







Lessons Learned from a Cooperative Box Experiment with Wild Baboons

William O’Hearn^{1,2*} , Louis Frank^{1,3} , Stefanie Keupp^{1,2} , and Julia Fischer^{1,2} 

¹Cognitive Ethology Laboratory, German Primate Center, Göttingen, Germany

²Leibniz ScienceCampus Primate Cognition, Göttingen, Germany

³Cognitive Neuroscience Laboratory, German Primate Center, Göttingen, Germany

*Corresponding author (Email: WOhearn@dpz.eu)

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Abstract – Choosing the right partners can mean the difference between success or failure at a cooperative task. Several studies in captivity have explored the extent to which animals can identify characteristics that make individuals better or worse at completing a joint task and whether animals use such information when choosing partners, with mixed evidence. Our study set out to test if free-ranging animals chose to cooperate with partners that provided a greater payoff in a cooperative task under natural conditions. We presented wild Guinea baboons (*Papio papio*) with paired boxes that yielded food only if operated simultaneously. The baboons could freely choose between potential partners that varied in their ability to extract food rewards from the boxes. During test trials, the baboons repeatedly solved the two-box task, though in a manner that suggests they failed to grasp the partner's role. Instead of varied partner choice, two males each monopolized access to one set of paired boxes and pulled with whichever partners sat next to them. Monopolization of the boxes did not extend to the food reward, which males allowed juveniles, females, and other males to feed on. Unfortunately, we were forced to terminate our study after only three days because the baboons behaved too aggressively toward researchers after test trials. Though we were unsuccessful in running our study to completion, our experiences can be useful for those planning cooperative field experiments in the future.

Keywords – Partner choice, Capability, Field experiment, Cooperation, Cognition, Baboons

Cooperative behaviors are powerful means by which animals work together to attain fitness benefits that individuals cannot gain alone (Hamilton, 1964). In the broadest sense, an animal behaves cooperatively when its action provides a benefit to the recipient of the action (West et al., 2007). In this sense, cooperation is defined without regard to the underlying cognitive processes or proximal mechanisms. However, cooperation can vary in cognitive complexity from two individuals co-performing similar actions, such as two female hyenas harassing a third (Smith et al., 2012), to whole groups of animals performing actions of shared labor, such as coordinated hunting in wolves and chimpanzees (Boesch & Boesch, 1989; MacNulty et al., 2014; Melis & Raihani, 2023). The first case requires only knowledge of oneself and the target, ignoring the behavior of the co-actor (Noë, 2006). The second case involves understanding the behavior of other actors and adjusting one’s behavior accordingly to form complimentary actions (Albiach-Serrano, 2015).

In our research, we aim to shed light on the cognitive processes by which animals achieve cooperation. Consequently, we consider animals as cooperators only if they act together to achieve their goals while taking one another’s behavior into account (Boesch & Boesch, 1989; Chalmeau & Gallo, 1995).

In cooperation, the willingness and capability of the partner matter just as much as those of the actor and deserve consideration in tests of cooperative exchanges.

Experimental tests of animal's abilities to cooperate, and the extent to which they understand the need to act together with a partner, are often assessed with a classic cooperation experiment: the "loose-string task" (Crawford, 1937). In this paradigm, two animals must simultaneously pull on both ends of a rope to move a platform baited with food within reach. If either individual pulls their end of the rope alone, the rope is pulled out of reach of the other actor, and the platform stays where it is – thus, simultaneous action is imperative. The loose-string task has been implemented, with modifications, in a wide range of non-human primates [chimpanzees, *Pan troglodytes* (Chalmeau & Gallo, 1995; Chalmeau, 1994; Hirata & Fuwa, 2007; Melis et al., 2006; Suchak et al., 2014)]; orangutans, *Pongo pymaeus* (Chalmeau, Lardeux, et al., 1997); Barbary macaques, *Macaca sylvanus* (Molesti & Majolo, 2016); capuchins, *Cebus apella* (Chalmeau, Visalberghi, et al., 1997; Mendres & De Waal, 2000; Visalberghi et al., 2000); cottontop tamarins, *Saguinus oedipus* (Cronin et al., 2005)], canids [domestic dogs, *Canus familiaris* (Ostojic & Clayton, 2014); wolves, *Canis lupus* (Marshall-Pescini et al., 2017); spotted hyaena, *Crocuta Crocuta* (Drea & Carter, 2009)], other mammals [elephants, *Elephas maximus* (Plotnik et al., 2011); Kune Kune pigs, *Sus scrofa domesticus* (Koglmüller et al., 2021); African crested porcupines, *Hystrix cristata* (Truax et al., 2022); giant otters, *Pteronura brasiliensis*, and Asian small-clawed otters, *Aonyx cinerea*, (Schmelz et al., 2017)], and birds [rooks, *Corvus frugilegus* (Seed et al., 2008); ravens, *Corvus corax* (Massen et al., 2015); African grey parrot, *Psittacus Erithacus* (Péron et al., 2011); Blue-throated macaws, *Ara glaucogularis* (Tassin De Montaigu et al., 2020); keas, *Nestor notabilis* (Heaney et al., 2017)].

The task has proved a valuable benchmark for cooperation in differing taxa because performance in the task can inform not only on the animal's ability to cooperate but also on how well the animals understand that success in the task is contingent on the actions of the partner (Drea & Carter, 2009; Noë, 2006). By assessing whether animals pull more often when a partner is present, whether animals wait for a partner before pulling, or the extent to which they look at, communicate with, or actively recruit the partner, researchers can learn about the way animals understand the role of the partner in a cooperative task (Melis et al., 2006; Mendres & de Waal, 2000).

The ability to choose one's partners is essential for initiating and maintaining cooperation (Claidière et al., 2015; House et al., 2014). Free partner choice allows animals to pair themselves with individuals that increase the likelihood that cooperation succeeds, or to choose partners with whom they can more equally share the spoils (Noë, 2001, 2006). Despite the importance of choosing one's partner, most experimental tests of cooperation are conducted in captivity using subject and partner in preassigned pairs – removing partner choice (Chalmeau, Visalberghi, et al., 1997; Chalmeau, 1994; Cronin et al., 2005; Heaney et al., 2017; Marshall-Pescini et al., 2017; Massen et al., 2015; Mendres & De Waal, 2000; Plotnik et al., 2011; Seed et al., 2008). Studies that allow partner choice are chiefly conducted with non-human primates and have found that subjects either fail to arrive at a cooperative solution, or only one dyad learns to solve the task, even when the animals received training (Burton, 1977; Chalmeau, Visalberghi, et al., 1997; Chalmeau & Gallo, 1995; Chalmeau, 1994; Fady, 1972; Petit et al., 1992). For example, both chimpanzees and capuchins demonstrated successful cooperation at tasks with preassigned pairs (Melis et al., 2006; Mendres & De Waal, 2000) but failed to establish cooperation in studies where subjects could choose between potential partners (Chalmeau, Visalberghi, et al., 1997; Chalmeau & Gallo, 1995; Chalmeau, 1994). In all these cases, the possibility of cooperation between individuals was limited by the social influences of the group, namely interference from dominant individuals or low levels of tolerance.

Cooperation in conditions allowing partner choice is often hampered by low levels of spatial tolerance among individuals, meaning the animals are unwilling to spend time, or eat food, close to one another (Burton 1977; Chalmeau 1994; Chalmeau & Gallo 1995; Chalmeau et al., 1997). Cooperation occurs more readily in more tolerant species, such as Guinea baboons (Formaux et al., 2023) or Tonkean macaques (*Macaca tonkeana*) (Petit et al., 1992). Even in relatively despotic societies, cooperation also occurs more often between more tolerant partners, such as kin (Silk, 2009), individuals close in dominance rank (Molesti & Majolo, 2016; Suchak et al., 2014), and friends (Bhattacharjee et al., 2023). For example, Barbary macaques were more likely to cooperate with individuals with whom they had existing strong

social bonds, compared to weak bonds, and preferred bold rather than shy partners for rope pulling (Molesti & Majolo, 2016). Such studies underline the importance of the proximate mechanisms underlying the initial choice of cooperative partners, i.e., individuals prefer known social partners bold enough to interact with an apparatus and tolerant enough to allow another to join. But what proximate mechanisms are essential for *continued* cooperation between partners? Once animals find partners with whom they can cooperate, do they prefer to continue cooperating with the same partner (attitudinal reciprocity, see de Waal, 2000; Schino & Aureli, 2009), or do they prefer the better of available co-operators, i.e., the partner that can complete a cooperative task more often or quickly than others?

To what extent animals can identify characteristics that would make individuals better or worse at completing a cooperative task is unclear. Several experiments show that animals prefer partners that cooperate over those that do not (Drea & Carter, 2009; Marshall-Pescini et al., 2017; Molesti & Majolo, 2016; Seed et al., 2008), including a recent study in which captive Guinea baboons (*Papio papio*) had a free choice of partners (Formaux et al., 2023). To our knowledge, only one study looked at non-human primate's preference for the more capable partner between two individuals who could both cooperate, i.e., the partner that would likely yield rewards more readily (Melis et al. 2006). Melis and colleagues (2006) gave captive chimpanzees the choice of two partners to help complete a loose-string task. They found that the chimpanzees preferentially chose the partner they saw succeed more often at the task the previous day. Yet, the chimpanzees' partner choice was limited compared to the options available within an open group setting. Thus, the next step in advancing the work of Formaux et al. (2023) and Melis et al. (2006) would be to test if individuals, given the full range of partner choices, choose to cooperate with partners that give them the greater payoff in a cooperative task. Ideally, such a study should be conducted in the wild to assess the animals' behavior under ecologically valid conditions.

In the current study, we presented wild Guinea baboons with access to two cooperative food boxes where they could freely choose their partners but where partners varied in the extent to which they could extract food from an experimental apparatus. After training the baboons to pull a lever alone for a food reward, we presented two sets of paired lever boxes, which only yielded rewards if both levers were pulled simultaneously. Furthermore, we designated all individuals as either "more-capable" or "less-capable" (see Methods subsection "Testing"). Pulling with a more-capable partner would yield a greater reward than pulling with a less-capable partner. Guinea baboons are generally relaxed and, excepting occasional conflicts, demonstrate extraordinary spatial tolerance, including in feeding contexts (reviewed in Fischer et al. 2017). Guinea baboons form coalitions during conflicts, exchange grooming bouts, perform extended play sessions with juveniles, and males cooperate in predator defense (Fischer et al., 2017). Moreover, Guinea baboons have been known to passively share meat from kills of infant antelopes and so demonstrate cooperation in the food domain (Goffe & Fischer, 2016). They are thus a tolerant and, on the whole, cooperative species well suited for a loose-string-style task. Additionally, a rank hierarchy among males could not be determined with certainty, and males show only weak effects of kin bias in their preferences for male social partners (Dal Pesco et al., 2021; Kalbitzer et al., 2015; Patzelt et al., 2014). As such, two of the largest factors affecting partner choices in other primate social systems, rank and kinship, seem less pertinent in this population, leaving greater opportunity for partner choice based on capability.

Our study aimed to investigate whether wild Guinea baboons could solve a two-lever task and whether they would choose the more-capable groupmates that provide more frequent rewards as cooperative partners. There were three possible outcomes for the baboons in this study: Outcome 1) The baboons could fail to learn to pull synchronously. Outcome 1 could indicate that the baboons do not meet preconditions for cooperative problem solving. Outcome 2) The baboons could learn to pull synchronously but not preferentially with more-capable partners, instead pulling with any available partner. Outcome 2 could indicate that the baboons could solve cooperative problems but either could not or would not optimize their reward outcomes, possibly because getting rewards with any frequency was sufficient. Outcome 3) The baboons learned to pull synchronously and preferentially with partners that gave food rewards more frequently, i.e., more-capable partners. Outcome 3 could indicate that the baboons are able to solve cooperative tasks and learn to identify and choose more-capable cooperative partners, resulting in better payoffs. We expected that wild Guinea baboons possessed the ability to complete a cooperative task

requiring two individuals. Furthermore, we predicted that the baboons would choose to complete the task with partners, which yielded a greater reward outcome. In other words, we expected outcome 3.

Methods

Ethics Statement

This research was conducted within the regulations set by Senegalese authorities and the guidelines for the ethical treatment of nonhuman animals set down by the Association for the Study of Animal Behaviour (ASAB Ethical Committee/ABS Animal Care Committee, 2023). Furthermore, our experiment adheres to the EU directive 2010/63/EU and national laws.

Field Site and Study Subjects

This experiment was conducted from March to May 2023 (3 months). The fieldwork was based at the field station “Centre de Recherche de Primatologie (CRP) Simenti” (13°01'34" N, 13°17'41" W) in the Niokolo-Koba National Park, Senegal. The climate is highly seasonal, with a dry season from November until May and a rainy season from June until October (Fischer et al., 2017).

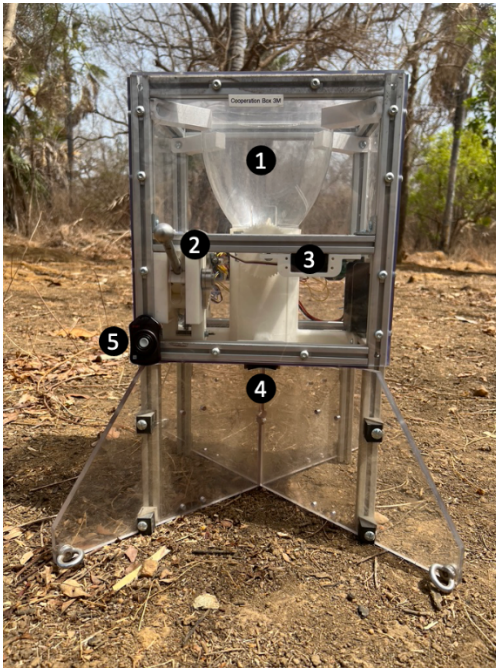
Guinea baboons (*Papio papio*) live in a nested multilevel society, the base of which are stable reproductive “units” comprised of a single reproductive male and one to several females with their offspring (Fischer et al., 2017; Goffe et al., 2016; Patzelt et al., 2014). Multiple units together form the higher nested social levels ‘party’ and ‘gang’ (Fischer et al., 2017; Goffe et al., 2016). Parties are composed of two to five units which spend most (> 68%) of their time together, while gangs are composed of two to four parties that travel and forage together regularly (12-68% of their time) (Patzelt et al., 2014).

The study subjects were wild baboons belonging to a single gang which were fully habituated to the presence of human observers. The gang comprised four parties: 5, 6I, 13, 15. Party 5 comprised four adult males and ten adult females, with three sub-adult males and twenty-eight juveniles arranged in three units (Table S1). Party 6I comprised three adult males, six adult females, two subadult males, one subadult female, and nine juveniles arranged in five units. Party 13 comprised four adult males, nine adult females, two subadult males, two subadult females, and eleven juveniles, which were part of three units. Party 15 comprised one adult male, one adult female, and one juvenile arranged in one unit. Subjects were individually identified by natural markings, body shape and size, and radio collars.

Field Experimental Procedure

Apparatus

The apparatus we used in this experiment was a food box consisting of a cereal dispenser with baboon-proofing modifications. The box (50.5 cm x 29 cm x 23 cm) had a skeleton of aluminum extrusions paneled with 5 mm clear polycarbonate sheets (Figure 1). The box consisted of an enclosed upper compartment containing the food dispenser (Figure 1, Element 1), lever assembly, servo, battery, control module, speaker, and accompanying wires. The upper compartment stood on aluminum legs attached to two 10 mm thick transparent plastic panels that crossed beneath the upper compartment. A steel lever, 11 cm long, protruded from the front side of the upper portion of the box (Figure 1, Element 2). When the lever was pulled from the full upright position to the lowest position, a servo was triggered (Figure 1, Element 3), which spun a gear in the cereal dispenser, releasing shelled peanuts to fall out the bottom of the upper compartment (Figure 1, Element 4) onto the ground in front of the box, where the operator baboon was seated. In this way, the lever operator had priority access to food rewards. The box also had a single-button remote control that could lock and unlock the box from a distance and make the box switch between different reward patterns in either the training or testing mode (Figure 1, Element 5).

Figure 1*Single Food Box with Lever*

Note. 1) the chamber where unshelled peanuts were stored before being released, 2) the lockable lever and ratcheted accompanying assembly, 3) the servo and gear assembly that spun to release peanuts from the upper peanut chamber, 4) the hole from which peanuts could drop to the ground in front of the operator, 5) the single button remote used to lock/unlock the lever (one click) or switch the box between modes (two clicks). For more details on the hardware, firmware, construction, and operations of the food box see the GitHub organization <https://github.com/CooperationboxExp> and accompanying repositories: Hardware DOI:10.5281/zenodo.14178666, Firmware DOI:10.5281/zenodo.14178677.

Training

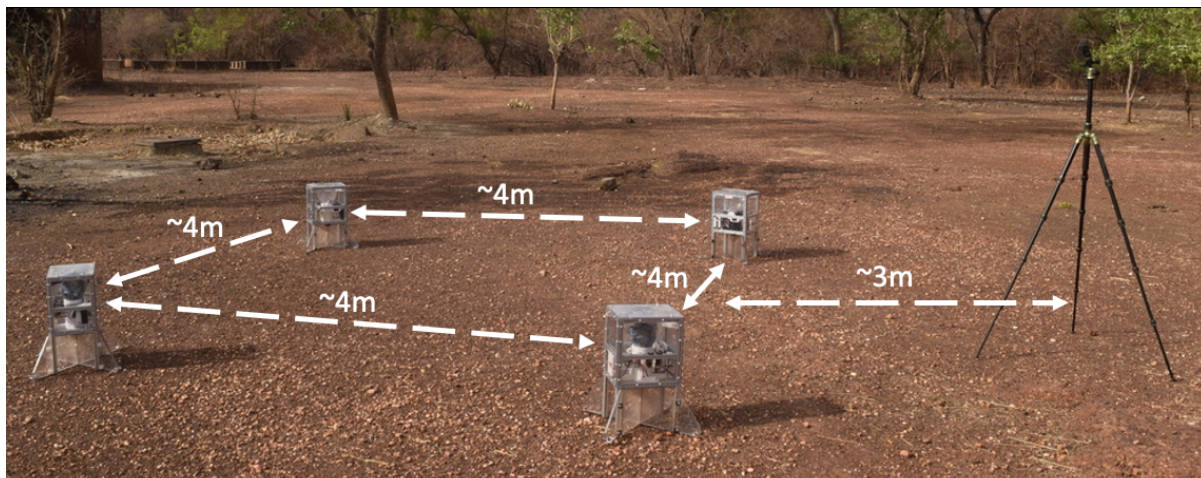
In the training phase, we aimed to train as many baboons as possible to operate the boxes’ levers. All adults and sub-adults of both sexes were deemed eligible for training. Individuals were first trained with a standard reward regime, where one lever pull resulted in one reward. We were concerned that once in the testing phase, if the baboons were accustomed to receiving rewards for each lever pull, they would quickly become frustrated when their early non-synchronous pulls were not rewarded. Once frustrated the baboons could revert to shaking the boxes or simply give up interacting with the boxes all together. To avoid this possibility, we sought to increase the baboon’s frustration tolerance by introducing a random reward schedule to the training. Individuals who completed the standard reward training were deemed to have learned the mechanics of the box and were then switched to a random reward schedule. In random mode, the box would choose a number between two and six for each reward. Once the baboon pulled the lever the desired number of times, they would receive a reward. An experimenter could switch between modes using the remote depending on whether the individual at the box was at the standard or random schedule stage of training.

For each training session, researchers found the baboons at their sleeping tree in the morning and placed four lever boxes in a rough square on the ground with ~ 4 m between each box (Figure 2). Boxes were staked to the ground to prevent the baboons from knocking them over, and a tarp was placed over them until the start of the session. Sessions were recorded with a GoPro Hero 8 with a wide-angle setting mounted on a tripod ~ 3 m from the boxes (Figure 2). Each box contained ~ 1 kg of peanuts. Once all boxes were staked down, the tarps were removed, giving the baboons access to the boxes. Each box was operated

by a separate researcher with a remote control. The operator of each box used shaping techniques to encourage individuals at the boxes to produce behaviors incrementally closer to the desired behavior. Operators rewarded desired behavior by pulling a string tied to the lever, which manually released a handful of peanuts (~ 9 g) as a reward. An individual in training could be rewarded first for approaching the box, then for inspecting the lever of the box, then for touching the lever, then for partially depressing the lever, and then for fully pulling the lever. During the training phase, 34 individuals approached the boxes (twelve adult/subadult females, thirteen adult/subadult males, and nine juveniles). Twenty-two of those individuals (five adult/subadult females, nine adult/subadult males, and nine juveniles) achieved at least one unassisted full pull of the lever (median number of pulls was 12). Operators communicated verbally with one another to track the progress of each individual’s training if individuals switched boxes during the training session.

Figure 2

Training Setup



Note. Four lever boxes in the training mode setting filmed by a nearby GoPro on a tripod. In the case of an active training session, each box had a researcher assigned as operator holding the box remote to switch between standard and random reward schemes, as well as a string to manually pull the lever to reward baboons being trained.

An individual met the training criterion, and was locked out of further pulls, if they fully pulled the lever themselves ten times in a single training session (nine individuals met this criterion: seven adult/subadult males and two juveniles). On the second day, if an individual met the criterion of ten pulls, they were considered fully trained on the standard reward regime and were allowed an additional ten pulls with the random reward regime. On all subsequent days an individual that was fully trained on the standard reward regime began training sessions with the random reward regime and was cut off at ten rewards. Any individual who received ten rewards in random mode on two separate days was considered fully trained. We originally planned to have 12-16 fully trained individuals, but it became apparent that no more than the six most invested adult males would reach the criterion. Hence, we moved on to the testing phase with those animals fully trained at that time.

Testing

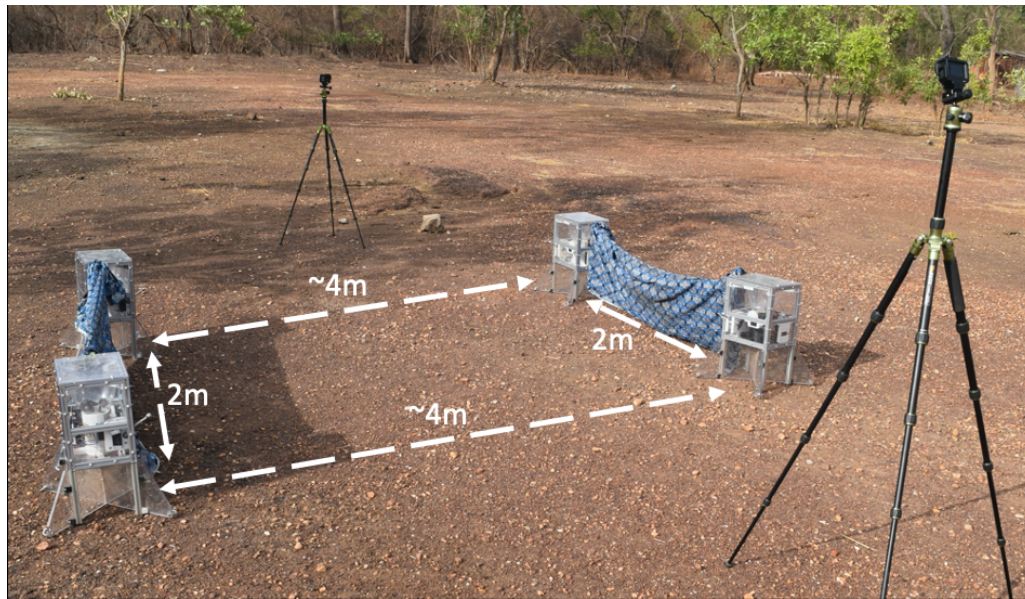
At the start of the testing phase, each member of the gang was assigned either the role “more-capable” or “less-capable”. Their role determined the possible payoffs for themselves and their partners in testing phase trials. All individuals who did not achieve full training in the training phase were designated as less-capable – this includes juveniles and individuals who never approached or interacted with the boxes. Of the six fully trained individuals, we selected three to be more-capable and the other three were designated

less-capable. In determining which of the six would be more-capable, we avoided individuals with strong pre-existing relationships, i.e., male-male dyads who most frequently approached and groomed one another in focal observations from the two months leading up to the experiment. We made this decision to reduce the probability that two more-capable individuals operated the boxes together at the start of the experiment and never experienced another partner pairing or payoff scheme. If two more-capable individuals were to operate the boxes together until the end of the testing phase, we would have no way to determine if their preference for one another was a result of their highly rewarding payoff scheme or a result of their existing relationship. Such a circumstance would also limit the opportunities of other baboons to operate the boxes with a more-capable individual. Fewer available more-capable partner pairings would reduce other individuals' experience with the higher payoff scheme and undermine the experiment by making it more difficult to determine if individuals' choices of cooperative partners were a result of partner capability (see below for details of possible payoff outcomes). To avoid this outcome, we chose as more-capable individuals, two infrequently associating males in party 6I (CSC and QNN) and one male in party 5 (SPC). Once the "capability" of all individuals was assigned, we began test presentations.

As in the training phase, for test sessions researchers found the baboons each morning and set out four boxes nearby. The key difference between training and testing was that in the testing phase the boxes were wirelessly linked to communicate with one another and physically linked by a 2 m long hanging piece of blue African wax fabric (Figure 3). The boxes were electronically paired such that two paired boxes would only release rewards if their levers were pulled within five seconds, i.e., a "synchronized pull". The number of synchronized pulls necessary to yield a reward differed based on the "capabilities" of the two individuals pulling the levers. For a more-capable/more-capable pair, a single synchronized pull yielded a reward. For a more-capable/less-capable pair, three synchronized pulls yielded a reward, and for a less-capable/less-capable pair, six synchronized pulls were needed to generate a reward. The boxes automatically locked for five seconds after every successful reward. The boxes also locked for two minutes after twelve successful synchronous pulls to discourage individuals from monopolizing the boxes and encourage individuals to move between boxes. Trial time was fixed at 30 minutes from the time the boxes were uncovered. Thus, to maximize the amount of food they received within the 30-minute trial time, individuals were incentivized, first, to learn to pull synchronously with a partner and, second, to choose a more-capable partner over a less-capable partner. Pulling with a more-capable partner would reduce the number of pulls and time needed to get a reward and increase the number of rewards acquired before the two-minute lock-out. A less-capable individual who choose a more-capable partner over a less-capable partner could halve the number of pulls needed per reward (from six to three) and double the number of rewards before lock-out (from two to four). A more-capable individual could do even better by choosing a more-capable partner over a less-capable partner, reducing by two-thirds the number of pulls needed (from three to one) per reward and tripling the number of rewards before lock-out (from four to twelve). The reason more-capable individuals could increase their return more than less-capable individuals is partly numeric. We assumed that the difference between one pull and two pulls per reward would not be sufficiently conspicuous. Hence, we opted for three, partly to offset the relative scarcity of opportunities for a more-capable individual to pull with another more-capable individual.

Test trials were recorded using two GoPro Hero8 cameras with a wide-angle setting facing one another on either side of the four boxes, recording a 360-degree view of the testing site (Figure 3).

Figure 3

Testing Setup

Note. Two sets of paired boxes connected by hanging African fabric placed between two inward facing GoPros on tripods. In the case of an active testing session, each set of paired boxes had a researcher assigned as operator holding the box remote to switch between setting for more-capable/less-capable, more-capable/less-capable, and less-capable/less-capable settings depending on the capability of the partners present at the paired boxes.

Video Coding

We extracted the identities of all individuals who participated in synchronous pulls from trial video recordings. We examined the animals’ behavior in recordings to see: 1) whether individuals pulled more often if a partner was present at the apparatus (Drea & Carter, 2009; Mendres & De Waal, 2000; Suchak et al., 2014; Visalberghi et al., 2000), 2) how often individuals looked at their partner during the cooperative situation (Chalmeau, Lardeux, et al., 1997; Chalmeau & Gallo, 1995; Hirata & Fuwa, 2007; Mendres & De Waal, 2000), and 3) whether individuals actively recruited a partner to join them at the apparatus (Hirata & Fuwa, 2007; Melis et al., 2006) (Table 1).

Table 1

Ethogram of Behaviors Measured in the Video Analysis of Trial Recordings

Behavior	Description
Recruitment behavior	A stereotyped “head turn and stare” behavior used recruit others to form a coalition or for individuals to greet others and move together toward the boxes (Dal Pesco & Fischer, 2023)
Pulling alone	Pulling the lever on one box when there was no individual present in front of the second paired box
Attention toward paired box	All instances of communication or repeated or sustained head orientation directed toward an individual at the paired box.

Results

Training Phase

The training phase of the study ran for ten days between March 27 and April 11, 2023. Only six individuals met the standard and random training criteria and were considered fully trained. We were limited to a relatively small number of individuals for three reasons: 1) box monopolizing males, 2) disinterested females, and 3) the loss of interest of one party. After the first four days of training, the primary males who had shown early interest in the boxes and had progressed furthest in training stopped leaving the boxes after completing their ten pulls. Instead, these males stayed, pulled the locked lever, or moved between boxes, trying levers, thereby preventing other individuals who still needed training from accessing the boxes. At the beginning of the training phase, our goal was to train around 12-16 individuals to operate the boxes. From this pool, we aimed to designate approximately one-third as more-capable individuals. However, because the box-monopolizing behaviors of the primary males hindered training, we were forced to move forward with the individuals who were able to access the boxes long enough to be trained. Furthermore, we found that females made poor training participants. Females showed little interest in pulling the lever and instead focused on eating food rewards already on the ground around the boxes. Many could pull the lever but chose to eat instead. Only if there was no male or juvenile available to pull the lever would females pull themselves. The highest number of pulls a female completed in a single day was six. Since 29 of the 48 adults and subadults we wanted to train were female (60.4%), this substantially limited our training options. The final limiting factor in training was the loss of interest from Party 13. Initially, we presented the boxes when all four parties in the gang were present, i.e., 5, 6I, 13, and 15. Members of all parties showed interest and interacted with the boxes on day one. But from day two of training onward, Party 13 was completely absent from training sessions. They were present when the boxes were set up but left shortly after members of the other parties began operating the boxes. Party 13 represented 17 of the 48 adults and subadults we worked with (35%).

Testing Phase

The test phase ran from May 9th to 11th 2023. The test phase was terminated after three days because the baboons' behavior toward researchers when the boxes were removed at the end of trials was deemed too aggressive to continue safely. In the three trials conducted before the termination of the study, 116 rewards were dispensed (day 1: 35, day 2: 40, day 3: 41). The baboons were, in fact, highly successful at the task, achieving a reward on average every 129 s at one set of boxes and every 74 s at the other. Nineteen dyads involving seven adult males, two adult females, one juvenile male, and five unknown juveniles achieved synchronous pull rewards (Table 2). Two adult males, one from each of the large parties, dominated the trials, each taking control of one set of paired boxes (Table 2). One adult male (SPP) from Party 5 received 85% (64/75) of the rewards obtained from box set A. Thirteen different dyads were rewarded at box set A and SPP was a member of nine of these trials. His main partner was another adult male (SPC) from Party 5, with whom he got 53% (40/75) of rewards from box set A. On the other set of boxes, box set B, CSC, an adult male from Party 6I, received 98% (40/41) of the rewards and was part of five of the nine dyads that received rewards from this box set. His main partner was KVU, a large juvenile male from Party 6I, with whom he got 85% (35/41) of rewards from box set B. Interestingly, unique dyads only ever used one of the two sets of boxes, never at both.

Table 2*Summary Table of Dyads that were Rewarded for Synchronous Pulls*

Dyad	Rewards gained	Capability	Party	Sex	Age
SPC_SPP	40	MORE_LESS	5_5	M_M	Adult_Adult
CSC_KVU	35	MORE_LESS	6I_6I	M_M	Adult_Juvenile
SPP_MKA	9	LESS_LESS	5_15	M_M	Adult_Adult
QNN_SPP	6	MORE_LESS	6I_5	M_M	Adult_Adult
SPC_MJV ⁽¹⁾	4	MORE_LESS	5_U	M_M	Adult_Juvenile
SPP_ABU	4	LESS_LESS	5_5	M_M	Adult_Sub_adult
SPC_MKA	3	MORE_LESS	5_15	M_M	Adult_Adult
QNN_MKA	2	MORE_LESS	6I_15	M_M	Adult_Adult
CSC_TRK	2	MORE_LESS	6I_6I	M_M	Adult_Adult
SPP_MJV ⁽¹⁾	2	LESS_LESS	5_U	M_M	Adult_Juvenile
CSC_SPP	1	MORE_LESS	6I_5	M_M	Adult_Adult
CSC_QNN	1	MORE_MORE	6I_6I	M_M	Adult_Adult
CSC_MJV ⁽¹⁾	1	MORE_LESS	6I_U	M_M	Adult_Juvenile
SPP_KVU	1	LESS_LESS	5_6I	M_M	Adult_Juvenile
SPP ⁽²⁾	1	LESS_	5_	M_	Adult_
SPP_ANE	1	LESS_LESS	5_5	M_F	Adult_Adult
SPP_LSL	1	LESS_LESS	5_5	M_F	Adult_Adult
SPC_ANE	1	MORE_LESS	5_5	M_F	Adult_Adult
ABU_MJV ⁽¹⁾	1	LESS_LESS	5_U	M_M	Adult_Juvenile

Note. ¹MJV refers unidentified middle juvenile male. As they are unidentified their party is U for unknown. ²This row is from one instance where SPP pulled the levers on both linked boxes within 5 seconds of one another.

Of the 116 rewards given in the three days, less-capable/less-capable dyads received 19, more-capable/less-capable dyads received 95, and only one was received by more-capable/more-capable dyads (Table 2). The prevalence of more-capable/less-capable dyads is likely due to the greater number of possible more-capable/less-capable compared to more-capable/more-capable dyads in the gang (Possible dyads: 3 more-capable/more-capable, 117 more-capable/less-capable, 741 less-capable/less-capable).

During trials, the individuals at the boxes paid little attention to others around them. The baboons' attention was fixed on the box where they sat or on the peanuts just around it. Males would look up from their task to greet a male or female who approached to sit and eat with them. However, the only attention we saw directed toward the operator of a paired box was when individuals would look toward the paired box, then leave their box to pull the lever of the paired box, greet its operator, and eat from peanuts on the ground nearby. We did not observe communication between individuals at boxes preceding synchronous lever pulls.

Discussion

We observed that specific males tended to monopolize the boxes, while females mainly concentrated on co-feeding to the point of ignoring the lever on the test apparatus. Moreover, one of the three parties of baboons lost interest in engaging with the task altogether. Thus, we trained fewer individuals to use the test

apparatus boxes than we intended. In the testing phase, we terminated the study after three days because the baboons behaved too aggressively towards the researchers during test trials. The resulting early termination of the experiment leaves us with minimal results to answer our initial question of whether wild Guinea baboons could solve a cooperative task and choose the more-capable partner for the cooperative task. Being aware of these limitations, we will interpret the few data we have and discuss what we learned from conducting this experiment.

Cooperation

The first goal of this study was to test if wild Guinea baboons could solve a cooperative two-lever task. We found that the baboons were able to solve the task by pulling the levers of the paired boxes synchronously, i.e., within five seconds of one another. However, their success does not necessarily mean they understood the cooperative nature of the task.

In our study, whether or not individuals pulled the lever appeared to be independent of the presence of a partner at the paired box. There were numerous instances of individuals, including the males most successful at getting rewards, pulling the lever in the absence of a partner. This evidence alone is inconclusive, as learning not to pull without a partner present takes time (Sigmundson et al., 2021), and even in experiments where the animals clearly understood the partner's role, pulling without a partner never fully disappeared (Cronin et al., 2005; Mendres & De Waal, 2000; Suchak et al., 2014). However, the baboons also did not appear to pay particular attention to the individual or individuals sitting at the box paired with theirs. The generally noisy atmosphere of the trials and the high level of activity around the boxes may have contributed to this inattention. Lastly, among the frantic scenes of the test trials, we saw no evidence of the baboons actively recruiting individuals to join them at their box or the paired box. We would have expected to see, for example, individuals use the exaggerated “head turn and stare” behavior to recruit others to form a coalition or for individuals to greet others and move together toward the boxes (Dal Pesco et al., 2021). Taken together, our observations of the baboons pulling alone, their absence of attention to the other box, and the absence of recruiting behavior, strongly indicate the baboons did not understand that the task they were rewarded for required coercion with another individual. It seems more likely that the baboons were pulling repeatedly until they got a reward, a strategy they learned in the random reward regime portion of the training phase.

The baboons' preference for an individually rewarding strategy is consistent with the actions of the poorly performing individuals in a recent study of cooperation in captive Guinea baboons (Formaux et al., 2023). This previous study found that when given the choice of rewarding a partner and themselves or only rewarding themselves, eight of 18 captive Guinea baboons showed a strong preference for rewarding themselves and the partner (Formaux et al., 2023). The authors' explanation for the 10 baboons that did not show a preference for cooperation was that those individuals were unaware that their actions were connected to the outcome for their partner and *vice versa*. These individuals had previously performed poorly in a different task involving a partner (Formaux et al., 2023). It appears our baboons similarly failed to recognize the role of the partner and acted alone. It is conceivable that, given more time, the baboons we studied would have worked out the cooperative aspect of the task. However, it is also possible they would continue using their “pull until rewarded” strategy indefinitely because it provided them with a sufficient stream of peanuts.

It is worth noting the one previous cooperation experiment conducted with wild Guinea baboons by Fady (1972). In their study, peanuts were placed under rocks of various sizes, including stones too large for the baboons to move singly. The goal of this study was to see if the baboons would spontaneously cooperate to move the heavy stones and gain the peanuts beneath. The baboons did not cooperate. A handful of females learned to dig under the rocks to reach the peanuts, and males learned to chase these females away and obtain their spoils. The males did not learn the digging behavior themselves. This paper was published in French in a not-so-well-known journal. Had we found the paper before running our experiment, we could have benefitted from their experience. Now, we can only remark on the striking similarity of our outcomes. In both studies, the wild Guinea baboons proved adept at using individual strategies to acquire

food rewards meant to be obtained via cooperation. In both studies, peanuts greatly excited the males into exerting their priority of food access to the point that it prevented cooperation. In our study, the males' monopolization of the task prevented us from training more individuals and eventually halted our experiment. In both studies, males proved highly inflexible in their approach to solving the task and lacked perseverance, quickly giving up when a behavior failed to provide immediate results. We corroborate the finding of Fady (1972) that Guinea baboons appear to be "practically incapable of instrumental cooperation in natural conditions" (p. 164).

In our study, the success of the baboon's "pull until rewarded approach" meant they never experienced failure or frustration in the cooperative task that may have forced them to change their approach. If the baboons had fewer successes in the testing phase, they might have been motivated to pay greater attention to the situation around them and discover the partner's role. Or perhaps they would simply have become frustrated and given up. In either case, the ease with which the baboons used an individually driven approach to succeed at our cooperative task marks a failure of our study design.

Capability

The second goal of this study was to test whether the baboons would choose partners whose cooperation yielded a greater payoff (more-capable) over partners who provided a lesser payoff (less-capable). Since the baboons appeared not to recognize the function of the partner in the task, they could not then determine that they were rewarded differently with different partners. Indeed, we saw no evidence that the baboons pulled preferentially with more-capable over less-capable individuals. The high incidence of more-capable/less-capable dyads in the test trials (95/116 rewards given) simply results from the two individuals most often at the boxes, SPP and CSC, being more-capable, while all but one other potential partner in the gang were less-capable. More generally, the constant presence of two more-capable males marks how little the trial set-up reflected the atmosphere of cooperation with free partner choice that we desired. In actuality, most individuals had the choice between one of two free boxes, which would pair them either with SPP or CSC. In choosing between the two, most individuals chose the male that belonged to the same party as themselves, which aligned with the tendencies of party members to congregate around one set of boxes.

Social Tolerance

Individuals SPP and CSC retained near-constant access to the boxes and displaced other individuals whenever they approached a box. Still, they also demonstrated a high degree of tolerance regarding food rewards from the boxes. During trials, individuals co-fed despite the food reward being dispensed into a narrow space directly before the lever operator. In the case of one dyad, we even saw co-lever-pulling – adult males from different parties sitting together, alternating pulls on the lever and then sharing the reward. It was common to see two adult males sitting shoulder to shoulder eating peanuts while one or two females and several juveniles took handfuls of peanuts from the ground in front of the males. In this way, the males most interested in the boxes demonstrated aspects of despotism by monopolizing access to the boxes themselves. They simultaneously demonstrated a high degree of tolerance by allowing others to feed on the food the boxes produced.

The apparent inconsistency of Guinea baboons monopolizing a food source but not the food itself may derive from the interaction of natural food tolerance in the species with the priority of resource access retained by adult males (Fady, 1972). The habitat of Guinea baboons in our research area has a high carrying capacity, providing the baboons with access to a range of food sources and water year-round (Zinner et al., 2021). As a result, Guinea baboons fight over food sources less often than closely related *Papio* species living in less resource-rich environments (Davidge, 1978; Kummer, 1968), and co-feeding at food sites is a part of their natural behavior (Patzelt et al., 2014). For example, the baboons sometimes come across small termite colonies early enough in their establishment that the baboons can break into the colony's interior. When this happens, individuals ranging in age and sex classes sit around the colony, within 1 m of

one another, and pick out the large warriors and larvae. Like in our study, the baboons co-feed on a nutrient-rich food source in a small space. This is not to say there is no competition for food in Guinea baboons. Competition is present, usually in the form of adult males displacing females and juveniles from a desired food item like freshly fallen coconuts. However, it is rare to see direct conflict over food among males, perhaps because of the strong male-male relationships that hold the units of a party together (Dal Pesco et al., 2021; Goffe et al., 2016). Thus, an adult male with access to our food boxes is unlikely to be displaced from the box. In addition, if a male knows how to pull the lever, he can access all the peanuts visible in the box. The combination of adult males' priority of food access and the species' general tendency to share food sites likely led to the situation we observed: males sat at the boxes, pulling while others fed around them.

The mixed monopolizing and sharing behavior of Guinea baboons might merit further investigation. An experimental approach might be to present food items varying in their desirability and shareability to examine the circumstances under which food sharing occurs. One could also provide specific individuals with highly desirable foods to test which classes of individuals can retain such an item and who must forfeit. An alternative approach could be to observe the Guinea baboon's natural behavior around highly desirable food items, such as in vertebrate meat-eating events and record how sharing and monopolizing behavior plays out in those contexts. It may also be interesting to see if there is a similar enmeshing of monopolizing and sharing behaviors in other tolerant species living in resource-rich environments. Do they also monopolize access to a food source but share the food itself?

Study Design Issues

In some ways, our study design failed to incite the baboons to cooperate because they succeeded at the presented task with an individual-driven approach. One aspect that likely contributed was the five-second window for synchronous pulls. Five seconds was too long, making it too easy for the baboons to make synchronous pulls by chance. If we were to re-run this experiment, we would shorten the synchronous window to 1 s or even less (Jaakkola et al., 2018). We would also consider modifying the set-up to more closely imitate the loose string paradigm where solitary action leads to the mechanism locking. This would discourage repeated solitary pulling by preventing either individual from getting rewarded until the levers reset. However, even with these additions, the study design may not succeed, and an alternate approach might serve better for testing cooperation in the wild.

Another choice that negatively impacted the success of the study was that the boxes were placed too far apart. The distance between the boxes was established to prevent one baboon from rushing between the boxes and pulling both levers alone – a behavior baboon SPP performed once in the test phase. However, putting the boxes closer together may have made it easier for the baboons to recognize their partner's role in the task. Furthermore, creating a physical connection between the two levers, for example, a bar stretching from one lever to the other, may have made the link between the boxes more obvious and encouraged the baboons to pay greater attention to their neighbors' actions. The need in our set-up for a physical connection between boxes highlights a disadvantage of using levers compared to a pullable rope linked to a moving tray (Mendres & de Waal, 2000; Molesti & Majolo, 2016). With the levers, the animals cannot see any physical outcome of their actions other than the dispensing of a reward. Whereas with a rope and tray the animals can see how the tray moves when they or their partner pulls on the rope and learn to adjust their actions for incremental improvement toward success.

The baboons' aggressive reactions at the end of test phase trials likely resulted from only a small number of individuals being able to access the high-quality food reward in the boxes. Trials in the testing phase were shorter than in the training phase, and more conditions had to be met for a reward of peanuts. As a result, fewer peanuts were dispensed in test trials, leaving the boxes partly filled with peanuts at the trial's end. Baboons who were accustomed to eating peanuts in the training trials but could not eat them in test trials were thus left frustrated and acted aggressively toward the experimenters when they removed boxes that still contained peanuts.

The co-feeding behavior of the baboons acted as an additional unexpected confound in our study design. The premise of our experiment was that the baboons could acquire a fixed amount of food based on their partner's ability to pull the lever synchronously and their capability. These two things determined how fast an individual could get food from the box as well as the maximum amount of food an individual could acquire in the 30-minute trial time. That was assuming a baboon ate all the food from the box. However, the baboons allowed others to eat the food reward with them. Some allowed only juveniles, some allowed juveniles and females, and some co-fed with other males. The variation in sharing we observed both between and within individuals disrupts the study predictions quite severely because the amount of food an individual ate was not solely dependent on their partner's abilities, but also on how much they tolerated co-feeding for a given reward. In this regard, the tolerant nature of the baboons coupled with their "pull until rewarded" strategy disrupted the reward scheme of the design and divorced partner contingent cooperation and partner capability from the size of the reward outcome.

Future Research

There are many elements in animal's natural environment that confound traditional experimental paradigms. This must be considered when taking methods used with captive animals into the field. Studies of cooperation in captivity with increased control over subjects are valuable for isolating the underlying cognition behind contingent cooperation and partner choice. However, to understand the interplay of partner interactions, like cooperative and partner choice, we must examine animals' behavior in their natural setting with all its complications. Doing so may mean coming to terms with failure, as in our case, and working to improve our study design's flexibility and robustness. Fortunately, new technologies and methods are available to help tackle the challenges of the field. Approaches using new tools like radio-frequency identification devices (RFID) (Firth et al., 2015; Kings et al., 2023) and multiple data type collecting collars (Farine et al., 2017; Harel et al., 2020) allow researchers to automate experimental set-ups for whole populations of animals and collect data semi-continuously over months. Studies implementing these tools have already begun yielding results. A recent experiment used wild jackdaws (*Corvus monedula*) ringed with RFID tags with two feeders equipped with RFID readers to run an automated social coordination task with a whole population for four months (Kings et al., 2023). Experimenters split the population into two treatment groups. They programmed the feeders to give low-quality food to birds alone, high-quality food to simultaneously landing birds of the same group, and to lock and provide no food to simultaneously landing birds of different groups. Over the course of the study, the birds learned to favor social associations with members of the same treatment group with whom they received high-quality food. Studies like these may present new avenues for modifying our traditional experimental designs to succeed at scale in the natural environments of the animals we study. In our study case, automate feeders and tagged individuals would allow us to leave the boxes in the baboons' home range continuously for months. We could remotely record if over time individuals learned to approach and operate the boxes more frequently with more-capable partners that yielded more frequent rewards.

Conclusion

We set out to conduct an ambitious cooperation and partner choice experiment in wild Guinea baboons. We found the baboons could solve our two-lever task without the use of contingent cooperation. Our experimental design proved insufficiently robust to determine if the baboons would choose more-capable cooperative partners for the task because of the baboons' aggressive attitudes during trials. Despite our experiment's early termination, our experience can be informative for researchers planning cooperation experiments with wild animals. Testing experimental paradigms in the field with all the challenges wild environments present is essential for testing our understanding of animal behavior.

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Data Availability Statement: There is no dataset associated with this manuscript. However, materials relating to the design, construction, and operation of the boxes used in this experiment can be found at the following GitHub organization <https://github.com/CooperationboxExp>, and its repositories: Hardware DOI:10.5281/zenodo.14178666, Firmware DOI:10.5281/zenodo.14178677. In addition, links to a YouTube playlist of video exemplars are available in the repository. All researchers who appear in the accompanying videos gave their informed consent with regard to the video’s distribution.

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Supplementary Materials

Table S1

The Unit and Party Associations of the Guinea Baboons within the Simenti Gang at our Field Site in Niokolo Koba National Park in the Second Quarter of 2023

Name	ID	Sex	Age category	Party	Unit
Lupin	LPN	M	Sub-adult	5	LPN
Nairobi	NRB	F	Sub-adult	5	LPN
Asha	ASA	F	Adult	5	SPC
Fanta	FTA	F	Adult	5	SPC
Kalissi	KLS	F	Adult	5	SPC
Sally	SLY	F	Adult	5	SPC
Spencer	SPC	M	Adult	5	SPC
Amidala	AMD	F	Adult	5	SPP
Anne	ANE	F	Adult	5	SPP
Liselotte	LSL	F	Adult	5	SPP
Marleen	MLE	F	Adult	5	SPP
Sepp	SPP	M	Adult	5	SPP
Jyn	JYN	F	Adult	5	VDR
Rey	REY	F	Adult	5	VDR
Vador	VDR	M	Adult	5	VDR
Abu	ABU	M	Sub-adult	5	
Fefe	FFE	M	Adult	5	
Moritz	MRZ	M	Sub-adult	5	
Palpatine	PPT	M	Adult	13	PPT
Pumpkin	PMP	F	Sub-adult	13	PPT
Lana	LNA	F	Sub-adult	13	TCO
Rumba	RUM	F	Adult	13	TCO
Taco	TCO	M	Adult	13	TCO
Taki	TKI	F	Adult	13	TCO
Wendy	WDY	F	Adult	13	TCO
Ganesh	GNS	F	Adult	13	XBO
Irene	IRN	F	Sub-adult	13	XBO
Mantova	MNT	F	Adult	13	XBO
Shiva	SHV	F	Sub-adult	13	XBO
Xibo	XBO	M	Adult	13	XBO
Zahara	ZHR	F	Adult	13	XBO
Snowball	SNW	M	Sub-adult	13	
Holly	HLL	F	Adult	15	MKA
Mika	MKA	M	Adult	15	MKA
Cindy	CND	F	Adult	6I	CSC
Cisco	CSC	M	Adult	6I	CSC
Liebling	LBL	F	Adult	6I	CSC
Odessa	ODS	F	Adult	6I	CSC
Indie	IND	M	Adult	6I	IND
Jess	JSS	F	Sub-adult	6I	IND
Dalmi	DLM	F	Adult	6I	QNN
Lischen	LSC	F	Sub-adult	6I	QNN
Quinn	QNN	M	Adult	6I	QNN
Bissap	BSS	F	Adult	6I	TRK
Triki	TRK	M	Adult	6I	TRK
Bela	BLA	M	Adult	6I	
Kuvo	KVU	M	Large juvenile	6I	