



Importance of a species' socioecology: Wolves outperform dogs in a conspecific cooperation task

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A number of domestication hypotheses suggest that dogs have acquired a more tolerant temperament than wolves, promoting cooperative interactions with humans and conspecifics. This selection process has been proposed to resemble the one responsible for our own greater cooperative inclinations in comparison with our closest living relatives. However, the socioecology of wolves and dogs, with the former relying more heavily on cooperative activities, predicts that at least with conspecifics, wolves should cooperate better than dogs. Here we tested similarly raised wolves and dogs in a cooperative string-pulling task with conspecifics and found that wolves outperformed dogs, despite comparable levels of interest in the task. Whereas wolves coordinated their actions so as to simultaneously pull the rope ends, leading to success, dogs pulled the ropes in alternate moments, thereby never succeeding. Indeed in dog dyads it was also less likely that both members simultaneously engaged in other manipulative behaviors on the apparatus. Different conflict-management strategies are likely responsible for these results, with dogs' avoidance of potential competition over the apparatus constraining their capacity to coordinate actions. Wolves, in contrast, did not hesitate to manipulate the ropes simultaneously, and once cooperation was initiated, rapidly learned to coordinate in more complex conditions as well. Social dynamics (rank and affiliation) played a key role in success rates. Results call those domestication hypotheses that suggest dogs evolved greater cooperative inclinations into question, and rather support the idea that dogs' and wolves' different social ecologies played a role in affecting their capacity for conspecific cooperation and communication.

cooperation | dogs | wolves | domestication | comparative cognition

In recent years, building on the hypothesis that dogs and humans may have gone through a process of convergent evolution, researchers have suggested that dogs—in addition to nonhuman primates—might be a good model for investigating the evolution of human social cognition (1–4). Due to intense selection during domestication, dogs are thought to have evolved genetic predispositions for cooperative interactions (5–7), a process suggested to mirror the “self-domestication” of humans, whereby having become more tolerant of one another, during our evolutionary history we evolved stronger cooperative tendencies compared with other members of our great ape family (8–10; but see ref. 11). Based on such hypotheses, compared with wolves, dogs are expected to show a higher propensity for cooperation, not just with humans but also with conspecifics (12).

Interestingly however, the socioecology of wolves and dogs would suggest the reverse. Wolves live in tight-knit family groups that strongly rely on cooperation for hunting, pup-rearing, and territorial defense (13–15). In contrast, studies of free-ranging dogs [which form 80% of the world-dog population (16, 17)] show that, although group hunting can occur, foraging is mostly carried out solitarily on human refuse (18, 19) and that there is little allomaternal care of pups (20–22). Indeed cooperation in free-living dogs appears to be largely limited to territorial defense (23, 24). Hence, based on the socioecology of the two species, we would expect wolves to perform at least as well as

dogs, if not better, in cooperative tasks with their conspecifics (25, 26).

To assess these contrasting hypotheses, we tested similarly raised pack-living wolves and dogs housed at the Wolf Science Center in Vienna (www.wolfscience.at/en/) in the cooperative loose-string paradigm (Fig. 1). In this task, food is placed on an out-of-reach tray. A loose string is looped through rings on the tray, with the two ends of the string placed within the animal's enclosure at such a distance that a single individual cannot reach both ends and pull them simultaneously. In test trials, two individuals are given access to the enclosure at the same time, and cooperation is observed if they coordinate their actions so as to simultaneously pull on the two ends of the rope, thereby moving the platform forward, allowing them to access the out-of-reach food. However, if only one end of the string is pulled, the other end becomes inaccessible and the tray cannot be moved forward anymore, rendering the trial unsuccessful. This task has been used with a wide range of species, from ravens to elephants [chimpanzees (27–29), macaques (30), elephants (31), gray parrots (32), rooks (33), ravens (34), kea (35, 36), and dogs (37)], with many succeeding in solving the task after being initially trained individually to pull the tray out by pulling both ends of the rope together.

Results

At the Wolf Science Center in Vienna, wolves and dogs live in conspecific packs, composed of between two and six individuals. Overall, we tested 12 wolves (8 male, 4 female) and 14 dogs (7 male, 7 female): that is, a total of 16 wolf dyads and 10 dog dyads (i.e., all of the available within-pack dyads) in different

Significance

A popular hypothesis is that during the course of domestication, dogs acquired a tamer temperament, showing increased tolerance and cooperative inclinations compared with their wolf relatives. This “domestication effect” is suggested to mirror how humans evolved a more tolerant and cooperative nature compared with chimpanzees. However, whereas wolves rely heavily on cooperation for hunting, pup-rearing, and territorial defense, dogs' reliance on cooperation is much reduced. Here we compared similarly raised and kept wolves and dogs on a cooperative string-pulling task and found that, in line with the different socioecology of the two species, wolves better cooperate with their conspecifics than dogs. Furthermore, cooperation in wolves was more successful among partners of similar rank and with a close social bond.

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Fig. 1. Wolves working in the loose-string paradigm. Image courtesy of Roobert Bayer (Wolf Science Center, Ernstbrunn, Austria).

conditions. Initial dyads (tested in the Spontaneous condition, see below) were chosen based on the closeness of their affiliative bonds, giving precedence—where possible—to mixed-sex dyads over single-sex dyads.

Animals were tested in a number of different conditions (see Fig. 2 for a decisional flowchart of conditions). First, each dyad was presented with the string-pulling apparatus with no prior training (Spontaneous condition). Dyads were simultaneously allowed into the enclosure and presented with six to eight sessions of six trials each, depending on performance/motivation [average of 36 (range 9–48) trials] (see *SI Materials and Methods* for details). If animals were successful on at least four trials in each of the last two sessions, the dyads were presented with the Two-tray condition, where two identical apparatuses were presented 10-m apart in the same enclosure and animals were released at the same time (six sessions, six trials per session). This condition tested whether partners could coordinate their actions in both space and time. Finally, following the Two-tray condition and regardless of the dyads' performance, subjects were presented with a Delay condition (six sessions, six trials per session). In this condition, one animal was released 10 s after the other, allowing us to test whether the subject released earlier would wait for their partner's arrival before pulling the rope.

If a dyad failed to solve the Spontaneous condition, the two individuals were tested in a different dyad. If they succeeded in the new dyad, they were retested with their former partner (for retesting information, see Table S1). In packs, where no dyad was successful, similarly to previous studies using the loose-string paradigm (37), each individual went through a training procedure, whereby the individual learned that when ropes were placed close enough to each other, holding both in the mouth and pulling would allow it to solve the task (*SI Materials and Methods*). Following this training procedure, dyads were tested again with a single apparatus (Fig. 2) (*SI Materials and Methods*).

Dog–Wolf Comparison. Seven wolf and eight dog dyads were compared in the Spontaneous condition. Wolf and dog dyads had comparable experiences with the task, in that either (i) both partners had never been exposed to the apparatus (i.e., they were completely task-naïve) or (ii) one individual had been tested previously with another pack member but had failed to solve the task (see Table S2 for details). All animals had previous experience of pulling a string to obtain an attached piece of food. Five of the seven wolf dyads succeeded in at least one trial (and across dyads success rates were in between 3% and 56% of trials), while only one of the eight dog dyads succeeded and only in one trial.

Next, four wolf dyads (three of which had been tested in the Spontaneous condition but with less than 10% success rate) (Table S2) and six dog dyads (four of which had been tested in the Spontaneous condition) (Table S2) were submitted to a training procedure similarly to previous studies, where they learned to solve the string-pulling task alone by taking both ends of the rope in their mouth and pulling (see *SI Materials and Methods* for details on training regimen). All dyads were then retested in six sessions of six trials each (Fig. 2 and Table S2). Three of the four wolf dyads succeeded in 14–92% of trials, while only two of the six dog dyads succeeded in a single trial (3%).

Overall, the wolves outperformed the dogs regardless of condition [generalized linear mixed-model (GLMM) $\chi^2 = 10.418$, $P < 0.0001$] and dyads were significantly more successful after individual training (GLMM: $\chi^2 = 38.64$; $P < 0.0001$; no species \times condition interaction: $\chi^2 = 1.94$; $P = 0.16$) (Fig. 3).

To investigate why wolves, but not dogs, successfully cooperated, we analyzed the behaviors exhibited by both individuals in a dyad during the first test session of both the Spontaneous and Posttraining conditions (i.e., when the wolves' and dogs' experiences with the task was still comparable).

Two elements are important for animals to be able to pull both ends of the rope at the same time and thus to succeed: (i) they need to explore and manipulate the apparatus sufficiently to discover the “correct” behavior and (ii) they need to tolerate each other's presence and activity at the apparatus.

To assess the first aspect, we compared wolves and dogs on the frequency with which individuals showed (i) rope-pulling behaviors (exhibited not at the same time as the partner, so it did not lead to success) and (ii) other nonfunctional behaviors (i.e., biting, scratching, pawing, and so forth), which allowed us to assess the rate of manipulation in wolves and dogs.

As regards individual rope pulling, a species-by-condition interaction emerged (GLMM: $\chi^2 = 4.01$, $P = 0.045$); hence, we ran separate models on the Spontaneous and Posttraining conditions. In the Spontaneous condition, wolves did significantly more individual rope-pulling than dogs (GLMM: $\chi^2 = 4.57$, $P = 0.03$; Spontaneous: dog mean 0.5, range 0–6; wolf mean 0.7, range 0–10). In Posttraining trials, no effect of species emerged (GLMM: $\chi^2 = 0.84$, $P = 0.35$; Posttraining: dog mean 1.6 range 0–11; wolf mean 1.7.5, range 0–13).

The relative frequency of the other nonfunctional manipulations of the apparatus did not differ between wolves and dogs (no effect of species GLMM: $\chi^2 = 1.47$, $P = 0.22$) and was not affected by condition (effect of condition GLMM: $\chi^2 = 1.09$, $P = 0.029$; no species \times condition: $\chi^2 = 0.96$, $P = 0.32$).

To assess whether wolf and dog dyads differed in their level of tolerance, we analyzed: (i) the latency it took both animals to be

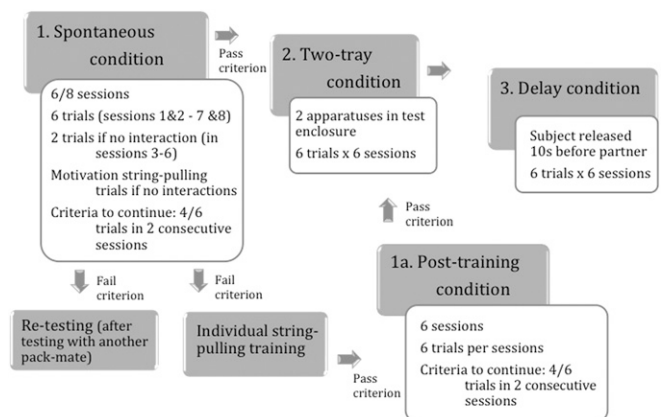


Fig. 2. Schematic depiction of the experimental procedure.

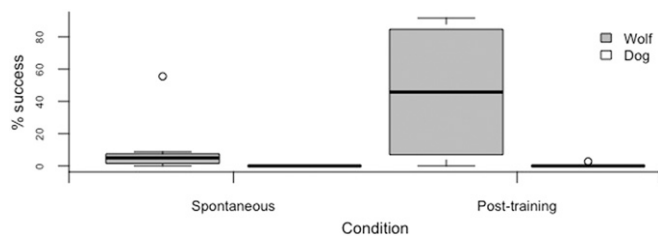


Fig. 3. Boxplots (median, interquartile range, outliers) showing the success rates (in percentage of trials in which dyads succeeded) for wolves and dogs in the Spontaneous and Posttraining conditions.

within one body length of the apparatus and the relative duration of trial time both individuals were simultaneously present at the apparatus, (ii) the likelihood that in a trial both animals would simultaneously manipulate the apparatus (i.e., biting, scratching, and pawing it), and (iii) the likelihood of dominant, aggressive, and submissive behaviors occurring during testing.

Wolf and dog dyads did not differ in the latency until both partners were close to the apparatus nor in the relative duration both individuals spent in proximity to the apparatus (latency: species: GLMM: $\chi^2 = 1.52$, $P = 0.22$; no interaction species \times condition: GLMM: $\chi^2 = 2.09$, $P = 0.15$; duration: GLMM: species: $\chi^2 = 0.008$, $P = 0.93$; no species \times condition interaction: $\chi^2 = 1.42$, $P = 0.23$). Wolf and dog dyads approached the apparatus faster in Posttraining than Spontaneous trials (GLMM: $\chi^2 = 4.9$, $P = 0.03$) and both species spent more time in proximity of the apparatus in Posttraining than Spontaneous trials (GLMM: $\chi^2 = 5.51$, $P = 0.02$).

However, wolf dyads were significantly more likely to simultaneously manipulate the apparatus, even if these were non-functional behaviors (e.g., biting, pawing, scratching, and so forth) than dog dyads (GLM: $\chi^2 = 4.85$, $P = 0.027$). Of course, wolves also significantly more frequently pulled the rope ends at the same time, leading to their higher success rate (see results relating to successful performance outlined above).

Dominant and aggressive behaviors (*SI Materials and Methods*) were rare in both wolves and dogs, occurring in a total of 12% of trials (wolves: 8 trials, 4 dyads; dogs: 10 trials, 5 dyads); the likelihood of these behaviors occurring was not affected by species (GLMM: $\chi^2 = 0.0001$, $P = 0.99$), but they were more likely to occur after the training (GLMM: $\chi^2 = 4.5$, $P = 0.044$; no species \times condition interaction: $\chi^2 = 0.047$, $P = 0.83$). Submissive behaviors (e.g., including withdrawing from the apparatus when another approached) also occurred rarely [i.e., in 11% of trials (wolves: 10 trials, 6 dyads; dogs: 6 trials, 3 dyads)] and the likelihood of their occurrence was affected by neither species nor condition (GLMM: species $\chi^2 = 1.59$, $P = 0.2$; condition $\chi^2 = 0.25$, $P = 0.61$; species \times condition interaction: $\chi^2 = 0.08$, $P = 0.78$).

Finally, as a potential measure of their coordination abilities, we evaluated gaze alternation behaviors (i.e., the rate of gazing from partner to apparatus and vice versa). No effect of species emerged (GLMM: $\chi^2 = 0.2$, $P = 0.65$ and no species \times condition $\chi^2 = 2.17$, $P = 0.14$), but gaze alternation was more frequent in both species after training (GLMM: $\chi^2 = 38.81$, $P < 0.0001$), potentially suggesting they had a better understanding of the need for the partner after individual string-pulling training.

Factors Affecting Wolves' Success. Due to the wolves' success, we continued to investigate their cooperative performance. A total of 16 wolf dyads were tested in the Spontaneous and Posttraining conditions and of these, 12 dyads succeeded in passing the set criterion (i.e., four of six trials in the last two sessions) to be tested in the Two-tray condition (*Table S1*); the latter condition requiring them to coordinate their actions in both space and time. To evaluate their understanding of the need for a partner, the wolves were subsequently presented with a Delay condition

in which the subject was released into the testing enclosure 10 s before the partner (*Fig. 2*).

We first compared success rate across conditions for those wolf dyads that did indeed pass criteria in the Spontaneous/Posttraining (One-tray), and therefore were presented with the subsequent Two-tray and Delay conditions and found no effect of condition ($n = 12$, GLMM: $\chi^2 = 0.08$, $P = 0.96$) (*Fig. 4*).

However, a learning effect was evident within each condition, since success rates increased across sessions in the Spontaneous and Posttraining (GLMM: $\chi^2 = 7.17$, $P < 0.0001$), Two-tray (GLMM: $\chi^2 = 19.19$, $P < 0.001$), and Delay (GLMM: $\chi^2 = 7.87$, $P = 0.005$) conditions.

In the Two-tray condition, dyads succeeded on both trays on average in 74% of the trials (range 20–100%) (*Table S1*). In accordance with other studies (e.g., refs. 27–29, 34, and 37), we found that the stronger the affiliative bond measured during daily observations (*SI Materials and Methods*) (GLM: $\chi^2 = 8.6019$, $P = 0.003$) (*Fig. 5*) and the smaller the rank distance (GLM: $\chi^2 = 25.82$, $P < 0.0001$) (*Fig. 6*), the better dyads were able to coordinate their actions and obtain rewards from both trays.

In the Delay condition, one individual (Shima) performed rather poorly (8% success). A second individual (Aragorn), who was tested with her, also performed poorly (22% of trials); however, on inspecting videos, it was clear that the responsibility for failures was mostly due to Shima. Hence, Aragorn was retested with another partner. The remaining subjects' performance ($n = 8$; including Aragorn's retest with another partner) showed a success rate of between 55% and 94% of trials in the Delay condition. A subject's performance (all tests included) was affected by the prior success rate they had with their partner in the Two-tray condition (GLM: $\chi^2 = 14.53$, $P < 0.0001$) and in the Spontaneous/Posttraining conditions (GLM: $\chi^2 = 21.15$, $P < 0.0001$).

Discussion

Overall, in line with the different socioecologies of dogs and wolves, and the latter's more conspicuous dependence on cooperative activities, results show that wolves consistently outperformed dogs in the cooperative string-pulling task.

Interest in the apparatus was comparable, since no differences emerged in the latency and duration of both animals being in proximity of the apparatus, nor the individual frequency of biting and pawing at it. However, in the Spontaneous condition, wolves manipulated the ropes more frequently than dogs, which likely increased the probability of dyads achieving success and learning from this experience. Differences in string-pulling frequencies between wolves and dogs are in line with studies showing that wolves tend to be more persistent in object manipulation than dogs, both in problem-solving tasks involving food (38, 39) and when exposed to novel objects (40, 41), and such basic differences

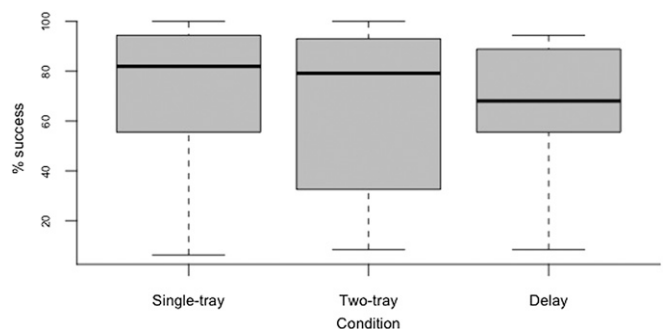


Fig. 4. Boxplots (median, interquartile range, outliers) showing the success rates (in percentage of trials in which dyads succeeded) for wolves across the three main conditions (Single-tray: Spontaneous, Retesting, and Posttraining; Two-tray and Delay conditions).

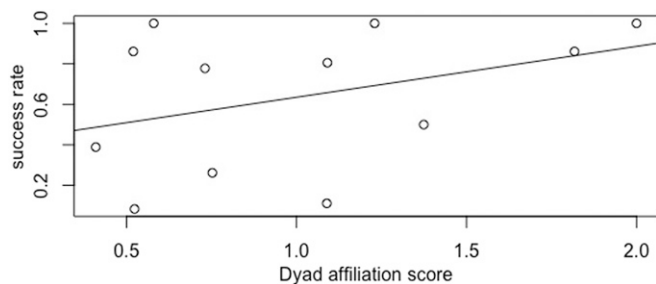


Fig. 5. The higher the wolf dyad's affiliation score, the more successful they were in coordinating their actions to solve both apparatuses in the Two-tray condition.

may play an important role when assessing wolves and dogs in cognitive tasks (42).

Another possibility is that wolves had a better understanding of the task requirements, thereby more frequently performing the "correct" string-pulling behavior. However, wolves and dogs have been shown to be on a par in tests of means-ends understanding (43), which is the task most related to the string-pulling apparatus used in the present study. Therefore, it seems unlikely that dogs and wolves differed in their understanding of the task.

Indeed, in the present study, differences in the rate of string-pulling per se were not sufficient to explain differences in cooperative success, since after individual training on the apparatus, the rate of string-pulling between wolves and dogs was comparable yet wolves continued to outperform dogs. Hence, in this condition dogs and wolves showed similar levels of interest and individuals equally frequently displayed the appropriate behaviors on the apparatus, but crucially wolves were better at coordinating these behaviors so that they both pulled at the same time, thereby succeeding.

Tolerance has been shown to be a key factor in cooperative success in a number of species (28, 29, 34). In the present test, in the first session, we found no obvious difference in the time wolves and dogs spent simultaneously in proximity of the apparatus, in the frequency of agonistic behaviors, and whether the dominant or subordinate animal manipulated the ropes, which indicates a comparable degree of tolerance around the apparatus. Furthermore, wolf and dog dyads tested did not differ in their social relationships, in that no significant effect of species emerged for either their affiliation score or their rank distance (*SI Materials and Methods*). However, crucially, whereas wolves pulled each end of the rope at the same time (leading to success), dogs did not, and hence never succeeded. Indeed, dogs tolerated each other's presence at the apparatus but they were significantly less likely than wolves to both engage in the task at the same time, most likely as a conflict-avoidance strategy over a coveted resource. This avoidance of a coveted resource in a potentially competitive context has been observed more often in dogs than wolves (44, 45), suggesting that there may be different social strategies adopted by the two species to avoid/resolve conflicts. Difference in such strategies may in turn affect cooperative success, where a shared resource is the ultimate aim.

Dogs in the present study performed very poorly, which contrasts with a study carried out with pet dogs, where the five dyads tested all succeeded in the cooperation task (37). It is likely that differences in the prior experience of dogs (pet dogs were all highly trained), and potentially methodological differences in the procedure, contributed to these discrepancies. But most importantly, pet dyads were composed of dogs living in the same household, where typically owners train their dogs not to engage in conflicts over resources, promoting a level of tolerance, which may facilitate cooperation. In contrast, pack dogs at the Wolf Science Center develop their social relationships with minimal

human interference, in that animals are removed only if levels of aggression lead to potentially serious injuries. In this setting, competition over resources is likely to be higher, and conflict-avoidance strategies (constraining cooperation) may be more prevalent than in a pet dog environment. The large variability in results across the two very different dog populations studied so far highlights the high behavioral plasticity of dogs, which is likely one of the major ingredients of their success as human's companions. In line with this, it would be of great value to test dog populations from the most diverse backgrounds on such a task (e.g., dogs selected for pack hunting, free-ranging dogs, highly trained working dogs, and so forth) to start teasing apart the factors promoting/inhibiting dogs' conspecific cooperation.

Nevertheless, current results of dogs and wolves living under comparable conditions show wolves being strikingly more prone to coordinate their actions in a cooperative task. This is in line with the notion that wolves' reliance on cooperative activities, such as group hunting, continues to place a high-selection pressure on their capacity for tolerance and coordinated actions. During the course of domestication, the alteration in dogs' socioecology, leading to a reduced reliance on conspecific cooperative activities, likely relaxed the selective pressures for such skills (26). Future comparisons of wolves' and dogs' cooperative abilities in more naturalistic tasks, such as territorial defense or third-party conflict support, may help to disentangle whether such differences relate specifically to coordinated actions on an apparatus (i.e., where a resource is at stake) or are more generally extended to other aspects of the animal's social environment.

In contrast to dogs, wolves overall showed a striking capacity to coordinate their actions in this task. Interestingly, when comparing the success rate of the 12 dyads across all three conditions, we found no significant difference (Fig. 4). These results suggest that during the single-apparatus condition, dyads learned the basic requirements of the task and were then able to flexibly apply them in the new contexts (Two-tray and Delay conditions). However, a number of elements appeared to be important in contributing to the wolves' success. Dyads significantly improved their performance across sessions within each condition, suggesting that after an initial success, the positive feedback allowed them to rapidly acquire the necessary associative rules to continue to succeed. Indeed, in the Delay condition, where the individual's understanding of the need for a partner was tested, the higher success rate of the subject was directly related to how often they had succeeded in the prior Two-tray and single apparatus (Spontaneous or Posttraining) conditions, suggesting that the animals learned the contingencies of the task during testing in these conditions.

Interestingly, besides the learning process, the social relationship played an important role in how well dyads succeeded in the Two-tray condition. Indeed in line with previous results in other species (28, 29, 34), we found that the strength of the social

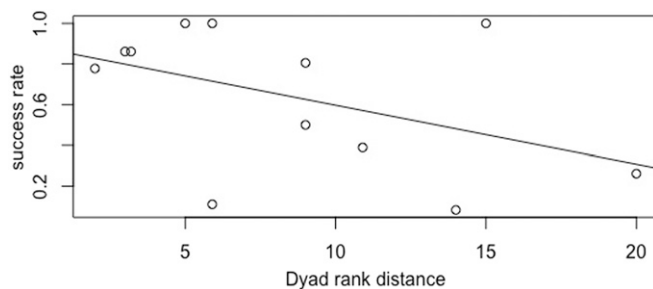


Fig. 6. The smaller rank distance between partners in a wolf dyad, the more successful they were in coordinating their actions to solve both apparatuses in the Two-tray condition.

bonds was associated with the success with which wolves were able to coordinate their actions to obtain a reward from both apparatuses. Furthermore, the closeness of the rank between individuals was also related to higher cooperation success, similarly to results from chimpanzees (46) and hyenas (47) [although studies in other species found the opposite effect, with higher cooperative success being related to increased rank distance between partners (30, 34)]. In the Two-apparatus condition, the coordination between partners is particularly important; therefore, it is possible that animals closer in rank paid closer attention to one another compared with partners in dyads with larger rank distances. Indeed studies in dogs suggest that subordinates will learn a task from a dominant more readily than vice versa (48), and in rhesus macaques, gaze-following has been observed to be more likely to occur the closer the rank distance between partners (49). Future studies will be needed to test this hypothesis further.

Overall, the present study questions the hypotheses that dogs, during the process of domestication, have become better cooperators than wolves, and cautions against using the wolf-dog comparison as a model for hypotheses regarding human “self-domestication.” Indeed, studies on captive pack-living wolves and dogs suggest that considering dogs a “tamer/friendlier” version of wolves is an oversimplification. Rather, dogs appear to exhibit different behavioral strategies than wolves when interacting with conspecifics: showing fewer formal signals of dominance but higher intensity of aggression (50–52), a more persistent use of avoidance and distance maintenance in managing conflicts in the feeding context (44, 45), and a reduced inclination to coordinate actions in a cooperative task (present results). Taken together,

such results suggest that changes in dogs’ socioecology, in particular their reduced dependence on conspecific cooperation in hunting and pup-rearing, may have significantly affected their intraspecific social behavior in a number of ways, highlighting the importance of taking socioecology into account in theories about domestication (26).

Materials and Methods

Details of the subjects, testing, training, coding of test and observations, as well as statistical analyses carried out are included in the *SI Materials and Methods*, Fig. S1, Tables S1–S4, Movies S1–S3, and Datasets S1 and S2. This study was discussed and approved by the institutional Ethics and Animal Welfare Committee at the University of Veterinary Medicine Vienna, in accordance with Good Scientific Practice guidelines and national legislation (Protocol number ETK-01/04/97/2014).

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