

Article

Teamwork Makes the String Work: A Pilot Test of the Loose String Task with African Crested Porcupines (*Hystrix cristata*)

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Abstract: Comparative researchers have heavily focused their studies of social cognition on species that live in large social groups, while neglecting other potential predictors of social cognition. African crested porcupines (*Hystrix cristata*) are relatively rare among mammals in that they are cooperative breeders that pair for life. Little is known about their social cognition, but they are good candidates for exploring cooperative behavior due to the need to coordinate behavior to cooperatively raise young. Cooperation, as defined in this study, is the process by which two or more participants perform independent actions on an object to obtain a reward for all parties. Humans are thought to outperform all other species in the frequency and magnitude of cooperative behaviors. Yet, only by studying a variety of species can researchers fully understand the likely selection pressures for cooperation, such as cooperative breeding. Here, we pilot tested the feasibility of the popular loose-string task with a mated pair of African crested porcupines, a task that required the porcupines to cooperatively pull ropes to access an out of reach platform baited with food rewards. Other species presented with this task were able to work together to receive rewards but did not always demonstrate understanding of the role of their partner. The porcupines achieved success but did not appear to coordinate their actions or solicit behavior from their partner. Thus, similar to other species, they may achieve success in this task without taking their partner's role into account. This study demonstrates that the loose string task can be used to assess cooperation in porcupines. However, further experiments are needed to assess the porcupine's understanding of their partner's role under this paradigm.

Keywords: cooperation; loose-string task; rodents; synchronized actions; cooperative breeding; pair bonds



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1. Introduction

Cooperation is of particular interest to comparative psychologists because individuals are expected to be self-interested; yet, cooperative behaviors have been observed in countless species in the wild (e.g., African wild dogs, *Lycan pictus*: [1]; carrion crow, *Corvus corone*: [2]; chimpanzees, *Pan troglodytes*: [3]; Florida scrub-jays, *Aphelocoma coerulescens*: [4]; lions, *Panthera leo*: [5]). The definition of cooperation has varied (e.g., [3,6,7]), but we define it as the process by which two or more participants perform independent but coordinated actions to obtain a reward for all parties. Cooperation benefits an individual when there is a greater chance of success, in terms of short-term consequences and in lifetime reproductive success, working with another individual compared to when working alone. Cooperation is expected in species that engage in repeated interactions with the same individuals and can remember and track the outcomes of those interactions. Thus, cooperation is seen as particularly beneficial in social species as groups can be comprised of related individuals [8] or long-lasting reciprocating partners [9], and it has been extensively studied in nonhuman primates, notably chimpanzees (e.g., [10–16]). Tests of less social species and non-primates can help to establish the evolutionary timeline for the emergence of precursors to cooperation, and to identify factors that may predict the presence of these capabilities [12,17,18].

When assessing the capacity for cooperation in other species, it is critical that partners can learn to coordinate their actions [19]. Here, we present a pilot test of the capacity to cooperate in the previously unstudied African crested porcupine (*Hystrix cristata*).

Despite the increasing breadth of species studied by comparative psychologists, the cognitive abilities of many species remain unexplored. A strong emphasis on studying group-living species, such as primates, canids, cetaceans and corvids (e.g., [10,11,20–24]) has led to the neglect of other aspects of sociality as predictors of social cognition, such as pair bonds and cooperative breeding [18]. Although cooperative breeding has emerged as a possible predictor of social cognitive abilities in primates [25,26], and birds [27–29], other groups present important opportunities for study. For example, within rodents, there exists a wide range of social structures (e.g., [30,31]), including the monogamous pair bonds of African crested porcupines—a large species of rodent, ranging from 10–15 kg, that inhabits Central and North Africa, as well as Central Italy [32,33]. These porcupines are good candidates for research on cooperative behavior due to their tendency to pair-bond and cohabitate in dens with other mated pairs [33]. Furthermore, partners share in parental duties, such that they alternate cub guarding in the den for the first two months of life [34]. The few existing studies of these species have been restricted to assessments of temporal activity patterns [32,35], observations of home site selection and fidelity to those locations [33,35], and scavenging behavior [36]. A single study of their cognitive abilities found that African crested porcupines could be successfully trained to touch and hold to a target for 30 s using a shaping procedure [37]. Thus, very little is currently known of their cognitive capacities, particularly in regard to social cognition. Our ultimate goal was to test their capacity to engage in cooperation in an experimental task, but, because porcupines have relatively poor vision [38], and little is known about their capacity to coordinate their actions, we needed to first test the feasibility of presenting them with an experimental task requiring behavioral coordination. To do so, we piloted the popular loose string paradigm (e.g., [12,39]) with a single mated pair of African crested porcupines.

Various paradigms have been employed to reveal a species' capacity to cooperate and the underlying cognitive mechanisms (e.g., simultaneous handle pulling: [40]; synchronized button pressing: [22]). Individuals can learn to engage in cooperation by learning associations between their own behaviors within the presence of a partner without understanding the essential role of the partner; thus, experimental studies are necessary to probe the mechanisms underlying their performance. One method for doing so, the loose-string task, a popular cooperation paradigm, involves two individuals pulling two ends of a rope attached to an out of reach platform baited with food. The rope is typically looped through a hole attached to the platform that allows the rope to come loose if only one individual pulls. Thus, two individuals must pull to access the platform, or it becomes inaccessible. Some previously tested species have excelled at this task (e.g., capuchins, *Cebus apella*: [41]; elephants, *Elephas maximus*: [42]; domestic dogs, [43]; wolves, *Canis lupus*: [44,45]), although others have shown difficulty in understanding the role of the partner (e.g., African gray parrots, *Psittacus erithacus*: [46]; keas, *Nestor notabilis*: [47]; rooks: [17]; domestic dogs, [44]; chimpanzees, [12]). Although the ecological relevance of the task for many tested species may be questioned, it is important to test the capacity for animals to learn to perform behaviors that have not been extensively shaped by natural selection to test their capacity for behavioral flexibility and the generalization of behavior to novel contexts. Typically, subjects are first trained to pull the ropes independently to achieve reward, either by allowing them access to both ropes for animals that use their hands or tying the ropes together for animals that pull using their mouths, beaks or one foot. Often, shaping procedures are implemented to ensure that subjects acquire proficiency with independent pulling before partners are introduced (e.g., [44,48]). When partners are introduced, the two may solve the task by both pulling backwards at the same time, although each individual may differ in the speed and force of their pulls. For instance, one of the elephants assessed by [42] solved the task by stepping on its side of the rope while its partner pulled the platform within reach. Subsequent phases introduce a partner with only one end of the rope being

available to each partner, thus necessitating that both partners pull simultaneously or pull for short distances alternately. In this phase, researchers assess whether the subjects look to each other to coordinate their actions or solicit pulling behavior from the partner. This allows researchers to determine whether subjects appreciate the role of their partner. Additional tests can be constructed in such a way that one partner's access to the rope is delayed, allowing researchers to assess whether the actor waits to pull until the partner is in position. Thus, this unique paradigm allows a test of the capacity of the subject to understand essential components of cooperation.

Tolerance (i.e., expressed as the ability to eat from the same food source within proximity of one another) has also been identified as directly impacting the results of these studies. The level of tolerance in a dyad predicts chimpanzee spontaneous cooperation and highly tolerant bonobos (*Pan paniscus*) cooperate more successfully than chimpanzees on highly monopolizable rewards [49,50]. Testing a familiar mated pair of porcupines maximized our likelihood of observing cooperative behavior.

We presented two African crested porcupines with the standard loose string task. We were unable to provide them additional planned opportunities to learn about the role of the partner similar to [46], who tested African gray parrots. However, our results serve as a pilot test of the capacity of porcupines to participate in a task requiring coordination and tolerance. The first phase ensured the individuals would pull a rope and that they associated pulling with a reward. In this phase, we assessed how quickly the porcupines interacted with the apparatus, pulled on the apparatus, and completed the task. In the second phase, the subjects were required to pull the rope simultaneously to move the apparatus within reach. In this phase, we assessed their ability to complete the task successfully, the speed at which they did so, and any soliciting behaviors that might have occurred. To probe their understanding, we evaluated whether the likelihood of pulling became more closely synchronized with the partner's initiation of pulling over sessions. This pilot test serves to improve our limited understanding of the social cognition of the African crested porcupine, but future testing is needed to assess their ability to learn to understand the role of their partner.

2. Materials and Methods

2.1. Participants

Two adult African crested porcupines, one female, Lady Gaga, and one male, Bedhead, were tested. These porcupines were housed at The Creature Conservancy, a nonprofit educational sanctuary in Ann Arbor, Michigan in the United States. This pair had been bonded for the duration of their time at this sanctuary. The porcupines had participated in some husbandry training prior to this study, including target training. They previously participated in a study investigating behavioral flexibility through presentation of a multi-access box and in a study investigating their ability to track the number of responses required in a particular spatial location (Vonk, unpublished). They were housed together in an indoor enclosure with intermediate access to an outdoor habitat depending on the weather (see Figure 1). The porcupines could choose not to participate in the study at any time.

2.2. Materials

The loose string paradigm [12] requires an out of reach tray baited with food. For this study, the tray was built out of a square piece of wood covered by metal sheets and was similar to the apparatus used by Heaney et al. [51]. In the first phase, the rope, made out of non-toxic manila and sisal, was fed around the back of the tray and kept in place by a U-shaped metal ridge attached to the back. The bait used for the porcupines depended on the food available to the researchers at The Creature Conservancy, but it was typically either sweet potatoes or apples. These foods were typical to the diet of the porcupines, but the specific items utilized in research were provided in addition to their daily diet. The food was placed in front of a metal barrier at the very front of the tray to prevent it from

sliding backward when the porcupines attempted to grasp it with their mouths (Figure 2). This design was modified after four sessions of the second phase to include extending arms that contained the food, which would protrude into the porcupines' habitat to allow them to retrieve the food more easily. A metal loop was also attached in the center of the tray to feed the rope through to ensure the tray would move in a straight trajectory and the rope would easily come loose (Figure 3).



Figure 1. Porcupine indoor habitat including testing area.



Figure 2. Apparatus used in Phase 1 and first 4 sessions of Phase 2.



Figure 3. Apparatus used in the last 8 sessions of Phase 2.

2.3. Procedure

2.3.1. Phase 1: Individual Pulling

To ensure the subjects were able to pull a rope to gain access to a reward, a training phase was implemented. Sessions consisted of 10 trials each, and subjects were given a maximum time limit of five minutes for each trial before the apparatus was removed (Some sessions consisted of fewer trials if the porcupines stopped participating (1 session for Bedhead, 1 session for Lady Gaga), or more than 10 trials if there was extra food (no more than 13 trials per session, this occurred in 5 sessions for Lady Gaga). Note that trials ranged from 5–10 within sessions in the original [12] study. If there were fewer than 10 trials, the session was not counted toward the criteria for changing training or phases. If there were more than 10 trials, only the first 10 trials were counted toward the criteria for changing training or phases.). Typically, one session per subject occurred per day. The porcupines were separated to test each subject individually through luring one individual into the outer portion of the enclosure with the food available to the experimenters at the Creature Conservancy (e.g., almonds, corn, sweet potatoes, bananas), while distracting the target subject with the same food in the inside portion of their enclosure similar to the procedure of [12]. Once one individual was successfully lured outside, the experimenter closed off the opening to the outer enclosure by sliding a metal door into place. This door was secured to ensure the other porcupine could not access this indoor room during testing. Once separated, training with the desired subject began. Previous studies have also trained subjects to pull the rope individually before interacting with a partner. In the original version of the task with chimpanzees, the chimpanzees were trained to pull both ends of the rope at the same time, or the rope would be pulled out of the apparatus and the trial would be a failure [12]. This is feasible with primates that use their hands with human-like dexterity. However, with other species that pull ropes with their mouths, beaks or one foot (e.g., domestic dogs, [44]; rooks, [48]), it is not feasible to have the subjects pull two ropes simultaneously. Porcupines use their mouths to manipulate objects, which we had witnessed in other studies (Vonk, unpublished). Thus, here, the two ends of the rope attached to the apparatus were tied together so that one animal alone could pull the apparatus forward (as in [44,51]). When training started, this rope was attached to the inaccessible apparatus so that only the rope was accessible to the porcupine through the gates in front of the enclosure.

At the start of the trial, the experimenter positioned the apparatus approximately 20 cm from the bars separating the test area from the porcupine's habitat and extended

the rope through the bars into the habitat. The trial lasted for five minutes or until the porcupine obtained the reward, whichever occurred first. If five minutes passed with no interaction with the rope, the trial was considered unsuccessful, and the apparatus was reset for the next trial. If the porcupine could not be lured back for the next trial, the session was ended. Once the porcupine obtained the reward, the apparatus was pulled back to the starting position and rebaited and the rope was placed back within the porcupine's habitat for the next trial without additional delay. The experimenter remained behind the bars on the outside of the enclosure on either side of the apparatus. The subject was required to pull the apparatus until it reached the front bars of their enclosure to access the reward. If the porcupine successfully pulled the apparatus to within reach but did not immediately take the reward, their attention was directed to the food or the experimenter handed them the food. This occurred more often with the female than the male, due to her being slower to find and retrieve the reward. Handing the food directly to the porcupines was necessary to ensure they received a reward soon following a correct response to reinforce the desired behavior and motivate continued participation. As these are program animals, it was essential to reduce frustration by ensuring they received rewards for performing desired actions. Once the porcupine pulled the apparatus flush, the experimenter would say "Yes!", the cue used by trainers at this facility to indicate the animal had reached criteria, and then the experimenter would pull the ropes outside of the enclosure.

This phase continued until both individuals reached criterion. The criterion required that the subjects responded correctly on 8/10 trials for two consecutive sessions on two different testing days without any prompting from the experimenter. If one individual reached criterion before the other, that individual received individual refresher sessions before moving on to simultaneous pulling to maintain criterion level performance up until Phase 2 could be implemented.

If the subject responded correctly on fewer than 5/10 trials within a session, shaping was introduced in the next session. For shaping, the experimenter rewarded the porcupine with small pieces of the desired food as soon as the porcupine engaged in the desired behavior (biting the rope and pulling, even if the rope did not move the desired distance). Once the porcupine had done so, and been rewarded three times (i.e., on three consecutive trials), the experimenter did not offer a reward until the porcupine pulled the apparatus to the desired distance on the fourth trial. If the porcupine needed to be lured back to the rope, a less desirable food was placed near it (e.g., corn). If the porcupine reached a criterion of five out of ten correct trials, that subject was presented with a regular training session without shaping procedures for the next session. If the porcupine exhibited less than five out of ten correct trials in that session, it continued to receive shaping on the subsequent session. Once both porcupines reached the final training criterion without shaping, both porcupines were moved on to Phase 2.

Immediately before starting Phase 2, both porcupines received a reminder session of Phase 1 in which they were required to achieve success on 8/10 trials without prompting.

2.3.2. Phase 2: Simultaneous Pulling

This phase included 12 sessions of approximately 10 trials each. Three sessions in Phase 2 consisted of 11 trials, 1 session consisted of 9 trials, and 1 session consisted of 7 trials. The same method as Phase 1 was utilized in this phase to determine which trials would have been considered toward the criterion. Two experimenters were present in this phase, each positioned on opposite sides of the apparatus. The apparatus was baited and made inaccessible to the porcupines. The tips of the extending arms were approximately 2 cm from the back of the bars. This meant that the apparatus had to be pulled approximately 20 cm to become flush with the bars. The rope was attached to the apparatus and untied so that there were two accessible ends. During this phase, both porcupines were required to be within 9 m of the front of their enclosure, within 30 cm of each other positioned side to side, and facing the apparatus to ensure they reached the rope at similar times before the rope was made accessible on each trial. Corn was used to lure them nearer to the dividing bars,

if necessary. When the porcupines were in position, each experimenter placed one of the rope ends into the enclosure simultaneously so that each rope end was an approximately equal distance from its respective porcupine on each side of the apparatus. Once the ropes were placed in the habitat, the porcupines had five minutes to obtain the rewards.

If only one subject pulled and the rope became fully detached from the apparatus so that the other end of the rope became inaccessible to the other porcupine, the rope was removed, and the apparatus was returned to its starting position and rebaited, and the trial was scored as unsuccessful. The experimenters did not provide any guidance or cueing and remained in position looking straight ahead at each other in profile to the porcupines during the trial. A trial was also considered unsuccessful when there was no response after five minutes, meaning neither porcupine had interacted with the rope via touching or biting. If the porcupines were successful, meaning that they had pulled the tray forward far enough that the baited cups on the extending arms were accessible to them through the bars of the enclosure, they received their reward. If one porcupine had not found its reward by the time the other porcupine was finishing its reward, the researchers would attempt to direct the porcupine to their reward or move the reward to the porcupine, if necessary to prevent stealing.

The apparatus was modified as described above after the first four sessions. Two extendable arms with cups for food were attached to the front of the apparatus, and a metal loop was attached near the front of the tray to thread the rope through (see Figure 3). The modifications were made for two reasons. First, the male could sometimes pull the apparatus close enough to receive rewards without the rope being detached even though the female was not pulling her end of the rope in synchrony. Second, the female porcupine continued to have difficulty obtaining food in this phase, which led to the male having an opportunity to consume her food. The modifications ensured the rope would come loose when pulled by only one individual and improved the female's ability to find the food. Once both subjects had consumed their rewards on successful trials, the apparatus was returned to its starting position and rebaited and the ropes were placed in the habitat to commence the next trial. The Supplementary Material Video S1 depicts a portion of a trial in this phase.

If the porcupines had reached the criterion of eight out of ten successful trials on four sessions across four testing days, they would have progressed to a planned delayed arrival phase.

2.3.3. Video Coding

One coder coded all trials from video for the following behaviors: success, latency to pull, latency for each to receive a reward (i.e., pulling apparatus flush with enclosure), first to pull the rope, and (in Phase 2 only), soliciting behaviors of one porcupine toward the other. For soliciting behaviors, we asked coders to identify any behaviors that a porcupine engages in that could be soliciting towards the other (i.e., behavior to elicit cooperation). We avoided specifying behaviors as we found no previous literature relevant to this species of porcupine, and we did not want to introduce bias in the coder's decisions. For the trial to be counted as a success in Phase 1, the porcupines were required to engage in the desired pulling behavior (i.e., biting the rope and pulling backward) without engaging in any other undesired behavior first (e.g., biting on the rope and pulling upwards while holding the rope with the front paws, scratching front paws on top of the rope more than once). In Phase 2, a trial was considered a success if both porcupines pulled the apparatus flush with the bars and accessed their reward. A second coder coded a randomly determined 20% of trials in each phase.

3. Results

3.1. Reliability

In Phase 1, reliability for success was represented by Cohen's Kappas; ($\kappa = 1.000$). Pearson correlations were conducted for the reliability between coders for latencies; (latency

to pull: $r = 0.998$, $p < 0.001$; latency to reward: $r = 0.998$, $p < 0.001$). In Phase 2, reliability for the following behaviors was represented by Cohen's Kappas; (first to pull: $\kappa = 0.344$; Lady Gaga soliciting behaviors towards Bedhead: $\kappa = 1.000$; Bedhead soliciting behaviors towards Lady Gaga: $\kappa = 1.000$). Pearson correlations were conducted for the reliability between coders for latencies; (Bedhead latency to pull: $r = 0.475$, $p = 0.007$; Lady Gaga latency to pull: $r = 0.816$, $p < 0.001$; latency to reward: $r = 0.938$, $p < 0.001$). The data of the primary coder were used for analyses, although we acknowledge a low level of agreement between the two coders for first to pull and Bedhead's latency to pull in Phase 2. This is likely due to Bedhead's more animated behaviors surrounding the rope, which made it difficult to determine precisely when he was pulling as defined in our coding instructions (e.g., pulling backward rather than upward).

3.2. Phase 1: Individual Pulling

The purpose of this phase was to ensure that the porcupines were capable of consistently performing the basic action required to cooperate in the later phases. Bedhead required 63 trials of individual training to reach criterion and Lady Gaga required 144 trials of individual training. Both subjects pulled on the rope in 100% of trials. For Bedhead, the average latency to interact with the apparatus was 7.42 s, the average latency to pull the rope was 10.03 s, and the average latency to receive the reward was 18.38 s. For Lady Gaga, the average latency to interact with the apparatus was 14.32 s, the average latency to pull the rope was 18.23 s, and the average latency to receive the reward was 26.31 s. Overall, Lady Gaga's response time was slower than Bedhead's response time. There was no evidence that they learned to pull more quickly over time (Figure 4).

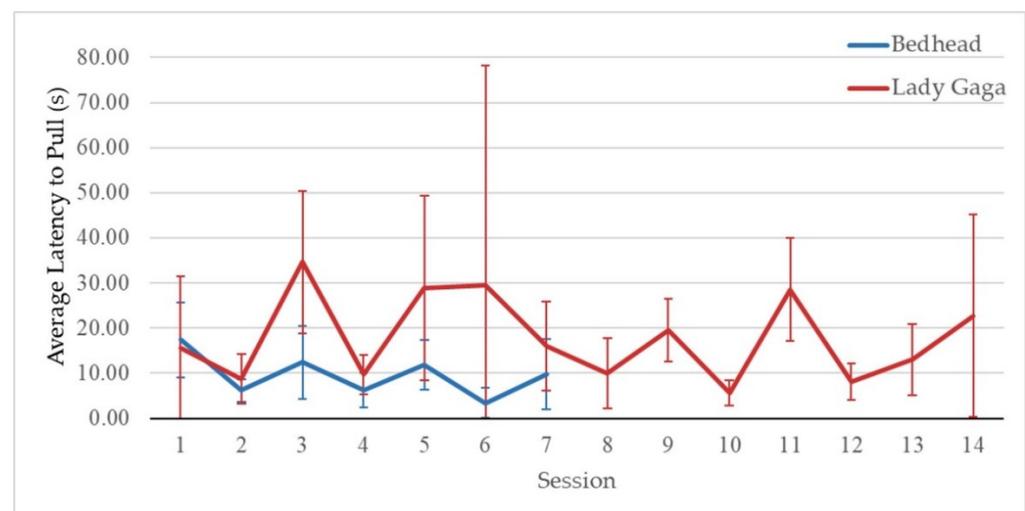


Figure 4. Average latency until first pull for each porcupine across sessions in Phase 1. Error bars depict standard deviations.

3.3. Phase 2: Simultaneous Pulling

This phase consisted of 12 sessions, the first 4 sessions (41 trials) with the first version of the apparatus, and the last 8 sessions (78 trials) with the updated version of the apparatus. However, the first 4 sessions were not included in analyses as those sessions allowed for success without cooperation. Thus, these initial sessions provided additional experience for the porcupines but did not contribute toward demonstration of cooperative behavior. In this phase, Bedhead pulled on the rope in 98.72% of trials and Lady Gaga pulled on the rope in 93.59% of trials. The average latency before Bedhead pulled on the rope was 2.40 s, and the average latency before Lady Gaga pulled on the rope was 2.62 s. Across all trials where at least one porcupine pulled, Bedhead was the first to pull in 39.74% of trials, Lady Gaga was the first to pull on the rope in 21.79% of trials, and they pulled on the rope simultaneously in 38.46% of trials. The average latency until the first pull for each

porcupine across all sessions is shown in Figure 5. There is no evidence of learning in that the porcupines did not become quicker at pulling the rope over time or increasingly likely to pull simultaneously. The average latency until success was achieved was 7.54 s.

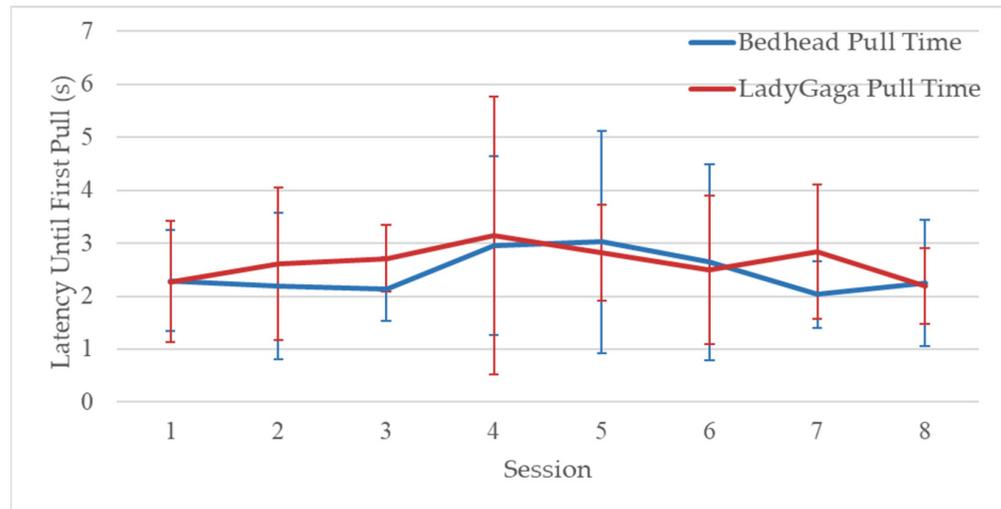


Figure 5. Average latency until first pull for each porcupine across sessions in Phase 2. Error bars depict standard deviations.

A Chi-square goodness of fit test was conducted to compare the frequency of the porcupines pulling simultaneously versus pulling separately across all sessions. All categories were expected to be equal. Overall, the porcupines were significantly more likely to pull individually ($N = 48$) than in a coordinated fashion ($N = 30$), $\chi^2(1) = 4.15, p = 0.04$. The latency until successful completion of the task is shown in Figure 6. Again, there is no evidence of learning across the sessions. As another indicator of what the porcupines might have understood about the need to coordinate their pulling, we examined the average latency for each porcupine to pull after the other porcupine pulled first. These data appear in Figure 7. Values of zero indicate that the porcupines pulled at the same time. There does not appear to be an increased likelihood to pull simultaneously with increased sessions. Figure 8 demonstrates the percentage of successful trials across Phase 2, which indicates that the porcupines did not become more likely to succeed over time. We also examined the possibility of soliciting behaviors between the porcupines. However, there were no recorded instances of such behavior.

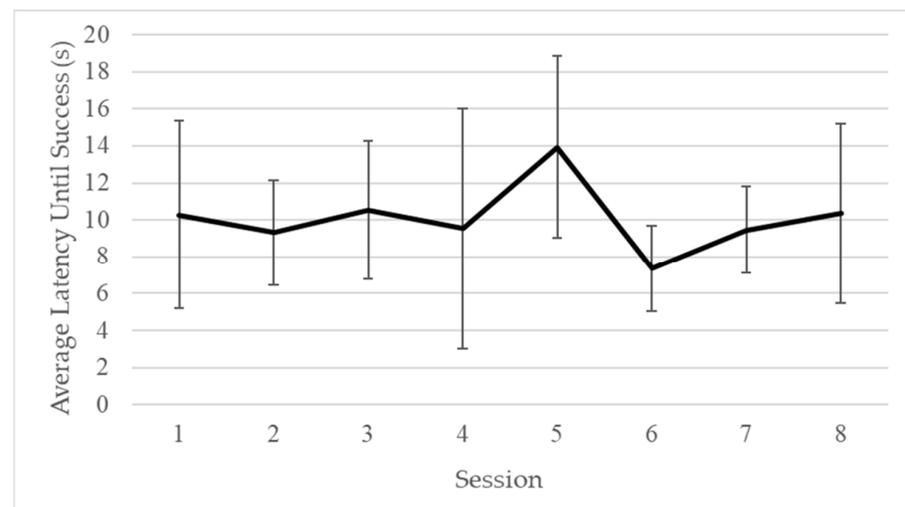


Figure 6. Time until success across sessions in Phase 2. Error bars depict standard deviations.

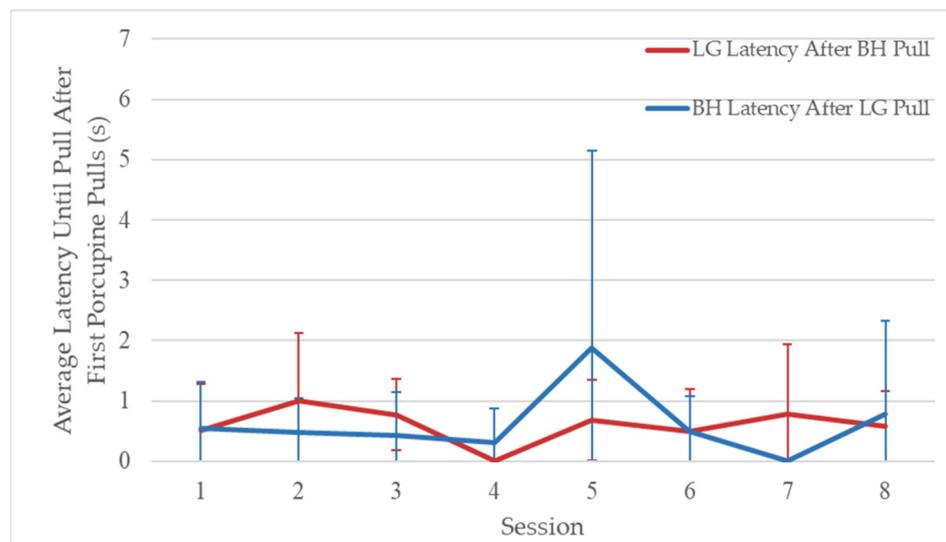


Figure 7. Latency for partner to pull after the initiating partner pulls in Phase 2. Error bars depict standard deviations. BH = Bedhead, LG = Lady Gaga.

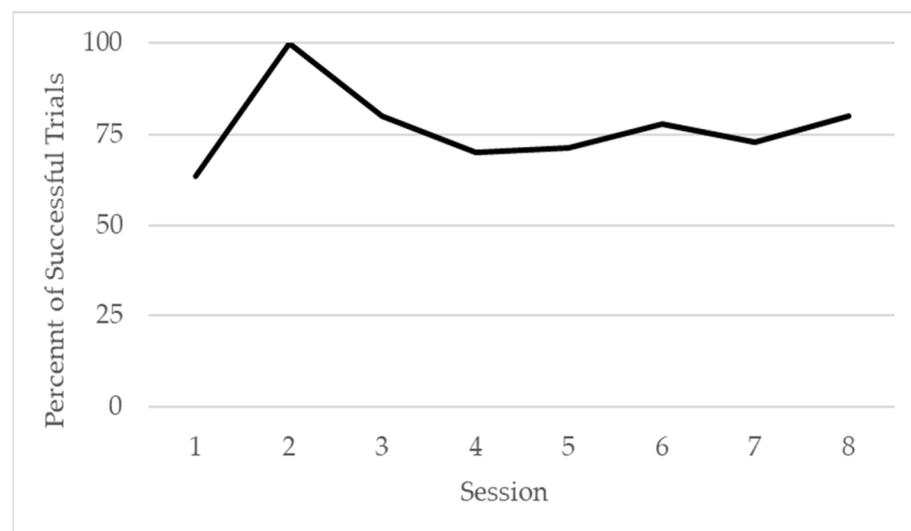


Figure 8. Percentage of Successful Trials across Phase 2.

4. Discussion

Other species widely considered good candidates for cooperative behavior, such as domestic dogs [44], chimpanzees [12] and keas [47,52] have struggled to succeed in the loose string task, although other members of the same species have succeeded [43,50,51]. The successful chimpanzees may have succeeded because the rope was longer in [50], which meant that they did not have to completely synchronize their behavior to succeed, which was also the case in the current study although it was necessary for both partners to pull in both studies. Even successful rooks [48] appeared to synchronize their pulling to external cues, rather than to their partner’s behavior. Hirata and Fuwa’s [12] chimpanzees also failed to look at their partner in the first 30 trials of the task or to engage in soliciting behaviors with their conspecific, although they did show soliciting behavior when paired with human partners. Although the porcupines tested here did not show soliciting behaviors to engage their partner, they did pull the ropes together often enough to succeed on 111 of the 119 trials presented in Phase 2. Whereas chimpanzees appeared to learn to be successful over time, the porcupines’ behavior did not appear to change across sessions.

As Hirata and Fuwa [12] noted, cross species comparisons are fundamental to determining the evolutionary roots of cooperative behavior. Here, we used this popular cooperative task for the first time with African crested porcupines—a species overlooked in studies of cooperation to date. Our findings confirm that the cooperative capabilities of the African crested porcupines can be assessed utilizing the loose string task. The porcupines were very likely to engage with the task, as both porcupines pulled on 100% of trials in the first phase and over 95% of trials in the second phase. There were individual differences in learning, as Bedhead reached the criteria for the second phase much more quickly than did Lady Gaga. Bedhead was also quicker to interact with the rope, pull on the rope, and to receive the reward compared to Lady Gaga, on average. This trend continued in Phase 2, as Bedhead was the first to pull on the rope in 46.28% of trials. No conclusions can be drawn regarding sex differences given the very small sample size. What can be confirmed is that the porcupines did learn to pull two ends of a rope to access separate rewards in most trials in the second phase, and the average time to complete the task decreased in the second phase by over 9 s for Bedhead and over 17 s for Lady Gaga compared to the average time of completion of each porcupine in the first phase. This increased speed in completing the task might be taken as a sign that the porcupines approached the task intentionally with the understanding that they could receive the rewards if the partner was in place.

As with previous implementations of the loose string task, we were able to show that porcupines could succeed in the task, and we assessed the extent to which they adjusted their own behavior to account for the behavior of their partner. Although the porcupines achieved some level of success, indicating that this task was appropriate for testing cooperation in porcupines, it did not appear that the porcupines improved their coordination on the task over time by monitoring their partner's actions. Specifically, the latency until the first pull for each porcupine, the latency until success, and the latency to pull after the first porcupine pulled did not decrease across sessions in Phase 2. We would have expected the porcupines to solve the task more quickly as they learned to intentionally coordinate their pulling as soon as the partner was in position. The conclusion that the porcupines were not attending to their partner is supported by the lack of soliciting behaviors from either porcupine toward the other and that the porcupines were significantly more likely to pull individually rather than together. Later phases were originally planned to provide porcupines the opportunity to learn to coordinate their behavior with their partner, but testing was unfortunately terminated due to COVID-19. Other species tested with delayed partner arrival conditions (i.e., when one partner has access to the rope before the other partner has arrived), have demonstrated at least some understanding of the necessity of a partner, for example, in kea [51], elephants [42], capuchins [41], domestic dogs [43], and wolves [44]. Although we were unable to assess the porcupines' understanding of the partner's role under a delayed partner arrival condition, we did not observe the signatures of this understanding in Phase 2, consistent with other researchers' observations with chimpanzees (e.g., [12]). Thus, our data suggest that porcupines may not spontaneously take the partner's role into account in the loose string task. Future work is needed to determine whether they can do so in other contexts.

Capuchins successfully cooperated more often when in visual contact with their partner [41]. The limited eyesight of the porcupines may hinder their ability to monitor their partner while completing this task, which may explain their lack of soliciting behaviors and synchronized pulling. However, other cues (e.g., auditory cues) to the partner's presence were available and the partners were positioned at a distance where they would have been visible to each other. The porcupines did not appear to decrease their time until the first pull across Phase 1 or increasingly synchronize their pulling actions across Phase 2, unlike wolves that improved their performance across sessions within every condition tested [44]. Thus, the porcupines may not integrate the feedback necessary for improved coordination across multiple trials. This may be due to the fact that porcupines do not forage cooperatively as hunting species may do. These difficulties in coordination are interesting given that previous research has pointed at the importance of strong social bonds for

cooperation in species such as wolves and chimpanzees [13,44], and the porcupines were a mated pair. Male-female dyads were found to perform better than same sex dyads in ravens, *Corvus corax* (i.e., a pair bonding species; [53]). It would be interesting to test different types of dyads in a larger sample of porcupines in future work.

Some challenges with this style of apparatus became apparent for this species. First, the poor eyesight of the African crested porcupine proved to be problematic in ensuring they were able to take the reward from the apparatus in a timely manner. The male was generally able to find the bait relatively quickly, possibly due to his quick responding, but this proved more difficult for the female. Thus, her understanding of the association between pulling and access to the food via the movement of the apparatus may have been hindered, as she may have understood the operant contingencies of the task (she received a reward after pulling the rope), but not the causal contingencies (pulling caused the reward to move closer to her) [3,54]. Allowing her extra time to find the reward would have given the male enough time to then take the reward meant for the female, which might have led to her not interacting with the apparatus in the future. Furthermore, these animals frequently participate in training procedures at the Creature Conservancy. Thus, it may be problematic for her future training if she learned that she does not receive a reward for her efforts, or if the timing of the reward is so delayed that she does not associate it with the task at hand. Thus, the reward was handed to her soon after she pulled, even though doing so might interrupt her causal understanding of the task. This is similar to the procedure used with dolphins (*Tursiops truncatus*) that were tossed a fish when they simultaneously pushed two buttons that were not connected to the delivery of food [22]. Thus, researchers have considered coordination of causally arbitrary actions as evidence for cooperation in previous research, mitigating against the concern that our methods could not evoke cooperation. Handing the reward to the porcupines on only successful trials would still allow the porcupines to learn the necessity of pulling synchronously for reward, albeit via association rather than by functional understanding (see also [43,55]).

However, there are other limitations of the current study. With only one male and one female porcupine, it is difficult to generalize to other captive members of the species, let alone their wild counterparts who have additional agency in mate selection. In particular, these porcupines were housed in a notably different environment from African crested porcupines in the wild, and this pair did not select each other as mates even though they were a mated pair. The Creature Conservancy also involves these porcupines in husbandry training, like target training; thus, they are likely more experienced with training procedures than other members of their species. However, any information that can enhance our limited understanding of porcupine cognition is of value, given its scarcity.

This research demonstrates that African crested porcupines are a promising species for the study of cooperative behaviors as they are capable of interacting with an apparatus that requires pulling as well as being capable of pulling together when given simultaneous access. They were also tolerant enough to receive rewards simultaneously and this did not inhibit participation in the task. However, given that the male was able to pull the apparatus mostly on his own in the first four sessions of Phase 2 and sometimes took the female's reward, it is possible that the female's performance was impacted by motivation. That is, a lack of motivation from sometimes not being rewarded for her effort, albeit this did not occur often and was remedied by the apparatus change. It would have been ideal to test her with other less forceful and dominant partners. Social tolerance has been cited as a necessary precursor to developing cooperative behaviors [43,56] and important for success on cooperative tasks in multiple species [17,49,50,53,57]. Future research is necessary to test porcupines' ability to learn about the role of their partner. However, given that this was the first experimental test of cooperation in this taxon, the results contribute to the ongoing understanding of the breadth of species exhibiting cooperation behaviors. This new information improves our understanding of their cognition, as there is currently no other research on their ability to problem solve.

Future Directions

To understand whether African crested porcupines can understand the role of their partner, future studies could implement a delayed partner arrival phase (e.g., [17,42,44,46,51]), which would have made the apparatus immediately available to one partner, while the other partner was just released from a distant location, requiring the individual closest to the apparatus to wait until the partner had reached the apparatus. This phase would test whether the individual understands that the partner is necessary to pull the apparatus forward and receive the reward and can inhibit their own pulling behavior in their absence. Due to the extended time until the partner arrives, it is possible that the animals may engage with the apparatus due to frustration rather than a misunderstanding of the necessity of a partner. The last phase of our experiment would have attempted to address this problem. In the planned covered rope phase, a randomly selected piece of the rope, out of the two sides available to the porcupines, would have been covered with a moveable blocker. This blocker would need to be removed before the porcupine closest to this rope end could access the rope and pull. This would allow the subject to facilitate the partner's response through allowing access to the rope.

Because porcupines burrow to den, it is possible that a method that would allow the porcupines to dig may be a more intuitive paradigm for this species. In the first phase especially, the porcupines were likely to attempt to scratch at the rope rather than pull utilizing their mouth. In future studies, an apparatus that would provide a benefit only if both porcupines dug together may be a better test of their cooperative abilities. We hope that the current results will encourage other researchers to probe the origins of cooperative behavior in other understudied species.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/jzbg3030034/s1>. Video S1: An example of a successful test trial. Bedhead and Lady Gaga pull their ropes simultaneously and each receive rewards.

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