A cooperation experiment in captive white-handed gibbons (*Hylobates lar*)

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1 Abstract

Cooperative behaviours among individuals play a crucial role in social interactions. There is a special interest in investigating the occurrence of cooperation among apes, because this knowledge could as well shed light on evolutionary processes and help understand the origin and development of cooperation in humans and primates in general. Gibbons are phylogenetically intermediate between the great apes and monkeys, and therefore represent a unique opportunity for comparisons. The aim of the present study was to discover whether or not gibbons (*Hylobates lar*) show cooperative behaviours among each other. In order to test for the respective behaviours, the gibbons were presented with a commonly used experimental cooperative problem-solving task. Additionally, social behaviours were recorded during behavioural observations. The gibbons in this study did not exhibit cooperative behaviours during the problem-solving task. Behavioural observations revealed that the gibbons spent significantly more time ‘out of arm reach to everyone’, suggesting that they are less involved in social interactions than other, more cooperative apes. Both findings combined support the “social brain hypothesis”, which predicts that cognitive abilities are constrained by the complexity of the animals’ social life. Based on previous findings of occurrences of cooperative behaviours in two other primate lineages (i.e. New World monkeys and Old World monkeys) it was suggested that cooperation in primates was a matter of a convergent evolutionary processes rather than a homologous trait.

Keywords: Cooperation, Gibbons, Hylobates, Primates, Problem-solving, Social behaviour

2 Introduction

Gibbons or small apes (Hylobatidae) form the sister group of the great apes (Hominidae) (Geissmann, 1995). Those two family groups separated 16.26 million years ago, according to mitochondrial analyses (Thinh et al., 2010). With currently 20 recognized species (four monophyletic genera) (Geissmann, personal communication, 2017), gibbons represent the richest group in species within the apes (Hominoidea). The natural habitat of these arboreal apes are the tropical rainforests in southeast Asia (Geissmann, 2003a), but due to ever-expanding threats all gibbon populations in the wild are declining. As a matter of fact, the International Union for Conservation of Nature (IUCN) classified one gibbon species as vulnerable, 14 species as endangered, and four species as critically endangered (Geissmann, 2014; IUCN, 2018). Main threats are habitat loss as a result of deforestation, forest fires, oil palm plantations, and fragmentation as well as air pollution caused by forest fires. Last but not least, gibbons are exposed to hunting due to sport and food purposes on one hand, and to be delivered into the illegal pet trade on the other hand (Cheyne, 2009; Geissmann, 2014).

Gibbons live in small family groups and their structure is generally described as socially monogamous (Chivers, 1977; Leighton, 1987). Fuentes (2000), however, suggested to change these characterizations towards a more flexible term. He proposed that gibbons exhibit a “stable small-grouped, two-adult pattern” (Fuentes, 2000). His findings go along with those of Brockelman et al. (1998). They also observed a slightly more flexible pair building and social structure than it was previously assumed. Gibbons are highly territorial and are known for their great calls to, amongst others, defend their territory-boundaries and to announce themselves to adjacent gibbon-groups (Chivers, 1977; Raemaekers and Raemaekers, 1985; Leighton, 1987; Ham et al., 2016).

Investigating great apes has long been of special interest because this knowledge could shed light on evolutionary processes and even help understand the origin and development of human kind, and primates in general. Gibbons are particularly interesting based on their proximity to the great apes and them being phylogenetically intermediate between the great apes and monkeys. This highlights their comparative relevance. However, gibbons have received much less of both research and attention than their famous cousins. Even though quite a number of studies have been done on gibbon behaviour (Parker, 1973; Shepherdson et al., 1989; Nicolson, 1998), their social structure (Palombit, 1994; Brockelman et al., 1998; Fuentes, 2000) and especially their communication (Geissmann, 1986; Geissmann, 1993; Nicolson, 1998), there is still a huge lack of knowledge about their cognitive capabilities. Nevertheless, occurrences of some fundamental behaviours have already been documented.

Cognitive capabilities are often associated with tool-use, which has already been shown to exist within gibbons. Captive hoolock gibbons (*Bunopithecus hoolock*) used a rake to obtain food that was out of their reach, furthermore, they did not require prior training to solve this task (Cunningham et al., 2006). During a study done by Rumbaugh (1970), a captive gibbon was observed to repeatedly use a piece of cloth as a sponge to collect water for drinking purposes. Another indication of tool-use was described in door-slamming behaviour of a captive female white-handed gibbon (*Hylobates lar*). She apparently displayed this behaviour to alter and accentuate a particular phrase of her morning song bouts (Geissmann, 2009).

When it comes to primate cognition, theory of mind is a much-discussed topic. It implies that an animal is aware of its own mental state and as well of that of other individuals (Premack and Woodruff, 1978). One way to investigate if an animal has self-awareness is the mirror-test. Regarding gibbons, it is a controversial topic whether they can actually recognize themselves or not. Inoue-Nakamura (1997), Hyatt (1998) and Suddendorf and Collier-Baker (2009) believe that gibbons do not recognize themselves in a mirror and that this cognitive ability, within primates, only applies to the great apes. On the contrary, Ujhelyi et al. (2000) reported that three out of four gibbons displayed behaviours that could, indeed, indicate self-recognition (e.g. head tilting, leg/ arm lifting, mouth opening). Heschl and Fuchsbichler (2009) proposed that siamangs (*Symphalangus syndactulus*) should also be considered as “potentially self-conscious”, after they displayed self-directed behaviours in front of a mirror during a long-term observation study. In the same study, however, the siamangs did not pass the mark-test (The studied animal is imperceptibly marked with, for instance, an odourless dye, on a for the animal not visible spot on its body. Afterwards, the animal’s performance in front of a mirror is observed and evaluated with regards to its reactions based on the possible raising of the marking’s awareness) (Heschl and Fuchsbichler, 2009).

Another indication for theory of mind or at least for higher intelligence is the ability of detecting and understanding the gaze of others. A three-year-old white-handed gibbon (*H. lar*) was able to use a humans’ gaze to attain hidden food (Inoue et al., 2004). These findings coincide with those of Horton and Caldwell (2006), who found pileated gibbons (*H. pileatus*) being competent of following visual directional cues from conspecifics as well as from humans. Yocom (2010), however, reported that the white-handed gibbons (*H. lar*) in her study were only able to follow a combined cue of eye gaze and head-posture but could not follow only eye gaze cues.

Going one step even further is the investigation of an individual’s possible comprehension of its own and its corresponding part within an interaction. And furthermore, if social or communicative techniques are applied to align their manners (Tomasello and Call, 1997), which is usually referred to as cooperation. Generally, cooperation is defined as “the behaviour of two or more individuals acting together to achieve a common goal” (Boesch and Boesch, 1989). The individuals are “in a situation in which neither can benefit alone, or at least not to the same degree, as when they act in concert” (Tomasello and Call, 1997). Even though it was long believed that cooperative behaviours were unique to the human kind, several studies revealed the fact that this is not the case and that various species, indeed, display cooperative behaviours (e.g. Boesch and Boesch, 1989; Boesch, 1994; Parish, 1996).

One of the most popular examples of cooperative behaviours observed in great apes is probably the hunting behaviour in chimpanzees (*Pan troglodytes*) (Boesch and Boesch, 1989; Boesch, 1994). Boesch (2002) described the procedures that Taï chimpanzees performed during collectively hunting. Every chimpanzee would undertake a different part with its own duties and functions. The roles differed in cognitive demands and could vary between the participators. The learning process of the hunting procedures is very time consuming, more specifically, it was reported that chimpanzees needed about 20 years to perfect their performances (Boesch, 2002). In captivity, chimpanzees also showed their ability for teamwork in problem-solving tasks (Chalmeau and Gallo, 1996; Melis et al., 2006; Hirata and Fuwa, 2007). They were presented with a platform that was baited with a food reward. In order to obtain the reward, the individuals had to pull two rope ends simultaneously which allowed them to pull the baited platform towards them. The tolerance level between certain individuals (e.g. in food-sharing situations), however, seemed to restrain the success of solving the cooperation test (Melis et al., 2006).

The same test was conducted with bonobos (*Pan paniscus*), a close relative of the chimpanzee. Hare et al. (2007) found no differences in the performances of bonobos and chimpanzees when the reward was shareable. Therefore, bonobos were also competent to successfully cooperate with their conspecifics (Hare et al., 2007). Was the reward monopolizable, on the other hand, bonobos appeared to be more successful and more effective in their cooperative performances than the chimpanzees (Hare et al., 2007). Even though no data exist on hunting behaviour in bonobos, females have been observed building coalitions to cooperatively assail the males (Parish, 1996).

Gorillas (*Gorilla gorilla*) have not received as much research as e.g. chimpanzees, in regards to cooperative behaviours. Nevertheless, wild male eastern gorillas (*G. beringei*) have been observed cooperating with other male group members in order to keep their females in the group (Sicotte, 1993). Most females leave their natal group after becoming mature and transfer to another gorilla group at least once in their lives (Harcourt et al., 1976; Harcourt, 1978). To impede the females from leaving, males have been observed to cooperatively herd their females. Herding behaviours were usually displayed in new and not well-established groups and with females that were neither currently pregnant nor rearing offspring (Sicotte, 1993). However, this kind of social interaction does not occur on a regular basis (Watts, 1989).

Bornean orangutans (*Pongo pygmaeus*), who were presented with a similar problem-solving task as the chimpanzees, performed cooperative behaviours in a comparable manner (Chalmeau et al., 1997). The orangutans' success rate increased over sessions and the individuals learned to coordinate and adjust their performances to one another. Additionally, it appeared to be the case that one individual would take the lead during the cooperation (Chalmeau et al., 1997). Völter et al. (2015) tested orangutan mothers and their juvenile offsprings for cooperative behaviours through an alternative scenario. The mother-offspring dyads were not required to complete a task simultaneously, but consecutively. The mother had to provide her juvenile with a certain tool that only the juvenile was able to use in order to release food rewards to both of them. The mothers actively handed the tool over to their offspring, however, this behaviour decreased when only the juveniles received the reward (Völter et al., 2015). All in all, even though this study was not based on the traditional rope-pulling cooperation test created by Hirata (2003; cited in Melis et al., 2006; Hirata and Fuwa, 2007), it indeed provides evidence for the existence of orangutans' understanding of their own and their conspecifics' role in a certain situation (Tomasello and Call, 1997).

Cooperative behaviours among animals have not only been observed in primates, but also in numerous other species. The same concept of the cooperation test that was initially designed for chimpanzees was applied to several animal species. Asian elephants (*Elephas maximus*) were highly successful in solving the cooperation task, and furthermore, demonstrated deeper understanding of their counterparts' role during the test (Plotnik et al., 2011). They waited with pulling behaviours until the partner's arrival and they seemed to understand that no pulling behaviour was necessary as long as the partner had no access to the other end of the rope (Plotnik et al., 2011).

Kuczaj et al. (2015) presented bottlenose dolphins (*Tursiops truncatus*) with this test and found that they were also able to successfully solve it. However, the authors discussed the ambiguity of the dolphins' behaviours and stated that it remained unclear if the dolphins actually took the role of their partner into account or if they merely tolerated another individual interacting with the same apparatus (Kuczaj et al., 2015). Subsequently, Eskelinen et al. (2016) discovered a significant increase of the whistle rate between the dolphins during mutual manipulations of the test tube. This was interpreted as a communicative strategy, possibly to exchange information and thus as a potential indication for the awareness of the partner's role during the interaction (Eskelinen et al., 2016).

When comparing the performances of wolves (*Canis lupus*) and dogs (breed unknown) during the cooperative problem-solving task, Marshall-Pescini at al. (2017) found that the wolves were able to synchronize their behaviours and therefore succeeded in the test. These results go along with those of Möslinger (2009). On the contrary, the dogs were not able to pull the ropes simultaneously and thus failed the test (Marshall-Pescini at al., 2017).

Spotted hyaenas (*Crocuta crocuta*) did not only solve the cooperative problem-solving task without any problems or even prior training, but they even appeared to be superior to chimpanzees in synchronizing their movements temporally as well as spatially (Drea and Carter, 2009).

Not only mammals participated in cooperative problem-solving tasks, but also birds have been tested. Rooks (*Corvus frugilegus*) showed their ability to successfully cooperate with their conspecifics in a comparable manner as chimpanzees did (Seed et al., 2008). Similar to chimpanzees, cooperation performances were more successful between individuals that had a higher tolerance level to one another. Unlike elephants, the rooks did not wait for their partners' arrival (Seed et al., 2008). Similar results were found after presenting the test to african grey parrots (*Psittacus erithacus*) (Péron et al., 2011).

At this stage, gibbons have not yet been investigated whether or not they exhibit cooperative behaviours among each other, and if they do to what extent. The only documented report on this subject emerged from Markowitz (1975; 1978). He claimed the occurrence of cooperative behaviours within a family group of captive white-handed gibbons (*H. lar*). However, it is difficult to assess the relevance of his report, because no quantitative data for the occurrence of cooperative behaviours were published. And furthermore, Markowitz' understanding of cooperation could be challenged, since it does not quite fall within the commonly accepted and used definitions (Boesch and Boesch, 1989; Tomasello and Call, 1997). He merely described one gibbon manipulating the given apparatus with the result that his mother received the food reward. The mother, correspondingly, was never actively participating in a mutual interaction but solely profited from her son's performances. Presumably, this kind of behaviour could better, if any, be interpreted as altruistic behaviour.

According to the "social brain hypothesis" or "Machiavellian intelligence"- hypothesis, cognitive abilities are constrained by the complexity of the animals' social life (Humphrey, 1976; Dunbar, 1998). Since gibbons are socially monogamous and live in small family groups, they would be expected to perform poorer in cooperative problem-solving tasks. Another argument for why gibbons would be predicted to be less successful than great apes but superior to monkeys is the theory that "brain size predicts cognitive abilities" (Benson-Amram et al., 2016). It implies that animals with a larger brain relatively to their body-mass are more likely to exhibit higher cognitive abilities (Benson-Amram et al., 2016). Findings from Reader and Laland (2002) suggest that "social learning, innovation, and tool use frequencies" are indeed "positively correlated with species' […] brain volumes". Matsuzawa (2007) reported a general increase in brain mass during primate evolutionary processes. The brain mass measured in gibbons (as well as in macaques) was in between that of the great apes and monkeys (Matsuzawa, 2007). Subsequently, gibbons would be expected to reveal an intermediate performance in cooperative problem-solving tasks.

2.1 Aims

The aim of the present study was to provide evidence for or against the existence of cooperative behaviours among gibbons. This information would contribute to the understanding of evolutionary processes and suggest when cooperative behaviours evolved.

Furthermore, the "social brain hypothesis" was tested in order to confirm or deny if the complexity of animals' social life could be indicative for their cognitive abilities.

3 Materials and methods

3.1 Location and time of data collection

The data collection was conducted in Kolmården Wildlife Park, situated close to Norrköping, Sweden. It took place from the 25th July 2017 until the 15th December 2017, Mondays to Fridays.

3.2 Animals

The animals engaged in this study were five white-handed gibbons (*Hylobates lar*) (Figure 1), living together in a family group consisting of an adult breeding pair and their three offspring. The group composition is listed in Table 1. Besides Elly, who was born in the Parken Zoo in Eskilstuna, Sweden, all gibbons were born in Kolmården, and were parent-reared. The age classes proposed by Geissmann (1993) for captive gibbons and siamangs were used in this report: infants from 0 to 2 years of age; juveniles 2.1 to 4 years; subadults 4.1 to 6 years; adults more than 6 years.

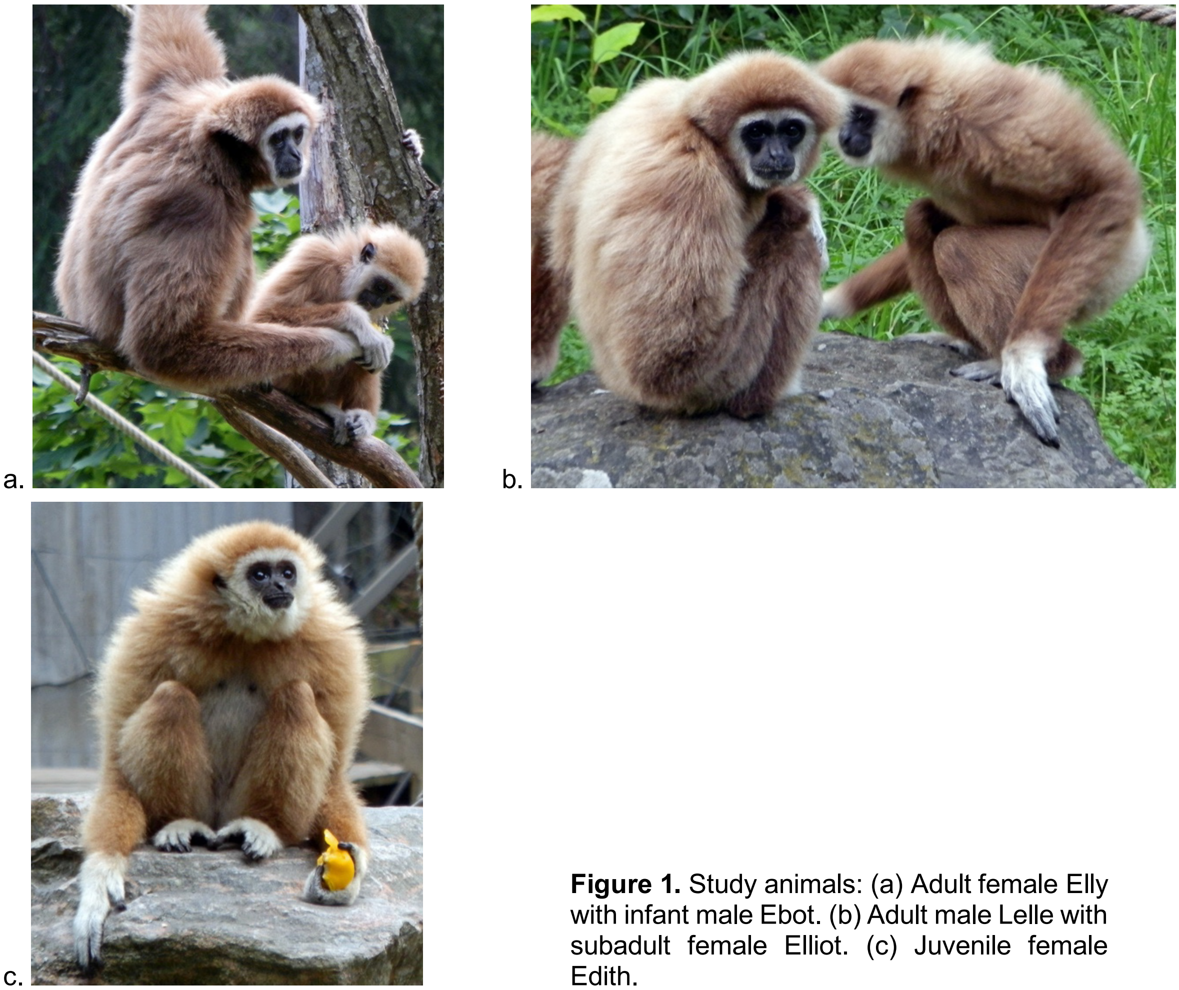

Figure 1. Study animals: (a) Adult female Elly with infant male Ebot. (b) Adult male Lelle with subadult female Elliot. (c) Juvenile female Edith.

Table 1. Composition of the gibbon study group.

Name	**Sex**	**Birth date**	**Age class at begin of study**
Lelle	Male	1 Oct 1987	Adult
Elly	Female	16 Mar 1988	Adult
Elliot	Female	7 Oct 2011	Subadult
Edith	Female	22 Dec 2013	Juvenile
Ebot	Male	30 Mar 2016	Infant

3.3 Housing

The gibbons' enclosure was subdivided into an indoor facility (Figure 2) and an outdoor facility (island). In total, 618.6 m^2 (83.6 m^2 indoors + 535 m^2 outdoor island) were available to the gibbons. Depending on the weather, the gibbons were free to choose between the inside and the outside area. During winter they were required to be kept inside. The facilities were cleaned by the animal keepers once a day with an additional annual major cleaning.

The animals were fed four times a day according to a more or less regular feeding schedule. Water was available at all times. In order to prevent boredom, to stimulate the gibbons' senses and to arouse their natural behaviours, they were provided daily with altering enrichment items.

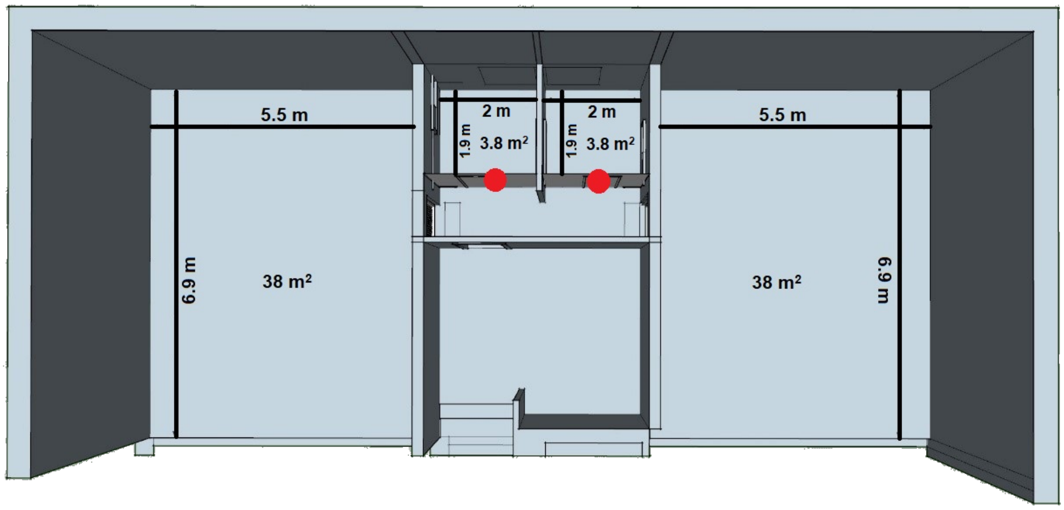

Figure 2. Birds-eye view of the indoor quarters with the corresponding sizes in square metres. Red dots indicating the location of training and test sessions. Image modified after Johannes Höök.

3.4 Procedure and apparatus

The study was divided into three parts, two training phases and one actual test phase. The training phases were established to generate and develop the gibbons' basic understanding of the physical properties and the causalities of the task. All sessions were carried out either by the ape keepers or the employed animal training coach at Kolmården and took always place in the indoor quarters (Figure 2). Two sessions per day were conducted on five days per week. The particular proceedings and apparatuses are described in the corresponding sections.

Participation in the training and test sessions was voluntary at all times. The gibbons were never food deprived and were always able to freely move around. Accordingly, the length of a session was not only dependent on, but also determined by, the gibbons' willingness to participate (from here on called 'motivation'). None of the gibbons had been part of a cognitive-ability-assessment study before. Additionally, they had not been actually trained prior this study. The gibbons were handled exclusively with protected contact (i.e. there was always a fence between keepers and trainer, and the animals). In all phases, the food rewards consisted of various kinds of fruits or cooked potatoes. Food rewards were equally distributed among the individuals, hence, monopolizing of the reward was impossible.

3.4.1 Phase 1: First training phase

In the first training phase the gibbons were required to learn to pull a single rope in order to receive a food reward. Every participating gibbon was offered individual training that was adapted to their needs and training level. Taking the experiences of Markowitz (1978) into account, a duration of approximately one month was planned for this phase.

The employed apparatus (Figure 3) was attached to the outside of the testing room, so the keepers could bait it without having to walk into the enclosure. A rope, hanging on the inside of the testing room, was attached to an elongated piece of plywood, called the "slide", that would drive in through the fence when the rope was pulled. Thereby the animal would access a food reward placed on the slide. A Plexiglas sheet was installed on the fence to hinder the gibbons from taking the reward directly from the slide, through the fence. A hanging rope was used to facilitate, or even enable the gibbons to grab it. Beck (1967) highlighted that the hand anatomy of gibbons was adapted to an arboreal lifestyle and thus does not allow the animals to easily pick items up. To obtain a realistic and reliable result, test methods have to be appropriately adjusted (Beck, 1967).

Each gibbon was assigned to their personal training station based on the location where they appeared to feel most comfortable. The gibbons that fulfilled the passing criterion after the first training phase went further to the second training phase. Since it was impossible to conduct a fixed number of trials, the passing criterion was based on their overall performances during this training phase. Within a minimum of 100 trials per individual, significantly more trials had to be scored as a success than as a failure.

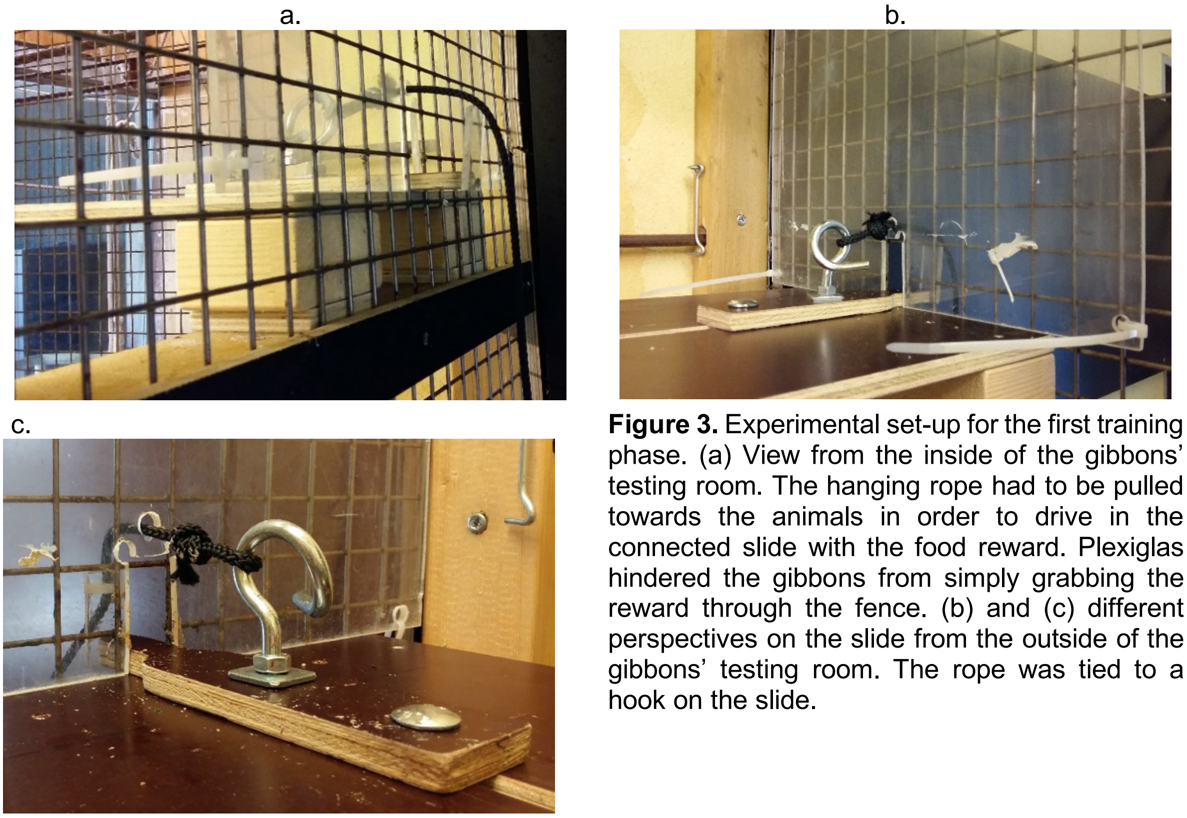

Figure 3. Experimental set-up for the first training phase. (a) View from the inside of the gibbons' testing room. The hanging rope had to be pulled towards the animals in order to drive in the connected slide with the food reward. Plexiglas hindered the gibbons from simply grabbing the reward through the fence. (b) and (c) different perspectives on the slide from the outside of the gibbons' testing room. The rope was tied to a hook on the slide.

3.4.2 Phase 2: Second training phase

In the second training phase the gibbons were supposed to learn that onwards two connected rope ends were required to be pulled simultaneously in order to get the food reward. The sessions in this phase were continued as individual training. A duration of approximately two months was planned for this phase.

The same apparatus was used as in the first phase, but it was partly altered (Figure 4). Two ends of the rope were hanging into the testing room. The original idea was that the rope would slip through if only one end was pulled. Since the set-up did not always function properly, the keepers were required to manually adjust the movements of the slide. That enabled the keepers to immediately reinforce the correct and wanted behaviour. To focus the gibbons' attention on the two rope ends and to encourage them to pull both of them, the keepers and the trainer occasionally waggled with the two rope ends.

However, to slowly accustom the gibbons to the new situation, the rope was temporarily tied to the slide (Figure 5). The fact that pulling any of the two rope ends could make the food reward accessible for a while kept the motivation at a high level and showed that both rope ends had a positive outcome. Once the gibbons had learned that both rope ends were beneficial the knot was untied.

To count the gibbons' action as correct, they had to pull both rope ends either with one hand each or both rope ends together with one hand. Using a foot instead of a hand for pulling also counted as correct. When the gibbons showed an understanding of the process, the distance between the two rope ends was progressively increased.

The gibbons that fulfilled the passing criterion after the second training phase went further to the test phase. Since it was impossible to conduct a fixed number of trials, the passing criterion was based on their overall performances during this training phase. Within a minimum of 100 trials per individual, significantly more trials had to be scored as a success than as a failure.

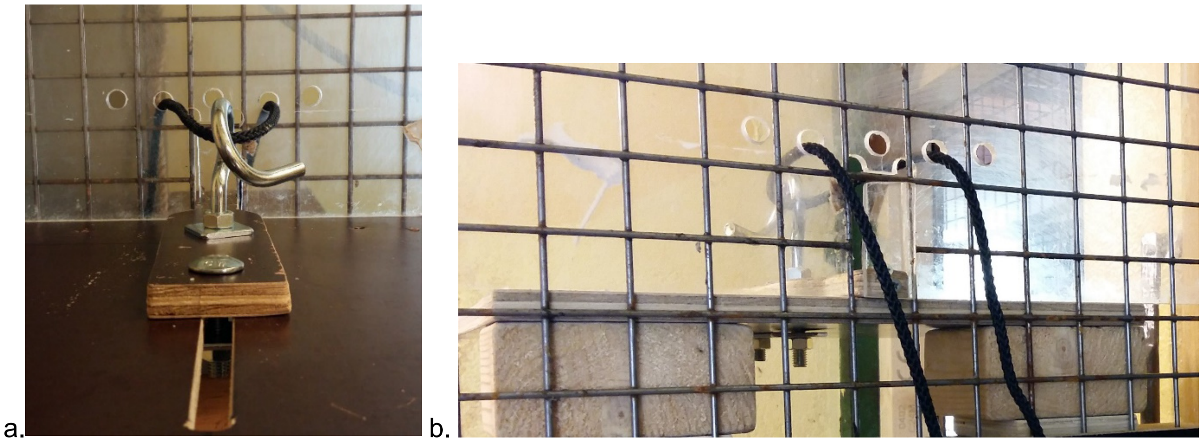

Figure 4. Experimental set-up for the second training phase. (a) View on the slide, on which the food reward was placed, from the trainer's side. The rope was slid around the hook with two ends presented to the gibbons. The two rope ends had to be pulled simultaneously in order to release the food reward. Plexiglas hindered the gibbons from simply grabbing the reward through the fence. The holes in the Plexiglas were used to increase the distance between the rope ends. (b) View from the gibbons' side. The two hanging rope ends had to be pulled simultaneously in order to drive in the slide with the food reward through the opening in the Plexiglas.

Figure 5. Experimental set-up for the second training phase with the rope tied to the slide's hook (with two ends presented to the gibbons). View from the trainer's side. This was done temporarily to keep the animals' motivation (willingness to participate) high while learning that pulling both rope ends would result in access to the food reward on the slide. Once the gibbons had learned that pulling both rope ends were beneficial the knot was untied. Plexiglas hindered the gibbons from simply grabbing the reward through the fence. The holes in the Plexiglas were used to increase the distance between the rope ends.

Young gibbons are dependent on their mother until the age of approximately 2 years (Burns and Judge, 2016), and therefore performances of the youngest offspring, Ebot, were not included.

Prior to the individual training routines, the gibbons were given some adaptation time towards the apparatuses and the new training situation and time to develop more trust and confidence towards the keepers. This was essential for a successful training.

The keepers were required to only bait the station when the corresponding gibbons were watching. This ensured the gibbons were aware of the on-going session. During the individual training, performances were documented on-site and the time from baiting the station until the animal successfully obtained the reward was recorded in order to establish how fast the gibbons solved the tasks and if they would improve over time.

All training sessions were recorded by two cameras, directed towards one testing location (Figure 2) each. The cameras used were a *GoPro Hero 4* and an *Olympus SP-610UZ*. If necessary, data was taken from the videos posterior to the training sessions.

3.4.3 Phase 3: Test phase

The test was based on the cooperation test developed by Hirata (2003; cited in Melis et al., 2006; Hirata and Fuwa, 2007). The two ends of the rope were too far apart (149 cm) for one animal to work the apparatus by itself. Thus, two animals were required to pull one end each at roughly the same time to receive the food reward. The test phase was purely experimental, no training was provided for the gibbons any longer. A time frame of approximately one and a half months was planned for conducting the test.

Figure 6 shows the experimental set-up for the test phase. Two individual training stations were combined to one test apparatus. Unfortunately, the original idea of having one rope employed that would slide through when only pulled on one side, did not work, because single gibbons were still able to release the slide with vigorous pulls. Therefore, the apparatus was modified to contain two single ropes. Each of them was connected to a retainer that blocked the other slide. If a gibbon pulled one rope end the slide was not released but the mechanism allowed to open the corresponding retainer. This enabled another gibbon to pull its slide out of the station while simultaneously unblocking the other retainer. Hence, the second slide was released as well. This mechanism made sure that actually two gibbons had to coordinate their actions and to work together.

In the first four test sessions the apparatus was baited, and the gibbons were given three minutes to figure out how to obtain the food reward. After three minutes the reward was discarded, and a new trial was initiated. This procedure was repeated three to five times, depending on the gibbons' motivation. During the three-minute test, all keepers left the testing area. This was done to prevent the gibbons getting upset with the keepers who were no longer allowed to reinforce their behaviours. Prior, the gibbons were reinforced for pulling behaviours but during the test situation they did not get any rewards for a simple pulling behaviour, since it required two pulling gibbons at the same time. Additionally, this stage of the study was designed to discover whether or not the gibbons understood the mechanism and if they would exhibit spontaneous cooperative behaviours in the absence of trained movements.

It appeared, however, that three-minute trials were too short to keep the gibbons motivated and interested since they barely participated after a short period of time. Therefore, the testing duration was prolonged to an approximately 75-minute trial. This did not only allow the gibbons to show interest in the apparatus according to their desire but also to return back and try again after a while.

All test sessions were recorded by a *GoPro Hero 4* and data was collected from the videos posterior to the test sessions. Performances of the individuals were taken into account when they effectively pulled a rope. If the rope was merely gently touched or the gibbons tried to obtain the reward in another way, it did not count as a recordable performance. If one individual pulled a rope repeatedly in succession, it was counted as one attempt as long as the individual did not leave its position in between. However, if every single pulling would have counted, regardless of leaving the position, it would not have made a difference in the results.

Behaviours were rated as cooperative when two simultaneous pullings were performed by two individuals with the result of both receiving the food reward.

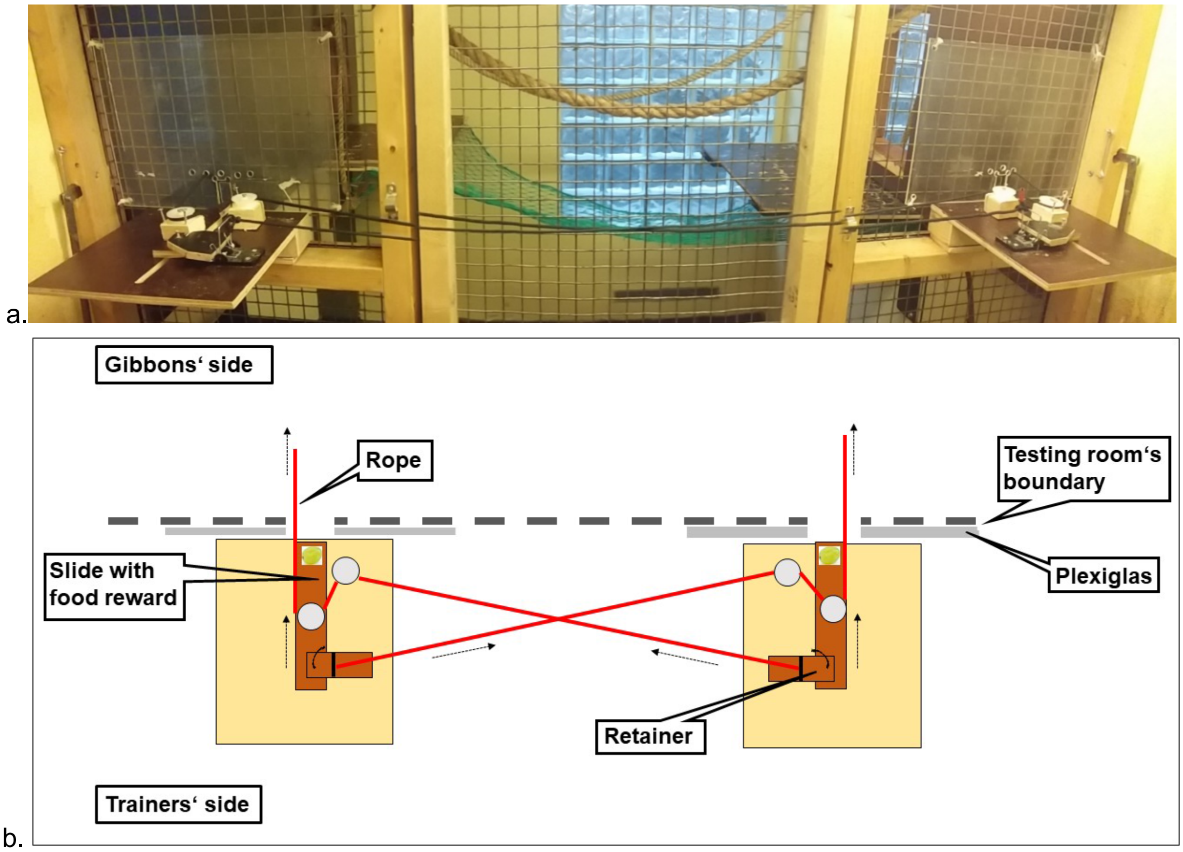

Figure 6. Experimental set-up for the test phase. (a) View from the trainer’s side. Two single ropes were connected to a retainer that blocked the respective slides. If a gibbon pulled one rope end, the slide was not released but the mechanism opened the corresponding retainer on the other animal’s slide. This enabled the latter to pull its slide through the opening in the Plexiglas while simultaneously unblocking the other slide. Hence, the second slide was released as well. Consequently, both gibbons had to coordinate their actions and to work together. (b) Schematic drawing of the same experimental set-up for the test phase.

3.4.4 Behavioural observations: Recording of social behaviours

Alongside the test phase, social behaviours were recorded during observation sessions. Each session lasted for one hour. Two sessions per day were conducted on five days per week. All observations were homogeneously distributed over the times of day. This ascertained that any possible changes of behaviour due to the time of day was taken into account in order to obtain the best possible and reliable image of the reality. A total of 66 hours of observations were carried out. For the behavioural recording, scan-sampling with a one-minute-interval was applied. Behaviours were recorded according to the ethogram shown in Table 2.

Table 2. Ethogram used during the one-hour behavioural observations.

Behaviour	**Descriptive term**
Social grooming	Individual is investigating and cleaning the fur or skin of a conspecific.
Social play	Individual is cavorting with another conspecific without displaying any obvious aggressive behaviours.
Conflict	Individual displays agitated behaviour towards, or in conjunction with, a conspecific.
Close contact	Individual is “hugging” or “cuddling” a conspecific or is carried by a conspecific.
Within arm reach	Individual is close enough to a conspecific to be able to grab or touch it and could be grabbed or touched by this conspecific.
Out of arm reach	Individual is too far away from a conspecific to grab or touch it and could not be grabbed or touched by this conspecific.
Out of sight	Individual is not visible to the observer and no other behaviour could be concluded when taking other conspecifics into account (e.g. out of arm reach to everyone).

3.5 Statistics

To test for significant differences between two frequencies, the non-parametric Chi-square-test was applied (Siegel and Castellan, 1988; Geissmann, 2003b).

In order to test for significant differences between three frequencies, the non-parametric Kruskal-Wallis-test was applied (Kruskal and Wallis, 1952). Subsequently, a *post-hoc* test with pairwise comparisons with Bonferroni correction was conducted (Armstrong, 2014). Both tests were performed using *IBM SPSS (Statistical Package for Social Science) version 25* for windows software.

Spearman rank correlation tests were computed using *StatView 5.0.1* software on an *iMac PowerMac 4.2* (for success rates) and *IBM SPSS version 25* for windows software (for progression rates) (Spearman, 1904). Correlation coefficients Rho (in absolute values) were interpreted according to Taylor (1990): $r_s \leq 0.35$ (weak correlation); $0.36 \leq r_s \leq 0.67$ (moderate correlation); $0.68 \leq r_s \leq 1$ (strong correlation).

A *p*-value ≤ 0.05 was considered as statistically significant.

4 Results

4.1 Descriptive features of the study

4.1.1 Training phase

The training phase was performed between the 25th July and the 31st October 2017. In total, there were 136 training sessions. Most of the sessions were carried out in the morning, because wild gibbons are reportedly more active in the morning (Chivers, 1977; Geissmann, 2003a) and because it was more compatible with the keepers' schedule. The second session of the day was usually conducted at noon or early afternoon (Figure 7).

The duration of a training session was dependent on the gibbons' participation and, therefore, varied. On average, a training session lasted for 11.47 minutes. The shortest session had a duration of 2 minutes and the longest lasted for 29 minutes.

For each individual the amount of training sessions per phase (first and second) varied, depending on how fast they adapted to the new situation and learned the first task. It was notable that juvenile female Edith required considerably less adaptation time (18 sessions) than adult male Lelle (54 sessions) and subadult female Elliot (38 sessions).

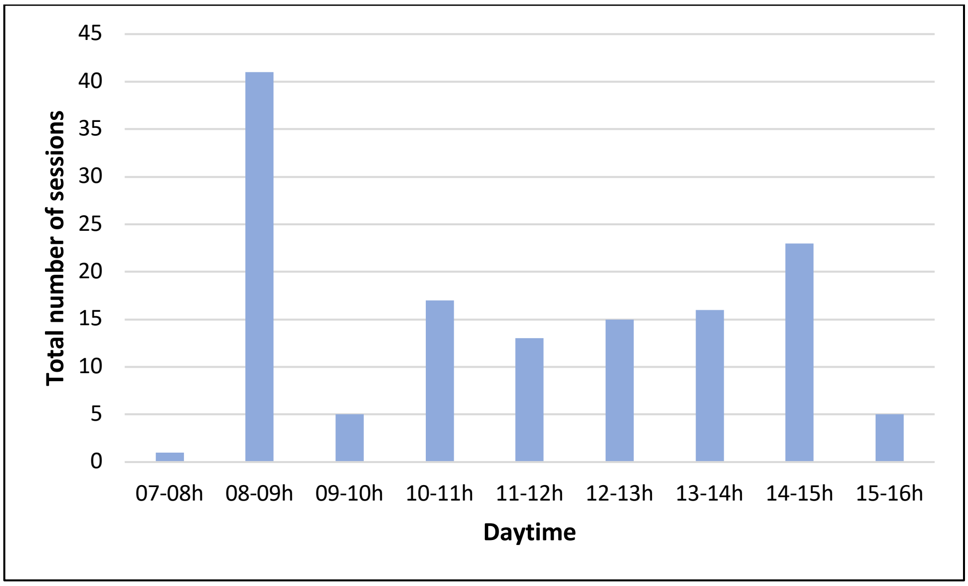

Figure 7. Distribution of the starting times of the sessions during the training phases over the daytime.

4.1.2 Test phase

The test phase was conducted between the 1st November and the 15th December 2017. Altogether, 66 test sessions were accomplished. The first test session of the day was mostly conducted between 8am and 11am, whereas the second test session took usually place between 1pm and 3pm (Figure 8).

The first nine sessions contained several trials which lasted for three minutes. On average, such a test session remained for 23.38 minutes. The shortest session had a duration of 18 minutes and the longest lasted for 32 minutes. From session five onwards the installed test apparatus was modified as descripted in the methods and shown in Figure 6.

As from session 10 the test procedure was changed, a test session lasted on average 74.21 minutes.

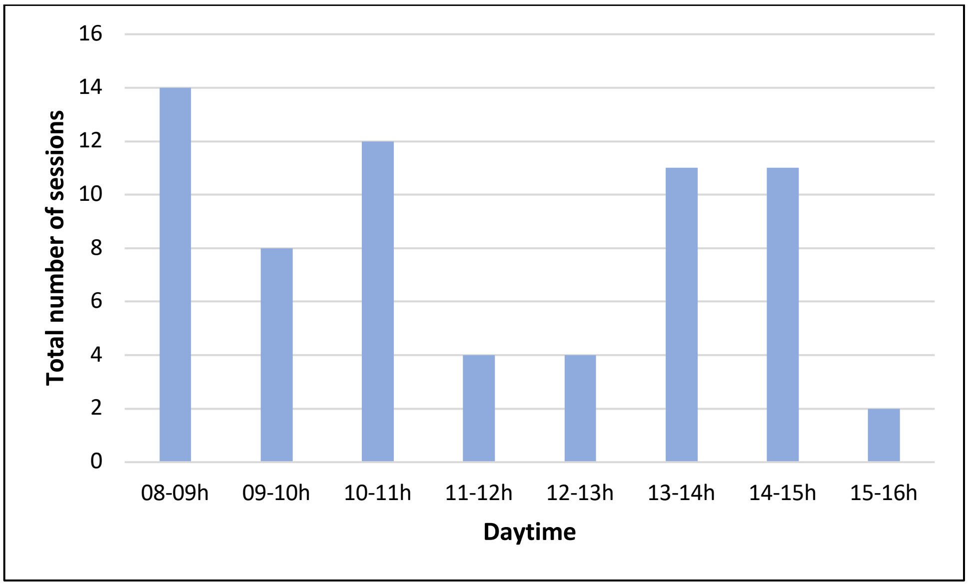

Figure 8. Distribution of the starting times of the sessions during the test phase over the daytime.

4.1.3 Behavioural observations

Behavioural observations were carried out between the 1st November and the 15th December 2017. A total number of 66 observations were conducted. As stated above, the starting times of the observations were homogeneously distributed over the day (Figure 9). Due to the study gibbons' daily activity pattern, the total number of sessions differed slightly in the beginning and at the end of the day.

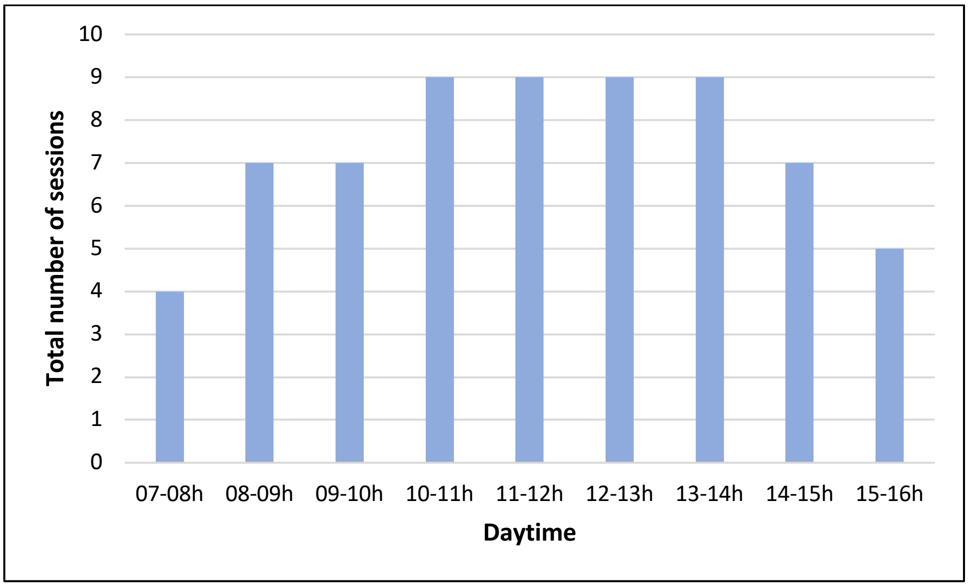

Figure 9. Distribution of the starting times of the one-hour behavioural observations over the daytime.

4.2 First training phase

4.2.1 Lelle

Adult male Lelle required 54 adaptation sessions, with 41 of which having the completed apparatus in place. He received 19 sessions of individual training, in which he correctly solved

138 out of 151 trials. This difference was significant (χ^2 *(1, N = 151) = 103.48, p < 0.001*), which confirmed that Lelle passed the first training phase and could continue with the second training phase.

Lelle solved the task on average in 4.11 seconds but with a median of 2.06 seconds (range 0.44–28.66 seconds). Looking at the progression of the mean time per session over time (Figure 10), a weak positive trend was suggested, but the correlation was not statistically significant (Spearman rank correlation, Rho = 0.127, n = 18, p = 0.616).

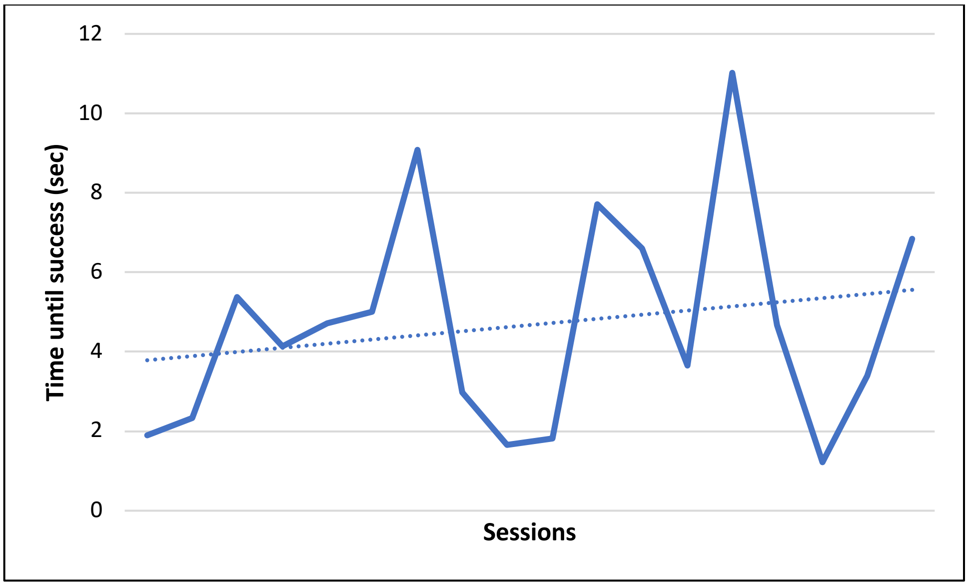

Figure 10. Means of the time until success per session during the first training phase. The dotted line indicates the progression over time (regression line) (*p* = 0.616). Data corresponds to adult male Lelle.

To determine if a positive success rate could be established, the ratio of correctly solved trials and failed trials over time was analysed and is illustrated in Figure 11. In order to examine whether or not a significant transition in Lelle's performance regarding the success rate could be detected, a Spearman Rank Correlation test was conducted. A weak negative trend was suggested but it was not statistically significant (Spearman rank correlation, Rho = -0.218, n = 19, p = 0.1811). Since the number of trials per training session was determined by Lelle's participation, there was no consistent number of trials per training session. In order to obtain a more reliable outcome, only sessions that contained at least 10 trials were included in further analysis (Figure 12). The reduced data still seemed to suggest a negative trend, but the correlation was not statistically significant (Spearman rank correlation, Rho = -0.387, n = 8, p = 0.2556). As a consequence, no positive success rate could be issued.

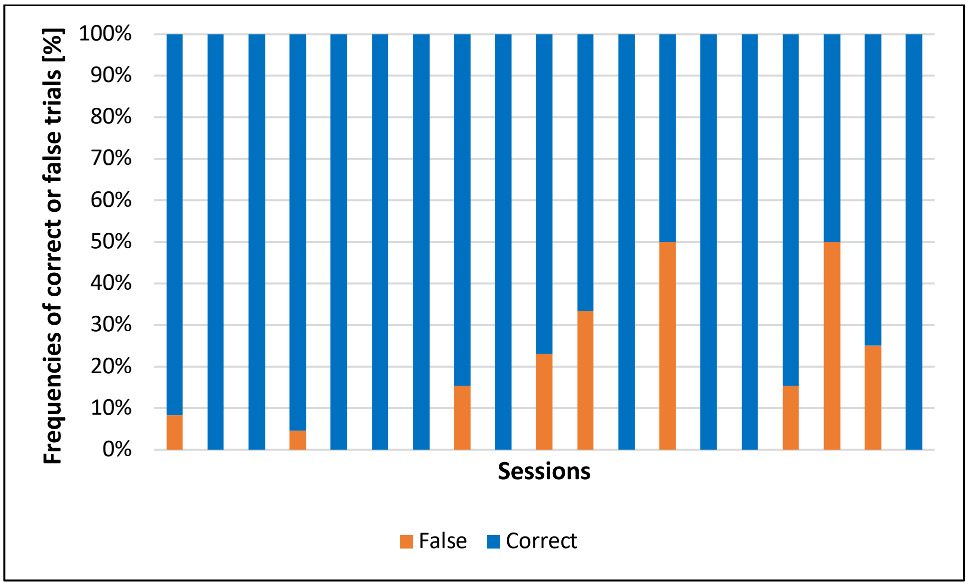

Figure 11. Ratio of correctly solved trials (blue) and failed trials (orange) over time of the first training phase. Data corresponds to the performance of adult male Lelle. All sessions are included.

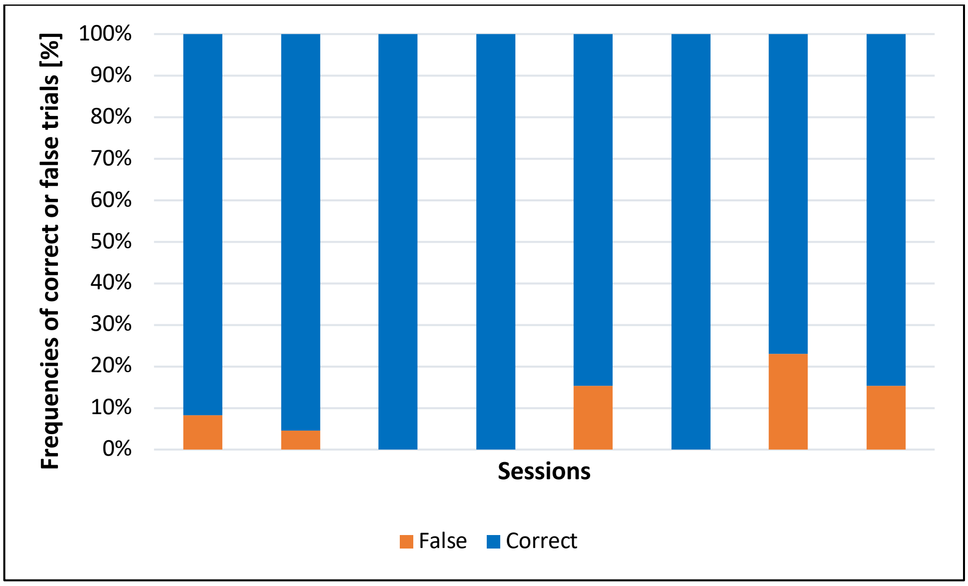

Figure 12. Ratio of correctly solved trials (blue) and failed trials (orange) over time of the first training phase. Data corresponds to the performance of adult male Lelle. Only sessions that contained at least 10 trials were included.

4.2.2 Elly

Adult female Elly required 58 adaptation sessions, with 45 of which having the completed apparatus in place. During this first training phase, she was only 13 times present in the training room, and she never even touched the rope. Accordingly, she could not be included in any further training or test sessions and therefore dropped out of this study.

4.2.3 Elliot

Subadult female Elliot required 38 adaptation sessions, with 30 of which having the completed apparatus in place. She received 51 sessions of individual training, in which she correctly solved 253 out of 271 trials. This difference was significant (χ^2 *(1, N = 271) = 203.78, p < 0.001*), which confirmed that Elliot passed the first training phase and could continue with the second training phase.

Elliot solved the task on average in 3.60 seconds but with a median of 1.75 seconds (range 0.13–54.59 seconds). Looking at the progression of the mean time per session over time (Figure 13), a decrease in time until success, more specifically, a moderately negative trend was suggested. This correlation was statistically significant (Spearman rank correlation, Rho = -0.554, *n* = 44, *p* < 0.01).

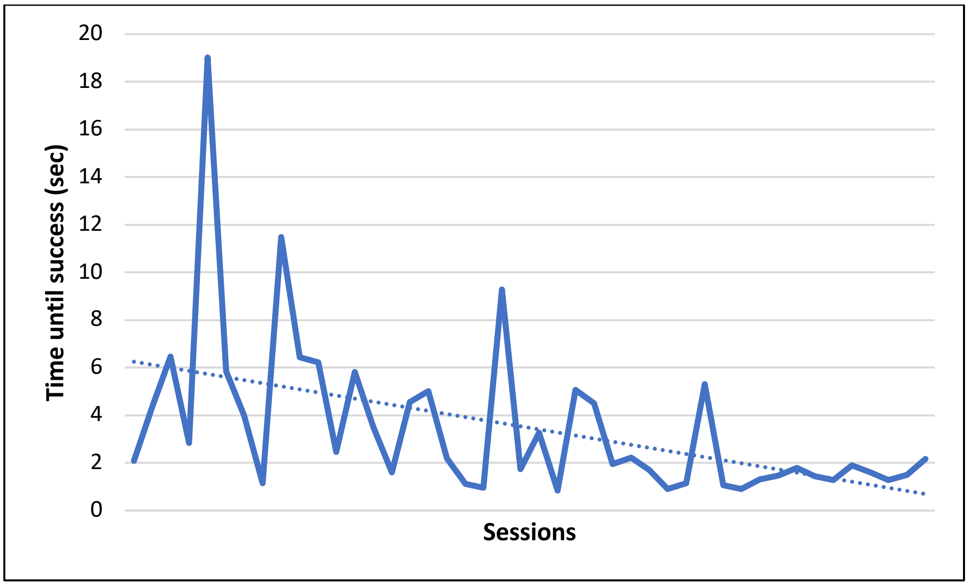

Figure 13. Means of the time until success per session during the first training phase. The dotted line indicates the progression over time (regression line) (*p* < 0.01). Data corresponds to subadult female Elliot.

To determine whether a positive success rate could be established, the ratio of correctly solved trials and failed trials over time was analysed and is illustrated in Figure 14. In order to examine whether or not a significant transition in Elliot's performance regarding the success rate could be detected a Spearman Rank Correlation test was conducted. A moderately positive trend was suggested, but the correlation was not statistically significant (Spearman rank correlation, Rho = 0.377, *n* = 46, *p* = 0.0860). Since the number of trials per training session was determined by Elliot's participation, there was no consistent number of trials per training session. In order to obtain a more reliable outcome, only sessions that contained at least 10 trials were included in further analysis (Figure 15). The reduced data still seemed to suggest a positive trend, but the correlation was not statistically significant (Spearman rank correlation, Rho = 0.434, *n* = 11, *p* = 0.2215). As a consequence, no positive success rate could be issued.

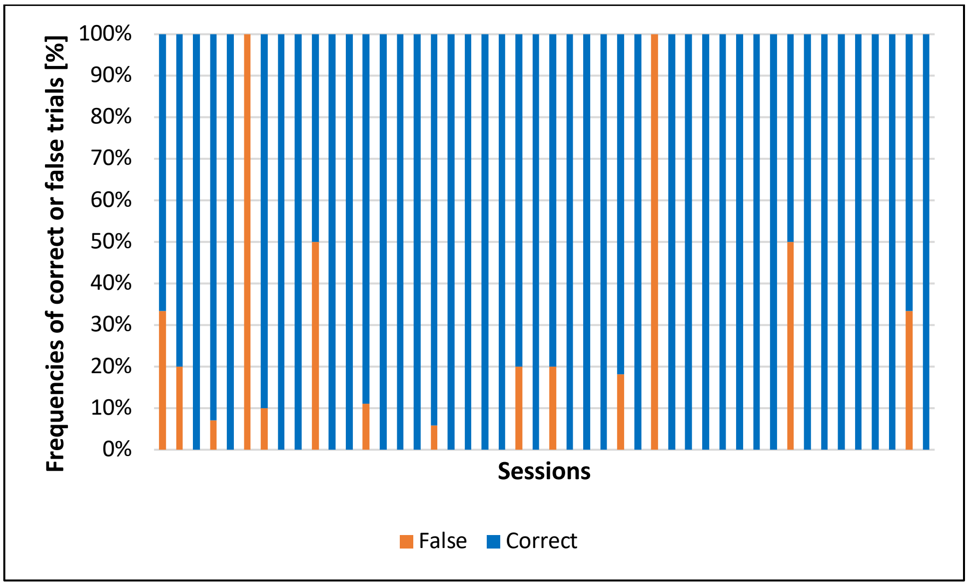

Figure 14. Ratio of correctly solved trials (blue) and failed trials (orange) over time of the first training phase. Data corresponds to the performance of subadult female Elliot. All sessions are included.

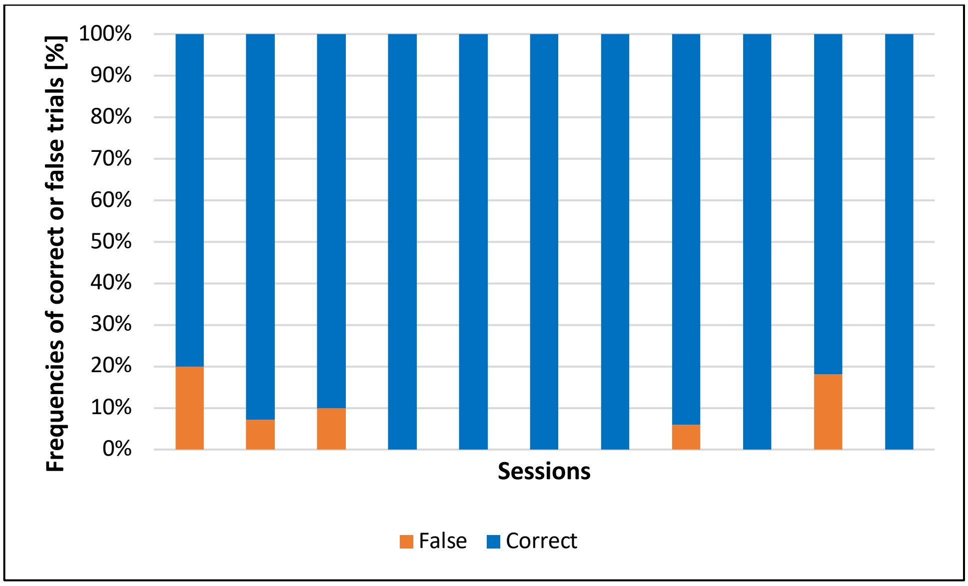

Figure 15. Ratio of correctly solved trials (blue) and failed trials (orange) over time of the first training phase. Data corresponds to the performance of subadult female Elliot. Only sessions that contained at least 10 trials were included.

4.2.4 Edith

Juvenile female Edith required 18 adaptations sessions, with 10 of which having the completed apparatus in place. She received 21 sessions of individual training, in which she correctly solved 190 out of 202 trials. This difference was significant (χ^2 *(1, N = 202) = 156.85, p < 0.001*), which confirmed that Edith passed the first training phase and could continue with the second training phase.

Edith solved the task on average in 4.13 seconds but with a median of 3.02 seconds (range 0.62–24.75 seconds). Looking at the progression of the mean time per session over time (Figure 16), a weak negative trend was suggested, but the correlation was not statistically significant (Spearman rank correlation, Rho = -0.306, $n = 18$, $p = 0.217$).

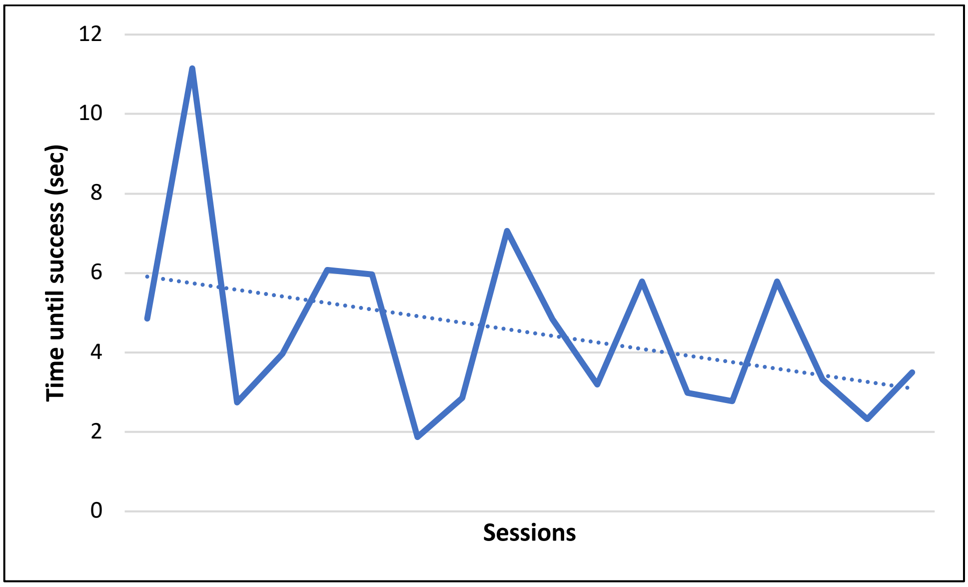

Figure 16. Means of the time until success per session during the first training phase. The dotted line indicates the progression over time (regression line) (p = 0.217). Data corresponds to juvenile female Edith.

To determine if a positive success rate could be established, the ratio of correctly solved trials and failed trials over time was analysed and is illustrated in Figure 17. In order to examine whether or not a significant transition in Edith's performance regarding a success rate could be detected a Spearman Rank Correlation test was conducted. A weak positive trend was suggested, but the correlation was not statistically significant (Spearman rank correlation, Rho = 0.296, n = 18, p = 0.3403). Since the number of trials per training session was determined by Edith's participation, there was no consistent number of trials per training session. In order to obtain a more reliable outcome, only sessions that contained at least 10 trials were included in further analysis (Figure 18). The reduced data still seemed to suggest a positive trend, but the correlation was not statistically significant (Spearman rank correlation, Rho = 0.269, n = 14, p = 0.4821). As a consequence, no positive success rate could be issued.

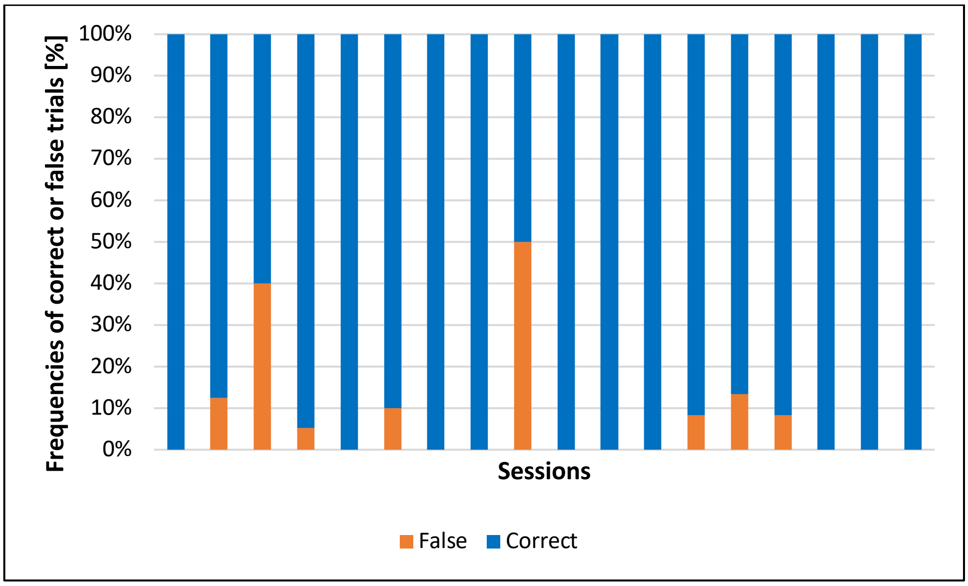

Figure 17. Ratio of correctly solved trials (blue) and failed trials (orange) over time of the first training phase. Data corresponds to the performance of juvenile female Edith. All sessions are included.

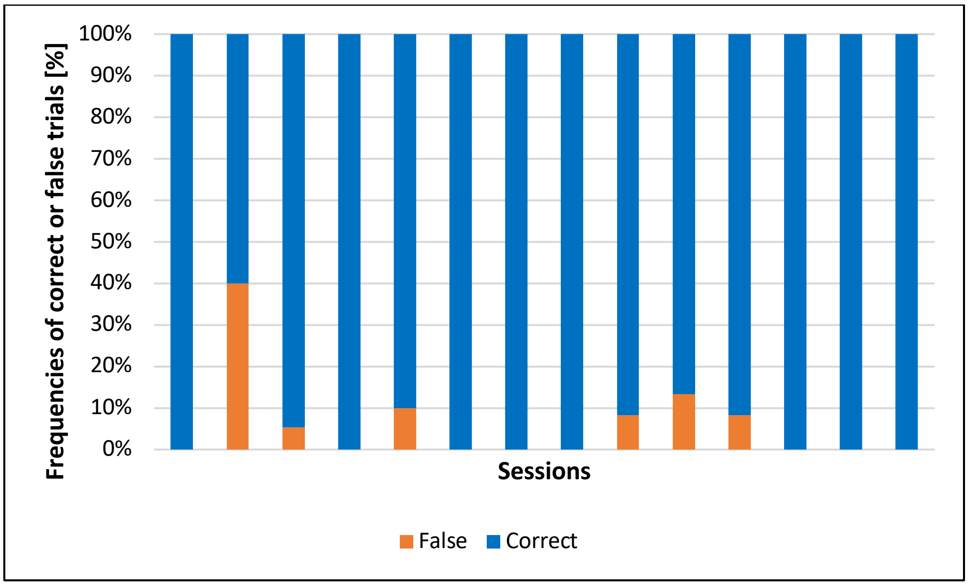

Figure 18. Ratio of correctly solved trials (blue) and failed trials (orange) over time of the first training phase. Data corresponds to the performance of juvenile female Edith. Only sessions that contained at least 10 trials were included.

4.2.5 Comparisons of performances between the individuals

Comparing all three successful individuals, juvenile female Edith adapted fastest to the new situation, whereas adult male Lelle was slowest. Edith learned to solve the task faster than Lelle or Elliot. However, on average and median, she needed slightly more time to solve the task, whereas subadult female Elliot was the fastest in successfully obtaining the rewards. The Kruskal-Wallis-test revealed that the three gibbons differed significantly among each other in the time they required to obtain the rewards ($H(2) = 35.742$, $p < 0.01$). The Bonferroni *post-hoc* test for pairwise comparisons showed that Edith differed significantly from both Elliot and Lelle ($p = 0.000$, and $p = 0.01$, respectively). The pair Lelle and Elliot, however, did not differ significantly ($p > 0.05$).

4.3 Second training phase

4.3.1 Lelle

Adult male Lelle received 63 sessions of individual training. To maintain his motivation, training units with one and with two rope ends were applied alternately. The distance between his two rope ends measured 12 cm. During the 157 trials, he never pulled the two rope ends at the same time, hence, he never solved this task. Accordingly, Lelle did not pass on to the cooperation test.

4.3.2 Elliot

Subadult female Elliot received 47 sessions of individual training. To increase her motivation and to help her adapt to the new situation, training units with one and with two rope ends were applied alternately for the first eight sessions. Afterwards, only two rope ends were employed. The rope distance measured 6 cm. In session 24 she pulled two rope ends for the first time. But after that, she pulled the two rope ends simultaneously again only from session 35 onwards. Out of 140 provided trials, she solved 19 correctly. This difference was significant (χ^2 *(1, N = 140) = 74.31, p < 0.001*), however, not in favour of correctly solved trials.

Elliot solved this task on average in 8.48 seconds but with a median of 4.97 seconds (range 0,88–31,69 seconds). There was no significant difference between the median times of both training phases (χ^2 (1, N = 6.72) = 1.54, $p > 0.20$). Looking at the progression of the mean time per session over time (Figure 19), an increase in time until success, more specifically a moderately positive trend was suggested, but the correlation was not statistically significant (Spearman rank correlation, Rho = 0.434, $n = 12$, $p = 0.159$).

She used only one hand to solve the task, with one exception when she used both hands.

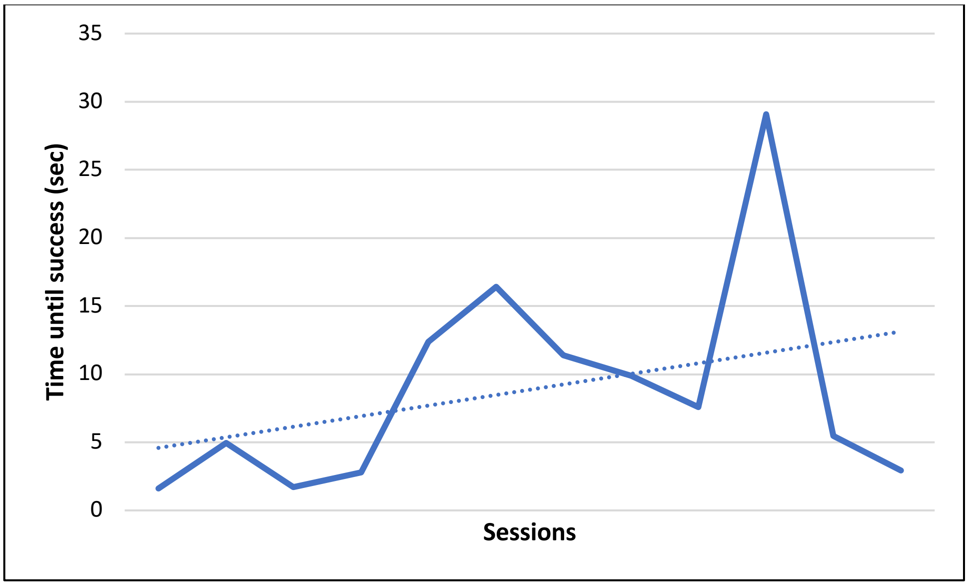

Figure 19. Means of the time until success per session during the second training phase. The dotted line indicates the progression over time (regression line) (p = 0.159). Data corresponds to subadult female Elliot.

To determine whether a positive success rate could be established, the ratio of correctly solved trials and failed trials over time was analysed and is illustrated in Figure 20. In order to examine whether or not a significant transition in Elliot's performance regarding a success rate could be detected a Spearman Rank Correlation test was conducted. A strong positive correlation was found which was statistically significant (Spearman rank correlation, Rho = 0.762, $n = 30$, $p < 0.0001$). Since the number of trials per training session was determined by Elliot's participation, there was no consistent number of trials per training session. Unfortunately, there were no sessions that featured at least 10 trials and therefore a reduced data set could not be analysed.

Even though it remains unclear whether Elliot conceived the task entirely, she exhibited an increasing success rate. On these grounds, and due to time limits, the training phase was eventually terminated, and she was admitted to the test phase.

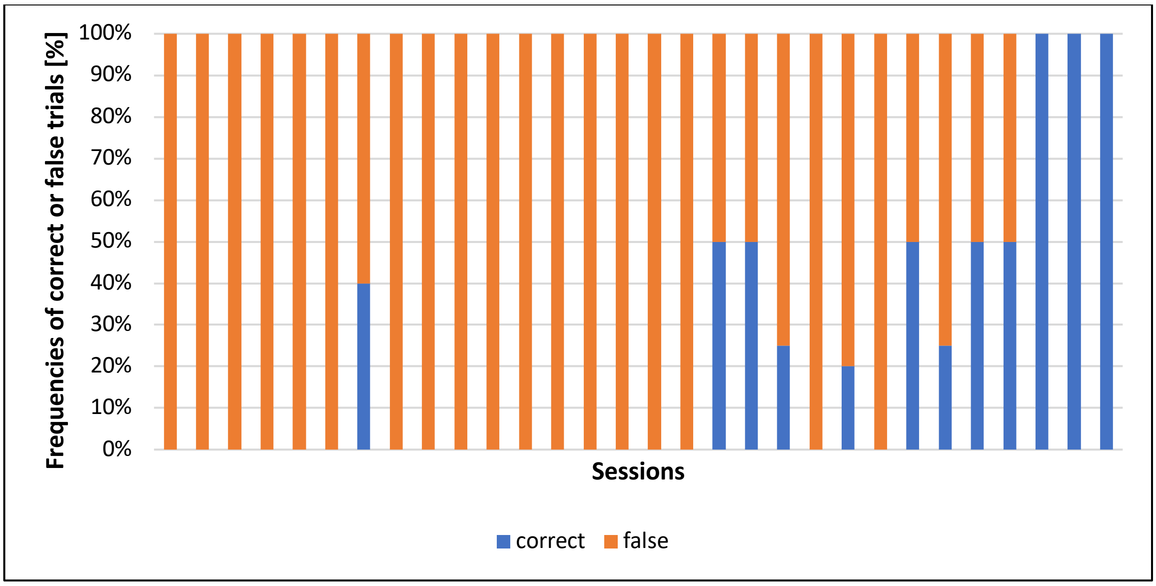

Figure 20. Ratio of correctly solved trials (blue) and failed trials (orange) over time of the second training phase. Data corresponds to the performance of subadult female Elliot. All sessions are included.

4.3.3 Edith

Juvenile female Edith received 97 sessions of individual training. Already in session seven she pulled two rope ends simultaneously for the first time. Out of 333 provided trials, she solved 105 correctly. This difference was significant (χ^2 *(1, N = 333) = 45.43, p < 0.001*), however, not in favour of correctly solved trials.

Edith solved this task on average in 12.11 seconds but with a median of 9.02 seconds (range 1.85–58.44 seconds). There was no significant difference between the median times of both training phases (χ^2 (1, N = 12.04) = 2.99, $0.10 > p > 0.05$). Looking at the progression of the mean time per session over time (Figure 21), a very weak positive correlation was suggested, but the correlation was not statistically significant (Spearman rank correlation, Rho = 0.071, $n = 54$, $p = 0.608$).

She tried several techniques (hand, foot, mouth) to solve the given task. Usually, she decided for using one hand and one foot.

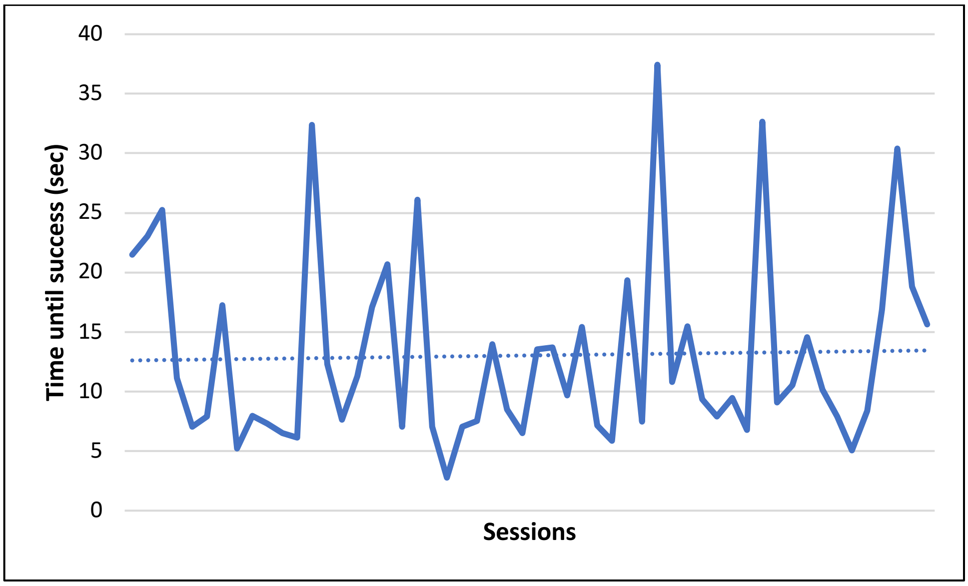

Figure 21. Means of the time until success per session during the second training phase. The dotted line indicates the progression over time (regression line) (*p* = 0.608). Data corresponds to juvenile female Edith.

Since Edith was generally very motivated and picked up the training routines quite fast, the distance between the two ropes could be gradually increased from session 74 onwards. At the beginning of the training phase, the rope distance measured 11 cm. With nine steps, the distance could finally be increased to 62 cm. During training it was occasionally required to go a step back again before being able to increase the distance one more time.

To determine whether a positive success rate could be established, the ratio of correctly solved trials and failed trials over time was analysed and is illustrated in Figure 22. In order to examine whether or not a significant transition in Edith's performance regarding a success rate could be detected a Spearman Rank Correlation test was conducted. A weak positive trend was found, but the correlation was not statistically significant (Spearman rank correlation, Rho = 0.299, $n = 71$, $p = 0.4590$). Since the number of trials per training session was determined by Edith's participation, there was no consistent number of trials per training session. In order to obtain a more reliable outcome, only sessions that contained at least 10 trials were included in further analysis (Figure 23). The reduced data exhibited a strong positive trend, and the correlation was found to be statistically significant (Spearman rank correlation, Rho = 0.881, $n = 8$, $p = 0.0201$).

Even though it remains unclear whether Edith conceived the task entirely, she exhibited an increasing success rate. On these grounds, and due to time limits, the training phase was eventually terminated, and she was admitted to the test phase.

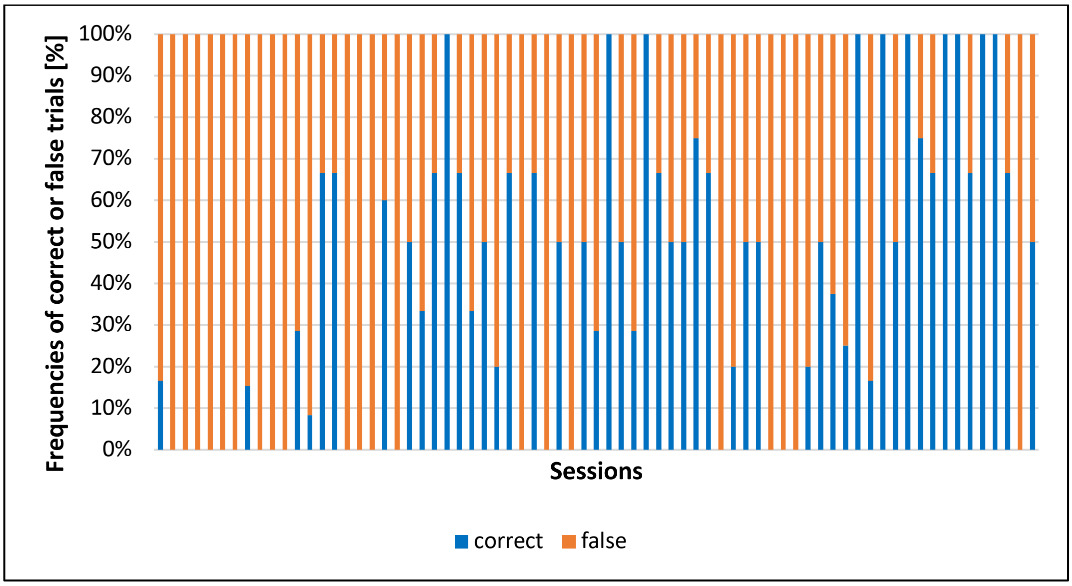

Figure 22. Ratio of correctly solved trials (blue) and failed trials (orange) over time of the second training phase. Data corresponds to the performance of juvenile female Edith. All sessions are included.

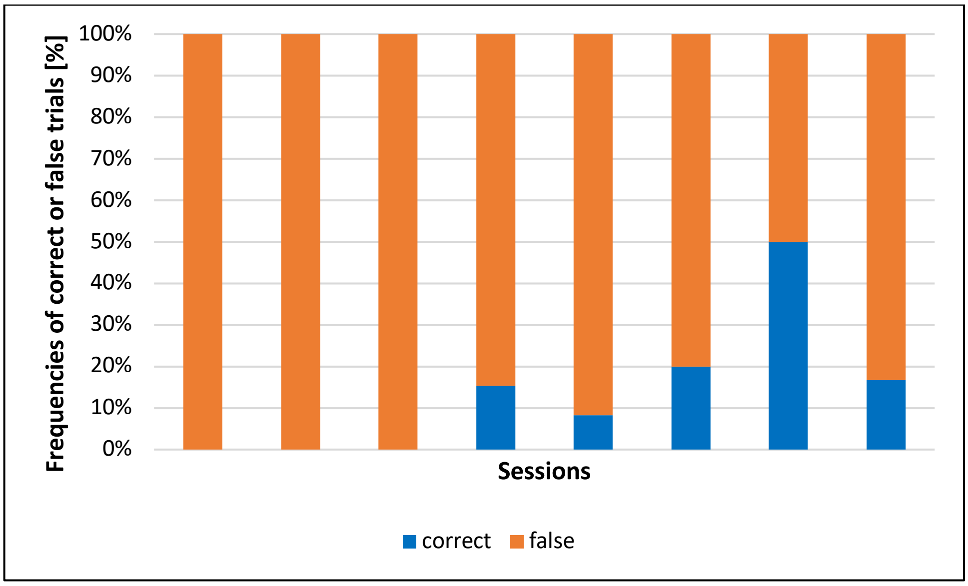

Figure 23. Ratio of correctly solved trials (blue) and failed trials (orange) over time of the second training phase. Data corresponds to the performance of juvenile female Edith. Only sessions that contained at least 10 trials were included.

4.3.4 Comparisons of performances between the individuals

Comparing Elliot's and Edith's performance during the second task, Edith was again faster in incrementally improving her performance than Elliot. Edith was in fact already confronted with the extension of the distance between the two rope ends, whereas Elliot did not reach that stage. Nevertheless, Elliot again solved the tasks faster than Edith (both on average and median), but the difference between the two gibbons was not statistically significant (χ^2 (1, N = 13.99) = 1.17, $p > 0.20$).

4.4 Test phase

During the test phase, the gibbons were on their own, i.e. the keepers and trainer did not reinforce their behaviours any longer. The aim was to establish whether or not they would work together to achieve a common goal. If they simply pulled on one rope end, they did not receive any reinforcements.

Since the apparatus could not always withstand their vigorous pullings, it had to be modified as described in section 2.4.3. Additionally, the time to investigate and to work with the apparatus was prolonged from several three-minute-trials to one 75-minute-trial in order to enable the gibbons to work at their own pace. On these grounds, the data were split into three parts.

Figure 24 depicts the gibbons' performances during those three parts. In all parts, the left rope was clearly pulled less often than the right rope. The Chi-square-test revealed all differences to be significant (original apparatus (3-min-trials): (χ^2 *(1, N = 57) = 16.86, p < 0.001*); modified apparatus (3-min-trials): (χ^2 *(1, N = 35) = 24.46, p < 0.001*); modified apparatus (75-min-trials): (χ^2 *(1, N = 49) = 45.08, p < 0.001*)). At the beginning of the test phase, the gibbons pulled the left rope 13 times, but then seemed to have lost interest in pulling the rope despite having more time.

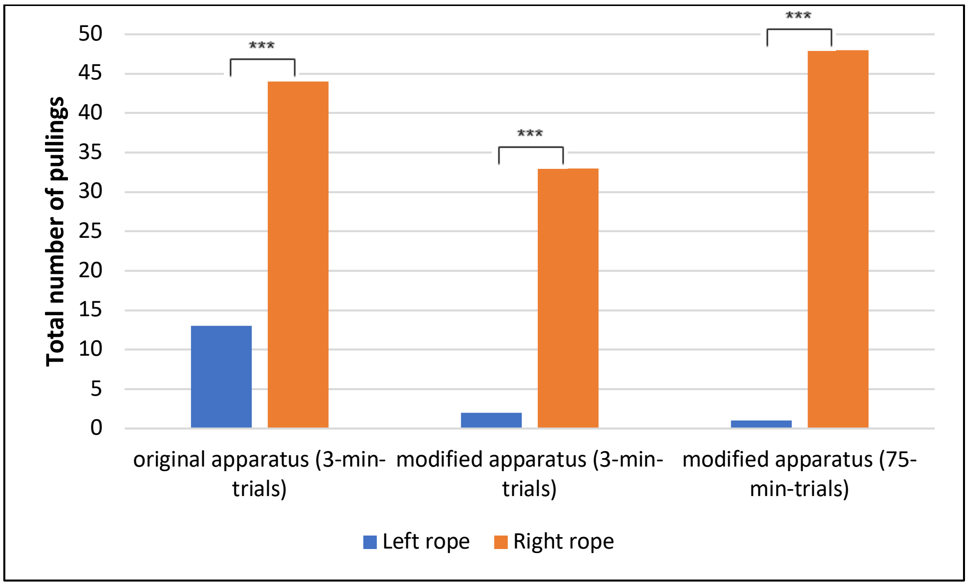

Figure 24. Total number of pullings for each rope (blue = left; orange = right) during the test phase. There are three different parts due to necessary adjustments of the test apparatus and timing. *** indicates *p* < 0.001.

In the test phase, Lelle pulled 24 times in total (Figure 25). This corresponds to the lowest number of pullings during the test phase of the three study animals. Besides one time, Lelle always pulled the right rope.

Elliot showed little more interest in the ropes with 40 pullings in total (Figure 26). Similar to Lelle, she focused her interest on the right rope; she only pulled the left rope twice.

Edith exhibited most interest in the ropes and pulled them 77 times in total (Figure 27). She pulled the left rope 13 times, possibly because she was trained on that side. However, during the 75-minute trials she did not pull the left rope anymore.

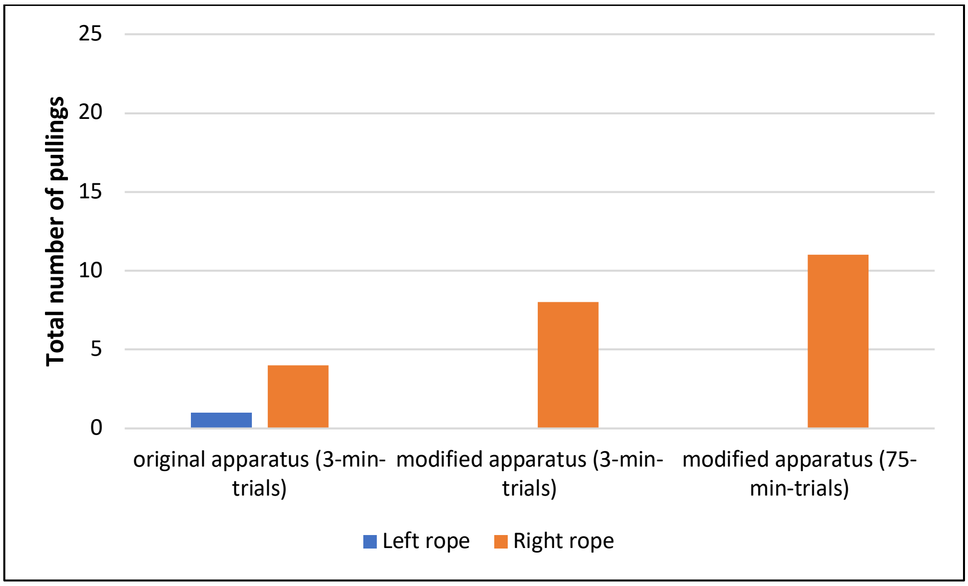

Figure 25. Total number of pullings by adult male Lelle on each rope (blue = left; orange = right) during all three parts of the test phase.

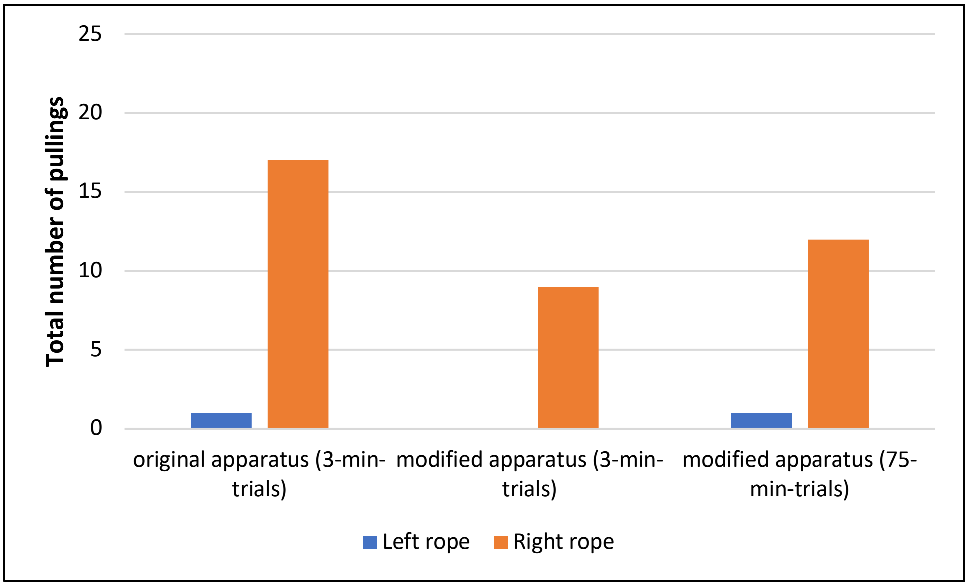

Figure 26. Total number of pullings by subadult female Elliot on each rope (blue = left; orange = right) during all three parts of the test phase.

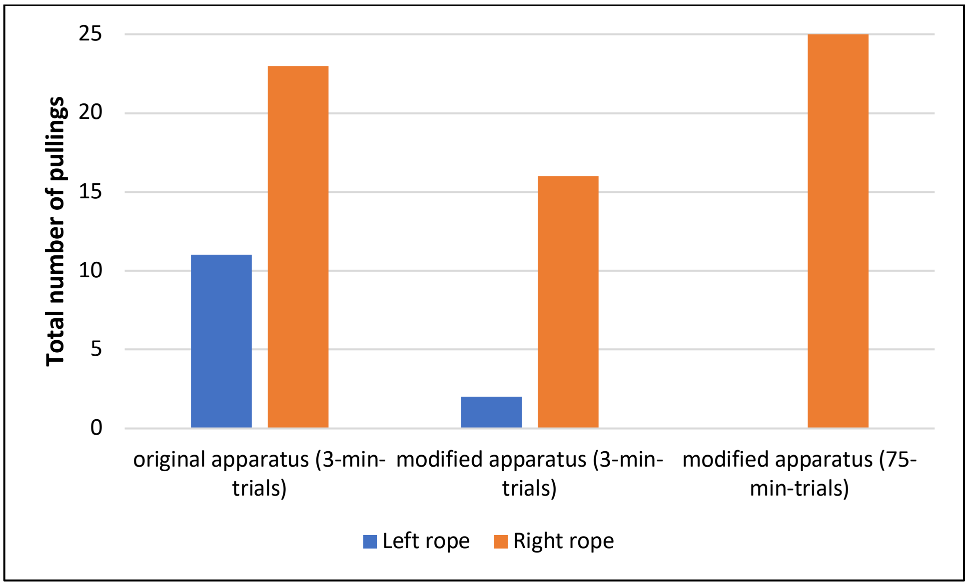

Figure 27. Total number of pullings by juvenile female Edith on each rope (blue = left; orange = right) during all three parts of the test phase.

Even though the gibbons did learn to pull the ropes, ultimately, no cooperation between them occurred. Furthermore, they seemed to lose interest in the apparatus after they figured out it did not work the same way as before.

Although no cooperation behaviour could be recorded, two individuals occasionally did sit together in front of the apparatus. Table 3 lists all dyads that sat together in front of the apparatus during all three parts of the test phase. If infant Ebot was ignored, at four occasions two individuals were sitting together in front of the apparatus. One was actively pulling one rope, while the other one was present, but not pulling the second rope. Interestingly, Edith was the possible cooperation partner in all four occurrences. Lelle and Elliot were both twice the counterpart of a possible cooperation dyad.

Table 3. Occurrences of two individuals sitting together in front of the apparatus for all three parts of the test phase. One was actively pulling the rope, the other was one just present but could have reached the other rope. Infant Ebot is included in the list but parentheses indicate he was not taken into account.

	Left rope	**Right rope**
Original apparatus (3-min-trials)	Edith present	Elliot pulling
	Edith present	Lelle pulling
	(Edith present	Ebot pulling)
	Elliot pulling	Edith present
Modified apparatus (3-min-trials)	(Ebot present	Edith pulling)
	(Ebot present	Lelle pulling)
Modified apparatus (75-min-trials)	Edith present	Lelle pulling

Even though infant male Ebot was not actively involved, or encouraged to participate, in the training, he started to pick up and imitate the behaviours his family members were supposed to learn. During the training, he curiously investigated the apparatuses and occasionally pulled the ropes. Whenever he successfully pulled a rope, he most certainly also received a food reward. However, his performance during the training sessions was not taken into account.

Ebot also tried to participate in the test sessions. A total number of 35 pullings were counted for Ebot, with one pull on the left rope, and 34 on the right rope (Figure 28).

Towards the end of the test phase he was only observed trying to receive the rewards through other techniques (e.g. trying to reach the reward on the slide by using his fingers instead of the ropes).

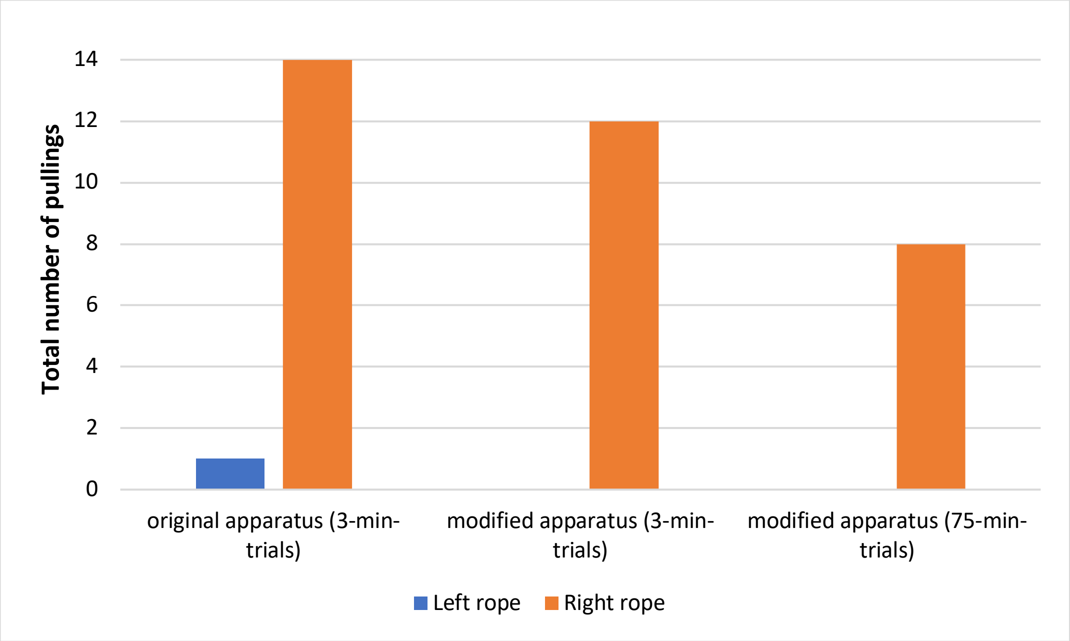

Figure 28. Total number of pullings by infant male Ebot on each rope (blue= left; orange= right) during all three parts of the test phase.

4.5 Behavioural observations

4.5.1 Distances between the animals

Observations and behavioural monitoring revealed that all gibbons spent most of their time ‘out of arm reach to everyone’. Hence, less time was spent in a reachable distance to other conspecifics or even being actively involved in any kind of social interactions. The Chi-square-test showed that the differences between ‘out of arm reach to everyone’ and the other two distance categories combined were significant for every individual (Lelle: χ^2 *(1, N = 3862) = 1.16x10*^{10}*, p < 0.001*; Elly: χ^2 *(1, N = 3514) = 360.81, p < 0.001*; Elliot: χ^2 *(1, N = 3715) = 944.31, p < 0.001*; Edith: χ^2 *(1, N = 3791) = 100.42, p < 0.001*; Ebot: χ^2 *(1, N = 3546) = 47,41, p < 0.001*). Compared to the other individuals, infant Ebot spent the least time (55.8%) ‘out of arm reach to everyone’, followed by juvenile Edith with 58.1%. Adult male Lelle spent the most time ‘out of arm reach to everyone’ (77.5%), followed by subadult Elliot with 75.2%.

The second most represented distance category for all individuals was ‘within arm reach to someone’. The highest value for this category was found for Edith (41.2%), and the lowest for Lelle (21.8%).

All individuals were hardly ever ‘in close contact to someone’ (0-3.7%). Obviously, the values for adult female Elly (3.6%) and infant Ebot (3.7%) were well matched, because Ebot was still dependent on his mother. The proportions of the three distance categories for each individual are illustrated in Figure 29.

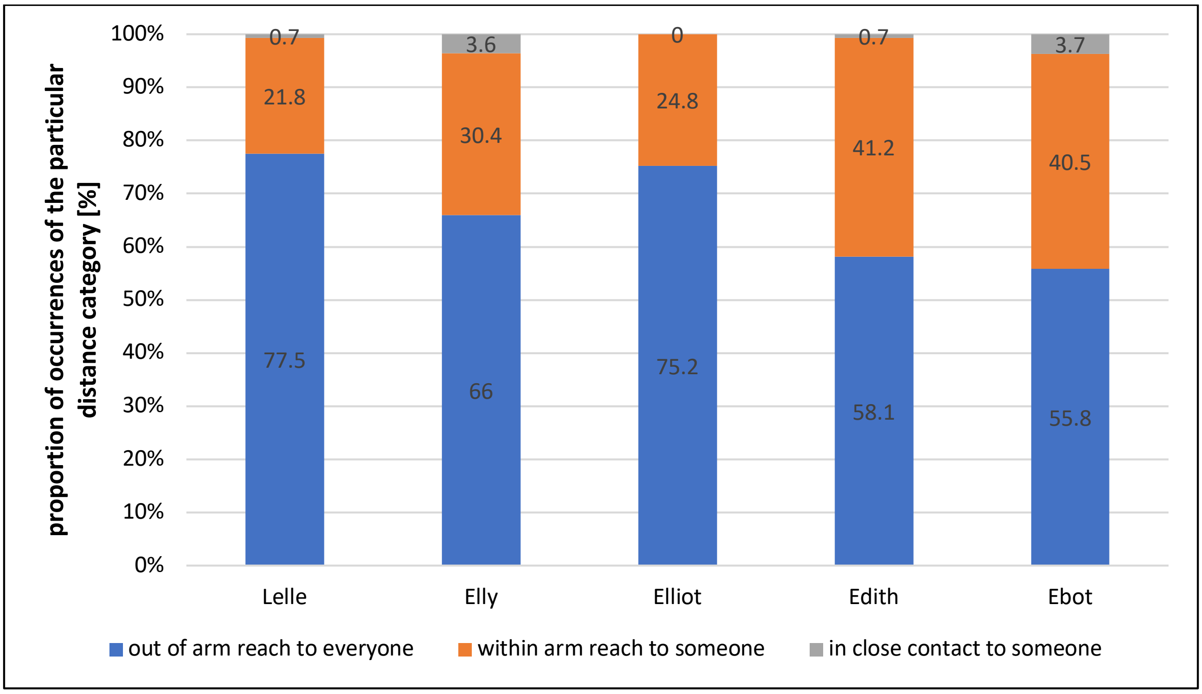

Figure 29. Proportion of occurrences of the three distance categories (blue=out of arm reach to everyone; orange=within arm reach to someone; grey=in close contact to someone) for each of the five family group members. Definitions for the distance categories are listed in the ethogram in Table 2.

4.5.2 Social behaviour

4.5.2.1 Social grooming

During observations, grooming behaviour for each individual was recorded. The data showed that most of the grooming behaviour was displayed by Edith. She performed this behaviour in 13.24% of the observed time. Lelle was the major recipient (9.47%), followed by Elly (2.69%). Elly performed grooming behaviour in 4.78% of the observed time, and it was mostly directed towards Ebot (1.68%) and Elliot (1.39%). However, Elliot, Ebot, and Lelle displayed grooming behaviour only scarcely, namely in 1.8%, 0.12%, and 0.05% of the observed time, respectively. The sociogram in Figure 30 presents the frequencies of grooming behaviour that occurred at least 0.5 times per hour.

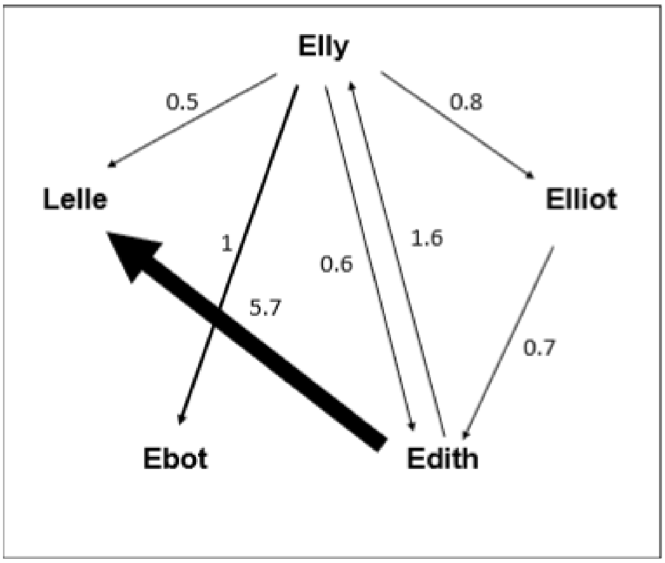

Figure 30. Sociogram for the frequency of grooming behaviour between the individuals. The direction of the behaviour is determined by the corresponding arrows, the frequency is indicated by the arrows' thickness. Associated values indicate occurrences per hour. Grooming behaviour that occurred less than 0.5 times per hour was not included in this sociogram.

4.5.2.2 Social play

Play behaviour between the individuals was also recorded. Most of the observed play behaviour occurred between Edith and Ebot (2.4 times per hour). Edith and Elliot played together 1.2 times per hour. Between Elliot and Ebot, play behaviour was recorded 0.6 times per hour. Lelle and Elly were both playing with their offspring only two times during the whole observation. The sociogram in Figure 31 presents the frequency of play behaviour that occurred at least 0.5 times per hour.

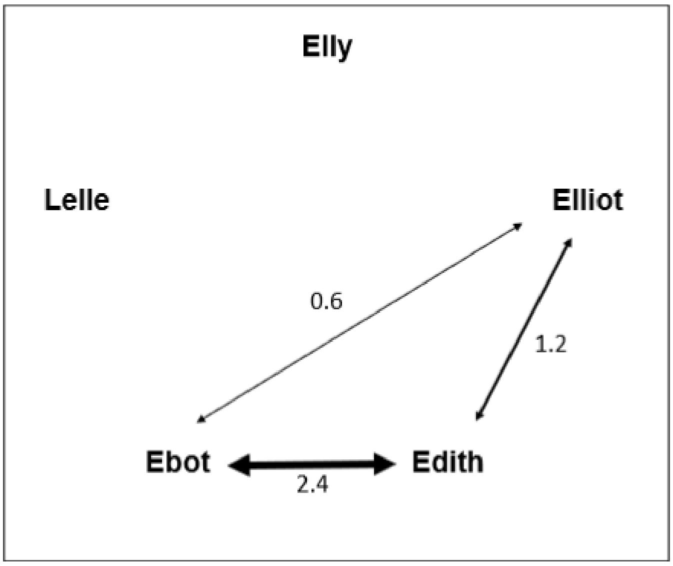

Figure 31. Sociogram for the frequency of play behaviour between the individuals. The direction of the behaviour is determined by the corresponding arrows, the frequency is indicated by the arrows' thickness. Associated values indicate occurrences per hour. Play behaviour that occurred less than 0.5 times per hour was not included in this sociogram.

4.5.2.3 Conflict

Conflict behaviour was almost never seen between the individuals. During the whole observation, it occurred once between Lelle and Edith, and once between Elly and Ebot.

5 Discussion

The aim of the present study was to discover whether or not cooperative behaviours occur among gibbons (*Hylobates lar*). The gibbons at Kolmården Wildlife Park in Sweden were presented with an experimental problem-solving task, in which two individuals were required to simultaneously pull a rope in order to receive a food reward. In the following, the particular steps of the study are discussed, and the results are put into context of previous research.

Since none of the participating gibbons had been part in a study before that examined their cognitive abilities, training and testing environment was completely novel to them. Therefore, adaptation and obtaining the animals' confidence required longer time than with animals that are participating in studies on a daily basis.

Even though Edith, Elliot and eventually Lelle took an active part in the training, Elly indicated no interest from the very beginning. It is not known whether she had bad experiences with humans in her youth, and is therefore more reluctant towards them, but the possibility should be taken into consideration. Throughout the study, however, she improved and gained more trust towards her keepers. That was shown in an increase of appearances from her side on one hand, and her allowing infant Ebot unrestrained interaction with the keepers on the other hand. If more time could have been invested, Elly would probably also have been successfully trained to pull the rope to obtain the food reward. Edith, Elliot and Lelle, however, showed that gibbons are able to pull a rope in order to receive a food reward. Furthermore, after having learned the task, they required only a few seconds to complete the tasks. Both findings go along with those of Beck (1967) whose gibbons were also able to solve all presented rope-pulling tasks. The gibbons in Beck's study required twice as long time to finish the task compared to the gibbons in the present study (mean of 8.75 sec. *versus* mean of 3.95 sec, respectively), but it should be noted that it was only a matter of seconds (Beck, 1967). Due to the lack of time, however, no control condition (e.g. available rope without food reward) could be included in the present study. Such a control condition should be considered for future examinations to further investigate the gibbons' extent of insight. Beck (1967) reported that his gibbons repeatedly pulled the rope even though no food reward was connected to it. This raises doubt that the individuals actually understood the physical properties of the task and possibly suggests that rope-pulling is merely a conditioned behaviour.

The second training phase, in which the individuals were supposed to learn to pull two ropes simultaneously, already suggested cognitive limitations. After having learned to pull one rope it proved difficult to broaden the learned behaviour. Adult male Lelle never managed to manipulate two rope ends at the same time, even though he seemed motivated to engage in the project. A reason for his limited flexibility could have been his advanced age (30 years). It is presumed that wild gibbons have a longevity of 25 to 35 years, in captivity it can reach up to an age of 60 years (Geissmann et al., 2009). Either way, Lelle's age may have influenced his learning capability, which could have resulted in a delayed learning process (Geinisman et al., 1995). Nevertheless, both Edith and Elliot revealed the onset of the asked behaviour. At the end of the second training phase, Elliot pulled the two rope ends together progressively more frequently and more confidently. For solving the task, she always used one hand. Edith's training progress was even more advanced. She was the first to discover that pulling two rope ends would deliver the reward. On the contrary to Elliot, she always used one hand and one foot for pulling the two rope ends. Since Edith was very motivated, the distance between the two rope ends could progressively be increased. An impediment during the training phase was the fact that the gibbons were quite sceptical towards novelties and changes. Even Edith, who appeared to be a curious and explorative character, would be initially reluctant to the slightest change. Another factor that might have had a decelerating impact on the learning process is that several keepers trained the animals. And even with an agreed and coordinated plan for training procedures, every keeper had their own personal style to conduct the training sessions. For both Elliot and Edith, a positive success rate was found, suggesting that they might have learned the behaviour eventually, if more time could have been invested.

During the actual test phase, no cooperative behaviours were displayed, and thus, the gibbons were not able to succeed in the problem-solving task. Since the gibbons could not be separated, all five individuals had access to the ropes. Therefore, performances of all individuals were analysed, even though not all of them fulfilled the passing criterion of the second training phase. The motivation level of all gibbons declined drastically after they discovered that a single rope pulling behaviour would no longer lead to success. Unlike for instance chimpanzees, the gibbons were more likely to lose interest and ignore the apparatus instead of persistently trying to achieve the reward, in one way or another. This goes along with the findings of previous studies (Cunningham, 2006; Martinez Sierra, 2013). Surprisingly, not even Edith showed a lot of excitement towards the ropes, even though she was the most successful one in both training phases. Both Cunningham (2006) and Martinez Sierra (2013) reported low levels of motivation in gibbons during cognitive investigations. They emphasized that low motivation, rather than the absence of cognitive abilities, could have restrained their success (Cunningham, 2006; Martinez Sierra, 2013). On the other hand, the modified testing apparatus might have been to advanced and the interplay of the two ropes were not obvious enough for the gibbons to grasp the concept.

Martinez Sierra (2013) further reported that juveniles displayed greater interest in novel devices than adults. These findings were consistent with those from the present study, because juvenile Edith as well as infant Ebot both interacted more often with the apparatus than their older conspecifics. It is well known that spatial exploration plays a crucial role during infants' cognitive development (Hazen, 1982).

Another interesting point was that Edith hardly ever pulled the rope on the left side which was in fact her training side. If she pulled a rope in the test situation it was almost always the one on the right side. One explanation for this choice could be the panel in front of the right rope. It was possibly more comfortable to sit or stand directly in front of the apparatus instead of hanging in front of it as it was required for the left rope. Additionally, this could be an indicator that she was not obtusely trained for one side but that she actually understood that pulling any of the two ropes, independent from which side, meant reinforcement. For future studies, however, it is suggested to arrange a more equal set-up design in order to prevent any kind of bias.

The behavioural observations revealed that all gibbons, including infant Ebot, spent most of their time 'out of arm reach to everyone', and, therefore, were not involved in any kind of social interaction. Similar results were found in siamangs (*Symphalangus syndactylus*), that were observed to gradually increase their intra-species distance with age (Pra and Geissmann, 1994). Elly and Ebot (i.e. mother and infant) had the highest values for spending time in close contact to another conspecific. This was expected since Ebot was still dependent on, and reared by, his mother. Both Lelle and Elliot were the ones spending the least time near their group members. The proportional distribution of the particular distance categories obtained for juvenile Edith were comparable to those for infant Ebot. More specifically, Edith spent less time alone and more time near her group members than both of her parents as well as her subadult sister Elliot. That was surprising since Edith was slightly closer to Elliot age- and developmental-wise than to Ebot and would have been expected to behave more similar to Elliot than to Ebot.

The juvenile female Edith presented herself as being highly social. It was remarkable that most of the social grooming behaviour was initiated and performed by her. The second most, and yet distinctly less, grooming behaviour was recorded for mother Elly towards Ebot, which again could be evaluated as mother-infant-care behaviour. Generally, the gibbons did not spend a great proportion of their activity budget with social grooming behaviour. Play behaviour only occurred between the offspring and here again, Edith was the one most often involved. A relatively low proportion of social interactions (which includes social grooming and play behaviour) has also been reported for the white-handed gibbon during field observations (annual mean of 11.3%) (Bartlett, 2003). Black-crested gibbons (*Nomascus concolor*) have also been observed to devote the least of their time to social interactions (Sheeran, 1993). Accordingly, conflict-related behaviours were hardly seen, neither in the present study nor in previous ones (Bartlett, 2003). Chimpanzees, by comparison, who exhibit a totally different social structure, were found to spent 2.05 minutes per hour with social grooming and 3.19 minutes per hour with social play (King et al., 1980). That corresponds to approximately twice as much social grooming (Edith not included) and thrice as much social play exhibited in chimpanzees compared to the gibbons of the present study.

In order to approach the origin of cooperative behaviours within the primate taxa, not only performances of the apes (Hominoidea) have to be taken into account but those of monkey species as well. Several species of Old World monkeys (Cercopithecinae) – the sister group of the apes – have been examined regarding their abilities to solve a given task in cooperation with their conspecifics. None of the monkey species were able to develop cooperative problem-solving skills. Species tested include the sooty mangabey (*Cercocebus fuliginosus*: Warden and Galt, 1943), guinea baboon (*Papio papio*: Fady, 1972), japanese macaque (*Macaca fuscata*: Burton, 1977), rhesus macaque (*M. mulatta*: Petit et al., 1992; Warden and Galt, 1943), and tonkean macaque (*M. tonkeana*: Petit et al., 1992).

Considering those results and the outcome of the present study, one could argue that cooperative behaviours evolved in Old World monkeys after the gibbons separated from the great apes. However, several studies reported occurrences of cooperative behaviours among various species of the New World monkeys (Platyrrhini). Two species of Callitrichidae have been tested. Cotton-top tamarins (*Saguinus oedipus*) appeared to be very successful in cooperating with a conspecific during problem-solving tasks (Cronin et al., 2005; Cronin and Snowdon, 2008). The authors even presumed that cotton-top tamarins would take the partners role as well as its presence into account (Cronin et al., 2005). In common marmosets (*Callithrix jacchus*), Werdenich and Huber (2002) could record cooperative behaviours for every individual, leastwise with one partner. Only fifty per cent of the pairs successfully solved the cooperative problem-solving task (Werdenich and Huber, 2002). The authors concluded that the cooperation success rate would depend on two factors: “On a specific distribution of roles and the tolerance of higher-ranking individuals” (Werdenich and Huber, 2002). Within the family Cebidae, white-headed capuchins (*Cebus capucinus*) were found not to be able to cooperatively solve a given problem (Warden and Galt, 1943), whereas brown capuchins (*Sapajus apella)* appeared to be highly successful in solving the cooperation task (Mendres and de Waal, 2000; de Waal and Davis, 2003; Hattori et al., 2005; Brosnan et al., 2006). Mendres and de Waal (2000) suggested that capuchins were able to take the partners’ role into account during the cooperative interaction.

Based on findings of earlier publications, the occurrence of cooperative behaviours in the two lineages, the New World monkeys (i.e. Callitrichidae and Cebidae) and the Old World monkeys and apes (i.e. Hominidae) could rather be explained as a result of convergent evolution. The gap between families that do and do not exhibit the corresponding behaviours seems to be too large in order to consider this trait to be a homology. More likely is that similar selective pressures and adaptations to comparable circumstances have independently caused the development of cooperative behaviours. All the mentioned mammal species that were successful in the cooperative problem-solving tasks have in common that they are not socially monogamous but live in groups with fluctuating social structures and flexible breeding compositions. This includes brown capuchin (*S. apella*: Izawa, 1980); tamarin and marmoset (*C. jacchus* and *S. oedipus*: Sussman and Garber, 1987); orangutan (*Pongo*: Singleton and van Schaik, 2002; Goossens et al., 2006); gorilla (*Gorilla*: Harcourt et al., 1976; Harcourt, 1978; Robbins et al., 2004); chimpanzee (*Pan troglodytes*: Gagneux et al., 1999); bonobo (*P. paniscus*: Gerloff et al., 1999); asian elephant (*Elephas maximus*: Vidya and Sukumar, 2005); bottlenose dolphin (*Tursiops truncatus*: Félix, 1997); wolf (*Canis lupus*: Sands and Creel, 2004); spotted hyaena (*Crocuta crocuta*: Frank, 1986).

As previously elucidated, gibbons live in small stable groups with few conspecifics to interact with and spend comparatively little time in social interactions compared to primates living in larger groups. Therefore, the present study's findings on the gibbons' social behaviours and their performances in the cooperation task appear to be compatible with the "social brain hypothesis" (cognitive abilities are constrained by the complexity of the animals' social life (Humphrey, 1976; Dunbar, 1998). Furthermore, Edith, who appeared to be most involved in social interactions, was also the one who learned the tasks faster and to a greater extent than the other gibbons. Similar differences were found in two orangutan species. The more companiable sumatran orangutan (*P. abelii*) was found to be more successful during problem-solving tests than its close relative, the more unsociable bornean orangutan (*P. pygmaeus*; Forss et al., 2016).

It remains unclear if brain size can actually be used as a predictor of cognitive abilities, since relative brain masses reported in Matsuzawa (2007) do not quite reflect scientific observations regarding cognitive abilities. However, Kudo and Dunbar (2001) found a positive correlation between the relative neocortex size and the social group size in primates. Unfortunately, gibbons were not included in that study.

5.1 Conclusion and outlook

In conclusion, the gibbons at Kolmården Wildlife Park in Sweden did not develop any cooperative behaviours among each other and spent comparatively little time in social interactions. These findings appear to support the "social brain hypothesis". However, the findings of the present study should be regarded with caution because of its small sample size of one gibbon group. Clearly, more gibbons should be examined.

In future experiments, control conditions should be included. Conditions without a cooperation partner as well as with prevented access to one of the two rope ends could shed light on the extent of insight in gibbons, given that they exhibit prior cooperative behaviours. Additionally, siamangs (*S. syndactulus*) should be included in future studies on cooperation in gibbons. Siamangs live sympatrically with white-handed gibbons (*H. lar*) and agile gibbons (*H. agilis*), respectively (Geissmann, 2003a). Yet, siamangs differ from the sympatric gibbon species in several respects of their social organisation. For instance, the father is actively involved in parenting including infant carrying (Alberts, 1987; Lappan, 2008) and siamangs appear to have more cohesive groups than white-handed gibbons (Chivers, 1976). It would be worthwhile to investigate whether siamangs are more successful in cooperative problem-solving tasks than white-handed gibbons.

5.2 Ethical considerations

Due to their proximity to humans, research on non-human primates is a controversial topic. The procedures of the study on hand were throughout non-invasive. To ensure that the gibbons were not harmed as well as that their exposure to potential stress was as low as possible, the animals were always kept in their (known) enclosure. Furthermore, they were only cared for and trained by regular staff members of Kolmården Wildlife Park. Neither the animal keepers nor any other person entered the enclosure when the gibbons were present. The gibbons were never captured or exposed to any kind of risks, furthermore, their participation during the study was voluntary at all times. The food rewards consisted of their regular diet, but only served as a supplement. This implies that the gibbons were never food deprived and their performances during the study had no impact on their daily amount of food.

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