                        Estimate Std. Error t value Pr(>|t|)
(Intercept)             0.450355   0.407922   1.104   0.2801
ObjectPipe              0.513878   0.324300   1.585   0.1256
Persistence             0.002867   0.001355   2.115   0.0446 *
Age                     0.042100   0.080686   0.522   0.6064
ObjectPipe:Persistence -0.001990   0.001362  -1.461   0.1565
------------------------------------------------------------------
Sigma link function:  logit
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  -1.3655     0.5367  -2.544   0.0175 *
------------------------------------------------------------------
No. of observations in the fit:  31
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  25
                      at cycle:  4

Global Deviance:     106.9416
            AIC:     118.9416
            SBC:     127.5456
******************************************************************
```

```
dropterm(Diversity.Dogs.ZIP, test = "Chisq")
Single term deletions for mu
Model: Motor.Diversity ~ Object * Persistence + Age
                   Df    AIC     LRT Pr(Chi)
<none>                118.94
Age                 1 117.22 0.27643  0.5991
Object:Persistence  1 119.00 2.06065  0.1511
summary(Diversity.Dogs.ZIP.2)
******************************************************************
Family: c("ZIP", "Poisson Zero Inflated")

Call: gamlss(formula = Motor.Diversity ~ Object + Persistence + Age,
      family = "ZIP", data = na.omit(dogs), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) 0.5632811  0.4018451   1.402 0.172820
ObjectPipe  0.3443769  0.3051545   1.129 0.269401
Persistence 0.0009430  0.0002494   3.781 0.000825 ***
Age         0.0465734  0.0805621   0.578 0.568166
------------------------------------------------------------------
Sigma link function:  logit
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  -1.3587     0.5402  -2.515   0.0184 *
------------------------------------------------------------------
No. of observations in the fit:  31
Degrees of Freedom for the fit:  5
      Residual Deg. of Freedom:  26
                      at cycle:  4

Global Deviance:     109.0023
            AIC:     119.0023
            SBC:     126.1722
******************************************************************
```

7.2.4.3.1.5.3 Zero Altered Negative Binomial

```
summary(Diversity.Dogs.ZANBI)
******************************************************************
Family: c("ZANBI", "Zero Altered Negative Binomial type I")

Call: gamlss(formula = Motor.Diversity ~ Object * Persistence + Age,
      family = "ZANBI", data = na.omit(dogs), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                        Estimate Std. Error t value Pr(>|t|)
(Intercept)             0.317742   0.596072   0.533    0.599
ObjectPipe              0.747607   0.534575   1.399    0.174
Persistence             0.003239   0.003607   0.898    0.377
Age                     0.036956   0.126409   0.292    0.772
ObjectPipe:Persistence -0.002434   0.003660  -0.665    0.512
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   -36.04   17960.53  -0.002    0.998
------------------------------------------------------------------
Nu link function:  logit
Nu Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  -1.0561     0.4105  -2.573   0.0153 *
------------------------------------------------------------------
No. of observations in the fit:  31
Degrees of Freedom for the fit:  7
      Residual Deg. of Freedom:  24
                      at cycle:  3

Global Deviance:     105.2878
            AIC:     119.2878
            SBC:     129.3258
******************************************************************
```

```
dropterm(Diversity.Dogs.ZANBI, test = "Chisq")
Single term deletions for mu
Model: Motor.Diversity ~ Object * Persistence + Age
                   Df    AIC     LRT Pr(Chi)
<none>                119.29
Age                 1 117.51 0.21815 0.64046
Object:Persistence  1 120.01 2.71950 0.09913 .
summary(Diversity.Dogs.ZANBI.2)
******************************************************************
Family: c(“ZANBI”, “Zero Altered Negative Binomial type I”)

Call: gamlss(formula = Motor.Diversity ~ Object + Persistence + Age,
       family = "ZANBI", data = na.omit(dogs), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) 0.4643207  0.5176760   0.897    0.378
ObjectPipe  0.5215666  0.4585333   1.137    0.265
Persistence 0.0008724  0.0005106   1.709    0.099 .
Age         0.0481085  0.1122336   0.429    0.672
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   -36.04   17960.53  -0.002    0.998
------------------------------------------------------------------
Nu link function:  logit
Nu Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  -1.0561     0.4105  -2.573   0.0153 *
------------------------------------------------------------------
No. of observations in the fit:  31
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  25
                      at cycle:  4

Global Deviance:     108.0073
            AIC:     120.0073
            SBC:     128.6113
```

7.2.4.3.1.5.4 Zero Inflated Negative Binomial

```
summary(Diversity.Dogs.ZINBI)
******************************************************************
Family: c(“ZINBI”, “Zero Inflated Negative Binomial type I”)

Call: gamlss(formula = Motor.Diversity ~ Object * Persistence + Age,
       family = "ZINBI", data = na.omit(dogs), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                        Estimate Std. Error t value Pr(>|t|)
(Intercept)             0.451127   0.518061   0.871    0.392
ObjectPipe              0.514607   0.488324   1.054    0.302
Persistence             0.002886   0.003560   0.810    0.425
Age                     0.041361   0.110586   0.374    0.711
ObjectPipe:Persistence -0.002010   0.003602  -0.558    0.582
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) -36.06855    0.01724   -2092   <2e-16 ***
------------------------------------------------------------------
Nu link function:  logit
Nu Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  -1.3647     0.5133  -2.659   0.0125 *
------------------------------------------------------------------
No. of observations in the fit:  31
Degrees of Freedom for the fit:  7
      Residual Deg. of Freedom:  24
                      at cycle:  4

Global Deviance:     106.9416
            AIC:     120.9416
            SBC:     130.9795
******************************************************************
```

```
dropterm(Diversity.Dogs.ZINBI, test = "Chisq")
Single term deletions for mu
Model: Motor.Diversity ~ Object * Persistence + Age
                   Df    AIC     LRT Pr(Chi)
<none>                120.94
Age                 1 119.22 0.27629  0.5991
Object:Persistence  1 121.00 2.06025  0.1512
```

```
summary(Diversity.Dogs.ZINBI.2)
******************************************************************
Family: c(“ZINBI”, “Zero Inflated Negative Binomial type I”)

Call: gamlss(formula = Motor.Diversity ~ Object + Persistence + Age,
      family = "ZINBI", data = na.omit(dogs), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) 0.5623289  0.4602342   1.222   0.2323
ObjectPipe  0.3433202  0.3993139   0.860   0.3975
Persistence 0.0009447  0.0004307   2.193   0.0371 *
Age         0.0467424  0.0987681   0.473   0.6398
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) -36.06932    0.01701   -2121   <2e-16 ***
------------------------------------------------------------------
Nu link function:  logit
Nu Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   -1.360      0.515   -2.64    0.013 *
------------------------------------------------------------------
No. of observations in the fit:  31
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  25
                      at cycle:  5

Global Deviance:     109.0018
            AIC:     121.0018
            SBC:     129.6057
```

7.2.4.3.1.6 Model AIC Values & Plots

Model	df	AIC
Diversity.Dogs.ZAP	6	117.2878
Diversity.Dogs.ZAP.2	5	118.007357
Diversity.Dogs.ZIP	6	118.9416379
Diversity.Dogs.ZIP.2	5	119.0022906
Diversity.Dogs.ZANBI	7	119.2878429
Diversity.Dogs.ZANBI.2	6	120.007344
Diversity.Dogs.ZINBI	7	120.941578
Diversity.Dogs.ZINBI.2	6	121.0018255

7.2.4.3.2 Wolves

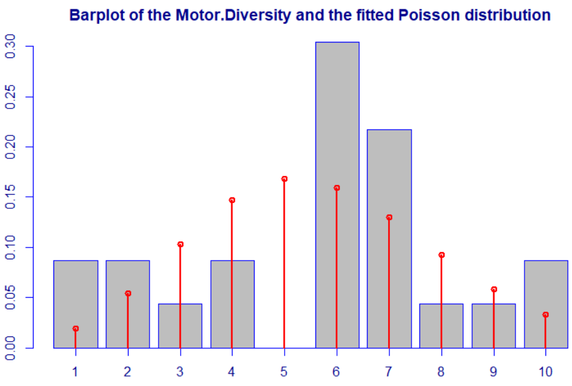
7.2.4.3.2.1 Response Variable Distribution

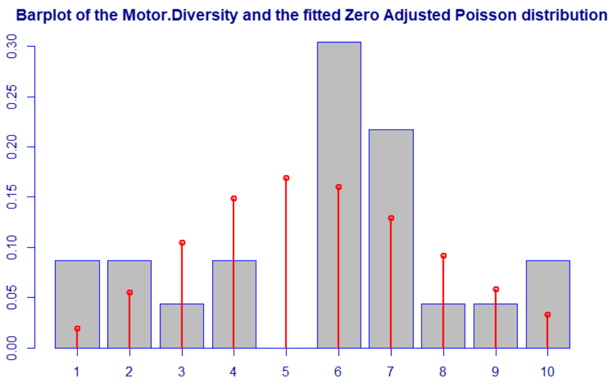
```
Wolves.Diversity.Distribution$fit
```

Distribution	AIC
PO	111.857751
DPO	113.200737
NBII	113.656754
NBI	113.656754
GPO	113.669782
PIG	113.69866
ZAP	113.70139
ZIP2	113.857751
ZIP	113.857751

Distribution	AIC
ZANBI	115.407244
ZAPIG	115.474817
NBF	115.656754
SI	115.656754
DEL	115.656754
ZINBI	115.656754
SICHEL	115.656754
BNB	115.681199
ZIPIG	115.69866

7.2.4.3.2.2 Density plots of examples of distributions used in final models





7.2.4.3.2.3 Model Distribution Selection

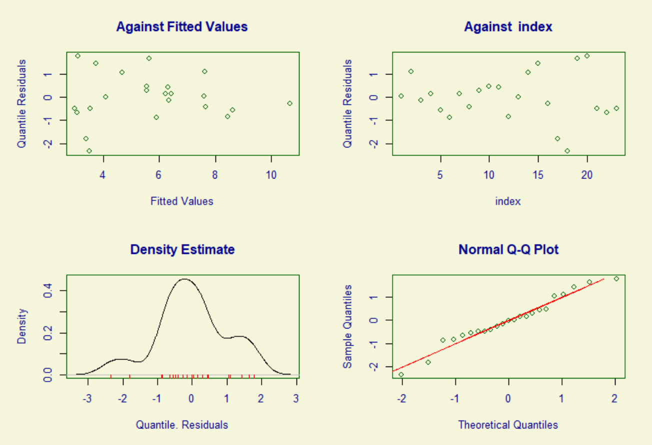
```
Diversity.Wolves.DISTRIBUTION <- gamlss(Motor.Diversity ~ Object*Persistence + Age,
                                 random = ~1|Individual,
                                 family = "DISTRIBUTION", data = wolves)
```

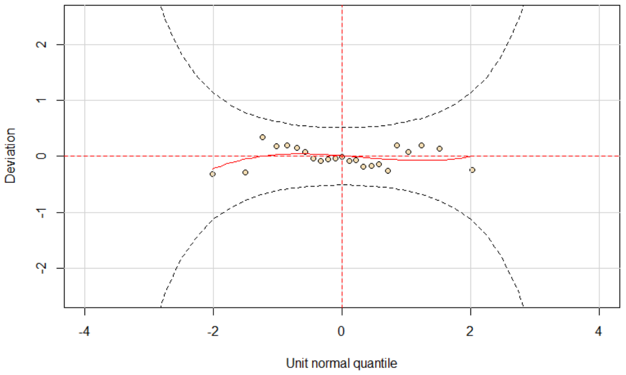
Model	df	AIC
Diversity.Wolves.DPO	6	101.744393
Diversity.Wolves.PO	5	103.02143
Diversity.Wolves.ZAP	6	104.368964
Diversity.Wolves.NBI	6	105.02143
Diversity.Wolves.GPO	6	105.021491
Diversity.Wolves.ZIP	6	105.022016

Model	df	AIC
Diversity.Wolves.ZANBI	7	106.369167
Diversity.Wolves.DEL	7	107.021477
Diversity.Wolves.ZIPIG	7	107.021944
Diversity.Wolves.NBF	7	107.022231
Diversity.Wolves.ZINBI	7	107.022231

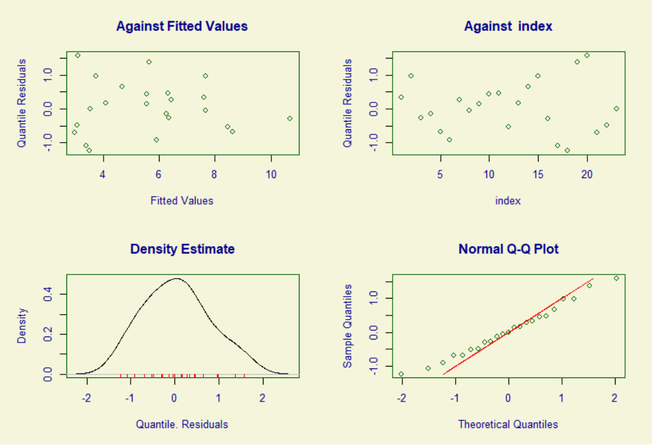
7.2.4.3.2.4 Model Diagnostics Plots

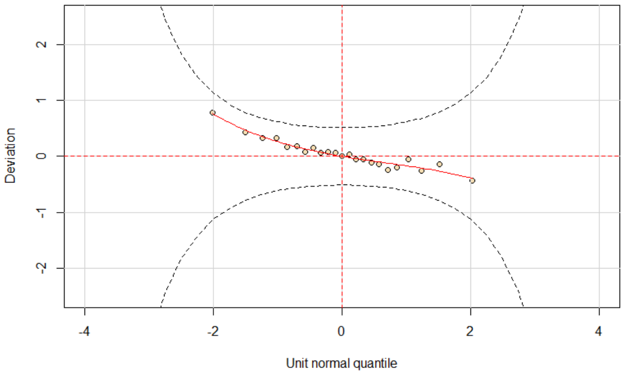
`plot(Diversity.Wolves.DPO) & wp(Diversity.Wolves.DPO)`



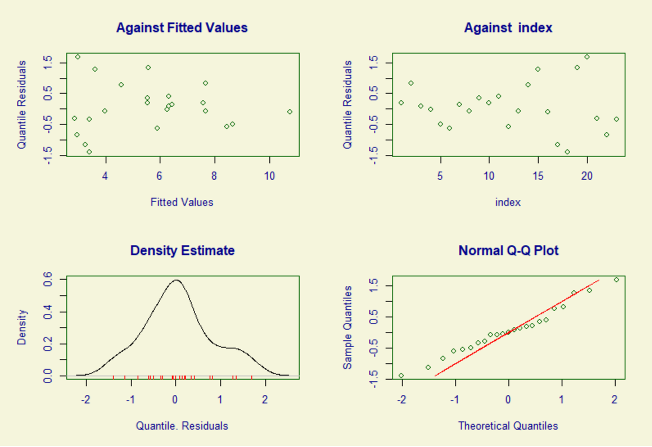


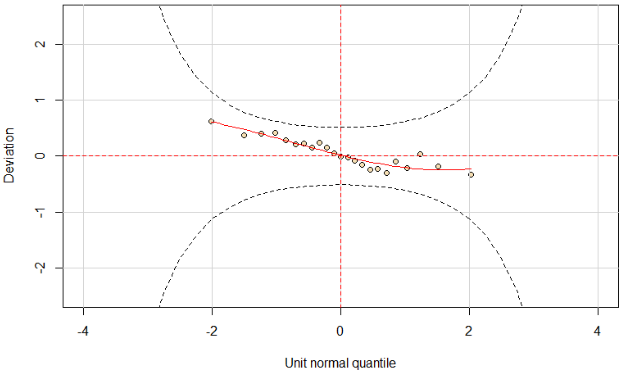
`plot(Diversity.Wolves.PO) & wp(Diversity.Wolves.PO)`



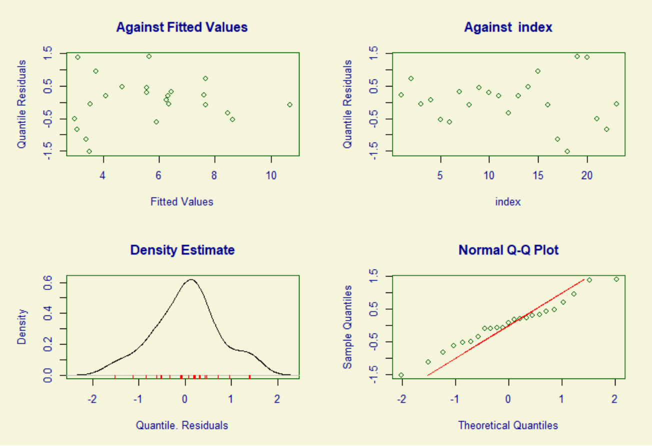


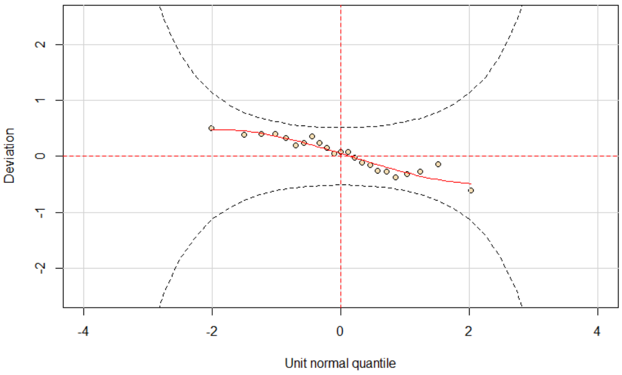
plot(Diversity.Wolves.ZAP) & wp(Diversity.Wolves.ZAP)



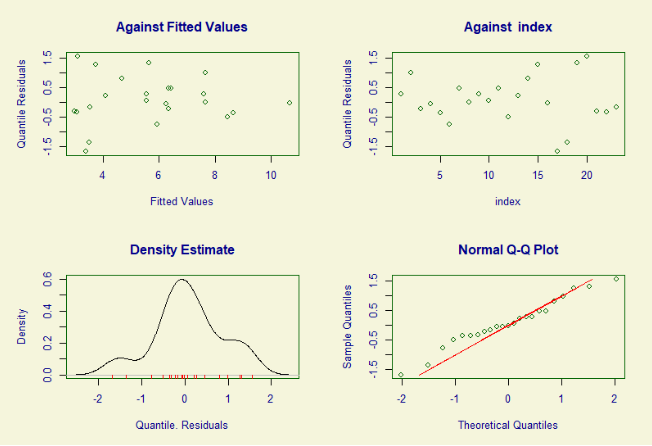


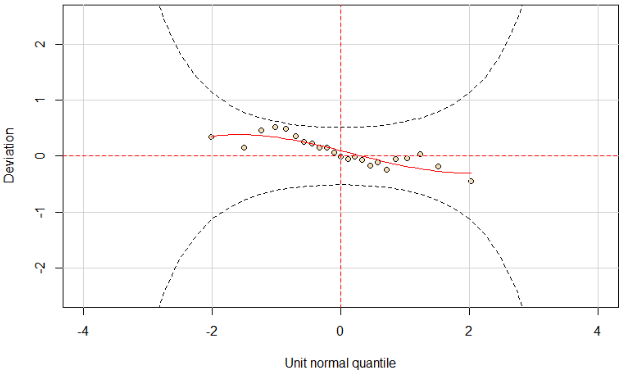
plot(Diversity.Wolves.NBI) & wp(Diversity.Wolves.NBI)



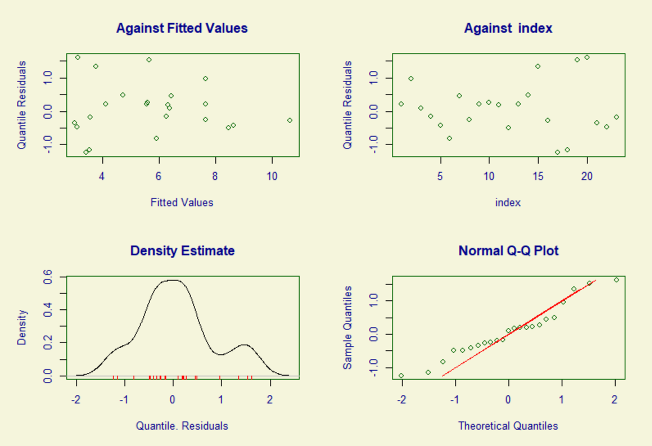


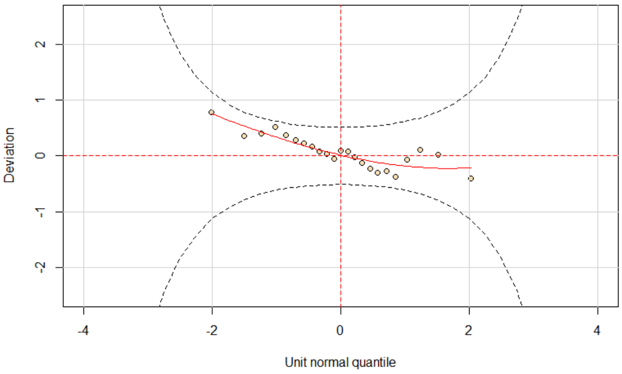
plot(Diversity.Wolves.GPO) & wp(Diversity.Wolves.GPO)



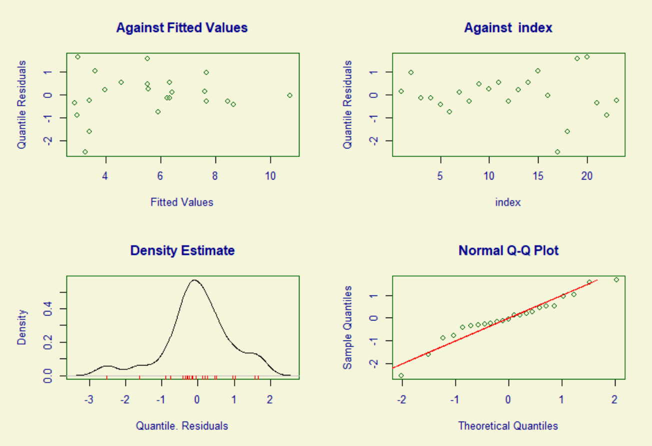


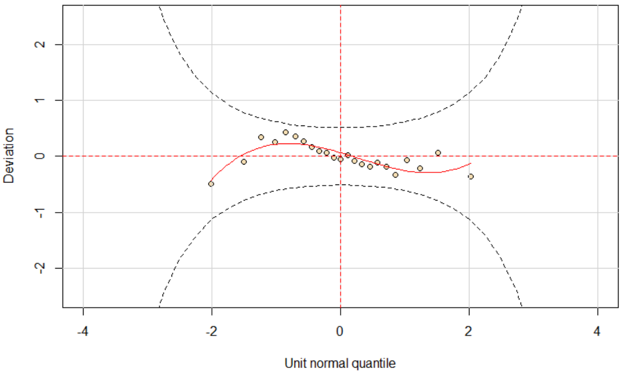
plot(Diversity.Wolves.ZIP) & wp(Diversity.Wolves.ZIP)



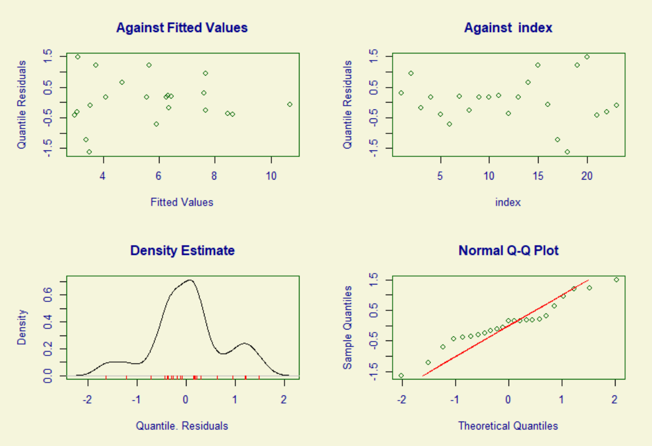


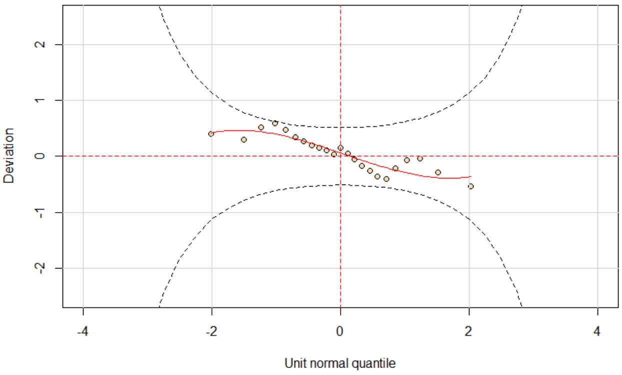
plot(Diversity.Wolves.ZANBI) & wp(Diversity.Wolves.ZANBI)



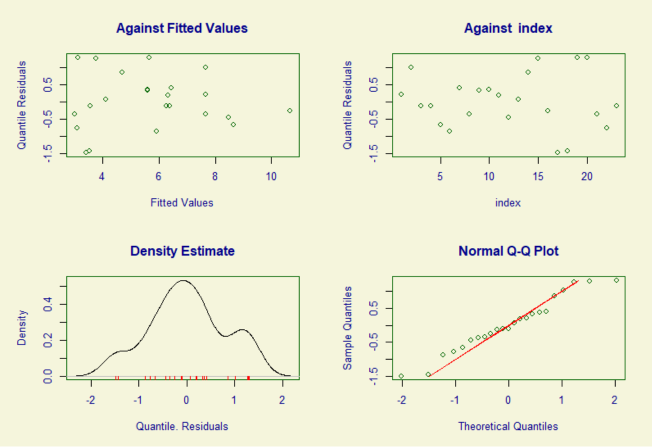


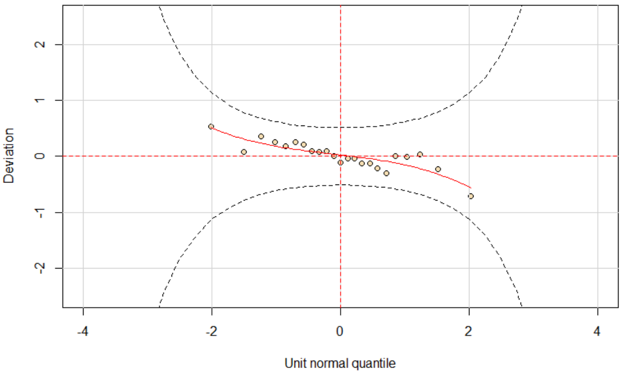
plot(Diversity.Wolves.DEL) & wp(Diversity.Wolves.DEL)



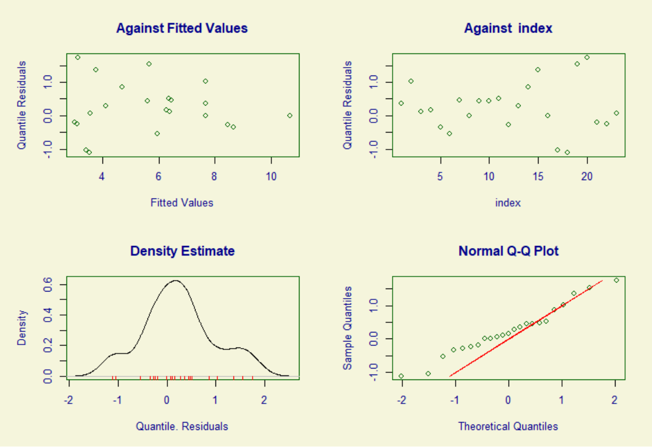


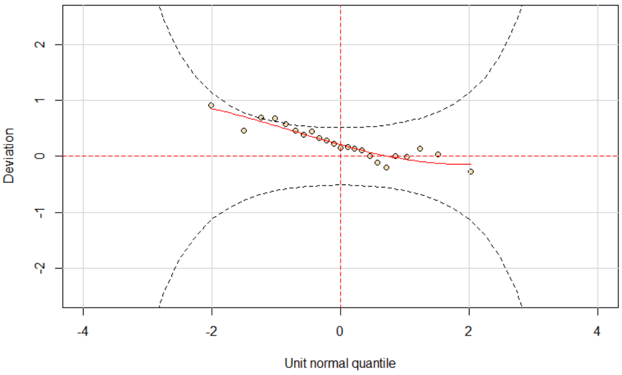
plot(Diversity.Wolves.ZIPIG) & wp(Diversity.Wolves.ZIPIG)



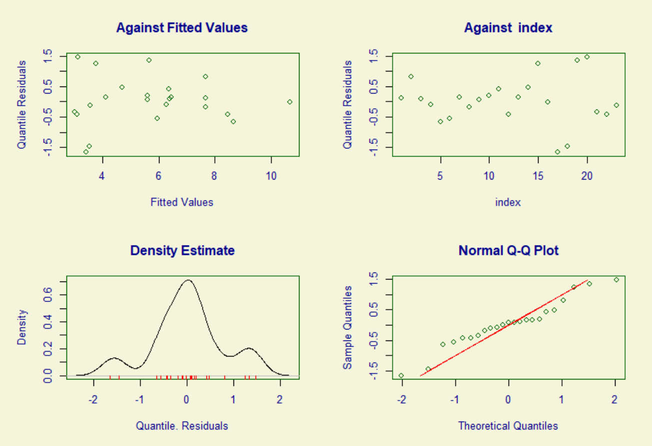


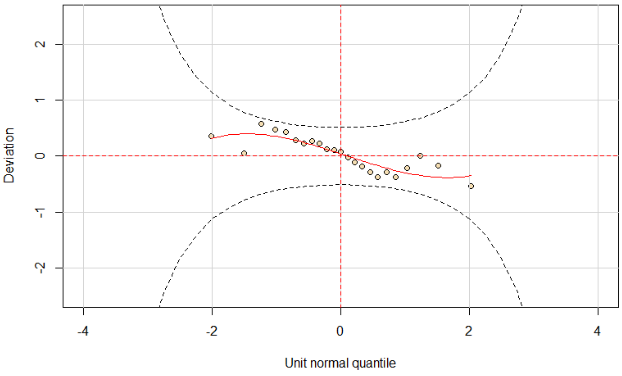
plot(Diversity.Wolves.NBF) & wp(Diversity.Wolves.NBF)





```
plot(Diversity.Wolves.ZINBI) & wp(Diversity.Wolves.ZINBI)
```





7.2.4.3.2.5 Model Reduction and Validation

7.2.4.3.2.5.1 Poisson

```
summary(Diversity.Wolves.PO)
******************************************************************
Family: c(“PO”, “Poisson”)

Call: gamlss(formula = Motor.Diversity ~ Object * Persistence + Age,
      family = "PO", data = na.omit(wolves), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)
(Intercept)             1.4140292  0.3902138   3.624  0.00194 **
ObjectPipe             -0.5530735  0.2559170  -2.161  0.04441 *
Persistence             0.0003478  0.0003086   1.127  0.27455
Age                     0.0545874  0.0512440   1.065  0.30085
ObjectPipe:Persistence  0.0006448  0.0003970   1.624  0.12173
------------------------------------------------------------------
No. of observations in the fit:  23
Degrees of Freedom for the fit:  5
      Residual Deg. of Freedom:  18
                      at cycle:  2

Global Deviance:     93.02143
            AIC:     103.0214
            SBC:     108.6989
******************************************************************
dropterm(Diversity.Wolves.PO, test = "Chisq")
Single term deletions for mu
Model: Motor.Diversity ~ Object * Persistence + Age
                   Df    AIC    LRT Pr(Chi)
<none>                103.02
Age                 1 102.17 1.1459  0.2844
Object:Persistence  1 102.94 1.9148  0.1664
```

```
summary(Diversity.Wolves.PO.2)
******************************************************************
Family: c(“PO”, “Poisson”)

Call: gamlss(formula = Motor.Diversity ~ Object + Persistence + Age,
       family = "PO", data = na.omit(wolves), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)  1.2142231  0.3675870   3.303  0.00374 **
ObjectPipe  -0.2832031  0.1764174  -1.605  0.12492
Persistence  0.0007218  0.0001938   3.724  0.00144 **
Age          0.0610446  0.0507405   1.203  0.24373
------------------------------------------------------------------
No. of observations in the fit:  23
Degrees of Freedom for the fit:  4
      Residual Deg. of Freedom:  19
                      at cycle:  2

Global Deviance:     94.93626
            AIC:     102.9363
            SBC:     107.4782
******************************************************************
```

7.2.4.3.2.5.2 Zero Adjusted Poisson

```
summary(Diversity.Wolves.ZAP)
******************************************************************
Family: c(“ZAP”, “Zero Adjusted Poisson”)

Call: gamlss(formula = Motor.Diversity ~ Object * Persistence + Age,
       family = “ZAP”, data = na.omit(wolves), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)
(Intercept)             1.4060427  0.3955977   3.554  0.00244 **
ObjectPipe             -0.5893984  0.2642837  -2.230  0.03950 *
Persistence             0.0003497  0.0003100   1.128  0.27492
Age                     0.0558551  0.0520286   1.074  0.29803
ObjectPipe:Persistence  0.0006804  0.0004022   1.692  0.10896
------------------------------------------------------------------
Sigma link function:  logit
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   -12.43     104.39  -0.119    0.907
------------------------------------------------------------------
No. of observations in the fit:  23
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  17
                      at cycle:  2

Global Deviance:     92.36896
            AIC:     104.369
            SBC:     111.1819
******************************************************************
```

```
dropterm(Diversity.Wolves.ZAP, test = "Chisq")
Single term deletions for mu
Model: Motor.Diversity ~ Object * Persistence + Age
                   Df    AIC    LRT Pr(Chi)
<none>                104.37
Age                 1 103.55 1.1825  0.2769
Object:Persistence  1 104.44 2.0692  0.1503
```

```
summary(Diversity.Wolves.ZAP.2)
******************************************************************
Family: c(“ZAP”, “Zero Adjusted Poisson”)

Call: gamlss(formula = Motor.Diversity ~ Object + Persistence + Age,
family = “ZAP”, data = na.omit(wolves), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)  1.1914525  0.3752959   3.175  0.00525 **
ObjectPipe  -0.3068588  0.1801701  -1.703  0.10574
Persistence  0.0007108  0.0001977   3.596  0.00207 **
Age          0.0651915  0.0516929   1.261  0.22336
------------------------------------------------------------------
Sigma link function:  logit
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   -12.43     104.39  -0.119    0.907
------------------------------------------------------------------
No. of observations in the fit:  23
Degrees of Freedom for the fit:  5
      Residual Deg. of Freedom:  18
                      at cycle:  2

Global Deviance:     94.43815
            AIC:     104.4381
            SBC:     110.1156
******************************************************************
```

7.2.4.3.2.5.3 Negative Binomial type I

```
summary(Diversity.Wolves.NBI)
******************************************************************
Family: c(“NBI”, “Negative Binomial type I”)

Call: gamlss(formula = Motor.Diversity ~ Object * Persistence + Age,
       family = “NBI”, data = na.omit(wolves), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)
(Intercept)             1.4140292  0.3911258   3.615  0.00198 **
ObjectPipe             -0.5530735  0.2629323  -2.103  0.04975 *
Persistence             0.0003478  0.0003595   0.968  0.34607
Age                     0.0545874  0.0512004   1.066  0.30045
ObjectPipe:Persistence  0.0006448  0.0004669   1.381  0.18420
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) -36.08189    0.01004   -3592   <2e-16 ***
------------------------------------------------------------------
No. of observations in the fit:  23
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  17
                      at cycle:  3

Global Deviance:     93.02143
            AIC:     105.0214
            SBC:     111.8344
******************************************************************
```

```
dropterm(Diversity.Wolves.NBI, test = "Chisq")
Single term deletions for mu
Model: Motor.Diversity ~ Object * Persistence + Age
                   Df    AIC    LRT Pr(Chi)
<none>                105.02
Age                 1 104.17 1.1459  0.2844
Object:Persistence  1 104.94 1.9148  0.1664
```

```
summary(Diversity.Wolves.NBI.2)
******************************************************************
Family: c(“NBI”, “Negative Binomial type I”)

Call: gamlss(formula = Motor.Diversity ~ Object + Persistence + Age,
family = “NBI”, data = na.omit(wolves), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)  1.2142231  0.3683111   3.297  0.00379 **
ObjectPipe  -0.2832031  0.1766578  -1.603  0.12540
Persistence  0.0007218  0.0002297   3.142  0.00537 **
Age          0.0610446  0.0507599   1.203  0.24390
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) -36.08192    0.01004   -3595   <2e-16 ***
------------------------------------------------------------------
No. of observations in the fit:  23
Degrees of Freedom for the fit:  5
      Residual Deg. of Freedom:  18
                      at cycle:  3

Global Deviance:     94.93626
            AIC:     104.9363
            SBC:     110.6137
******************************************************************
```

7.2.4.3.2.5.4 Generalised Poisson

```
summary(Diversity.Wolves.GPO)
******************************************************************
Family: c(“GPO”, “Generalised Poisson”)

Call: gamlss(formula = Motor.Diversity ~ Object * Persistence + Age,
       family = “GPO”, data = na.omit(wolves), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
                         Estimate Std. Error t value Pr(>|t|)
(Intercept)             1.4101449  0.7615412   1.852    0.0805 .
ObjectPipe             -0.5505080  0.4935132  -1.115    0.2793
Persistence             0.0003530  0.0009641   0.366    0.7185
Age                     0.0546569  0.0911584   0.600    0.5563
ObjectPipe:Persistence  0.0006471  0.0010982   0.589    0.5630
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   -25.83   20851.44  -0.001    0.999
------------------------------------------------------------------
No. of observations in the fit:  23
Degrees of Freedom for the fit:  6
      Residual Deg. of Freedom:  17
                      at cycle:  3

Global Deviance:     93.02149
            AIC:     105.0215
            SBC:     111.8345
******************************************************************
```

```
dropterm(Diversity.Wolves.GPO, test = "Chisq")
Single term deletions for mu
Model: Motor.Diversity ~ Object * Persistence + Age
                   Df    AIC    LRT Pr(Chi)
<none>                105.02
Age                 1 104.17 1.1468  0.2842
Object:Persistence  1 104.94 1.9169  0.1662
```

```
summary(Diversity.Wolves.GPO.2)
******************************************************************
Family: c(“GPO”, “Generalised Poisson”)

Call: gamlss(formula = Motor.Diversity ~ Object + Persistence + Age,
       family = “GPO”, data = na.omit(wolves), control = con, random = ~1 | Individual)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)  1.2131412  0.6203147   1.956   0.0654 .
ObjectPipe  -0.2791210  0.3151429  -0.886   0.3869
Persistence  0.0007308  0.0005000   1.462   0.1602
Age          0.0604934  0.0824273   0.734   0.4720
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   -36.04   20851.44  -0.002    0.999
------------------------------------------------------------------
No. of observations in the fit:  23
Degrees of Freedom for the fit:  5
      Residual Deg. of Freedom:  18
                      at cycle:  3

Global Deviance:     94.93842
            AIC:     104.9384
            SBC:     110.6159
******************************************************************
```

7.2.4.3.3 Model AIC Values & Plots

Model	df	AIC
Diversity.Wolves.PO.2	4	102.936263
Diversity.Wolves.PO	5	103.02143
Diversity.Wolves.ZAP	6	104.3689642
Diversity.Wolves.ZAP.2	5	104.4381486
Diversity.Wolves.NBI.2	5	104.936263
Diversity.Wolves.NBI	6	105.02143
Diversity.Wolves.GPO.2	5	104.938424
Diversity.Wolves.GPO	6	105.021491

7.2.4.4 Individual Consistency Models

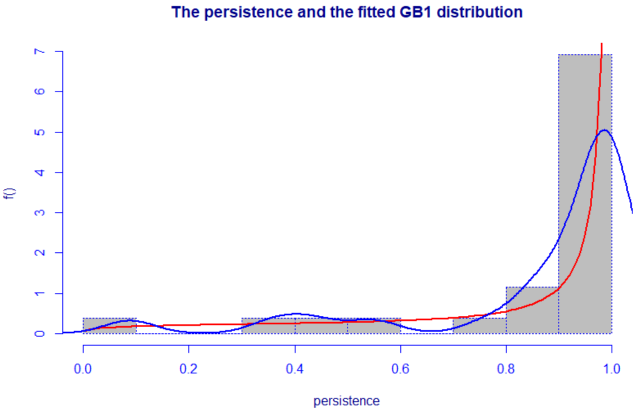
7.2.4.4.1 Consistency in Persistence

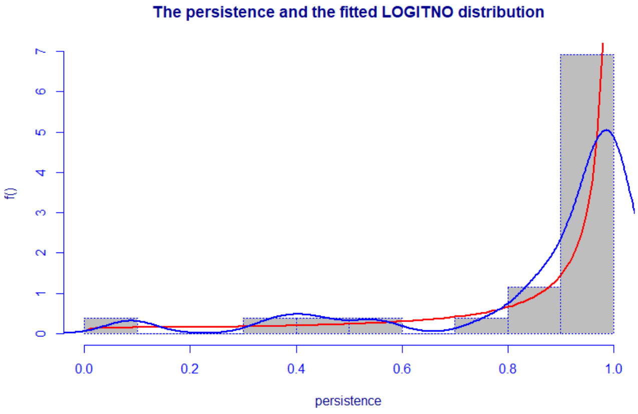
7.2.4.4.1.1 Response Variable Distribution

```
Persistence.Consistency.Distribution$fit
```

Distribution	AIC	Errors in Plot?	Distribution	AIC	Errors in Plot?
LOGITNO	-90.4823	No	BEOI	-79.7263	Yes
GB1	-88.2188	No	BEZI	-79.7263	Yes
BE	-81.7263	No	BEINF1	-79.7263	Yes
BEo	-81.7263	No	SIMPLEX	-77.8157	No
BEINF0	-79.7263	Yes	BEINF	-77.7263	Yes

7.2.4.4.2 Density plots of examples of distributions used in final models





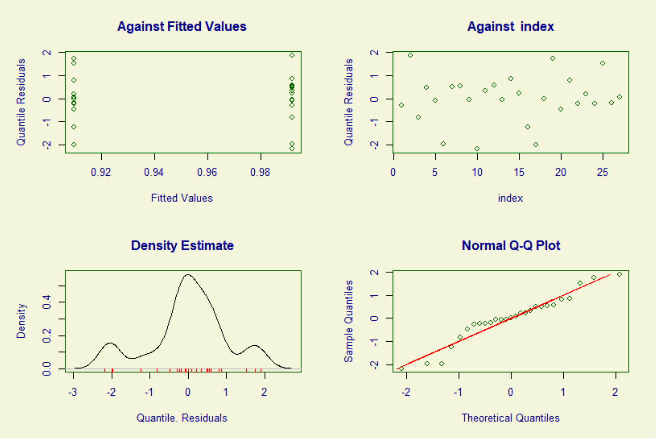
7.2.4.4.3 Model Distribution Selection

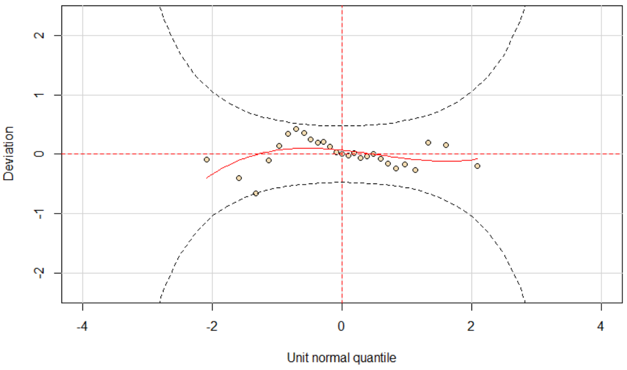
```
Persistence.Consistency.DISTRIBUTION <- gamlss(persistence ~ Species,
                                         family = "DISTRIBUTION", data = consistency)
```

Model	df	AIC	Residuals Outside CI
Persistence.Consistency.LOGITNO	3	-95.2377192	1
Persistence.Consistency.GB1	5	-91.8139533	0
Persistence.Consistency.BE	3	-83.2899177	4
Persistence.Consistency.BEo	3	-83.0986407	3
Persistence.Consistency.SIMPLEX	3	-78.5299752	8

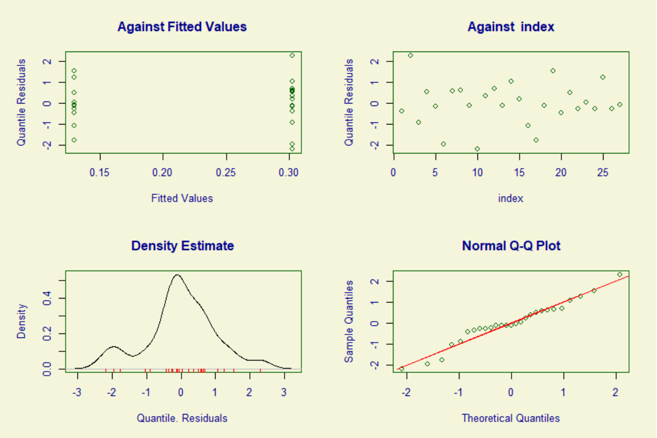
7.2.4.4.4 Model Diagnostics Plots

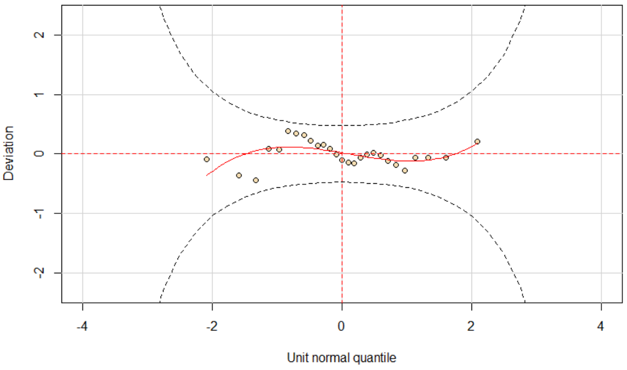
```
plot(Persistence.Consistency.LOGITNO) & wp(Persistence.Consistency. LOGITNO)
```



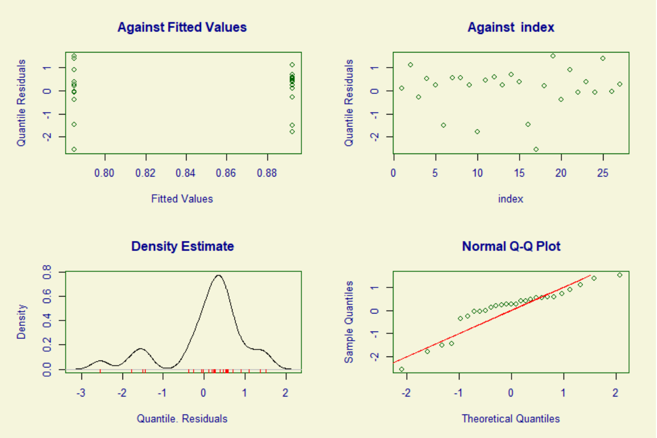


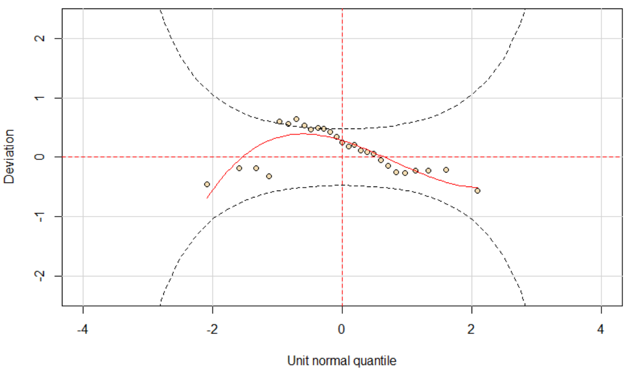
```
plot(Persistence.Consistency.GB1) & wp(Persistence.Consistency.GB1)
```



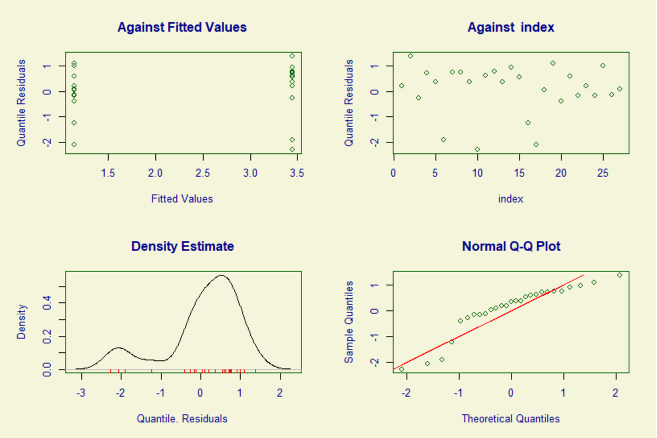


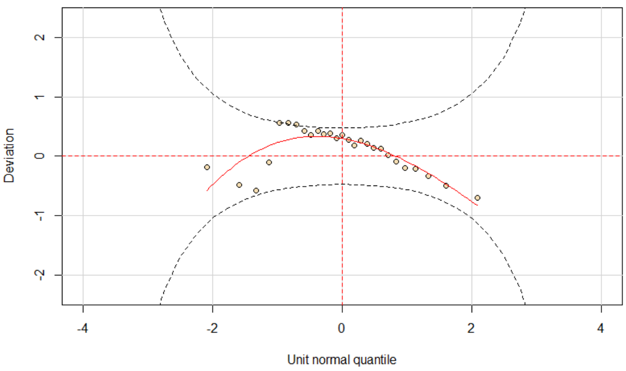
`plot(Persistence.Consistency.BE) & wp(Persistence.Consistency.BE)`



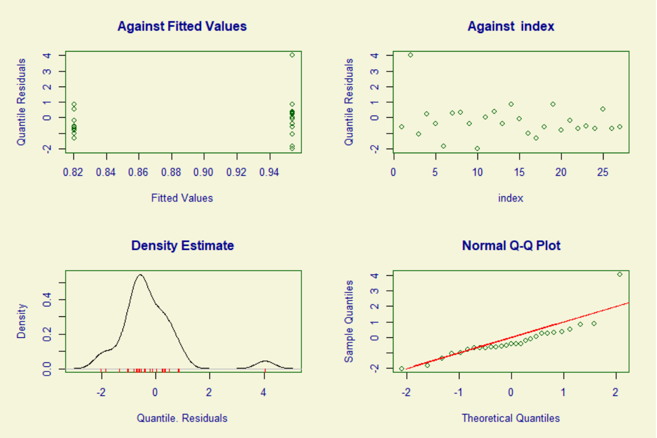


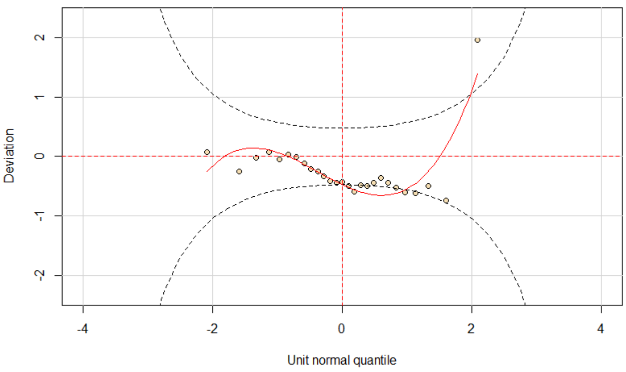
`plot(Persistence.Consistency.BEo) & wp(Persistence.Consistency.BEo)`





`plot(Persistence.Consistency.SIMPLEX) & wp(Persistence.Consistency.SIMPLEX)`





7.2.4.4.5 Model Validation

7.2.4.4.5.1 Generalised Beta type 1

```
summary(Persistence.Consistency.GB1)
******************************************************************
Family:  c("GB1", "Generalized beta type 1") 

Call:  gamlss(formula = persistence ~ Species, family = "GB1",  
       data = na.omit(consistency), control = con) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  logit
Mu Coefficients:
            Estimate Std. Error t value Pr(>|t|)  
(Intercept)  -0.8357     0.8077  -1.035   0.3120  
SpeciesWolf  -1.0719     0.4640  -2.310   0.0306 *
------------------------------------------------------------------
Sigma link function:  logit
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   0.4096     0.3414     1.2    0.243
------------------------------------------------------------------
Nu link function:  log 
Nu Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)    4.715      1.121   4.205 0.000366 ***
------------------------------------------------------------------
Tau link function:  log 
Tau Coefficients:
            Estimate Std. Error t value Pr(>|t|)  
(Intercept)   1.4259     0.7247   1.968   0.0619 .
------------------------------------------------------------------
No. of observations in the fit:  27 
Degrees of Freedom for the fit:  5
      Residual Deg. of Freedom:  22 
                      at cycle:  79 
 
Global Deviance:     -101.814 
            AIC:     -91.81395 
            SBC:     -85.33477 
******************************************************************
```

7.2.4.4.5.2 Logit Normal

```
summary(Persistence.Consistency.LOGITNO)
******************************************************************
Family:  c("LOGITNO", "Logit Normal") 

Call:  gamlss(formula = persistence ~ Species, family = "LOGITNO",  
       data = na.omit(consistency), control = con) 

Fitting method: RS() 
------------------------------------------------------------------
Mu link function:  logit
Mu Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)   4.8053     0.6005   8.002 3.14e-08 ***
SpeciesWolf  -2.4954     0.9007  -2.770   0.0106 *  
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)   0.8440     0.1361   6.202 2.08e-06 ***
------------------------------------------------------------------
No. of observations in the fit:  27 
Degrees of Freedom for the fit:  3
      Residual Deg. of Freedom:  24 
                      at cycle:  2 
 
Global Deviance:     -101.2377 
            AIC:     -95.23772 
            SBC:     -91.35021 
******************************************************************
```

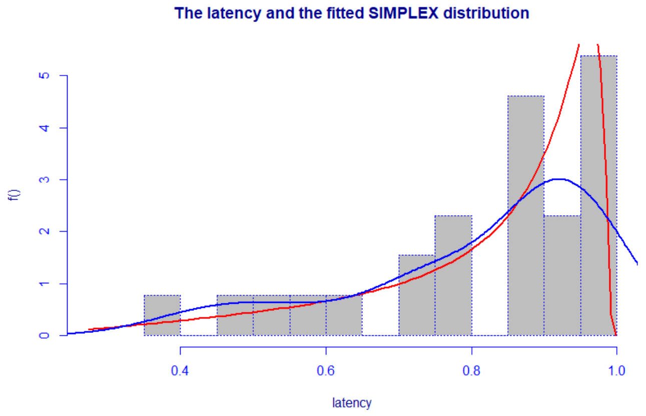
7.2.4.4.6 Consistency in Contact Latency

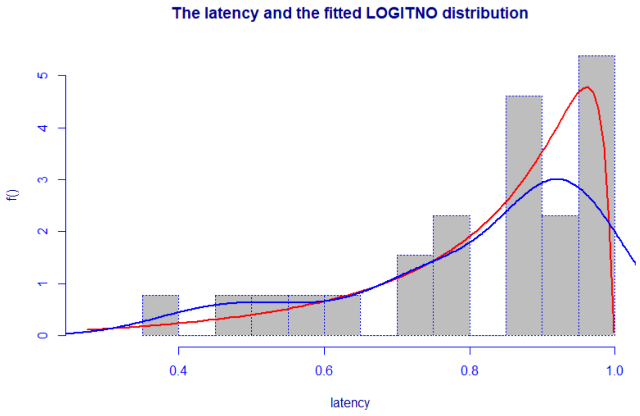
7.2.4.4.6.1 Response Variable Distribution

```
Latency.Consistency.Distribution$fit
```

Distribution	AIC	Errors in Plot?	Distribution	AIC	Errors in Plot?
SIMPLEX	-35.8643	No	BEINF0	-29.4833	Yes
LOGITNO	-34.118	No	BEINF1	-29.4833	Yes
GB1	-31.593	Yes	BEOI	-29.4833	Yes
BEo	-31.4833	No	BEZI	-29.4833	Yes
BE	-31.4833	No	BEINF	-27.4833	Yes

7.2.4.4.7 Density plots of examples of distributions used in final models





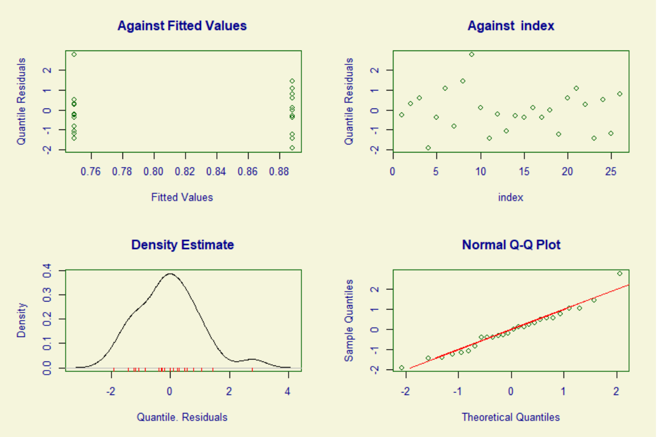
7.2.4.4.8 Model Distribution Selection

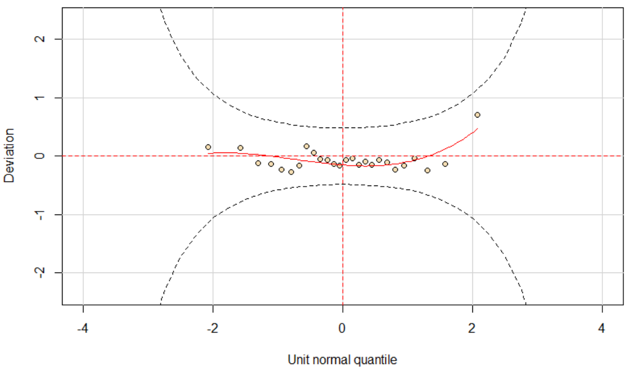
```
Latency.Consistency.DISTRIBUTION <- gamlss(latency ~ Species,
                                   family = "DISTRIBUTION", data = consistency)
```

Model	df	AIC
Latency.Consistency.SIMPLEX	3	-39.7189678
Latency.Consistency.LOGITNO	3	-39.6086058
Latency.Consistency.BEo	3	-39.5609832
Latency.Consistency.BE	3	-35.9167115

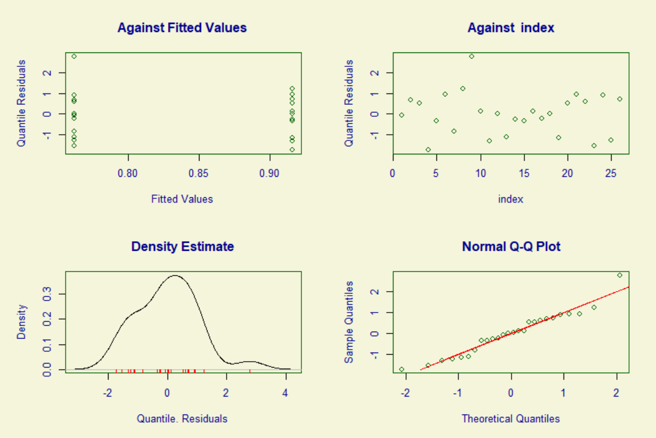
7.2.4.4.9 Model Diagnostics Plots

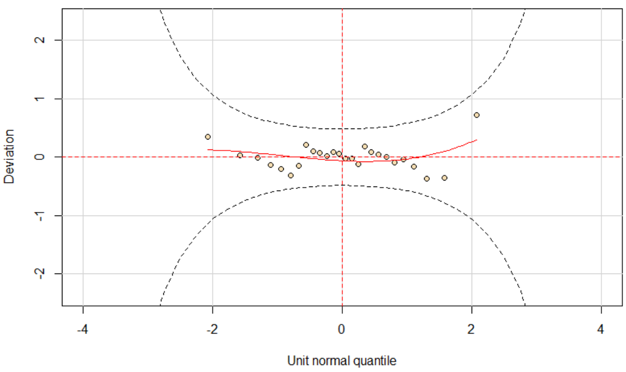
```
plot(Latency.Consistency.SIMPLEX) & wp(Latency.Consistency.SIMPLEX)
```



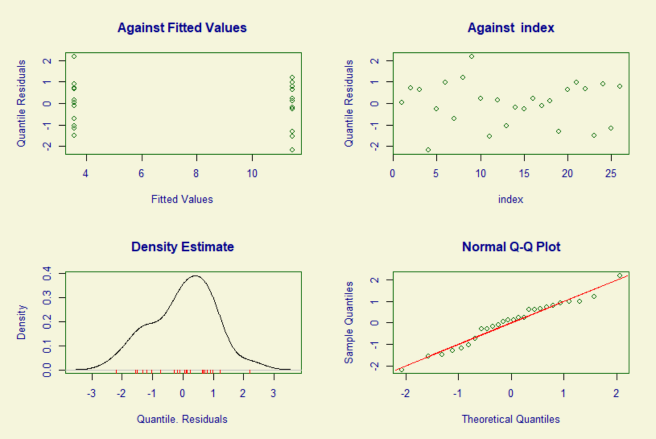


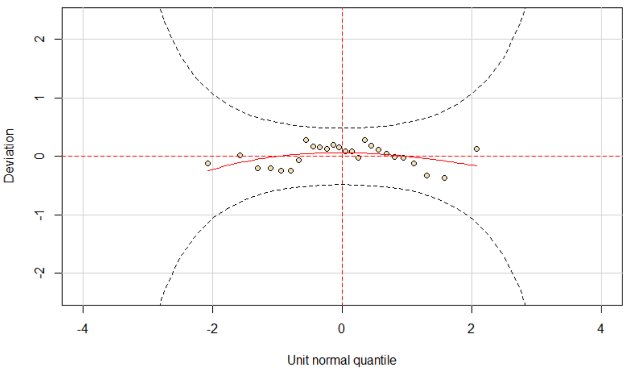
`plot(Latency.Consistency.LOGITNO) & wp(Latency.Consistency. LOGITNO)`



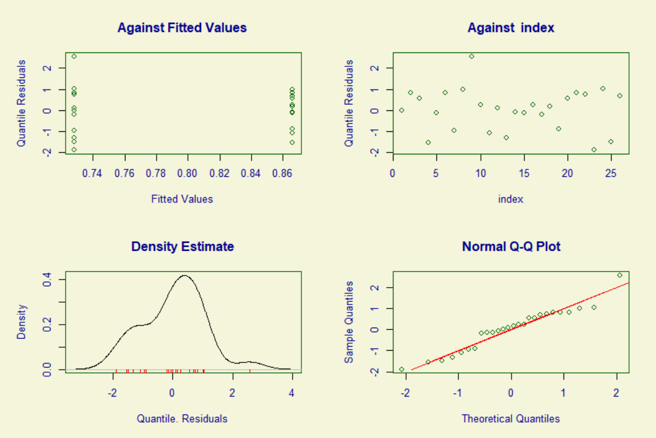


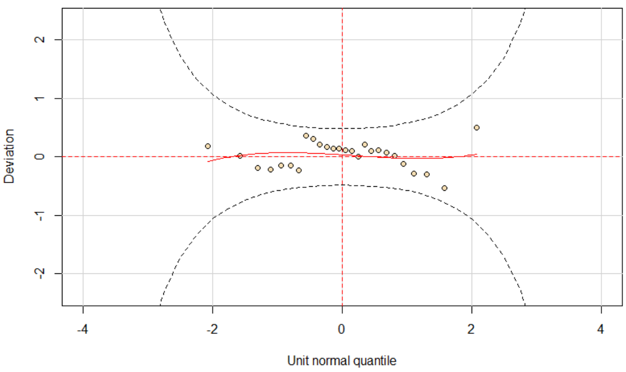
`plot(Latency.Consistency.BEo) & wp(Latency.Consistency.BEo)`





`plot(Latency.Consistency.BE) & wp(Latency.Consistency.BE)`





7.2.4.4.10 Model Validation

7.2.4.4.10.1 Simplex

```
summary(Latency.Consistency.SIMPLEX)
******************************************************************
Family: c("SIMPLEX", "Simplex")

Call: gamlss(formula = latency ~ Species, family = "SIMPLEX",
      data = na.omit(consistency), control = con)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  logit
Mu Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   2.0691     0.2399   8.624 1.16e-08 ***
SpeciesWolf  -0.9757     0.3729  -2.616   0.0154 *
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   1.2116     0.1387   8.737 9.16e-09 ***
------------------------------------------------------------------
No. of observations in the fit:  26
Degrees of Freedom for the fit:  3
      Residual Deg. of Freedom:  23
                      at cycle:  3

Global Deviance:     -45.71897
            AIC:     -39.71897
            SBC:     -35.94468
******************************************************************
```

7.2.4.4.10.2 Logit Normal

```
summary(Persistence.Consistency.LOGITNO)
******************************************************************
Family: c("LOGITNO", "Logit Normal")

Call: gamlss(formula = latency ~ Species, family = "LOGITNO",
      data = na.omit(consistency), control = con)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  logit
Mu Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   2.3858     0.2698   8.844 7.36e-09 ***
SpeciesWolf  -1.2220     0.4147  -2.946  0.00725 **
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   0.0438     0.1387   0.316    0.755
------------------------------------------------------------------
No. of observations in the fit:  26
Degrees of Freedom for the fit:  3
      Residual Deg. of Freedom:  23
                      at cycle:  2

Global Deviance:     -45.60861
            AIC:     -39.60861
            SBC:     -35.83432
******************************************************************
```

7.2.4.4.10.3 Beta Original

```
summary(Persistence.Consistency.BEo)
******************************************************************
Family: c("BEo", "Beta original")

Call: gamlss(formula = latency ~ Species, family = "BEo",
      data = na.omit(consistency), control = con)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  log
Mu Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)    2.438      0.325   7.504 1.26e-07 ***
SpeciesWolf   -1.173      0.343  -3.420  0.00234 **
------------------------------------------------------------------
Sigma link function:  log
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   0.3687     0.2520   1.463    0.157
------------------------------------------------------------------
No. of observations in the fit:  26
Degrees of Freedom for the fit:  3
      Residual Deg. of Freedom:  23
                      at cycle:  10

Global Deviance:     -45.56098
            AIC:     -39.56098
            SBC:     -35.78669
******************************************************************
```

7.2.4.4.10.4 Beta

```
summary(Persistence.Consistency.BE)
******************************************************************
Family: c("BE", "Beta")

Call: gamlss(formula = latency ~ Species, family = "BE",
      data = na.omit(consistency), control = con)

Fitting method: RS()
------------------------------------------------------------------
Mu link function:  logit
Mu Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   1.8643     0.2463   7.570 1.09e-07 ***
SpeciesWolf  -0.8799     0.3241  -2.715   0.0124 *
------------------------------------------------------------------
Sigma link function:  logit
Sigma Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  -0.6192     0.1867  -3.316  0.00301 **
------------------------------------------------------------------
No. of observations in the fit:  26
Degrees of Freedom for the fit:  3
      Residual Deg. of Freedom:  23
                      at cycle:  5

Global Deviance:     -41.91671
            AIC:     -35.91671
            SBC:     -32.14242
******************************************************************
```

7.3 Article 3

Marshall-Pescini S+*, Rao A+, Virányi Z, Range F. The role of domestication and experience in 'looking back' towards humans in an unsolvable task. *Sci Rep. Nature Publishing Group; 2017;7: 46636*.
(DOI: 10.1038/srep46636).

7.3.1 Supplementary Results

Table S1: Results of the linear mixed model on the latency to success in the solvable trials.

Latency to success	df	χ^2	P
Trial	1	116.83	<0.0001
Group	3	58.08	<0.0001
Trial:Group	3	0.93	0.82

Table S2: Corrected post-hoc group comparisons for the latency to success in the solvable trials.

Group comparison (latency to success)	z	P
Free-ranging vs. Pets	2.53	0.056
WSC dogs vs. Pets	0.07	0.9
Free-ranging vs. WSC dogs	2.43	0.069
Wolves vs. WSC dogs	5.02	<0.001
Wolves vs. Free-ranging	7.17	<0.001
Wolves vs. Pets	5.47	<0.001

Mean seconds to success across all three solvable trials: Wolves: 4.2; Pets: 6.4; Free-ranging dogs 19.7; WSC dogs: 14.4.

Table S3: Corrected post-hoc group comparisons of the time spent interacting with the apparatus in the unsolvable trial.

Group comparison (persistence)	t	P
Free-ranging vs. Pets	1.05	0.72
WSC dogs vs. Pets	0.08	0.99
Free-ranging vs. WSC dogs	0.91	0.79
Wolves vs. WSC dogs	4.32	<0.001
Wolves vs. Free-ranging	3.12	0.015
Wolves vs. Pets	4.73	<0.001

Wolves: Mean = 110 seconds, Range = 39.4 – 178.7 seconds;
WSC dogs: Mean = 46.6 seconds, Range = 32.4 – 69.6 seconds;
Free-ranging Dogs: Mean = 60.46 seconds, Range = 20.5 – 110.3 seconds;
PD mean = 48 seconds, Range = 5.8 – 155.9 seconds.

Table S4: Results of the generalized linear model (binomial) run on the likelihood of 'looking back' occurring in the unsolvable trial, in relation to persistence and group.

Occurrence of looking back	df	χ^2	P
Group	3	11.85	0.008
Persistence	1	21.7	<0.0001
Group:Persistence	3	1.8	1

Table S5: Results of the linear model on the latency to look back in the unsolvable trial, considering only those animals that exhibited the behaviour.

Latency to look back	df	F	P
Group	3	1.04	0.38
Persistence	1	11.9	0.001
Group:Persistence	3	0.67	0.57

Table S6: Results of the linear model on the duration of looking back in the unsolvable trial, considering only those animals that exhibited the behaviour.

Duration of looking back	df	F	P
Group	3	2.02	1.22
Persistence	1	33.41	0.001
Group:Persistence	3	0.14	0.94

Table S7: Results of the generalized linear model on the frequency of looking at the person in the unsolvable trial, considering only those animals that exhibited the behaviour.

Frequency of looking back	df	χ^2	P
Group	3	5.22	0.16
Persistence	1	27.79	0.0001
Group:Persistence	3	3.68	0.3

Table S8: Corrected post-hoc group comparisons of the time spent looking back at the person in the unsolvable trial, including only animals that exhibited this behaviour, following a model which did not include persistence as an explanatory factor.

Group comparison (duration of looking back)	t	P
Free-ranging vs. Pets	0.45	0.97
WSC dogs vs. Pets	0.08	0.99
Free-ranging vs. WSC dogs	0.5	0.96
Wolves vs. WSC dogs	4.19	0.001
Wolves vs. Free-ranging	3.42	0.006
Wolves vs. Pets	4.4	0.001

Looking back duration for Wolves: Mean = 7.35 seconds, Range = 0.8 – 25 seconds;
WSC-dogs: Mean = 14 seconds, Range: 4 – 28 seconds;
Pet Dogs: Mean = 12 seconds, Range = 3 – 25 seconds;
Free-ranging Dogs: Mean = 13 seconds, Range = 4 – 28 seconds.

Table S9: Corrected post-hoc group comparisons for the frequency of looking back at the person in the unsolvable trial, including only animals that exhibited this behaviour, following a model which did not include persistence as an explanatory factor.

Group comparison (frequency looking back)	z	P
Free-ranging vs. Pets	0.62	0.92
WSC dogs vs. Pets	0.59	0.93
Free-ranging vs. WSC dogs	0.07	0.99
Wolves vs. WSC dogs	3.33	0.005
Wolves vs. Free-ranging	3.26	0.006
Wolves vs. Pets	2.97	0.015

Looking back frequency for Wolves: Mean = 73, Range = 1 – 25;
WSC Dogs: Mean = 14, Range = 4 – 28;
Pet Dogs: Mean = 12, Range = 3 – 25;
Free-ranging Dogs: Mean = 13, Range = 4 – 28.

Table S10: Results of the generalized linear model on the frequency of gaze alternations in the unsolvable trial.

Frequency of gaze alternation	**df**	**χ^2**	**P**
Group	3	8.74	0.033
Persistence	1	11.39	0.0007
Group:Persistence	3	0.54	0.91

Table S11: Corrected post-hoc group comparisons for the frequency of gaze alternation between person and apparatus (or vice versa) in the unsolvable trial (including all animals).

Group comparison (frequency gaze alternations)	**z**	**P**
Free-ranging vs. Pets	2.07	0.15
WSC dogs vs. Pets	2.55	0.05
Free-ranging vs. WSC dogs	0.23	0.99
Wolves vs. WSC dogs	1.48	0.44
Wolves vs. Free-ranging	1.27	0.57
Wolves vs. Pets	0.31	0.99

Gaze alternation frequency for Wolves: Mean = 1.8, Range = 0 – 7;
WSC Dogs: Mean = 7.3, Range = 1 – 20;
Pet Dogs: Mean = 2.9, Range = 1 – 17;
Free-ranging Dogs: Mean = 6, Range = 1 – 14.

Table S12: Results of the generalized linear model on the duration of human interaction.

Duration interact person	**df**	**F**	**P**
Group	3	1.7	0.19
Persistence	1	7.69	0.007
Group:Persistence	3	0.83	0.48