ORIGINAL PAPER



Dog rivalry impacts following behavior in a decision-making task involving food

Christy L. Hoffman¹ · Malini Suchak¹

Received: 6 September 2016/Revised: 31 March 2017/Accepted: 4 April 2017/Published online: 18 April 2017 © Springer-Verlag Berlin Heidelberg 2017

Abstract Dogs learn a great deal from humans and other dogs. Previous studies of socially influenced learning between dogs have typically used a highly trained demonstrator dog who is unfamiliar to the observer. Because of this, it is unknown how dynamics between familiar dogs may influence their likelihood of learning from each other. In this study, we tested dogs living together in two-dog households on whether individual dogs' rivalry scores were associated with performance on a local enhancement task. Specifically, we wanted to know whether dog rivalry impacted whether an observer dog would approach a plate from which a demonstrator dog had eaten all available food, or whether the observer dog would approach the adjacent plate that still contained food. Dog rivalry scores were calculated using the Canine Behavioral Assessment and Research Questionnaire and indicated each dog's tendency to engage aggressively with the other household dog. Low-rivalry dogs were more likely to approach the empty plate than high-rivalry dogs when the observer dog was allowed to approach the plates immediately after the demonstrator had moved out of sight. This difference between low- and high-rivalry dogs disappeared, however, when observer dogs had to wait 5 s before approaching the plates. The same pattern was observed during a control condition when a human removed the food

Electronic supplementary material The online version of this article (doi:10.1007/s10071-017-1091-9) contains supplementary material, which is available to authorized users.

Christy L. Hoffman hoffmanc@canisius.edu

from a plate. Compared to low-rivalry dogs, high-rivalry dogs may pay less attention to other dogs due to a low tolerance for having other dogs in close proximity.

Keywords Multi-dog · Dog rivalry · Local enhancement · Social learning

Introduction

Observing others provides a rich opportunity for social animals to gain knowledge about their environment. Numerous studies have found evidence of socially influenced learning in a variety of species, ranging from fish to mammals (Brown and Laland 2003; Galef and Laland 2005). Dogs tend to be particularly adept at acquiring information from others. Dogs will follow others around obstacles (Pongrácz et al. 2001, 2003, 2004, 2008), learn about the location of food from others (Heberlein and Turner 2009), and even imitate specific actions to solve problems (Miller et al. 2009; Range et al. 2011; Pongrácz et al. 2012). Further, unlike many ape species that have been tested, dogs learn as well from humans as from conspecifics (Pongrácz et al. 2001, 2003, 2004; Kubinyi et al. 2003a, b; Miklósi and Soproni 2006; Kubinyi et al. 2009), and some dogs are actually better at learning from humans than from other dogs (Pongrácz et al. 2012). This tendency to learn from humans may be automatic. Range et al. (2011) demonstrated that dogs have a natural, inherent tendency to follow their owner's actions; if a task requires them to avoid copying their owners, they have to actively work against this tendency and are slower to learn the task.

There is ample evidence that dogs are highly influenced by social information, yet not much is known about the

¹ Department of Animal Behavior, Ecology, and Conservation, Canisius College, 2001 Main Street, Buffalo, NY 14208, USA

factors that mediate dogs' tendencies to copy conspecifics' actions. Research on other species has shown that many factors may influence an individual's propensity to learn from others, including developmental stage, personality, and the relationship between the demonstrator and the observer (Coussi-Korbel and Fragaszy 1995; Nicol and Pope 1999; Marchetti and Drent 2000; Schwab et al. 2008; Horner et al. 2010; Lonsdorf and Bonnie 2010; van de Waal et al. 2010). For example, great tits that scored high on exploratory behavior were more likely to follow a tutor to a new bird feeder than "slow" explorers (Marchetti and Drent 2000). One factor that may influence dog-dog social learning is dominance. Pongrácz et al. (2008) found that, compared to dogs classified as dominant in their own households, dogs classified as subordinate were more likely to correctly perform a detour task if given the opportunity to observe an unfamiliar dog solving the task. In this context, dominance rank was treated as a personality characteristic that influences an individual's tendency to learn. It has been argued, however, that dominance is not a stable personality trait and is, instead, a relationship construct that emerges from interactions between individuals (Bradshaw et al. 2009, 2016). Testing dogs with unfamiliar demonstrators leaves it unclear how dominance status, if viewed as an emergent property of an established relationship between dogs, impacts how one learns from unfamiliar dogs.

Rivalry may be an alternative measure that is useful for examining individual differences in social learning in dogs. As measured by the Canine Behavioral Assessment and Research Questionnaire (C-BARQ; Hsu and Serpell 2003), a validated survey completed by dog owners, dog rivalry reflects how likely dogs are to be aggressive toward other (familiar) dogs in the household. The dog rivalry subscale consists of four statements and requires that the owner rate the dog's recent tendency to display aggressive behavior in each of the contexts on a scale of 0 (no aggression) to 4 (serious aggression, characterized by snapping, biting, or attempting to bite). These are the four statements: "Towards another (familiar) dog in your household"; "When approached at a favorite resting/ sleeping place by another (familiar) household dog"; "When approached while eating by another (familiar) household dog"; and "When approached while playing with/chewing a favorite toy, bone, object, etc., by another (familiar) household dog." Dog rivalry is likely to play a role in social learning. In other species, low levels of tolerance, typically operationalized as high levels of aggression between individuals, tend to interfere with social learning (Coussi-Korbel and Fragaszy 1995; Lonsdorf and Bonnie 2010). Thus, we would expect that high-rivalry dogs would similarly be less likely to learn from conspecifics.

As the C-BARQ measure of dog rivalry specifically measures aggression between known dogs, it is particularly applicable to dogs who live together. Studying household dogs in relation to each other deviates from most prior studies, which have typically relied upon a trained demonstrator who has no preexisting relationship with the dog being tested (Pongrácz et al. 2004, 2008; Range et al. 2007; Miller et al. 2009; Tennie et al. 2009, but see Heberlein and Turner 2009). While this setup has yielded considerable control over the demonstrator's behavior and allowed researchers to test specific and sometimes complex actions (e.g., Range et al. 2007; Miller et al. 2009), there is a major gap in our understanding of how the preexisting relationship between dogs who know each other may impact social learning. In the current study, we looked at the influence of local enhancement on dogs living in twodog households. Enhancement tasks are ideally suited to this kind of study because they do not require a trained demonstrator, which would be necessary for more complex emulation or motor imitation tasks, and thereby allow dogs in a household to take turns being both the demonstrator and the observer. As evidence suggests that dog rivalry scores on the C-BARQ are impacted by context-specific factors (Rayment et al. 2016), we tested the dogs in their home to capture the influence of their relationships with each other as authentically as possible.

In the first experiment, we tested whether one dog was likely to automatically follow the other. We hypothesized that dogs who scored high in dog rivalry would be less susceptible to local enhancement. In Experiment 2, we examined whether the results of Experiment 1 could be attributed to automatic influences on behavior or extinction from approaching an option that turned out to be unrewarded. We hypothesized that if the behavior is automatic, inserting a delay between observing the other dog's action and the opportunity to follow would interfere with local enhancement.

Experiment 1

Method

Participants

We tested dogs residing in two-dog households within 30 miles of Buffalo, NY (USA). Participants were selected from a pool of households in which owners had completed an online survey about their dogs' behaviors and relationships with other dogs and the owner. Dogs who had a history of severe aggression or fear, based on owners' reports on the Canine Behavioral Assessment and Research Questionnaire (C-BARQ; Hsu and Serpell 2003), or whose

owners indicated during a telephone screen that one or both of their dogs had a bite history or would be uncomfortable with the study procedures, did not participate in the study. Fifty dogs from 25 households participated in the experiment, and we had complete data for 47 of those dogs. One dog did not successfully complete the task. Due to a malfunction with our video recording device, we were missing data from both Human Control conditions for one dog and the no delay Human Control condition for another dog. The dogs ranged between 7 months and 13 years old (mean = 5.16 years; SD = 2.75), and they had lived in the home for at least 5 months but for no more than 13 years (mean = 4.39 years, SD = 2.74). Twenty-six of the 50 dogs were female, and four of the dogs were intact. Table 1 provides detailed information about each dog.

Materials and procedure

The methods used in the study were approved by the Canisius College Institutional Animal Care and Use Committee (protocol number 20140402) prior to the start of the study. Study procedures conformed to New York State and United States federal laws regarding the use of animals in research. CH and MS made a preliminary study visit to each household. The purpose of this visit was to allow the dogs to become acquainted with the experimenters who would be handling them on leash during the study, to explain the study paradigm to the dogs' owners, to consult with owners regarding the optimal location within the home for conducting the experiment, and to collect consent forms and copies of rabies certificates.

During the research team's second visit, a research assistant (RA) accompanied CH and MS to participants' homes. All members of the research team were blind to the dogs' rivalry scores at the time of the experiment. Dogs were randomly assigned as Dog A or Dog B prior to arrival at the home. In addition, we randomized whether the dogs in a household completed all parts of the dog demonstrator task or the human control task first. The experiment was set up as shown in Fig. 1 in the largest room available on the main floor of the house. Two paper plates (diameter 25.6 cm; depth 1 cm) were placed 1–2 m apart from each other, depending upon the amount of space in the home and the size of the dog participants. A video camera was positioned on a tripod about 1 m behind the plates to capture dogs' movements toward the plates.

Dog demonstrator task CH held Dog A with her eyes open and facing the plates while MS held Dog B with her eyes closed and her back to the plates. Both dogs were on a 1.5 m lead (shortened to 0.5 m). The dogs stood parallel to one another 2–3 m from the plates, depending upon space constraints and the size of dog participants. Once dogs were in position, the RA stood between the two plates and shook the food container to capture the dogs' attention. The RA then placed a few pieces of food on each plate simultaneously, being sure to place equal amounts of food on the plates. After loading the plates, the RA picked up the food container, moved away from the plates, and left the room so as not to affect the dogs' behavior. CH walked Dog A to one of the plates and allowed Dog A to eat all the food that was on that plate. The plate to which CH walked Dog A was randomly determined for each trial prior to the study visit. We did, however, ensure that Dog A took food at least once from each side during each three-trial block. After Dog A had eaten all the food from the plate, CH walked Dog A out of Dog B's line of sight without allowing Dog A to come into contact with the other plate. MS remained unaware of which plate Dog A visited. In the first three trials, MS then loosened the leash and allowed Dog B to approach the plates immediately (no delay condition); in the latter three trials, she made Dog B wait 5 s before loosening the leash and allowing him to approach (delay condition). For all six trials, MS did not open her eyes until the dog had begun approaching the plates. Dog B was allowed to eat the remaining food, regardless of whether he directly approached the plate that still contained food (i.e., the full plate). Approximately 5 min after the six trials were completed, we ran six additional trials in which the dogs switched roles: Dog B was the first dog to approach the plates and Dog A was the second.

Human control task The plates were set up in this task as they were in the dog demonstrator task. CH handled Dog A on the leash as in the dog demonstrator task; although for this task, she closed her eyes and turned her back to the plates. MS kept Dog B in another room and out of visual contact with Dog A. Once Dog A was in position, the RA stood between the two plates and shook the food container to capture Dog A's attention. The RA placed a few pieces of food on each plate simultaneously, being sure to place equal amounts of food on the plates. Immediately thereafter, the RA picked up one plate and dumped all the food from that plate back into the food container. Next, the RA picked up the food container and left the room so as not to affect Dog A's behavior. The plate that the RA emptied of food was randomly determined for each trial prior to the study visit. We did, however, ensure that the RA took food at least once from each side during each three-trial block. CH remained unaware of which plate no longer contained food. In the first three trials, CH loosened the leash and allowed Dog A to approach the plates immediately (no delay condition); in the following three trials, she made Dog A wait 5 s before loosening the leash and allowing him to approach (delay condition). For all six trials, CH did not open her eyes until the dog had begun approaching the plates. Dog A was allowed to eat the remaining food, regardless of whether he approached the full plate directly.

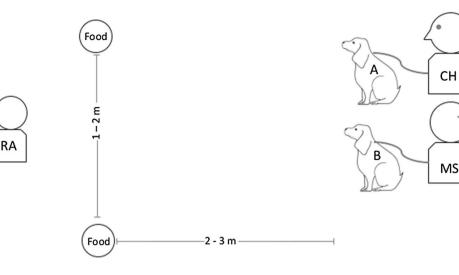
Dog's name	Pair	Age (years)	Length of time in household (years)	Sex	Intact?	Rivalry classification	How acquired by owner	Breed reported by owner	First trial type
Baylee	Baylee and Dookie	2.0	1.5	Female	No	Low	Shelter, pound, or rescue	Puggle/Staffordshire Terrier mix	Dog demonstrator
Dookie	Baylee and Dookie	7.0	6.0	Male	No	High	Newspaper or online ad	Labrador Retriever	Dog demonstrator
Charlie	Charlie and Szafi	3.5	3.5	Male	No	Low	Shelter, pound, or rescue	Lab/Hound mix	Human demonstrator
Szafi	Charlie and Szafi	2.5	2.0	Female	No	Low	Shelter, pound, or rescue	German Shorthaired Pointer	Human demonstrator
Buddy	Chloe and Buddy	6.0	4.0	Male	No	Low	Shelter, pound, or rescue	American Staffordshire Terrier	Dog demonstrator
Chloe	Chloe and Buddy	4.0	4.0	Female	No	Low	Shelter, pound, or rescue	Doberman Pinscher	Dog demonstrator
Bailey	Diego and Bailey	2.0	1.6	Female	No	High	Found as a stray	Poodle mix	Human demonstrator
Diego	Diego and Bailey	1.8	1.5	Male	No	Low	Friend or family member	American Pit Bull Terrier mix	Human demonstrator
Gracie	Gracie and Penny	13.1	13.1	Female	No	Low	Breeder	Bearded Collie	Human demonstrator
Penny	Gracie and Penny	3.3	3.3	Female	No	Low	Breeder	Bearded Collie	Human demonstrator
Kali	Kali and Sawyer	6.8	6.5	Female	No	High	Shelter, pound, or rescue	Labrador Retriever mix	Human demonstrator
Sawyer	Kali and Sawyer	6.2	5.9	Male	No	Low	Shelter, pound, or rescue	Dalmatian/German Shorthaired Pointer mix	Human demonstrator
Koda	Koda and Sky	2.0	2.0	Female	No	Low	Newspaper or online ad	Siberian Husky	Dog demonstrator
Sky	Koda and Sky	5.0	4.0	Female	No	High	Shelter, pound, or rescue	Siberian Husky	Dog demonstrator
Boozer	Milo and Boozer	12.0	12.0	Male	No	Low	Breeder	Labrador Retriever	Dog demonstrator
Milo	Milo and Boozer	9.0	3.0	Male	No	Low	Friend or family member	Bichon Frise	Dog demonstrator
Chewie	Mimi and Chewie	8.0	8.0	Female	No	High	Newspaper or online ad	Chihuahua/Pug Mix	Human demonstrator
Mimi	Mimi and Chewie	4.5	4.0	Female	No	Low	Shelter, pound, or rescue	Cane Corso	Human demonstrator
Gracie	Moose and	1.5	1.3	Female	No	Low	Breeder	Great Dane	Human

Table 1 (Table 1 continued								
Dog's name	Pair	Age (years)	Length of time in household (years)	Sex	Intact?	Rivalry classification	How acquired by owner	Breed reported by owner	First trial type
Moose	Moose and Gracie	0.6	0.5	Male	Yes	High	Breeder	Great Dane	Human demonstrator
Hudson	Murphy and Hudson	7.5	1.5	Male	No	High	Shelter, pound, or rescue	Labrador Retriever	Human demonstrator
Murphy	Murphy and Hudson	3.5	3.3	Male	No	High	Newspaper or online ad	Golden Retriever	Human demonstrator
Bodi	Mush and Bodi	7.5	7.5	Male	No	Low	Breeder	Australian Shepherd	Human demonstrator
Mush	Mush and Bodi	7.0	6.0	Male	No	High	Shelter, pound, or rescue	Australian Shepherd	Human demonstrator
Dora	Nora and Dora	5.0	3.5	Female	No	High	Shelter, pound, or rescue	Pit bull/Labrador Retriever mix	Dog demonstrator
Nora	Nora and Dora	5.0	3.5	Female	No	Low	Shelter, pound, or rescue	Pit bull/Labrador Retriever mix	Dog demonstrator
Izzy	Nora and Izzy	6.0	6.0	Female	No	Low	Breeder	Newfoundland	Dog demonstrator
Nora	Nora and Izzy	8.0	8.0	Female	No	High	Newspaper or online ad	Golden Retriever/Newfoundland mix	Dog demonstrator
Daisy	Poppy and Daisy	8.3	8.1	Female	No	Low	Breeder	Golden Retriever	Human demonstrator
Poppy	Poppy and Daisy	2.5	2.3	Female	No	Low	Shelter, pound, or rescue	Golden Retriever	Human demonstrator
Lloyd	Porter and Lloyd	3.0	2.0	Male	No	Low	Shelter, pound, or rescue	Labrador Retriever mix	Dog demonstrator
Porter	Porter and Lloyd	4.0	3.3	Male	No	Low	Shelter, pound, or rescue	Hound/Greyhound mix	Dog demonstrator
Ralphie	Ralphie and Sadie	4.6	4.3	Male	No	High	Shelter, pound, or rescue	American Eskimo	Dog demonstrator
Sadie	Ralphie and Sadie	5.0	4.5	Female	No	Low	Friend or family member	Labrador Retriever	Dog demonstrator
Dylan	Rooney and Dylan	8.0	8.0	Male	No	High	Breeder	Pembroke Welsh Corgi	Dog demonstrator
Rooney	Rooney and Dylan	3.0	3.0	Male	Yes	High	Breeder	Pembroke Welsh Corgi	Dog demonstrator
Duke	Ruby and Duke	7.0	6.0	Male	No	High	Shelter, pound, or rescue	Labrador Retriever	Human demonstrator
Ruby	Ruby and Duke	7.5	7.5	Female	No	High	Shelter, pound, or rescue	Husky/Shepherd mix	Human demonstrator

Dog'sPairAgeLength of time in householdSetname(years)(years)(years)MaBuchananSasha and4.54.5MaBuchananBuchanan6.56.5FerBuchananSasha and6.56.5FerBuchananSasha and6.56.5FerAthenaSherlock and7.05.0MaAthenaSherlock and7.05.0MaAthenaAthena7.05.0MaAthenaTia and Caleb6.06.0MaGrizzlyTippy and9.04.5MaGrizzlyTippy and6.33.23.0TippyTippy and6.06.0FerGrizzlyTippy and6.33.23.0CrescentVader and3.23.0FerUderVader and3.23.0FerBuoyZe and Buoy2.02.0Ma	Table 1 continued	continued								
nanSasha and Buchanan4.54.5Buchanan6.56.56.5Buchanan6.56.56.5Buchanan3.53.0Athena7.05.0Athena7.05.0Athena7.05.0Athena7.05.0Athena7.05.0Athena7.05.0Athena7.05.0Athena9.04.5Grizzly0.7Tippy and6.56.0Grizzly3.23.0Ader and1.61.3Crescent1.61.3Crescent2.02.0Ze and Buoy1.11.0	Dog's name	Pair	Age (years)	Length of time in household (years)	Sex	Intact?	Rivalry classification	How acquired by owner	Breed reported by owner	First trial type
Sasha and Buchanan6.5 6.56.5 BuchananaSherlock and Athena3.5 3.03.0ckSherlock and Athena7.0 5.05.0ckSherlock and Athena7.0 5.05.0ckSherlock and Athena7.0 5.05.0ria and Caleb6.0 6.06.06.0rippy and 	Buchanan	ŝ	4.5	4.5	Male	No	High	Breeder	Newfoundland	Human demonstrator
 Sherlock and 3.5 3.0 Athena Athena Ck Sherlock and 7.0 5.0 Athena Tia and Caleb 6.0 6.0 Tia and Caleb 4.0 0.7 Tippy and 9.0 4.5 Grizzly Tippy and 6.5 6.0 Grizzly Mathematical and 1.6 1.3 Crescent Ze and Buoy 1.1 1.0 	Sasha	Sasha and Buchanan	6.5	6.5	Female	No	High	Newspaper or online ad	Poodle mix	Human demonstrator
 ck Sherlock and 7.0 5.0 Athena Tia and Caleb 6.0 6.0 Tia and Caleb 4.0 0.7 Tippy and 9.0 4.5 Grizzly Tippy and 6.5 6.0 Grizzly nt Vader and 3.2 3.0 Crescent 1.6 1.3 Crescent 2.0 2.0 Ze and Buoy 1.1 1.0 	Athena	Sherlock and Athena	3.5	3.0	Female	No	Low	Shelter, pound, or rescue	Dutch Shepherd	Human demonstrator
Tia and Caleb6.06.0Tia and Caleb4.00.7YTippy and Grizzly9.04.5Tippy and Grizzly6.56.0Tippy and Grizzly3.23.0Tippy and Grizzly1.61.3Tippy and Grizzly1.61.3Tippy and Grizzly2.02.0Tippy and Grescent2.0Tippy and Grescent2.0Tippy and Grescent2.0Ze and Buoy1.11.0	Sherlock	Sherlock and Athena	7.0	5.0	Male	No	Low	Shelter, pound, or rescue	Jack Russell Terrier mix	Human demonstrator
Tia and Caleb4.00.7yTippy and9.04.5Grizzly6.56.0Grizzly3.23.0rit< Vader and	Caleb	Tia and Caleb	6.0	6.0	Male	No	High	Friend or family member	Mastiff/Labrador Retriever mix	Dog demonstrator
y Tippy and 9.0 4.5 Grizzly 6.5 6.0 Grizzly 3.2 3.0 Art Vader and 3.2 3.0 Crescent 1.6 1.3 Crescent 2.0 2.0 Ze and Buoy 2.0 2.0	Tia	Tia and Caleb	4.0	0.7	Female	No	Low	Shelter, pound, or rescue	Vizsla/Pit Bull mix	Dog demonstrator
Tippy and Grizzly6.5 6.0fizzly6.0Grizzly3.2Vader and Crescent3.2Vader and Crescent1.6Labor1.6Ze and Buoy2.0Ze and Buoy1.1Labor1.1	Grizzly	Tippy and Grizzly	9.0	4.5	Male	No	Low	Friend or family member	Labrador Retriever/Rottweiler mix	Human demonstrator
nt Vader and 3.2 3.0 Crescent 3.2 3.0 Vader and 1.6 1.3 Crescent 2.0 2.0 Ze and Buoy 2.0 2.0 Ze and Buoy 1.1 1.0	Tippy	Tippy and Grizzly	6.5	6.0	Female	No	Low	Friend or family member	German Shepherd/Border Collie mix	Human demonstrator
Vader and1.61.3Crescent2.0Ze and Buoy2.0Ze and Buoy1.1	Crescent	Vader and Crescent	3.2	3.0	Female	No	High	Newspaper or online ad	Great Pyrenees	Dog demonstrator
oy Ze and Buoy 2.0 2.0 Ze and Buoy 1.1 1.0	Vader	Vader and Crescent	1.6	1.3	Male	No	Low	Shelter, pound, or rescue	Labrador Retriever/Great Pyrenees mix	Dog demonstrator
Ze and Buoy 1.1 1.0	Buoy	Ze and Buoy	2.0	2.0	Male	Yes	Low	Breeder	Newfoundland	Dog demonstrator
	Ze	Ze and Buoy	1.1	1.0	Female	Yes	Low	Breeder	French Bulldog	Dog demonstrator

D Springer

Fig. 1 The experimental setup. Figure depicts the positioning of the two experimenters (CH and MS) and two dogs in relation to the food plates. The research assistant (RA) was present to put the food on the plates, but moved out of sight before the dogs approached



No delay

Full plates choser

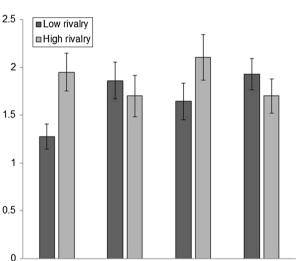
Approximately 5 min after the six trials were completed, we ran six additional trials in which CH handled Dog B while MS kept Dog A in another room out of Dog B's sight.

Video coding Videos of each dog's performance on the trials were coded by one of two research assistants. These assistants were blind to dogs' rivalry scores. When a dog directly approached the full plate, the choice was recorded as 1, and when the dog either directly approached the empty plate or walked toward the empty plate before ultimately approaching the full plate, the choice was recorded as a 0. For each set of three trials, scores for individual dogs ranged from 0 (i.e., full plate was never directly approached) to 3 (i.e., full plate was approached directly on every trial). To establish inter-rater reliability, both research assistants coded the same set of 48 trials. The assistants agreed on 47 of the 48 trials (Cohen's Kappa = 0.95).

Results

The median score on the C-BARQ dog rivalry subscale was 0.25. Twenty dogs (40%) scored above the median, and we classified those individuals as high rivalry. We classified dogs scoring at or below the median as low rivalry. In some households, both dogs were classified as high rivalry (N = 4 households) or low rivalry (N = 9), and in others, one was classified as high rivalry and the other as low rivalry (N = 12).

Figure 2 depicts the average number of full plates highand low-rivalry dogs chose with and without delays and with dog and human demonstrators. A repeated measures ANOVA examining the effects of rivalry classification of the focal dog (between-subjects variable), rivalry classification of the dog demonstrator (between-subjects variable), species of demonstrator (within-subjects variable), and



695

Fig. 2 Approaches to the full plate during Experiment 1. A lower number of approaches to the full plate indicate that the observer dog was following the demonstrator dog. There was a significant interaction whereby low-rivalry dogs were less likely to approach the full plate than high-rivalry dogs in the no delay condition

No delay

Human Control

Delay

Delay

Dog Demonstrator

whether the trials included a 5-s delay (within-subjects variable) showed a significant interaction between rivalry classification and whether the trials included a 5-s delay ($F_{1,43} = 8.73$, p = 0.005). Simple effects analyses indicated that high- and low-rivalry dogs did not differ in their tendencies to approach the full plate in the delay condition (p = 0.260), but that high-rivalry dogs were more likely to approach the full plate than low-rivalry dogs in the no delay condition (p = 0.030). There was no difference in how high-rivalry dogs performed in the no delay and delay conditions (p = 0.253), but low-rivalry individuals were more likely to approach the full plate in the delay condition than in the no delay condition (p = 0.002) (Table 2).

Effect	F	df	Р
Delay	0.558	1,43	0.459
Species	0.847	1,43	0.363
Rivalry classification of focal	0.573	1,43	0.453
Rivalry classification of dog demonstrator	1.210	1,43	0.277
Delay \times species	1.128	1,43	0.294
Delay \times rivalry classification of focal	8.726	1,43	0.005*
Delay \times rivalry classification of dog demonstrator	0.092	1,43	0.764
Species \times rivalry classification of focal	0.285	1,43	0.596
Species \times rivalry classification of dog demonstrator	0.380	1,43	0.541
Rivalry classification of focal × rivalry classification of dog demonstrator	0.714	1,43	0.403
Delay \times species \times rivalry classification of focal	0.906	1,43	0.346
Delay \times species \times rivalry classification of dog demonstrator	0.063	1,43	0.802
Delay \times rivalry classification of focal \times rivalry classification of dog demonstrator	0.604	1,43	0.441
Species \times rivalry classification of focal \times rivalry classification of dog demonstrator	0.639	1,43	0.429
Delay \times species \times rivalry classification of focal \times rivalry classification of dog demonstrator	1.389	1,43	0.245

 Table 2 Results from the repeated measures ANOVA examining the effects of delay condition, species, and rivalry classification of focal and demonstrator dogs on plate choice

* Denotes p < 0.01

Discussion

In the dog demonstrator and human control trials that were part of Experiment 1, low-rivalry dogs went to the empty plate more than high-rivalry dogs when the dogs were allowed to make their choice immediately. Remarkably, they did this even though the amount of food available on each plate was visible to the dogs for the duration of each trial. Attention to the empty plate may be a result of local enhancement, where the actions of one individual attract another individual's attention to a particular location. These results suggest that low-rivalry dogs, as compared to high-rivalry dogs, may be more susceptible to local enhancement and, therefore, more likely to copy other dogs' and humans' actions.

The propensity of high-rivalry dogs to go straight to the full plate more often than low-rivalry dogs when there was no delay supports the idea that dogs who engage with conspecifics in an aggressive manner are less affected by local enhancement. Although dog rivalry as a measure is specific to dog-dog interactions, whether the demonstrator was a dog or human did not significantly impact the behavior of high- or low-rivalry dogs. Across the board, dogs who scored high in rivalry were not particularly susceptible to local enhancement. A previous C-BARQbased study found that breeds scoring high on dog rivalry also tended to score high on owner-directed aggression (Serpell and Duffy 2014). Additionally, scores on the dog rivalry subscale are positively associated with scores on the stranger-directed aggression subscale (Rayment et al. 2016). Such findings suggest that the personality traits that one might expect to be associated with high-rivalry dogs, such as competitiveness or resource protection, may generalize beyond dog-dog interactions.

We note some consistency between our results and those from Pongrácz et al. (2008). This may be because some of the questions Pongrácz et al. (2008) used to assess dominance in dogs were directly related to aggression (e.g., "If the dogs start to fight, which dog usually wins?"; p. 77), and similarly, the dog rivalry subscale of the C-BARQ focuses on inter-dog aggression; thus, there may be some correspondence between these two approaches. In both Pongrácz et al.'s (2008) study and ours, dogs who showed more aggressive traits followed a dog demonstrator less. However, Pongrácz et al. (2012) reported that dominance hastened the speed at which dogs learned from a human demonstrator on a two-action test, whereas we found that low-rivalry dogs' choices were more strongly impacted by a demonstrator, regardless of whether the demonstrator was a dog or human. Pongrácz et al. (2008) found no effect of dominance on latency to follow a human on a detour task. Thus, further research may be needed to better elucidate the ways in which dog-dog relationship dynamics impact dogs' tendencies to learn from a human demonstrator.

In the delay trials, dogs had to wait 5 s before making a choice, and this appeared to lessen the impact of local enhancement on dogs' choices, particularly in the dog–dog condition. When there was a 5-s delay prior to approaching the plates, low- and high-rivalry dogs performed similarly. There are a couple of reasons why this may have occurred. First, since the delay trials (trials 4–6) occurred after the no delay trials (trials 1–3), extinction might explain why the

dogs made fewer approaches to the empty plate during the delay trials. Since a direct approach to the empty plate delayed the time to reward, whereas a direct approach to a full plate would lead to immediate reward, the dogs may have learned through trial and error to go directly to the full plate. Another possible explanation is that the local enhancement observed in the low-rivalry dogs in the no delay condition was a result of impulsive or automatic behavior, which could be overcome by making the dogs wait before they were allowed to approach the plates. Experiment 2 was designed to distinguish between these alternative explanations by repeating the experiment with a new set of dogs who were only tested with the delay condition and had no experience with the no delay condition.

Experiment 2

Method

Participants

The same inclusion criteria described in Experiment 1 were used in Experiment 2. We collected C-BARQ and experimental data from 24 dogs from 12 two-dog households, and we had complete data for all dogs. The dogs ranged in age from 1 to 12 years (mean = 5.93; SD = 2.90). They had lived in the home at least 6 months but no more than 12 years (mean = 5.37, SD = 3.18). Eleven of the 24 dogs were female, and only one dog was intact. For a more detailed description of each dog, see Table 3.

Materials and procedures

All dogs participated in the dog demonstrator task and human control task, which were set up the same way as described for Experiment 1. Each dog completed three trials for each task type, and during each trial, the dog had to wait 5 s before approaching the plates.

Video coding Two research assistants used the videos to code dogs' behaviors on all trials using the same coding rules used in Experiment 1. Furthermore, as in Experiment 1, the assistants were blind to dogs' dog rivalry scores, and scores for individual dogs ranged from 0 to 3. The assistants agreed on 278 of the 288 trials (Cohen's Kappa = 0.93).

Results

Nine of the 24 dogs scored above the median of 0.25 on the C-BARQ subscale and so were classified as high rivalry, with the remaining 15 dogs classified as low rivalry. In some households, both dogs were classified as high rivalry

(N = 3 households) or low rivalry (N = 6), and in others one was classified as high rivalry and the other as low rivalry (N = 3).

The ratio of high-rivalry to low-rivalry dogs in Experiment 2 did not differ from the ratio in Experiment 1 $[\chi^2(74) = 0.043, df = 1, p = 0.837]$. The average ages and average lengths of time in the home of participants in Experiment 1 and Experiment 2 did not differ significantly (age: t = -1.107, df = 72, p = 0.272; time in home: t = -1.362, df = 72, p = 0.178), nor did the ratio of males to females $[\chi^2(74) = 0.247, df = 1, p = 0.619]$.

Figure 3 depicts the average number of full plates highand low-rivalry dogs chose in Experiment 2 when there was a 5-s delay and the demonstrator was either a dog or a human. A repeated measures ANOVA examining the effects of rivalry classification of focal dog (between-subjects variable), rivalry classification of dog demonstrator (between-subjects variable), and species of demonstrator (within-subjects variable) indicated that none of the main effects nor interactions were significant (Table 4).

Discussion

In Experiment 2, rivalry did not impact the dogs' tendencies to directly approach the full plate. In fact, the results are markedly similar to the results from the delay trials in Experiment 1. This suggests that the delay itself, rather than trial order, eliminates any effect of local enhancement in low-rivalry dogs. Other studies have found that imitation in dogs can result from automatic impulses that dogs have to actively work around to prevent (Range et al. 2011). It is also possible that some dogs became distracted during the 5-s delay, causing them to forget which plate the demonstrator had visited. Our results suggest that low-rivalry dogs are more inclined than high-rivalry dogs to follow other dogs in their household and other humans unless forced to wait before responding to a stimulus. Future research might examine whether there is any relationship between dog rivalry and personality traits, such as competitiveness or impulsivity, which might explain the differences observed in the no delay dog demonstrator trials.

General discussion

Our findings are consistent with findings from numerous previous studies that have shown that dogs' behaviors can be heavily influenced by humans and other dogs (Pongrácz et al. 2001, 2003, 2004; Kubinyi et al. 2003a, b; Heberlein and Turner 2009; Kubinyi et al. 2009; Miller et al. 2009; Range et al. 2011). However, we found variation regarding how strongly dogs were impacted by others. When allowed

Dog's name	Pair	Age (years)	Length of time in household (years)	Sex	Intact?	Rivalry classification	How acquired by owner	Breed reported by owner	First trial type
Aly	Aly and Lily	8.0	8.0	Female	No	High	Breeder	Golden Retriever	Dog demonstrator
Lily	Aly and Lily	12.0	12.0	Female	No	Low	Breeder	Golden Retriever	Dog demonstrator
Bentley	Bently and Jeep	5.0	5.0	Male	No	High	Breeder	Bernese Mountain Dog	Human demonstrator
Jeep	Bently and Jeep	3.0	1.0	Male	No	Low	Shelter, pound, or rescue	Cocker Spaniel	Human demonstrator
Carly	Carly and Marlo	5.0	5.0	Female	No	Low	Breeder	Golden Retriever	Human demonstrator
Marlo	Carly and Marlo	3.5	3.5	Male	No	Low	Breeder	Golden Retriever	Human demonstrator
Charlie	Charlie and Penny	10.0	10.0	Male	No	Low	Friend or family member	Cavalier King Charles Spaniel	Dog demonstrator
Penny	Charlie and Penny	5.0	0.5	Female	No	Low	Shelter, pound, or rescue	King Charles Spaniel/English Toy Spaniel mix	Dog demonstrator
Coco	Coco and Spike	4.0	3.8	Female	No	Low	Friend or family member	Beagle/Labrador Retriever mix	Dog demonstrator
Spike	Coco and Spike	4.0	3.8	Male	No	Low	Friend or family member	Beagle/Labrador Retriever mix	Dog demonstrator
Cole	Cole and Nikki	9.0	0.6	Male	No	Low	Breeder	Labrador Retriever	Dog demonstrator
Nikki	Cole and Nikki	7.0	5.0	Female	No	High	Shelter, pound, or rescue	Great Dane	Dog demonstrator
Digby	Digby and Teddy	10.0	9.8	Male	No	Low	Newspaper or online ad	Bichon Frise/Shih Tzu mix	Dog demonstrator
Teddy	Digby and Teddy	8.7	8.0	Male	No	Low	Newspaper or online ad	Terrier mix	Dog demonstrator
Chloe	Hunter and Chloe	3.2	3.0	Female	No	Low	Friend or family member	German Shepherd/American Staffordshire Terrier mix	Human demonstrator
Hunter	Hunter and Chloe	7.3	7.0	Male	No	Low	Shelter, pound, or rescue	Siberian Husky mix	Human demonstrator
Lola	Phoebe and Lola	1.5	1.5	Female	No	Low	Shelter, pound, or rescue	Caim Terrier mix	Human demonstrator
Phoebe	Phoebe and Lola	2.0	0.9	Female	No	Low	Shelter, pound, or rescue	Australian Shepherd mix	Human demonstrator
Gabby	Rudy and	1.2	1.1	Female	Yes	High	Breeder	Golden Retriever	Dog

698

 $\underline{\textcircled{O}}$ Springer

Table 3	Table 3 continued								
Dog's name	Pair	Age (years)	Length of time in household Sex (years)		Intact? Rivalry classific	Rivalry classification	How acquired by owner	How acquired by Breed reported by owner owner	First trial type
Rudy	Rudy and Gabby	8.0	8.0	Male	No	High	Breeder	English Cocker Spaniel	Dog demonstrator
Clyde	S'more and Clyde	8.0	6.0	Male	No	High	Shelter, pound, or rescue	Beagle	Human demonstrator
S'more	S'more and Clyde	6.0	6.0	Male	No	High	Newspaper or online ad	Beagle	Human demonstrator
Ziggy	Ziggy and Zoey	5.0	5.0	Male	No	High	Shelter, pound, or rescue	Chihuahua/Miniature Pinscher mix	Human demonstrator
Zoey	Ziggy and Zoey	6.0	6.0	Female No	No	High	Newspaper or online ad	Pomeranian/Chihuahua mix	Human demonstrator

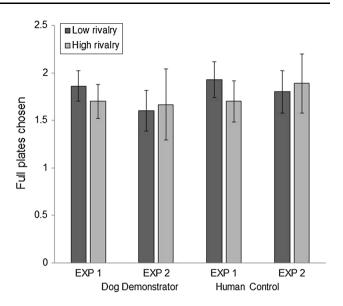


Fig. 3 A comparison of Experiment 1 (EXP1) and Experiment 2 (EXP 2) delay trials

to make a decision quickly, low-rivalry dogs were more heavily influenced by dog and human demonstrators than high-rivalry dogs, but this difference between high-rivalry and low-rivalry dogs disappeared when dogs were forced to wait 5 s before approaching the plates. Because the demonstrator and observer dogs lived together in the same household, the preexisting social relationship between the dogs is particularly likely to have influenced how attentive they were to the dog demonstrator dog and, as a result, their performance on the task.

Based on our analyses, we cannot be entirely certain whether dogs approached the empty plate because they were unaware that it no longer contained food or because the demonstrator's behavior weighed more heavily on their choice than the presence or absence of food. However, given that the local enhancement effect disappeared when there was a 5-s delay and that dogs were always allowed to approach the full plate regardless of which plate they approached first, it seems that the absence of food may not have factored into low-rivalry dogs' decisions in the no delay condition in Experiment 1.

It is important to note that when the observer dog was making his or her choice, the demonstrator was out of view and that the demonstrator dog's rivalry score did not impact which plate the focal dog approached. Thus, our findings speak to the degree to which a dog's tendencies to engage in rivalry-related behaviors with a familiar dog are associated with decision-making behaviors that occur after watching the familiar dog perform a behavior, rather than any overt aggression over the food source itself. Dogs' rivalry-related propensities may have impacted their attention during the observation phase. This would be

Effect	F	df	Р
Species	0.431	1,19	0.519
Rivalry classification of focal	0.012	1,19	0.913
Rivalry classification of dog demonstrator	0.012	1,19	0.913
Species \times rivalry classification of focal	0.108	1,19	0.746
Species \times rivalry classification of dog demonstrator	0.970	1,19	0.337
Rivalry classification of focal \times rivalry classification of dog demonstrator	0.110	1,19	0.743
Species \times rivalry classification of focal \times rivalry classification of dog demonstrator	0.431	1,19	0.519

Table 4 Results from the repeated measures ANOVA examining the effects of species and rivalry classification of focal and demonstrator dogs on plate choice

consistent with results in other species where individual differences in attention to a demonstrator resulted in individual differences in social learning (Schwab et al. 2008; Horner et al. 2010; van de Waal et al. 2010). Furthermore, Pongrácz et al. (2008) postulated that subordinate dogs, compared to dominant dogs, learned to solve a detour task faster after watching a dog demonstrator because dominant and subordinate dogs may differ in their attentiveness to other dogs.

Of note, there was not always one high-rivalry and one low-rivalry dog within a household in our study. In some households, both dogs were classified as high-rivalry, and in others, they were both classified as low-rivalry. Importantly, the dog rivalry subscale captures overt actions, such as growling, that are associated with a lack of tolerance for familiar conspecifics, but it does not capture more subtle actions associated with a lack of tolerance, such as actively avoiding conspecifics. In this way, rivalry deviates from the more commonly used measure of social tolerance in other species. Although definitions and measures of tolerance vary, it is typically defined as the willingness of an individual to tolerate proximity of, and potential competition from, another individual (Kummer 1968). To determine whether tolerance in and of itself influences social learning in dogs, more basic observational research to establish the patterns of proximity in dogs living in multidog households will need to be conducted in situ and/or a dyadic survey measure of tolerance developed. Currently, the literature on the social relationships of dogs living in the same household is not particularly comparable to information about social relationships in other species.

Even though the C-BARQ dog rivalry subscale prompts are specific to dogs living in the same household, the personality traits or behavioral characteristics of dogs that lead them to be classified as high- or low-rivalry may influence other behavioral traits as well. For example, high rivalry in dogs is thought to be linked to tendencies to be competitive or protective of resources (McMillan et al. 2016; Rayment et al. 2016). Our data alone cannot disentangle exactly what personality traits or relationship characteristics are responsible for the differences observed between high- and low-rivalry dogs. One idea a future study might explore is whether the disinclination of highrivalry dogs to automatically imitate or follow others results from a failure to tolerate having other dogs, and possibly humans, in close proximity, or a tendency to be competitive.

Across both experiments, dogs showed similar patterns of behavior in the human control task as in the dog demonstrator task. That dogs' choices tended to be impacted by human demonstrators similarly to how they were impacted by dog demonstrators is not surprising. There is a large body of evidence showing the variety of ways dogs learn from humans (Pongrácz et al. 2001, 2003, 2004; Kubinyi et al. 2003a, b; Miklósi and Soproni 2006; Kubinyi et al. 2009). However, it is important to note that although the behavior of the human and dog demonstrators resulted in the food disappearing from one of the plates, the actions of the human and dog demonstrators were not functionally similar. Whereas dog demonstrators consumed food from one of the two plates, the human demonstrator both baited and manually removed the food from one of the plates. In an experiment by Prato-Previde et al. (2008), dog preference for a particular food source was impacted by whether dogs saw their owners pretending to eat food. Had the human demonstrator in our experiments pretended to eat the food, we expect the impact of the human demonstrator on local enhancement in the no delay trials may have been even stronger.

On a broader level, our research suggests a greater need for dog cognition studies that are conducted in the context of dogs' normal relationships and environments. Up to this point, much of dog cognition research has been focused on dogs interacting with humans or unknown dogs. While this body of research has certainly demonstrated that dogs are able to learn from others in a wider variety of contexts than perhaps any other species tested, understanding the nature of established dog–dog relationships needs more attention from researchers. This study constitutes a first step toward better understanding that dynamic.

Data availability

All data generated or analyzed during this study are included as a supplementary file.

Acknowledgements We would like to thank our participants and their families for generously allowing us to visit their homes and Julie Hecht for helpful discussions regarding in-home data collection procedures. Thanks to Courtney Baird, Robert Frantz, Olivia Morello, Cameron Surratt, and Enya Van Poucke for assistance with data collection and video coding. We also extend our thanks to the following research assistants who were funded by the Canisius Earning Excellence Program: Colleen Bates, Stephanie Handley, Natalie Roberts, Erin Smith, Kaylee Stutz, and London Wolff.

References

- Bradshaw JW, Blackwell EJ, Casey RA (2009) Dominance in domestic dogs—useful construct or bad habit? J Vet Behav Clin Appl Res 4:135–144. doi:10.1016/j.veb.2008.08.004
- Bradshaw JW, Blackwell EJ, Casey RA (2016) Dominance in domestic dogs—A response to Schilder et al. (2014). J Vet Behav Clin Appl Res 11:102–108. doi:10.1016/j.jveb.2015.11. 008
- Brown C, Laland KN (2003) Social learning in fishes: a review. Fish Fish 4:280–288. doi:10.1046/j.1467-2979.2003.00122.x
- Coussi-Korbel S, Fragaszy DM (1995) On the relation between social dynamics and social learning. Anim Behav 50:1441–1453. doi:10.1016/0003-3472(95)80001-8
- Galef BG, Laland KN (2005) Social learning in animals: empirical studies and theoretical models. Bioscience 55:489–499
- Heberlein M, Turner DC (2009) Dogs, *Canis familiaris*, find hidden food by observing and interacting with a conspecific. Anim Behav 78:385–391. doi:10.1016/j.anbehav.2009.05.012
- Horner V, Proctor D, Bonnie KE et al (2010) Prestige affects cultural learning in chimpanzees. PLoS ONE 5:e10625. doi:10.1371/ journal.pone.0010625
- Hsu Y, Serpell JA (2003) Development and validation of a questionnaire for measuring behavior and temperament traits in pet dogs. J Am Vet Med Assoc 223:1293–1300. doi:10.2460/ javma.2003.223.1293
- Kubinyi E, Miklósi Á, Topál J, Csányi V (2003a) Social mimetic behaviour and social anticipation in dogs: preliminary results. Anim Cogn 6:57–63. doi:10.1007/s10071-003-0163-1
- Kubinyi E, Topál J, Miklósi A, Csányi V (2003b) Dogs (*Canis familiaris*) learn their owners via observation in a manipulation task. J Comp Psychol 117:156. doi:10.1037/0835-7036.117.2. 156
- Kubinyi E, Pongrácz P, Miklósi Á (2009) Dog as a model for studying conspecific and heterospecific social learning. J Vet Behav Clin Appl Res 4:31–41. doi:10.1016/j.veb.2008.08.009
- Kummer H (1968) Social organization of hamadryas baboons. University of Chicago Press, Chicago
- Lonsdorf EV, Bonnie KE (2010) Opportunities and constraints when studying social learning: developmental approaches and social factors. Learn Behav 38:195–205
- Marchetti C, Drent PJ (2000) Individual differences in the use of social information in foraging by captive great tits. Anim Behav 60:131–140. doi:10.1006/anbe.2000.1443

- McMillan FD, Vanderstichel R, Stryhn H et al (2016) Behavioural characteristics of dogs removed from hoarding situations. Appl Anim Behav Sci 178:69–79
- Miklósi Á, Soproni K (2006) A comparative analysis of animals' understanding of the human pointing gesture. Anim Cogn 9:81–93. doi:10.1007/s10071-005-0008-1
- Miller HC, Rayburn-Reeves R, Zentall TR (2009) Imitation and emulation by dogs using a bidirectional control procedure. Behav Process 80:109–114. doi:10.1016/j.beproc.2008.09.011
- Nicol CJ, Pope SJ (1999) The effects of demonstrator social status and prior foraging success on social learning in laying hens. Anim Behav 57:163–171. doi:10.1006/anbe.1998.0920
- Pongrácz P, Miklósi Á, Kubinyi E et al (2001) Social learning in dogs: the effect of a human demonstrator on the performance of dogs in a detour task. Anim Behav 62:1109–1117. doi:10.1006/ anbe.2001.1966
- Pongrácz P, Miklósi Á, Kubinyi E et al (2003) Interaction between individual experience and social learning in dogs. Anim Behav 65:595–603. doi:10.1006/anbe.2003.2079
- Pongrácz P, Miklósi Á, Timár-Geng K, Csányi V (2004) Verbal attention getting as a key factor in social learning between dog (*Canis familiaris*) and human. J Comp Psychol 118:375. doi:10. 1037/0735-7036.118.4.375
- Pongrácz P, Vida V, Bánhegyi P, Miklósi Á (2008) How does dominance rank status affect individual and social learning performance in the dog (*Canis familiaris*)? Anim Cogn 11:75–82. doi:10.1007/s10071-007-0090-7
- Pongrácz P, Bánhegyi P, Miklósi Á (2012) When rank counts dominant dogs learn better from a human demonstrator in a twoaction test. Behaviour 149:111–132. doi:10.1163/ 156853912X629148
- Prato-Previde E, Marshall-Pescini S, Valsecchi P (2008) Is your choice my choice? The owners' effect on pet dogs'(*Canis lupus familiaris*) performance in a food choice task. Anim Cogn 11:167–174
- Range F, Viranyi Z, Huber L (2007) Selective imitation in domestic dogs. Curr Biol 17:868–872. doi:10.1016/j.cub.2007.04.026
- Range F, Huber L, Heyes C (2011) Automatic imitation in dogs. Proc R Soc Lond B Biol Sci 278:211–217. doi:10.1098/rspb.2010. 1142
- Rayment DJ, Peters RA, Marston LC, De Groef B (2016) Investigating canine personality structure using owner questionnaires measuring pet dog behaviour and personality. Appl Anim Behav Sci 180:100–106. doi:10.1016/j.applanim.2016.04.002
- Schwab C, Bugnyar T, Schloegl C, Kotrschal K (2008) Enhanced social learning between siblings in common ravens, Corvus corax. Anim Behav 75:501–508. doi:10.1016/j.anbehav.2007.06. 006
- Serpell JA, Duffy DL (2014) Dog breeds and their behavior. In: Horowitz A (ed) Domestic dog cognition and behavior. Springer, Berlin pp 31–57
- Tennie C, Glabsch E, Tempelmann S et al (2009) Dogs, Canis familiaris, fail to copy intransitive actions in third-party contextual imitation tasks. Anim Behav 77:1491–1499. doi:10. 1016/j.anbehav.200903.008
- van de Waal E, Renevey N, Favre CM, Bshary R (2010) Selective attention to philopatric models causes directed social learning in wild vervet monkeys. Proc R Soc Lond B Biol Sci rspb20092260. doi:10.1098/rspb.2009.2260