Department of Physics, Chemistry and Biology

Master Thesis

Using predator models to induce anti-predator behaviors in two captive tamarin (Callitrichidae) species at Parken Zoo

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Titel/Title:

Using predator models to induce anti-predator behaviors in two captive tamarin (Callitrichidae) species at Parken Zoo

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Sammanfattning/Abstract:

Animals can suffer from impaired anti-predator responses when held in captivity without predation pressure for several generations. One way of preventing degradation of these possibly vital behaviors can be to use predator models as environmental enrichments in captive environments. During this study, anti-predator behaviors of two tamarin species, Brazilian bare-faced tamarin (Saguinus bicolor) and cotton-headed tamarin (Saguinus oedipus), were studied over several months. Both species were presented with two predator models (stuffed fox and rubber snake) and corresponding controls (covered fox and plastic plant) in 17 sessions, each with movement of stimuli in exposure period. The results revealed that the Brazilian bare-faced tamarins showed more anti-predator responses towards both the fox and the snake than the controls, while the cotton-headed tamarins only showed higher responses towards the fox compared to the control. A habituation effect towards both predator models was discovered in the Brazilian bare-faced tamarins. The most effective predator model was established to be the fox while it could not be assessed that movement had any effect. Conclusions of predator models, particularly a stuffed fox, being an effective way of inducing anti-predator behaviors in these tamarin species could be made, although warnings for possible habituation effects should be issued. By using predator models in the zoo, the future generations of these tamarins could be better prepared for a life in the wild when they are to be reintroduced.

Nyckelord/Keyword:

Anti-predator, Callitrichidae, Predator model, Zoo

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Contents

1 Abstract

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2 Introduction

More than 1,000 different species are held in captivity all over the world in zoos and aquariums that are part of the World Association of Zoos and Aquariums, WAZA (WAZA, 2012). Many of these species are threatened to some degree and are therefore kept in captivity for conservation purposes. But since the wild is hard to mimic in the zoos, the captive environments are often different from the natural habitat. In the absence of predators and without competition over resources, the captive animals have very different evolutionary pressures acting on them compared to their free living relatives. The natural selection acting in the wild is replaced by a different selection controlled by the management. This can lead to that some behaviors become degraded. To a large extent it is, however, unknown exactly what effect this change in selection pressure has on captive animals.

One group of behaviors that can be sensitive to changes in selection pressures are anti-predator behaviors. As stated by Alcock (2009, page 196), you can apply a cost-benefit approach to anti-predator behavior. If the cost of an anti-

predator behavior exceeds the benefits it will not be selected for. In absence of predators, anti-predator behavior should only imply a cost and no benefit at all. A selection that acts without predation pressure is usually called a relaxed selection (Caro & Eadie 2005). In the long run a relaxed selection can lead to that animals bred in captivity for several generations get impaired ability to cope with their predators in the wild. Altering of anti-predator behaviors when predation is absent has been confirmed in several different studies. Blumstein & Daniel (2005) saw a decreased occurrence of anti-predator vigilance in macropod marsupials living on predator-free islands compared to those living on the mainland. Similar results were revealed in New Zealand robins (*Petroica australis*) by Maloney & McLean (1994) where mainland robins responded more strongly to the predator stout than the island robins that had lost contact with predators did. A further study by Cooper Jr et al. (2009) confirmed similar results in the Balearic lizard (*Podarcis lilfordi*) that showed stronger anti-predator responses if inhabiting an island with higher predation pressure than the lizards inhabiting an island with lower predation pressure. Evidence for degradation of anti-predator behaviors has also been observed in species living in captivity. McPhee (2003) saw that the probability of mice taking cover after seeing a predator decreased with the number of generations they were bred in captivity. When studying rhesus monkeys (*Macaca mulatta*), Mineka et al. (1980) saw that lab-reared monkeys showed only mild responses towards models of snakes compared to wild-reared monkeys that showed considerable fear towards the snakes. Studies showing that animals living in captivity have maintained anti-predator behaviors are present as well. Captive-born meerkats (*Suricata suricatta*) studied by Hollén & Manser (2007) used the same alarm calls as reported in the wild and in similar contexts. They could also discriminate between fecal scents from potential predators and fecal scents from non-predators. Gaudioso et al. (2011) saw no difference in survival between red-legged partridges (*Alectoris rufa*) bred in farms for generations and red-legged partridges coming directly from wild parents. Furthermore, Maran et al. (2009) could not find any evidence indicating the number of generations bred in captivity had any effect on the European mink's (*Mustela lutreola*) survival after release.

Not only the degree to which behaviors change, but also with which speed relaxed selection alters behaviors is debated. In a study by Blumstein et al. (2004) on tammar wallabies (*Macropus eugenii*), it was revealed that isolation from predators could lead to a rapid decrease in predator recognition in as fast as only 130 years. Another study, on the other hand, concluded that isolation from predators for up to 20 000 years lead only to partial alteration of anti-predator behaviors in stickleback fish (Messler et al. 2007). These two different studies show evidence of very different degrees and velocities of which relaxed

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selection can act. The same study of Messler et al. (2007) also showed that anti-predator behaviors that had been lost through relaxed selection could be regained and elicited to a historically present predator after a time of a new predator being present. This phenomenon is called reverse selection and was acquired in the stickleback fishes in as fast as only 25 years. Further, a study by Håkansson & Jensen (2008) revealed that although two different populations of captive red junglefowl (*Gallus gallus*) showed different responses to a simulated attack by an avian predator model in the first generation, they became more similar after only four generations living in the same environment. These studies show that behaviors are changed and even regained to different degrees and with different speeds.

There are different theories about the genetic versus the environmental component concerning anti-predator behaviors. The multi-predator hypothesis predicts that the genes coding for anti-predator behaviors are pleiotropic, meaning that they can function also in non-predatory situations and therefore persist without presence of predators or at least in presence of only one type of predator (Blumstein 2006). One example of where anti-predator behaviors seems to be linked to a totally different behavior, was revealed trough the studies of Masataka (1993), where it was seen that squirrel monkeys (*Saimiri sciureus*) raised in captivity and fed with live insects showed as much anti-predator behaviors towards a live snake as wild-born individuals. Whereas the captive-born individuals that were fed only fruit and monkey chow, on the other hand, did not show these behaviors. Blumstein & Daniel (2001) continued the reasoning by showing that tammar wallabies from two different islands with only avian predators or both avian and mammalian predators, showed the same type of anti-predator behaviors when put in the same environment. This suggests that the group of tammar wallabies from the island where only avian predators were present still had maintained the appropriate anti-predator behaviors relevant for all type of predators. All the studies above suggest that there is a strong genetic component to anti-predator behavior in these species. According to Blumstein (2002), some anti-predator behaviors are innate but others have to be learned. The behaviors with a genetic component, as he calls the more "hard-wired" ones, can persist for several thousands of years without contact with predators. The behaviors that require experience on the other hand, are lost quickly, maybe as fast as in a single generation, but can also be regained in case of encountering with predators again. The importance of environment concerning the development of anti-predator behaviors is stated in a study by Beani & Dessí-Fulgheri (1998), where the parent-reared partridges showed more of some anti-predator behaviors compared to the ones reared without parents, when presented to a raptor. Interesting results concerning importance of nature versus nurture have also been found in primates. Mineka et al. (1984) studied

the effects of parent's fear towards snakes on young rhesus monkeys. In this study, the young rhesus monkeys did not show anti-predator behaviors towards a real, toy or model snake until they had seen their parents behave fearfully towards these snakes.

As made clear above, evolution of anti-predator behavior is complex and can include both genetic and environmental components depending on species. A fact that can further complicate the picture is that also the different senses involved in predator recognition can evolve differently within the same species. Blumstein et al. (2000) saw that tammar wallabies living on an island isolated from mammalian predators for 9500 years showed anti-predator behaviors towards different models of predators but not towards sounds of predators. With further studies on marsupials, Blumstein (2002) could formulate the theory that visual predator recognition is not lost after thousands of years of predator isolation in these species but olfactory and acoustic predator recognition have to be learned after this time. The authors suggest that this is due to the fact that visual predator recognition has been preserved under relaxed selection because mammalian predator morphology is convergent, while recognition of predator vocalizations have not been preserved since different predator vocalizations are not convergent.

As mentioned before, animals living in captivity might encounter a relaxed selection. When it comes to conservation of animals, a relaxed selection is not desirable. If the individuals held in captivity or their descendants are planned to be released back into the wild, many behaviors necessary for their survival in the wild might have been degraded. This makes interventions to maintain these behaviors in the captive environment necessary for conserving animals in captivity. Particularly the deprivation of anti-predator behaviors in captive animals might be a severe problem when conservation measures, such as reintroduction, are taken. Therefore, the possibility of preventing loss of anti-predator behaviors or improving them is of great importance. There has been some research conducted that has investigated the possibility of inducing anti-predator behaviors in captive animals. One example is with the New Zealand robin where presentation of predator models together with vocalizations or with simulated chasings taught young robins to respond fearfully to a predator model (McLean et al. 1999). Also within small monkey species of the family Callitrichidae, evidence for possible stimulation of anti-predator responses directed towards models has been found. Cagni et al. (2011) saw that marmosets increased gazing, alarm/mobbing calls and time spent close to another individual when exposed to a snake model. They also decreased foraging and time spent near the location of the snake model. But even without using models that are supposed to mimic real predators, anti-predator behaviors can be elicited.

Campbell & Snowdon (2007) managed to induce mobbing behavior in cotton-headed tamarins (*Saguinus oedipus*) when presenting them to a regular duster. The tamarins performed attack-like lunges towards the stimulus while vocalizing with open mouth.

The possibility of eliciting anti-predator behaviors in captive animals by using models could be used as a method to ensure that vital behaviors necessary for survival in the wild are not impaired in these species. In zoos, it might therefore potentially be successful to use predator models as environmental enrichments when it comes to preserving vital behaviors. The zoo community has a long history of using different environmental enrichments to ensure good welfare in their animals, both physically and mentally. Main efforts have been done to minimize management and diet effects on the well-being of animals (Mellen & MacPhee 2001). Different food presentations, complex environments and novel objects that stimulate species appropriate behaviors or give a diversity to an otherwise boring and constant daily routine include the most common environmental enrichments appearing in zoos all over the world (Swaisgood & Shepherdson 2005). But enrichments that deal with species appropriate behaviors of prey animals are very few, although for example Mellen & MacPhee (2001) encourage consideration to the species anti-predator behaviors when designing enrichments.

Two different tamarin species belonging to the family Callitrichidae held at Parken Zoo in Eskilstuna were used in this study, the Brazilian bare-faced tamarin (*Saguinus bicolor*) and the cotton-headed tamarin (*Saguinus oedipus*). These tamarin species are naturally living in Brazil and Colombia and are highly threatened. The Brazilian bare-faced tamarin is classified as endangered by the IUCN mainly due to habitat loss and range replacement by the golden-handed tamarin (*Saguinus midas*) while the cotton-headed tamarin is classified as critically endangered due to destruction of habitat. Both population sizes of these species have decreased substantially over the past three generations (18 years), more exactly by more than 50% for the Brazilian bare-faced tamarin and by more than 80% for the cotton-headed tamarin. Population sizes are uncertain but estimates have suggested that there are around 2,350 respectively 6,000 individuals left in the wild (IUCN 2012). Because of their placements in the red list categories, the two species are a part of European Endangered Species Breeding Programs (EEP:s) that is organized by the European Association of Zoos and Aquariums (EAZA), which means that the European zoos within the EAZA have a common conservation program concerning breeding. The idea is that these species someday will be reintroduced into the wild, and therefore efforts to keep these species in a way so that they maintain as many natural behaviors as possible, are included in the program (Parken Zoo 2012). Natural

predators of these monkeys include snakes and felids (Corrêa & Coutinho 1997, Emmons 1987). Although there are few reported observations of predator attacks in the wild, the present observations report anti-predator behaviors such as vocalizations (tzik), gazing and mobbing behavior (Corrêa & Coutinho 1997, Bezerra & Souto 2008). Mobbing behavior is defined as "the convergence of animals around their potential predator" and has been observed both in wild and captive Callitrichidae, sometimes in association with tzik calls (Campbell & Snowdon 2007, Corrêa & Coutinho 1997).

2.1 Aim

There are only a few earlier studies that have investigated this possibility of inducing anti-predator behaviors in captive animals by using a predator model. There are even fewer or none that have investigated the effects on tamarin's anti-predator behaviors over a longer time period by using different predator models that also include movement. A study of this kind would therefore fill a gap in the field of ethology/conservation biology and contribute to valuable discussions about how to prepare captive species for a life in the wild. Furthermore, it would encourage additional research within the same field. The purpose with this study was to evaluate the effects of presenting different predator models to two different tamarin species during a longer time period. This idea was initially raised by Parken Zoo which wanted this project to be performed as a part of their strive to shape environmental enrichments for prey species with focus on stimulating anti-predator behaviors. If the models tested in this study can induce anti-predator behaviors, they can possibly be used in the zoo as environmental enrichments with the purpose of mimicking situations in the wild and by that increase the possibility of maintaining vital anti-predator behaviors. The study might also be helpful in deciding the optimal way of using these predator models. In this project several different aspects associated with the use of these predator models were investigated and tested in two captive tamarin species:

a) Do tamarins at Parken Zoo show different initial reactions towards two predator models compared to the control models?

b) Do tamarins at Parken Zoo show different frequencies of anti-predator behaviors and/or different frequencies of calm behaviors (where the extreme would be taking contact with stimuli) during presentation of two predator models compared to the control models?

c) Do the possible anti-predator responses shown towards the predator models last after exposure?

d) Which of the two predator model is the most effective one?

e) Does movement of the predator models increase anti-predator responses?

f) Does the frequency of anti-predator behaviors and/or calm behaviors showed during presentation of the two predator models change over time when the models are used for a longer time period?

3 Material & methods

3.1 Study animals

The Brazilian bare-faced tamarin group consists of three individuals, one 3-year old female (Sabine), one six-year old male (Arthur) and one juvenile less than 1-year old (Jamie). Sabine is the fourth or fifth generation born in captivity (depending on if you count generations on the mother´s or the father's side) while Arthur is the third or fifth generation and Jamie the fourth or sixth generation born in captivity. The cotton-headed tamarin group consists of two individuals which are both males (Zeus and Caracas). They are nine-year old brothers of the fourth generation born in captivity. During time of the study they were held in indoor enclosures of 54.8 m^3 (the Brazilian bare-faced tamarins) and 28.7 m^3 (the cotton-headed tamarins). The Brazilian bare-faced tamarins had access to an outdoor enclosure of 58.3 m^3 in the beginning of the study while no outdoor access was present for the cotton-headed tamarins. Based on the fact that outdoor access was only present at a few times and the tamarins only being outside for very short time periods, the effect of this was disregarded in the results. Enclosures were of similar design for both groups, equipped with windows, shelves, branches and ropes and a mesh separating the enclosure from the corridor. The cotton-headed tamarin group was previously free-living in the park which might have led to them experiencing more encounters with different potential predators such as snakes, birds of prey or larger mammals than the Brazilian bare-faced tamarin group. For ethical reasons, a risk assessment of presenting the tamarins to models of predators was done before designing the experiment where it was estimated that it was of low or medium stress to the tamarins.

3.2 Experiment one

In the first experiment, a stuffed fox representing natural predators of mammalian carnivores was used. The fox, which were placed outside the mesh wall in front of the enclosure, was revealed by the keepers taking away the blanket hiding it (fig. 1 number 1). It was then presented still for five minutes before it was dragged on its wheels about one meter forward (fig. 1 number 2).

There it was left still for five minutes before it was covered with the blanket again and removed. As control, the same model but with an additional blanket of different color covering it was used in the same way. The control was included in order to exclude the possibility of behaviors recorded only being a reaction to any novel moving object of the same size. A blanket concealing the fox was put up between the walls of the corridor in order to prevent the tamarin group that were not taking part in the experiment from seeing the fox.
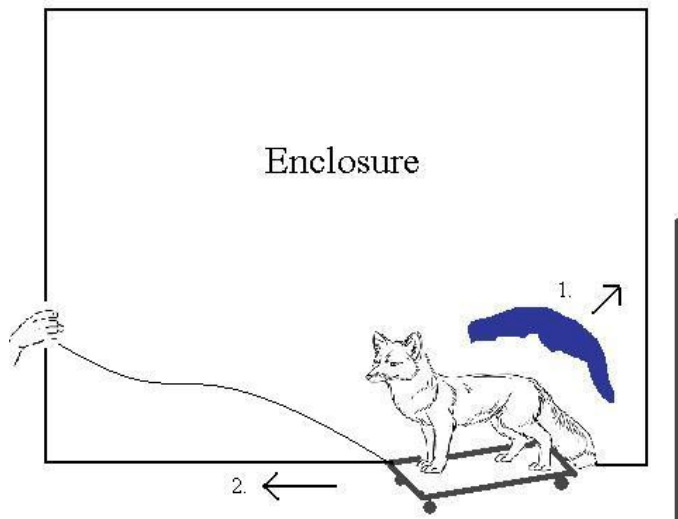
Figure 1. Experimental set-up for experiment one.

3.3 Experiment two

The second experiment involved a larger snake model of grey color, 180 centimeter of length and four centimeter in diameter, representing natural predators of tree-living boa snakes. It was placed on a shelf inside the enclosure before it was uncovered (fig. 2, number 1) and left still for 5 minutes. A movement was then simulated by pulling a thin fishing line attached to the snake's head (fig. 2, number 2), and it was then left still again for 5 minutes before it was removed by the keepers. The control was represented by a plastic plant placed at the same location to exclude the possibility of behaviors recorded only being a reaction to any novel object inside the enclosure. The reason for choosing a plastic plant as control was that this had been done in other research on Callitrichidae species (Cagni et al. 2011) and also because of the stimuli´s placement inside the enclosure. If a covered snake would have been used, the tamarins might have removed the blanket covering it and the results would thereby not reflect the response to the control but instead the response to the predator model.
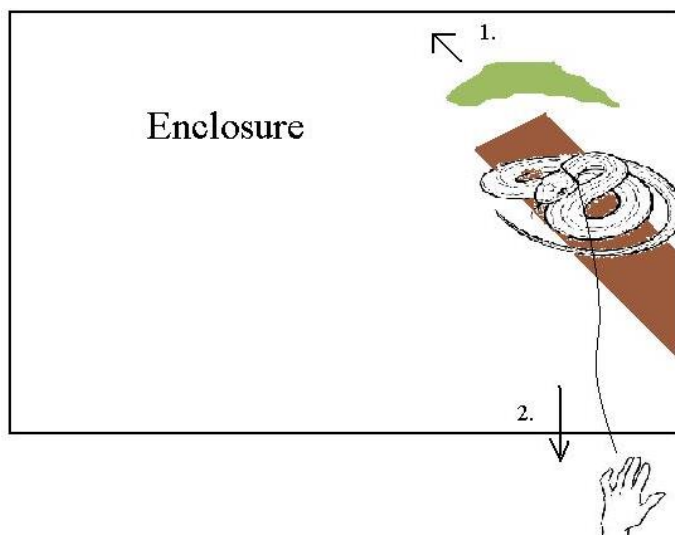
Figure 2. Experimental set-up for experiment two.

3.4 Recordings & analyses

Recordings and analysis were performed in the same way for both experiments and species. Behaviors recorded (listed in table 1) were chosen based on own behavioral observations of the tamarins and a pilot study conducted on the squirrel monkeys (*Saimiri ssp.*) at the park as well as by studying previous research on Callitrichidae (Barros et al. 2002, Cagni et al. 2011, Friant et al. 2008). The behaviors were registered throughout the whole sessions by rotating focal animal sampling with a 1/0 sampling every 15 seconds where the focal animal was switched every second minute. The individual that started as focal animal as well as the order of focal animals was chosen randomly. Behaviors were recorded for 10 minutes before the presentation of the stimuli started (pre-exposure period), during the presentation of the stimuli which consisted of two 5 minutes periods (exposure before movement period and exposure after movement period) and for 10 minutes after the stimuli had been removed (post-exposure period). The initial reaction of each individual was also recorded, where the measure was defined as the following: No reaction (not looking at the stimulus in moment of uncovering), Stay (looking but staying put at same location), Approach (looking and getting closer to stimulus) and Retreat (looking and getting away from stimulus). The initial reactions were registered on a later occasion by watching a video recorded during the experiment session. Contact with stimuli was also noted during each session, independent of whether it was the focal animal that made contact with the stimulus or not. Sessions of each different stimulus (snake model, snake control in form of plastic plant, stuffed fox and fox control in form of covered fox) were performed in association to feedings at two different times of day (11.30 a.m. and 2.30 p.m.)

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with mostly 20-72 hours in between (except for between the two weeks break of data collection during the Christmas holiday). The two different experiments with predator models and corresponding controls were performed for five days a week and in total of sixteen weeks according to a random schedule, resulting in 17 replicates of each stimulus.

Table 1. Ethogram with a functional and a descriptive term of all the recorded behaviors, where behavior 1-4 are classified as anti-predator behaviors, 5-11 are classified as calm behaviors and 12-14 as other behaviors.

Functional	Descriptive
1. Gazing	Gazing with open eyes and body still towards stimulus
2. Vocalization	Vocalizing with clearly open mouth or creating tzik sounds
3. Conspecific contact	Being closer than 20 cm to conspecific while looking at stimulus
4. Moving away	Moving more than one body length away from stimuli directly after looking
5. Foraging	Drinking, manipulating, chewing or putting food in mouth
6. Scratching	Scratching self with hands or feet or by rubbing body against features
7. Social interaction	Grooming, huddling, playing or mating with conspecific
8. Looking window	Looking outdoors through window when standing or sitting on window frame, shelf or branch closest to window
9. Investigating	Investigating floor bark, shelves or walls by using hands
10. Moving closer	Moving more than one body length closer to stimulus while looking
11. Stimuli contact	Being closer than 15 cm to stimulus or mesh protecting between
12. Locomotion	Moving more than one body length in any direction without looking at stimulus
13. Touching mesh	Touching mesh with hands, feet or body when either still or climbing
14. In box	Being out of sight by placing whole body in shelter box

3.5 Calculations & statistics

Frequency of each behavior for the different tamarin groups (the Brazilian bare-faced tamarin group and the cotton-headed tamarin group) was created by

calculating the mean values of the individual frequencies. To test for differences between the experimental stimuli and corresponding control (fox versus covered fox and snake versus plant), the behavior frequencies of each tamarin group from each exposure period was tested separately in a non-parametric Wilcoxon signed ranks test. Behavior frequencies from each behavioral group (anti-predator behaviors, calm behaviors and other behaviors) and from the two exposure periods (exposure before movement and exposure after movement) were summed together and tested for differences between predator stimuli and control with the same statistical test. To compare the different predator models, behavior frequencies from the sessions were tested against each other in a Mann Whitney U-test both separately and fused together in behavior groups. Frequency of the different anti-predator behaviors from before respectively after movement within data from sessions with the predator models were also tested in the same way to examine if movement of the predator models had any behavioral effects. To test for differences in behaviors before and after presentation of stimuli, a Wilcoxon signed ranks test was also done with behavior frequencies from the pre- and post-exposure periods collected during exposures with the fox and the snake.

No statistical test was done with the initial reactions as assumptions required by the statistical tests were not fulfilled. Sample sizes from reactions to each stimuli presentation were not equal due to loss of some data when the camera malfunctioned. The initial reactions were instead summed up so that the numbers of each reaction towards the different stimuli sessions could be displayed.

To test for behavioral changes over time, the frequencies of each behavior and the number of day of study was tested in a linear regression analyses. The same test was also done with anti-predator behaviors fused together.

4 Results

4.1 Results for the Brazilian bare-faced tamarins

4.1.1 Initial reactions in experiment one

The initial reaction was generally represented by "No reaction" and "Stay". When presented to the still fox, the tamarins reacted with "Stay" the most times (24 times), "No reaction" fewer times (13 times), "Approach" even fewer times (four times) and "Retreat" the least times (five times). Five reactions towards this stimulus could not be noted. To the covered fox they also reacted most times with "Stay" (22 times), "No reaction" fewer times (18 times), "Retreat" even fewer times (six times) and "Approach" only one time. Data from four

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stimuli presentations could not be obtained. When a moving fox was simulated, "Stay" was again the most common reaction (22 times). "Retreat" was the second most common reaction (12 times), while "Approach" was less common (seven times) and "No reaction" the least common reaction (two times). From these stimuli presentations, data of eight presentations could not be obtained. To the moving covered fox, they reacted mostly with "Stay" (24 times), while "Retreat" was the second most common reaction (nine times), "No reaction" the third (six times) and "Approach" the least common reaction (two times). Ten reactions could not be reported for this stimulus. These results are presented in figure 3.
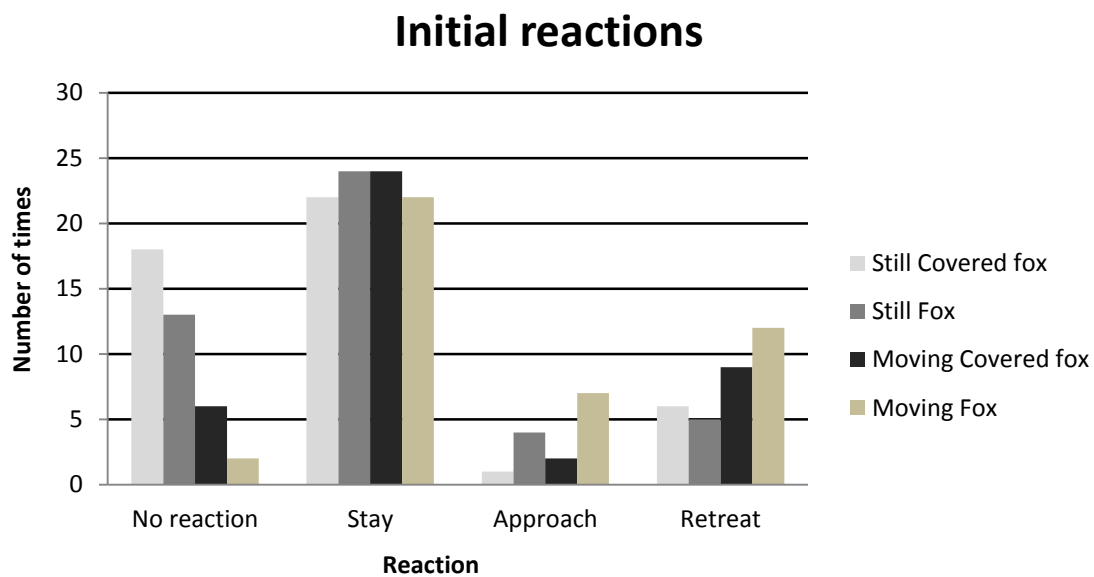
Initial reactions

Figure 3. Number of times that the tamarins reacted with different initial reactions where the different stimuli are represented by different bars.

4.1.2 Behavioral differences between predator stimulus and control in experiment one

When performing the Wilcoxon signed ranks test significant differences in behavior frequencies between sessions with the predator stimulus (fox) and the control (covered fox) was found in both exposure periods.

In the exposure before movement period, the following behaviors were significantly more common in session with the fox than the covered fox: "Gazing" ($z=-3.554$, $p<0.001$), "Vocalization" ($z=-3.242$, $p<0.001$) and "Moving closer" ($z=-2.677$, $p<0.01$). "In box" was instead significantly more frequent when presented with the covered fox than the fox ($z=-2.362$, $p<0.01$). Behavior frequencies which were significantly different between sessions with

the fox and sessions with the covered fox during the exposure before movement period are presented in table 2.

Table 2. Frequencies of behaviors with significant differences between the predator model (fox) and the control (covered fox) shown within the exposure before movement period of the 17 sessions where the significantly higher values are in bold style.

Gazing		Vocalization		Moving closer		In box	
Fox	Covered fox	**Fox**	Covered fox	**Fox**	Covered fox	Fox	**Covered fox**
0.42	0.25	**0.38**	0.17	**0.25**	0.00	0.00	**0.00**
0.71	0.04	**0.67**	0.08	**0.17**	0.00	0.00	**0.00**
0.50	0.21	**0.42**	0.00	**0.29**	0.00	0.00	**0.04**
0.63	0.08	**0.29**	0.04	**0.17**	0.00	0.00	**0.17**
0.54	0.25	**0.25**	0.08	**0.08**	0.00	0.04	**0.00**
0.46	0.29	**0.46**	0.00	**0.04**	0.00	0.00	**0.08**
0.63	0.17	**0.38**	0.21	**0.25**	0.00	0.00	**0.38**
0.79	0.04	**0.38**	0.04	**0.08**	0.00	0.00	**0.42**
0.50	0.21	**0.42**	0.17	**0.04**	0.00	0.00	**0.29**
0.42	0.25	**0.29**	0.21	**0.04**	0.00	0.00	**0.04**
0.50	0.13	**0.42**	0.00	**0.08**	0.04	0.00	**0.00**
0.25	0.29	**0.25**	0.21	**0.00**	0.00	0.00	**0.00**
0.50	0.04	**0.25**	0.25	**0.00**	0.00	0.08	**0.00**
0.75	0.00	**0.17**	0.29	**0.13**	0.00	0.00	**0.13**
0.50	0.17	**0.21**	0.21	**0.00**	0.00	0.00	**0.00**
0.38	0.33	**0.17**	0.00	**0.00**	0.17	0.00	**0.00**
0.42	0.08	**0.21**	0.00	**0.08**	0.00	0.00	**0.46**

When instead looking at data from the exposure after movement period, "Gazing" (z=-3.523, p<0.001), "Locomotion" (z=-2.501, p<0.01) and "Vocalization" (z=-2.789, p<0.01) had significantly higher behavior frequencies in sessions with the fox compared to the covered fox. There were no significant differences where the behaviors instead were more common during presentations of the covered fox compared to the fox. Behavior frequencies which differed significantly between sessions with the fox and sessions with the covered fox during exposure after movement period can be viewed in table 3.

Table 3. Frequencies of behaviors with significant differences between the predator model (fox) and the control (covered fox) shown within the exposure after movement period of the 17 sessions where the significantly higher values are in bold style.

Gazing		Locomotion		Vocalization	
Fox	Covered fox	**Fox**	Covered fox	**Fox**	Covered fox
0.33	0.00	**0.46**	0.63	**0.33**	0.00
0.50	0.04	**0.88**	0.58	**0.33**	0.00
0.71	0.25	**0.79**	0.71	**0.46**	0.00
0.83	0.08	**0.50**	0.50	**0.33**	0.00
0.67	0.33	**0.54**	0.54	**0.38**	0.00
0.71	0.13	**0.67**	0.54	**0.42**	0.00
0.83	0.00	**0.79**	0.54	**0.42**	0.00
0.79	0.04	**0.54**	0.13	**0.21**	0.08
0.33	0.08	**0.46**	0.58	**0.17**	0.17
0.58	0.13	**0.79**	0.29	**0.42**	0.21
0.58	0.04	**0.63**	0.29	**0.13**	0.04
0.46	0.08	**0.71**	0.75	**0.13**	0.04
0.71	0.08	**0.63**	0.67	**0.17**	0.21
0.50	0.08	**0.58**	0.50	**0.17**	0.25
0.67	0.04	**0.50**	0.33	**0.04**	0.21
0.17	0.17	**0.79**	0.46	**0.04**	0.04
0.58	0.13	**0.71**	0.42	**0.13**	0.00

After adding behavior frequencies of the same behavior group (anti-predator behaviors, calm behaviors or other behaviors) together, as well as frequencies from the two exposure periods, a significant result from the Wilcoxon signed ranks test was discovered. The test showed that anti-predator behaviors were more common during sessions with the fox than sessions with the covered fox (z=-3.622, p<0.001, fig. 4).
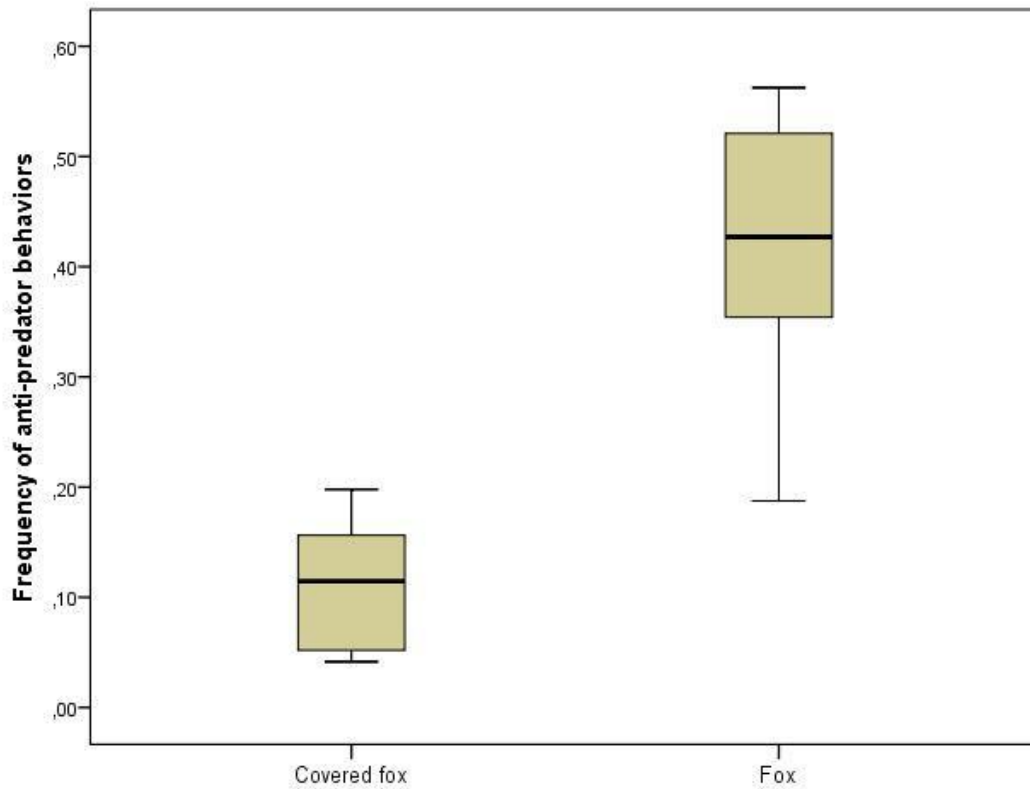
Figure 4. Boxplot of frequency of anti-predator behaviors performed during sessions with fox and sessions with covered fox where outliers are represented by stars or circles.

4.1.3 Behavioral differences between pre- and post-period in experiment one

When testing for differences in behavior frequencies between pre- and post-exposure period, some significant results were discovered. The behaviors that were significantly more common in pre-exposure period than in post-exposure period were "Vocalization" ($z=-2.687$, $p<0.01$) and "Touching mesh" ($z=-2.132$, $p<0.05$). Behavior frequencies were on the opposite significantly higher in post-exposure period than in pre-exposure period for "Foraging" ($z=-2.700$, $p<0.01$). Behavior frequencies with significant differences between pre- and post-exposure periods during sessions with the fox are displayed in table 4.

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Table 4. Frequencies of behaviors with significant differences between the pre- and the post- exposure periods shown within the 17 sessions with the fox where the significantly higher values are in bold style.

Vocalization		Foraging		Touching mesh	
Pre	Post	Pre	**Post**	**Pre**	Post
0.08	0.02	0.00	**0.27**	**0.00**	0.00
0.04	0.00	0.17	**0.52**	**0.00**	0.00
0.13	0.00	0.19	**0.04**	**0.04**	0.17
0.04	0.00	0.00	**0.25**	**0.13**	0.00
0.06	0.02	0.21	**0.33**	**0.15**	0.00
0.00	0.00	0.04	**0.15**	**0.04**	0.08
0.04	0.06	0.06	**0.69**	**0.17**	0.08
0.08	0.08	0.04	**0.71**	**0.21**	0.02
0.00	0.00	0.15	**0.06**	**0.21**	0.00
0.08	0.00	0.02	**0.25**	**0.04**	0.00
0.00	0.00	0.00	**0.48**	**0.06**	0.29
0.00	0.00	0.04	**0.29**	**0.35**	0.10
0.06	0.02	0.27	**0.50**	**0.33**	0.06
0.04	0.00	0.13	**0.31**	**0.21**	0.29
0.02	0.00	0.00	**0.33**	**0.27**	0.10
0.00	0.00	0.13	**0.25**	**0.33**	0.08
0.00	0.00	0.46	**0.10**	**0.13**	0.00

4.1.4 Behavioral differences between before and after movement in experiment one

No significant differences in any of the anti-predator behaviors between frequencies shown before movement and after movement of the fox were discovered.

4.1.5 Initial reactions in experiment two

The initial reaction was generally represented by "No reaction" and "Stay" also in experiment two. When presented to the still snake, the tamarins reacted the most times with "Stay" (19 times), "No reaction" fewer times (six times), "Approach" even fewer times (four times) and "Retreat" the least times (two times). 20 reactions to these presentations could not be noted. To the plant they also reacted with "Stay" the most times (21 times),"No reaction" fewer times (16 times), "Approach" even fewer times (four times) and "Retreat" only one time. Measurements of nine reactions towards these presentations could not be done. When a moving snake was simulated, "Stay" was the most common reaction as well (22 times) while "Approach" was the second most common

reaction (eight times), "No reaction" the third (seven times) and "Retreat" the least common reaction (five times). To these presentations, measurements of nine reactions are missing. To the moving plant they again reacted with "Stay" the most times (18 times), "No reaction" fewer times (16 times), "Approach" even fewer times (seven times) and "Retreat" the least times (two times). Eight reactions to these presentations could not be noted. These results are further displayed in figure 5.
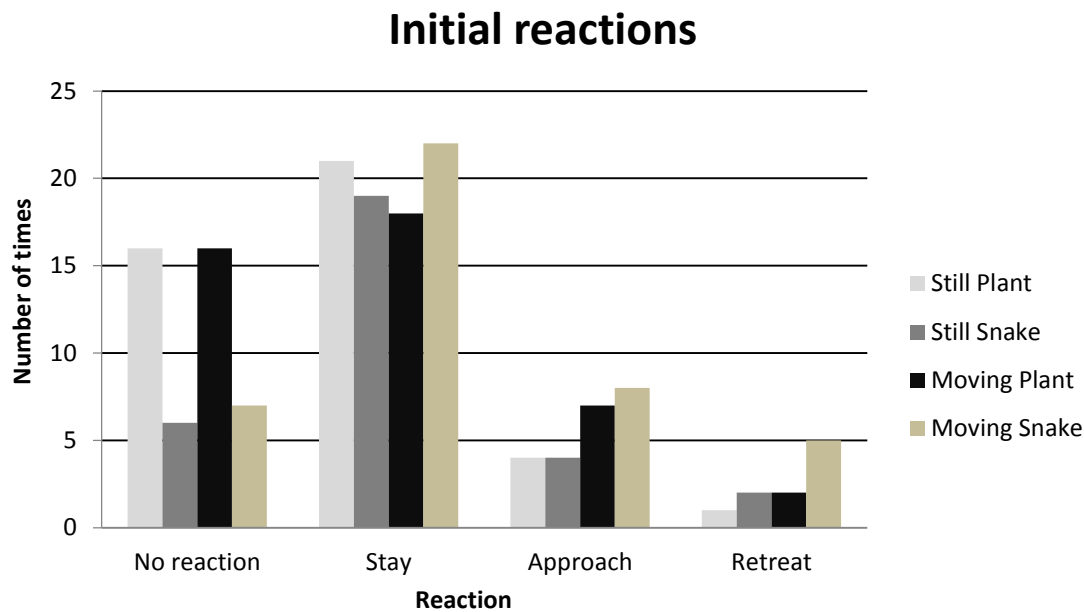
Initial reactions

Figure 5. Number of times that the tamarins reacted with different initial reactions where the different stimuli are represented by different bars.

4.1.6 Behavioral differences between predator stimulus and control in experiment two

When performing the Wilcoxon signed ranks test significant differences in behavior frequencies between sessions with the predator stimulus (snake) and the control (plant) was found in both exposure periods.

In the exposure before movement period, significant differences between behavior frequencies from sessions with the snake compared to sessions with the plant was found in "Gazing" ($z=-3.531$, $p<0.001$) and "Vocalization" ($z=-3.460$, $p<0.001$) which had highest frequencies during sessions with the snake. The behavior frequencies which had significant differences between the sessions with the snake and sessions with the plant are displayed in table 5.

Table 5. Frequencies of behaviors with significant differences between the predator model (snake) and the control (plant) shown within the exposure before movement period of the 17 sessions where the significantly higher values are in bold style.

Gazing		Vocalization	
Snake	Plant	**Snake**	Plant
0.63	0.00	**0.58**	0.04
0.46	0.13	**0.17**	0.00
0.33	0.00	**0.38**	0.00
0.50	0.08	**0.29**	0.08
0.75	0.25	**0.21**	0.33
0.46	0.21	**0.17**	0.00
0.25	0.21	**0.29**	0.08
0.33	0.08	**0.63**	0.42
0.44	0.13	**0.19**	0.00
0.58	0.21	**0.25**	0.13
0.42	0.17	**0.33**	0.00
0.42	0.04	**0.17**	0.13
0.21	0.04	**0.29**	0.04
0.29	0.08	**0.17**	0.00
0.46	0.00	**0.25**	0.00
0.21	0.29	**0.17**	0.13
0.50	0.13	**0.42**	0.00

Significant differences within the data from exposure after movement were found in the behaviors "Gazing" (z=-3.626, p<0.001) and "Vocalization" (z=-3.167, p<0.001) which had higher frequencies during sessions with the snake compared to sessions with the plant. No significant differences where behavior frequencies were higher during sessions with the plant compared to sessions with the snake were discovered. The behavior frequencies which were significantly different between sessions with the snake and sessions with the plant are shown in table 6.

Table 6. Frequencies of behaviors with significant differences between the predator model (snake) and the control (plant) shown within the exposure after movement period of the 17 sessions where the significantly higher values are in bold style.

Gazing		Vocalization	
Snake	Plant	**Snake**	Plant
0.58	0.00	**0.25**	0.13
0.79	0.04	**0.46**	0.04
0.46	0.00	**0.42**	0.00
0.63	0.04	**0.46**	0.04
0.33	0.25	**0.08**	0.00
0.50	0.13	**0.38**	0.00
0.33	0.05	**0.08**	0.00
0.46	0.17	**0.25**	0.13
0.38	0.00	**0.17**	0.17
0.46	0.13	**0.13**	0.04
0.58	0.00	**0.33**	0.00
0.42	0.04	**0.29**	0.00
0.38	0.17	**0.13**	0.00
0.29	0.17	**0.17**	0.00
0.21	0.08	**0.13**	0.00
0.33	0.25	**0.04**	0.00
0.29	0.13	**0.00**	0.13

Significant differences from the Wilcoxon signed ranks test between sessions with the snake and sessions with the plant within behavior groups and exposure periods together was found in anti-predator behaviors which had higher frequencies during sessions with snake (z=-3.622, p<0.001, fig. 6).
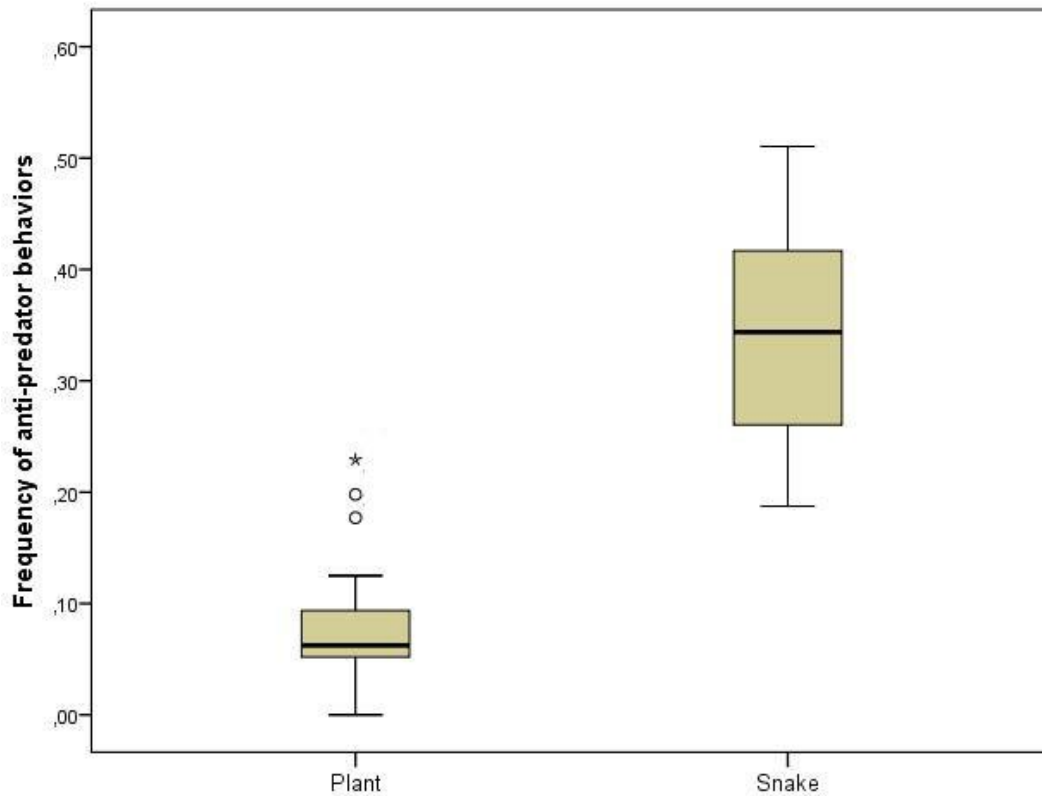
Figure 6. Boxplot of frequency of anti-predator behaviors performed during sessions with snake and sessions with plant where outliers are represented by stars or circles.

4.1.7 Behavioral differences between pre- and post-exposure period in experiment two

In the second experiment, behavioral differences between the pre- and post-exposure periods were also found. "Scratching" ($z=-2.418$, $p<0.01$) and "Investigating" ($z=-2.070$, $p<0.05$) were significantly more common for pre-exposure period than post-exposure period. Behaviors that were significantly more common during post-exposure period than pre-exposure period were "Foraging" ($z=-3.198$, $p<0.001$) and "In box" ($z=-2.748$, $p<0.01$). Behavior frequencies for behaviors with significant differences between pre- and post-exposure periods are shown in table 7.

Table 7. Frequencies of behaviors with significant differences between the pre- and the post-exposure periods shown within the 17 sessions with the snake where the significantly higher values are in bold style.

Foraging		Scratching		Investigating		In box	
Pre	**Post**	**Pre**	Post	**Pre**	Post	Pre	**Post**
0.44	**0.38**	**0.23**	0.10	**0.04**	0.00	0.00	**0.06**
0.13	**0.40**	**0.17**	0.21	**0.02**	0.00	0.00	**0.00**
0.04	**0.38**	**0.52**	0.10	**0.00**	0.00	0.00	**0.15**
0.23	**0.33**	**0.40**	0.35	**0.02**	0.00	0.00	**0.17**
0.02	**0.38**	**0.08**	0.35	**0.00**	0.00	0.08	**0.00**
0.00	**0.48**	**0.33**	0.19	**0.00**	0.00	0.02	**0.13**
0.48	**0.52**	**0.19**	0.17	**0.00**	0.00	0.00	**0.00**
0.08	**0.38**	**0.19**	0.19	**0.04**	0.00	0.00	**0.00**
0.04	**0.50**	**0.25**	0.08	**0.04**	0.00	0.00	**0.15**
0.00	**0.54**	**0.31**	0.15	**0.00**	0.00	0.00	**0.13**
0.21	**0.44**	**0.13**	0.13	**0.00**	0.00	0.00	**0.25**
0.04	**0.02**	**0.33**	0.21	**0.00**	0.00	0.00	**0.00**
0.19	**0.13**	**0.25**	0.08	**0.00**	0.00	0.06	**0.46**
0.00	**0.13**	**0.38**	0.10	**0.00**	0.00	0.00	**0.00**
0.00	**0.06**	**0.31**	0.19	**0.00**	0.00	0.10	**0.17**
0.06	**0.29**	**0.17**	0.15	**0.00**	0.00	0.04	**0.06**
0.04	**0.23**	**0.33**	0.25	**0.00**	0.00	0.00	**0.35**

4.1.8 Behavioral differences between before and after movement during experiment two

No significant differences in any of the anti-predator behaviors between before and after movement of the snake were discovered.

4.1.9 Behavioral differences between presentations with the different predator models

In this species, significant differences where frequencies of anti-predator behaviors were higher towards the fox than the snake were found in "Moving closer" ($z=-1.990$, $p<0.05$, table 8) in the exposure before movement period and "Gazing" ($z=-2.509$, $p<0.05$, table 9) in the exposure after movement period.

Table 8. Frequencies of behaviors with significant differences between sessions with the fox and sessions with the snake during exposure before movement period where the significantly higher values are in bold style.

Gazing	
Fox	Snake
0.33	0.58
0.50	0.79
0.71	0.46
0.83	0.63
0.67	0.33
0.71	0.50
0.83	0.33
0.79	0.46
0.33	0.38
0.58	0.46
0.58	0.58
0.46	0.42
0.71	0.38
0.50	0.29
0.67	0.21
0.17	0.33
0.58	0.29

Table 9. Frequencies of behaviors with significant differences between sessions with the fox and sessions with the snake during exposure after movement period where the significantly higher values are in bold style.

Moving closer	
Fox	Snake
0.25	0.21
0.17	0.21
0.29	0.17
0.17	0.00
0.08	0.13
0.04	0.04
0.25	0.00
0.08	0.00
0.04	0.00
0.04	0.00
0.08	0.00

0.00	0.00
0.00	0.04
0.13	0.00
0.00	0.00
0.00	0.00
0.08	0.04

Results from when testing anti-predator behaviors fused together as well as exposure periods between the two predator models, a significant difference was found where frequencies were higher towards the fox than the snake (z=-4.497, p<0.001, fig. 7).
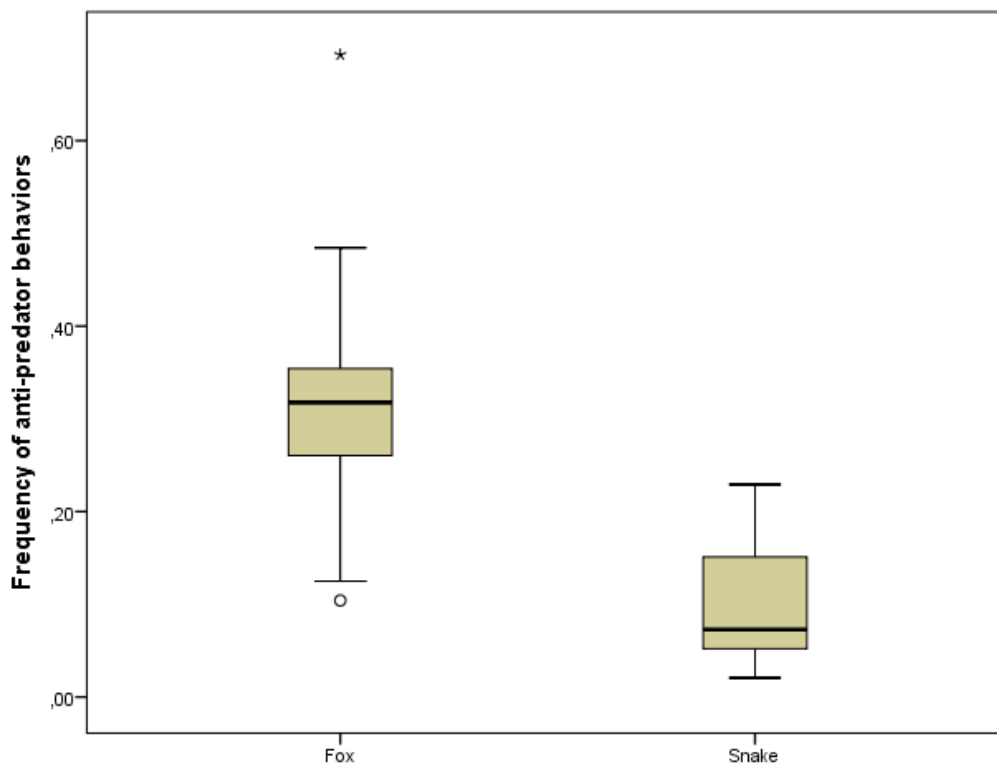
Figure 7. Frequency of anti-predator behaviors performed during sessions with fox and sessions with snake, where outliers are represented by stars or circles.

4.1.10   Contact with stimuli

Over the sessions, the Brazilian bare-faced tamarin group made contact with all the different stimuli. Most times they made contact with the plant, more exactly ten times, six times before movement and four times after movement. With the covered fox they made contact five times, where four times was before movement and one time was after movement. With the fox they made contact

three times where two were before movement and one after movement. Last, they made contact with the snake one time in the exposure before movement period.

4.1.11   Behavioral changes over time

When performing regression analyses on each behavior over time, some significant results was found. During exposure before movement period, a decrease over time was found for the behaviors "Vocalization" (R^2=0.467, B=-0.002 p<0.05) and "Moving closer" (R^2=0.537, B=-0.002, p<0.05) when presented with the fox. Also within data from the exposure after movement period with the snake, a significant negative relationship with day of study was discovered in the behaviors "Gazing" (R^2=0.429, B=-0.004 p<0.05) and "Vocalization" (R^2=0.432, B=-0.004, p<0.05). When putting anti-predator behaviors as well as exposure periods together, a significant negative relationship between behavior frequencies performed during sessions with fox and day of study was also found (R^2=0.660, B=-0.002, p<0.01, fig. 8) as well as a significant negative relationship between anti-predator behaviors performed during sessions with snake and day of study (R^2=0.697, B=-0.003, p<0.05, fig. 8).

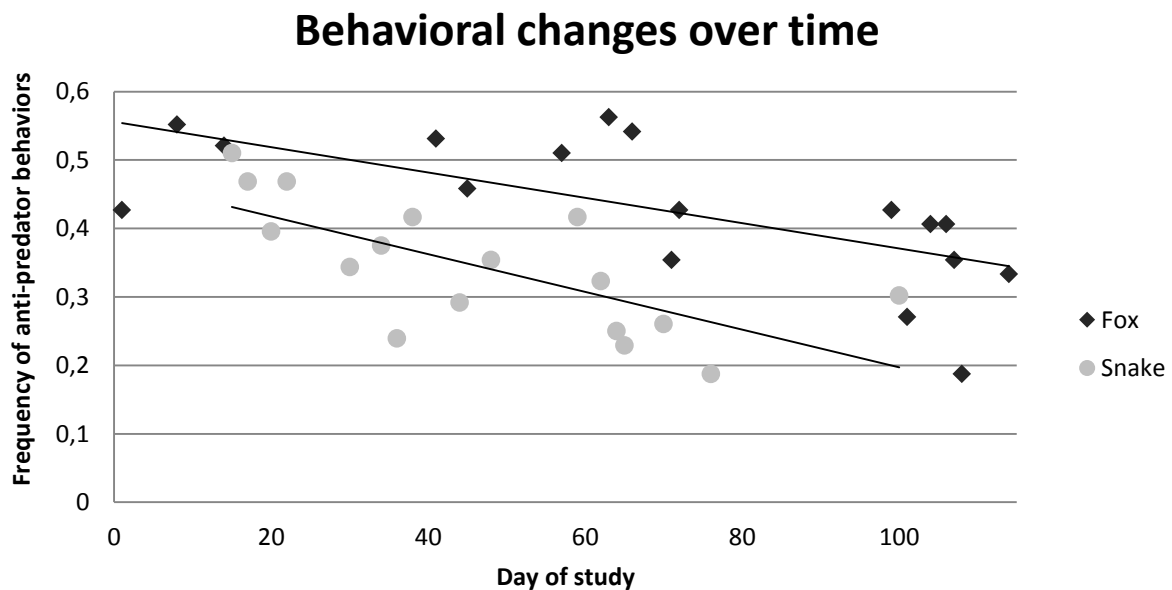*Figure 8. Relationships between the frequency of the anti-predator behaviors and day of study for sessions with fox and sessions with snake.*

4.2 Results for the cotton-headed tamarins

4.2.1 Initial reactions in experiment one

The initial reaction was generally represented by "No reaction" and "Stay" also in this tamarin group. When presented to the still fox, the tamarins reacted with "Stay" the most times (18 times), "No reaction" fewer times (12 times), "Retreat" the less times (two times) and "Approach" none of the times. Measurements of two reactions are missing for these presentations. To the covered fox they also reacted with "Stay" the most times (14 times"), No reaction" fewer times (10 times), "Approach" only one time and "Retreat" none of the times. From these presentations, data of nine reactions could not be noted. When a moving fox was simulated, they also reacted with "Stay" the most times (19 times), "No reaction" fewer times (nine times), "Retreat" even fewer times (three times) and "Approach" none of the times. Three reactions to these presentations could not be measured. To the moving covered fox they instead reacted with "Stay" 18 times, "No reaction" seven times, "Retreat" four times and "Approach" none of the times. Measurements of five reactions to these presentations are missing. The results are further shown in figure 9.
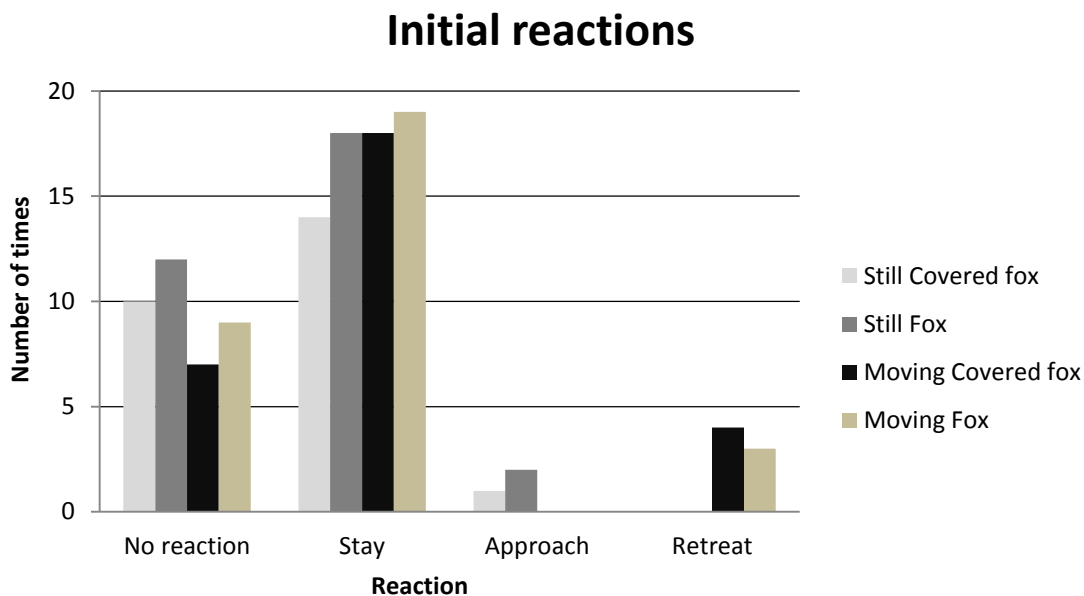

Figure 9. Number of times that the tamarins reacted with different initial reactions where the different stimuli are represented by different bars.

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4.2.2 Behavioral differences between predator stimulus and control in experiment one

When performing the Wilcoxon signed ranks test significant differences in behavior frequencies between sessions with the predator stimulus (fox) and the control (covered fox) was found in both exposure periods also in this species.

In the exposure before movement period, a significant difference where the behavior frequency was higher for fox compared to covered fox, was found in the behavior "Vocalization" ($z=-2.061$, $p<0.05$). A significant difference where the behavior frequency instead were higher for covered fox compared to fox was discovered in the behavior "Looking window" ($z=-1.954$, $p<0.05$). Behavior frequencies with significant differences between sessions with the fox and sessions with the covered fox are displayed in table 10.

Table 10. Frequencies of behaviors with significant differences between sessions with the predator model (fox) and the control (covered fox) shown within the exposure before movement period of the 17 sessions where the significantly higher values are in bold style.

Vocalization		Looking window	
Fox	Covered fox	Fox	**Covered fox**
0.19	0.00	0.00	**0.19**
0.60	0.00	0.00	**0.04**
0.50	0.06	0.00	**0.06**
0.10	0.27	0.00	**0.00**
0.56	0.21	0.00	**0.00**
0.38	0.35	0.00	**0.00**
0.40	0.04	0.00	**0.13**
0.21	0.67	0.06	**0.00**
0.50	0.40	0.00	**0.19**
0.44	0.21	0.00	**0.00**
0.31	0.23	0.00	**0.00**
0.31	0.40	0.00	**0.00**
0.25	0.10	0.00	**0.00**
0.25	0.04	0.00	**0.13**
0.04	0.13	0.00	**0.00**
0.60	0.00	0.00	**0.00**
0.13	0.17	0.00	**0.00**

In the exposure after movement period, "Gazing" had significantly higher frequencies during sessions with the fox than sessions with the covered fox (z=-2.939, p<0.01). The behavior frequencies are presented in table 11.

Table 11. Frequencies of behaviors with significant differences between the predator model (fox) and the control (covered fox) shown within the exposure after movement period of the 17 sessions where the significantly higher values are in bold style.

Gazing	
Fox	Covered fox
0.04	0.00
0.77	0.29
0.27	0.15
0.21	0.08
0.29	0.35
0.15	0.10
0.29	0.27
0.42	0.13
0.40	0.21
0.15	0.08
0.23	0.15
0.19	0.29
0.27	0.21
0.38	0.23
0.38	0.10
0.54	0.40
0.15	0.08

When adding frequencies from the same behavior group together as well as data from the two exposure periods, anti-predator behaviors were significantly more common during sessions with the fox than sessions with the covered fox (z=-3.197, p<0.01, fig. 10).
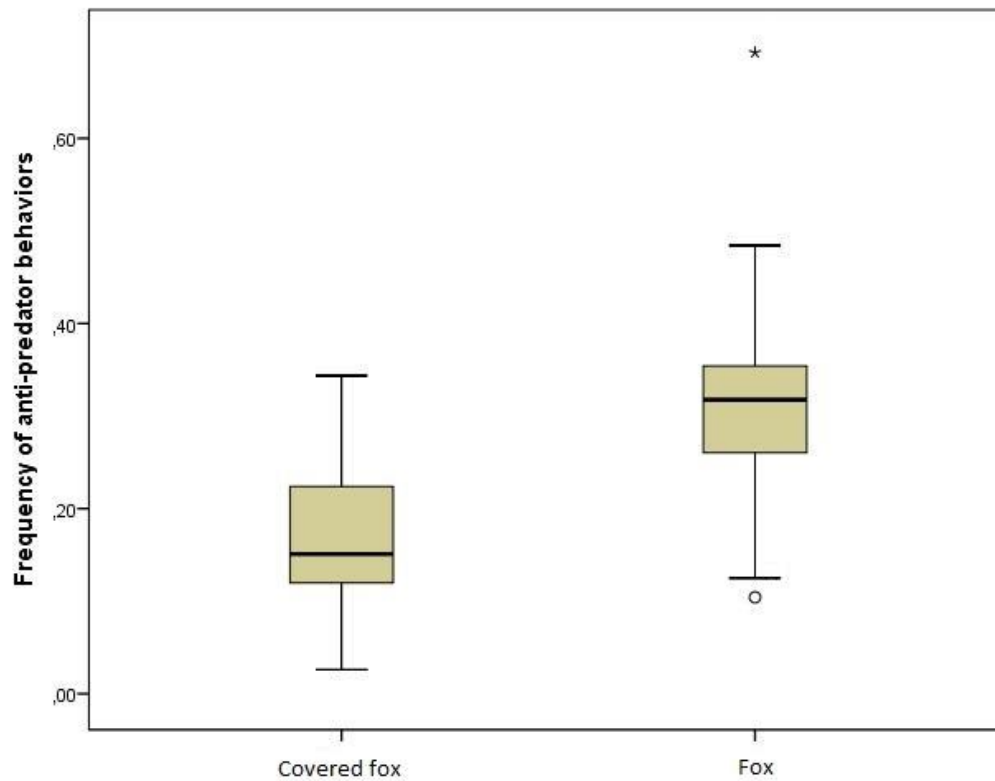
Figure 10. Boxplot of frequency of anti-predator behaviors performed during sessions with fox and sessions with covered fox where outliers are represented by stars or circles.

4.2.3 Behavioral differences between pre- and post-exposure period in experiment one

Also in this species, some behavioral differences between pre- and post-exposure periods were discovered. Several behaviors were significantly more abundant in pre-exposure period, more exactly, "Locomotion" ($z=-2.509$, $p<0.01$), "Social interaction" ($z=-2.560$, $p<0.01$) and "Touching mesh" ($z=-2.108$, $p<0.05$). One behavior had instead significantly higher frequencies in post-exposure period, more exactly, "Foraging" ($z=-2.769$, $p<0.01$). Behavior frequencies where significant differences between pre- and post-exposure periods were present can be viewed in table 12.

Table 12. Frequencies of behaviors with significant differences between pre- and post-exposure period shown within the 17 sessions with the fox where the significantly higher values are in bold style.

Locomotion		Foraging		Social interaction		Touching mesh	
Pre	Post	Pre	**Post**	**Pre**	Post	**Pre**	Post
0.70	0.13	0.10	**0.73**	**0.15**	0.08	**0.04**	0.00
0.80	0.47	0.26	**0.20**	**0.04**	0.00	**0.07**	0.09
0.50	0.59	0.00	**0.44**	**0.08**	0.03	**0.05**	0.08
0.90	0.66	0.00	**0.34**	**0.08**	0.00	**0.20**	0.02
0.77	0.61	0.03	**0.56**	**0.09**	0.00	**0.14**	0.02
0.47	0.34	0.13	**0.57**	**0.10**	0.00	**0.17**	0.04
0.56	0.42	0.00	**0.40**	**0.04**	0.00	**0.10**	0.02
0.61	0.70	0.20	**0.03**	**0.16**	0.06	**0.31**	0.22
0.76	0.69	0.08	**0.28**	**0.05**	0.00	**0.46**	0.07
0.23	0.45	0.00	**0.80**	**0.00**	0.00	**0.31**	0.15
0.67	0.55	0.02	**0.10**	**0.04**	0.00	**0.17**	0.34
0.54	0.33	0.17	**0.42**	**0.00**	0.15	**0.17**	0.00
0.44	0.24	0.06	**0.18**	**0.03**	0.00	**0.03**	0.04
0.72	0.42	0.31	**0.09**	**0.00**	0.00	**0.34**	0.05
0.76	0.74	0.04	**0.47**	**0.07**	0.00	**0.38**	0.19
0.78	0.50	0.20	**0.24**	**0.02**	0.00	**0.14**	0.03
0.55	0.63	0.23	**0.21**	**0.05**	0.00	**0.06**	0.24

4.2.4 Behavioral differences between before and after movement in experiment one

Significant differences in behavior frequencies between before and after movement of the fox were discovered in "Vocalization" ($z=-2.237$, $p<0.05$) which had higher frequencies before than after movement. Behavior frequencies with significant differences between before and after movement during sessions with the fox are shown in table 13.

Table 13. Frequencies of behaviors with significant differences between the exposure before movement and exposure after movement period where the significantly higher values are in bold style.

Vocalization	
Before	After
0.19	0.21
0.60	0.60
0.50	0.35
0.10	0.19
0.56	0.10
0.38	0.00
0.40	0.19
0.21	0.38
0.50	0.19
0.44	0.04
0.31	0.08
0.31	0.15
0.25	0.33
0.25	0.19
0.04	0.50
0.60	0.25
0.13	0.04

4.2.5 Initial reactions in experiment two

The initial reaction, was generally represented by "No reaction" and "Stay" also in experiment two. When presented to the still snake, the tamarins reacted with "Stay" the most times (18 times), "No reaction" fewer times (seven times), "Retreat" even fewer times (four times) and "Approach" the least times (one time). Four reactions to these presentations could not be noted. To the plant they reacted with "Stay" 12 times, "No reaction" nine times, "Retreat" two times and "Approach" also two times. To these presentations, measurements of nine presentations are missing. When a moving snake was simulated, they reacted with "Stay" 14 times, "No reaction" 11 times, "Retreat" two times and "Approach" one time. Measurements of five reactions to these presentations could not be obtained. To the moving plant they reacted with "No reaction" the most times (20 times), "Stay" fewer times (13 times) while they never reacted with "Approach" and "Retreat". These results are presented in figure 11.
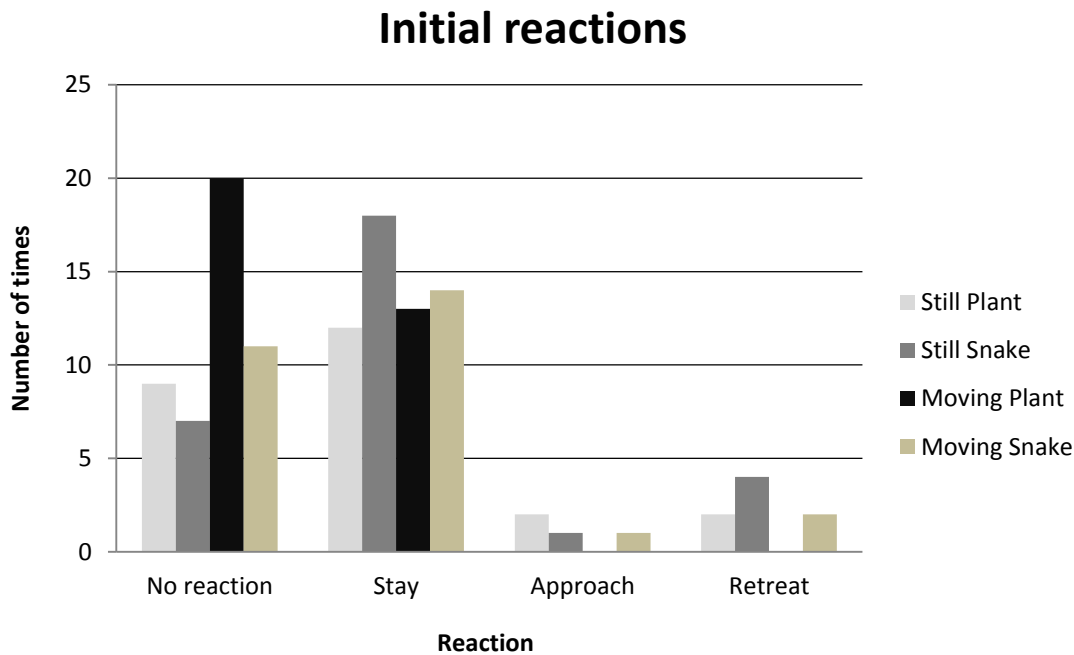
Initial reactions

Figure 11. Number of times that the tamarins reacted with different initial reactions where the different stimuli are represented by different bars.

4.2.6 Behavioral differences between predator stimulus and control in experiment two

When performing the Wilcoxon signed ranks test significant differences in behavior frequencies between sessions with the predator stimulus (snake) and the control (plant) was found in both exposure periods.

In the exposure before movement period, no significant differences were found of behaviors which had higher frequencies during sessions with the snake than sessions with the plant. A significant difference where frequencies instead were significantly higher during sessions with plant than sessions with snake was discovered in the behavior "Gazing" ($z=-3.419$, $p<0.001$). The behavior frequencies which significantly differed between the snake and the plant are shown in table 14.

Table 14. Frequencies of behaviors with significant differences between the predator model (snake) and the control (plant) shown within the exposure before movement period of the 17 sessions where the significantly higher values are in bold style.

Gazing	
Snake	**Plant**
0.00	**0.35**
0.04	**0.08**
0.04	**0.33**
0.00	**0.08**
0.15	**0.46**
0.06	**0.21**
0.13	**0.35**
0.06	**0.00**
0.04	**0.27**
0.25	**0.35**
0.10	**0.31**
0.10	**0.31**
0.08	**0.08**
0.10	**0.29**
0.00	**0.23**
0.00	**0.23**
0.00	**0.23**

In the exposure after movement period, significant differences in behavior frequencies between sessions with the snake and sessions with the plant, was found only in the behavior "Social interaction" ($z=-2.136$, $p<0.05$) which were more common during sessions with the snake. "Gazing" ($z=-3.292$, $p<0.001$) and had instead higher frequencies during sessions with the plant than sessions with the snake. The frequencies of behaviors that significantly differed between sessions with the snake and sessions with the plant are presented in table 15.

Table 15. Frequencies of behaviors with significant differences between the predator model (snake) and the control (plant) shown within the exposure after movement period of the 17 sessions where the significantly higher values are in bold style.

Gazing		Social interaction	
Snake	**Plant**	**Snake**	Plant
0.06	**0.25**	**0.00**	0.00
0.04	**0.10**	**0.10**	0.00
0.04	**0.23**	**0.00**	0.00
0.21	**0.23**	**0.00**	0.00
0.19	**0.48**	**0.00**	0.00
0.04	**0.25**	**0.00**	0.00
0.04	**0.27**	**0.00**	0.00
0.15	**0.23**	**0.00**	0.04
0.23	**0.13**	**0.00**	0.00
0.10	**0.27**	**0.04**	0.00
0.17	**0.35**	**0.10**	0.00
0.17	**0.21**	**0.10**	0.00
0.00	**0.04**	**0.00**	0.00
0.08	**0.31**	**0.00**	0.00
0.06	**0.10**	**0.06**	0.00
0.08	**0.44**	**0.00**	0.00
0.08	**0.21**	**0.06**	0.00

When testing behavior frequencies from the same behavior group together, as well as frequencies from both exposure periods, a significant difference was found in anti-predator behaviors that were significantly more performed during sessions with the plant than sessions with the snake (z=-3.362, p<0.01, fig. 12).
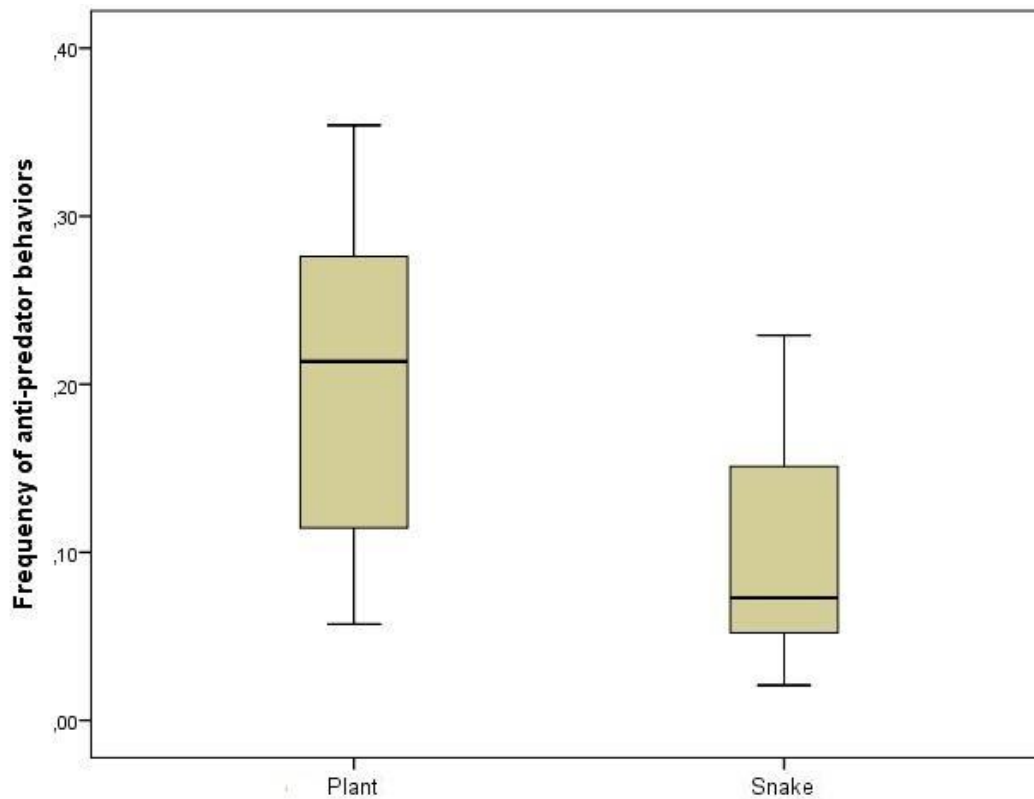
Figure 12. Boxplot of frequency of anti-predator behaviors performed during sessions with snake and sessions with plant where outliers are represented by stars or circles.

4.2.7 Behavioral differences between pre- and post-exposure period in experiment two

In the second experiment, no significant results for behavioral differences between pre- and post-exposure period were found.

4.2.8 Behavioral differences between before and after movement in experiment two

Significant differences in anti-predator behaviors performed before and after movement of the snake were discovered in "Vocalization" ($z=-1.969$, $p<0.05$), where frequencies were higher before than after movement. The behavior frequencies are displayed in table 16.

Table 16. Frequencies of behaviors with significant differences between the exposure before movement and exposure after movement period during sessions with the snake where the significantly higher values are in bold style.

Vocalization	
Before	After
0.00	0.04
0.13	0.00
0.00	0.00
0.48	0.10
0.27	0.00
0.42	0.08
0.35	0.13
0.06	0.00
0.08	0.00
0.33	0.19
0.00	0.00
0.08	0.13
0.15	0.00
0.16	0.00
0.10	0.13
0.00	0.00
0.08	0.04

4.2.9 Behavioral differences between presentations with the different predator models

Also in this species, significant differences between anti-predator behavior frequencies from sessions with the different predator models were found. In the exposure before movement period, "Vocalization" ($z=-2.846$, $p<0.01$) had higher frequencies towards the fox than the snake. The behavior frequencies of vocalization in exposure before movement are displayed in table 17.

Table 17. Frequencies of behaviors with significant differences between sessions with the fox and sessions with the snake in the exposure before movement period where the significantly higher values are in bold style.

Vocalization	
Fox	Snake
0.19	0.00
0.60	0.13
0.50	0.00
0.10	0.48
0.56	0.27
0.38	0.42
0.40	0.35
0.21	0.06
0.50	0.08
0.44	0.33
0.31	0.00
0.31	0.08
0.25	0.15
0.25	0.16
0.04	0.10
0.60	0.00
0.13	0.08

In the exposure after movement period two behaviors had higher frequencies towards the fox than the snake, more exactly "Gazing" (z=-3.784, p<0.001) and "Vocalization" (z=-3.673 p<0.001). The frequencies of these behaviors are shown in table 18.

Table 18. Frequencies of behaviors with significant differences between sessions with the fox and sessions with the snake in the exposure after movement period where the significantly higher values are in bold style.

Gazing		Vocalization	
Fox	Snake	**Fox**	Snake
0.04	0.06	**0.21**	0.04
0.77	0.04	**0.60**	0.00
0.27	0.04	**0.35**	0.00
0.21	0.21	**0.19**	0.10
0.29	0.19	**0.10**	0.00
0.15	0.04	**0.00**	0.08
0.29	0.04	**0.19**	0.13
0.42	0.15	**0.38**	0.00
0.40	0.23	**0.19**	0.00
0.15	0.10	**0.04**	0.19
0.23	0.17	**0.08**	0.00
0.19	0.17	**0.15**	0.13
0.27	0.00	**0.33**	0.00
0.38	0.08	**0.19**	0.00
0.38	0.06	**0.50**	0.13
0.54	0.08	**0.25**	0.00
0.15	0.08	**0.04**	0.04

When fusing anti-predator behaviors as well as exposure periods together and testing for differences between the predator models, a significant difference was found also in this species where higher frequencies was performed towards the fox than the snake (z=-2.396, p<0.05, fig. 13).
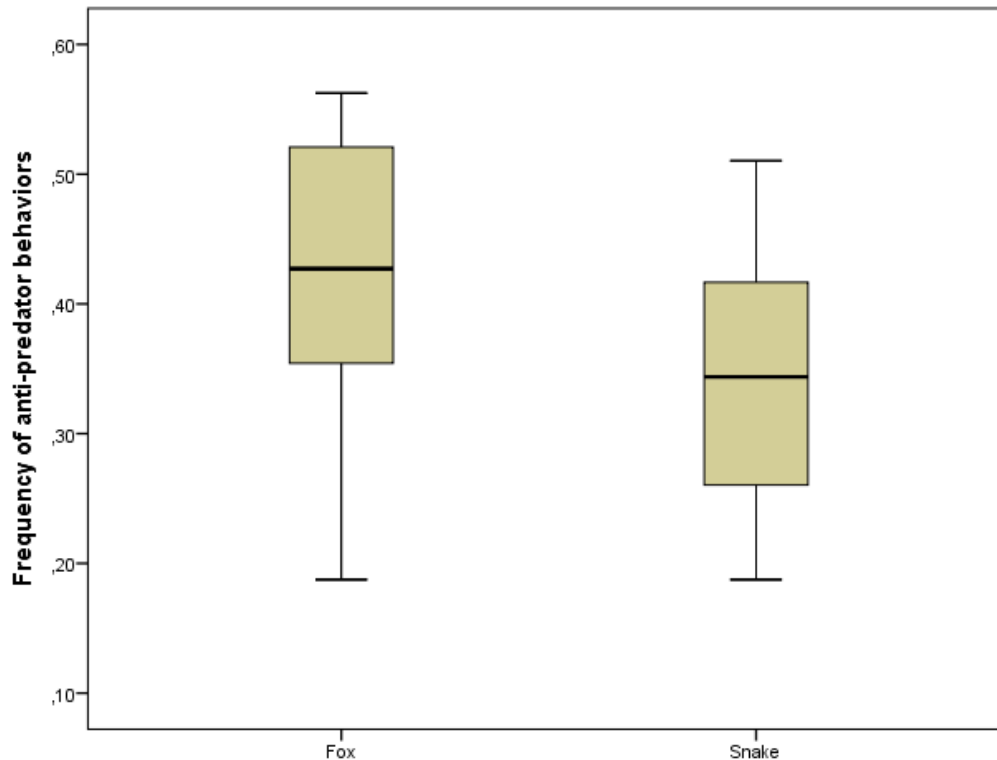
Figure 13. Frequency of anti-predator behaviors performed during sessions with fox and sessions with snake, where outliers are represented by stars or circles.

4.2.10 Contact with stimuli

The cotton-headed tamarins made less contact with the stimuli than the Brazilian bare-faced group. Three times they made contact with the snake where one time was before movement and two times were after movement. They also made contact with the plant and one time in before movement exposure period.

4.2.11 Behavioral changes over time

Also in the cotton-headed tamarins, evidence for behavioral changes over time was discovered. With the moving snake, a significant positive relationship between behavior frequencies and day of study was found in the behavior "Locomotion" (R^2=0.235, B=0.003, p<0.05). For presentation with the moving plant, a significant negative relationship between the behavior "Foraging" (R^2=0.291, B=-0.004, p<0.05) and day of study was revealed. No significant relationship between anti-predator behaviors and day of study was found in this tamarin group.

5   Discussion

5.1   Initial reactions

Most of the times both species of tamarins reacted with "No reaction" or "Stay" while they reacted with "Approach" or "Retreat" fewer times. The differences in initial reactions towards the stimuli are small in most cases, which means that no conclusions from these data alone can be made.

Within both species, "No reaction" was more abundant with the still objects than the moving ones in the first experiment. This is probably since a moving object elicits more fear response than a still one because it could be an attacking predator. A factor that might have added up to this effect is the dragging of the wagon which caused some noises while dragged across the floor. The uncovering of the still objects was more subtle and might therefore not catch the attention of the tamarins as often. Something that further strengthens the conclusion that a moving object is more scaring than a still one is that reactions with "Retreat" were more common with the moving objects than with the still ones. Interestingly, both species reacted more times with "Approach" to the fox than to the covered fox. This could be due to the fact that these "Approach" actually represents a part of mobbing behavior where the tamarins are moving closer in order to scare the fox away.

Also in the second experiment with the snake and the plant, the differences between the initial reactions towards the objects were generally not large. There were, however, some differences between the two species. In both species, "No reaction" was more common towards the plant than the snake. That the uncovering of the still plant was recorded as "No reaction" more often than the uncovering of the snake can be explained by that they indeed saw the plant but decided to not put too much attention to it which made it look like they did not react at all. "No reaction" also represented a larger part with the still objects compared to the moving ones in the Brazilian bare-faced tamarin group, which further imply that a moving object creates stronger reactions than a still one. A tendency for "Approach" being more abundant towards still plant than the still snake was found in the Brazilian bare-faced tamarins, which could be a sign of curiosity. It might be confusing that "Approach" is interpreted as mobbing behavior when performed towards the fox, but interpreted as a sign of curiosity when performed towards the plant. But this could be motivated since when doing the behavioral studies over the whole sessions, tendencies for approaching as a part of mobbing behavior when performed together with other anti-predator behaviors, were only seen in the sessions with the fox and not in the other sessions. The Brazilian bare faced tamarin's reactions of "Retreat" were again most abundant to the moving predator model, in this case the snake, which

indicate that the moving snake was seen as the most threatening. The cotton-headed tamarins reacted differently than the Brazilian bare-faced tamarin group. In the cotton-headed tamarins, the still plant elicited the most reactions of "Retreat" and the most reactions of "Stay" were shown towards the still snake. It is unlikely that this is because the cotton-headed tamarins experienced the plant as more threatening than the snake. It is instead more likely that it is due to the fact that this group was previously free-living in the park. The tamarins have seen many different objects and animals when moving freely in the park and have therefore habituated more than the other group to new objects. The bright-colored plastic plant might have stood out more than the grey rubber snake and thus elicited higher fear response. It might even be so that the relaxed selection has had different effects on the two groups. Perhaps anti-predator behaviors directed to predator snakes have been more degraded in the cotton-headed tamarins than in the other tamarin group due to differences in genetic connection of these behaviors.

It is hard to draw any conclusions from the initial reactions towards the different objects. Firstly because, as mentioned previously, the differences between the number of each reaction are not that big and secondly because the definitions of each reaction are questionable themselves. A "Stay" that was defined as "looking at stimuli but staying put at same location" could indeed be that the tamarins perceived the stimuli as not threatening at all and simply decided that it was nothing to pay attention to, or it could also be that they were so afraid that they did not dare to move. Furthermore, no statistical analyses could be done with this data. The measure of the initial reactions was included in the method so that in case of behavioral responses being shown for a very short period of time, reactions could still be discovered. On their own, these results are not very useful, but together with the behavioral studies over the whole sessions, they can provide valuable information.

5.2 Behavioral differences between predator stimulus and control

When instead looking at the behavior frequencies shown during the whole presentations of the stimuli, results pointing in the same direction as the results from the initial reactions were found. The Brazilian bar-faced tamarin group showed higher frequencies of "Gazing" and "Vocalization" towards the fox than towards the covered fox during both exposure periods. The cotton-headed tamarins reacted similar as the Brazilian bare-faced tamarin group. Higher frequencies of "Vocalization" towards fox was seen in the exposure before movement period and "Gazing" had higher frequencies for fox in the after movement period. More "Gazing" and "Vocalization" confirms anti-predator responses towards the fox in both species. The Brazilian bare-faced tamarins also performed more "Moving closer" towards the fox than the covered fox in

exposure before movement period. This could either be explained by curiosity or by a tendency to mobbing behavior. The latter is the most likely since anti-predator behaviors also were performed in significantly higher frequencies at the same time. In the after movement period, the Brazilian bare-faced tamarin group also showed higher frequencies of "Locomotion" for the fox than the covered fox. That particular behavior is probably a part of fearful behavior as well. When observing this group, it was quite clear that more locomotion could be a sign of stress or fear when performed together with gazing and vocalizations. This was clearly displayed when the tamarins saw a large bird flew past the window. The cotton-headed tamarin group performed more "Looking window" towards the covered fox than the fox in the exposure before movement period. "In box" was performed at higher frequencies during sessions with covered fox than sessions with fox by the Brazilian bare faced tamarins in exposure before movement period. These behaviors, which were typically performed during calm situations, further confirm that the covered fox was not seen as a threat by any of the tamarin groups.

When fusing data of the four anti-predator behaviors and the two exposure periods together, the conclusions made above could be confirmed. There were more anti-predator behaviors performed during sessions with the fox than sessions with the covered fox for both tamarin groups. This suggests that the fox was an effective model to induce anti-predator response in these groups.

As for the second experiment with the snake and plant, differences between the predator model and the control discovered when looking at initial reactions were confirmed. The Brazilian bare-faced tamarin group showed higher frequencies of "Gazing" and "Vocalization" during sessions with snake compared to sessions with the plant in both exposure periods. The occurrence of anti-predator behaviors indicates that the snake was seen as threatening in this group. The cotton-headed tamarin group on the other hand performed more of the anti-predator behavior "Gazing" towards the plant than the snake in both exposure periods. The calm behavior "Social interaction" was in addition shown more with the snake compared to the plant in exposure after movement period. This strengthens the theory that the plant somehow elicits stronger fear response than the snake in this group.

The results above were further supported when testing the anti-predator behaviors and the two exposure periods together. More anti-predator behaviors were shown towards the snake than the plant in the Brazilian bare-faced tamarin group while the cotton-headed tamarin group instead showed higher frequencies of anti-predator behaviors towards the plant than the snake. It can therefore be concluded that the snake is an effective predator model to induce anti-predator

response in the Brazilian bare-faced tamarin group, but not in the cotton-headed tamarin group.

Results in agreement with the ones in this study have previously been shown for Callitrichidae, where anti-predator behaviors have been elicited towards different predator models (Barros et al. 2002, Cagni et al. 2011, Dacier et al. 2006). The results from the present study, showing that anti-predator behaviors are still present in these captive tamarins, indicate that visual predator recognition could be at least partly innate in these species. There are not frequent encounters with potential predators in most captive environments, especially not close up, although some zoos allow visitors to bring dogs into the park. Previous research has shown that anti-predator behaviors within other species must be learned by observing parents behave fearfully towards predators or predator models (Beani & Dessí-Fulgheri 1998, Mineka et al. 1984, Shier & Owings 2007). But the results obtained in this study do not imply that this would be the case in these tamarin groups since anti-predator behaviors have been maintained without predator presence when growing up in the zoo. The tamarins used in this study have only been in captivity for a few generations which means that the relaxed selection have not been present for long, hence anti-predator behaviors might not had been degraded yet. Previous studies on other taxa have shown a wide variety of with which speed relaxed selection can act (Blumstein et al. 2004, Messler et al. 2007) which makes predictions on how long anti-predator behaviors can persist within future generations of these tamarins impossible.

Degradation of anti-predator behaviors has been found in several different taxa (Blumstein & Daniel 2005, Cooper Jr et al. 2009, Maloney & McLean 1994, McPhee 2003, Mineka et al. 1980). But a maintained anti-predator response has also been found (Gaudioso et al. 2011, Hollén & Manser 2007, Maran et al. 2009). From the present study, we cannot say whether these groups have impaired anti-predator responses or not. To be able to conclude anything regarding that, we would have to compare these results with the results from studies of anti-predator responses in wild tamarin groups.

Due to the variety of quality in anti-predator behaviors among other taxa, it is interesting to compare the results from this study with previous research on the same species. Buchanan-Smith et al. (1993) found olfactory discrimination in cotton-headed tamarins. The tamarins showed higher anxiety response towards predatory compared to non-predatory faecal scents. Another study by Friant et al. (2008) discovered that captive born cotton-headed tamarins could not discriminate between vocalizations from predators and vocalizations from non-predators. When connecting this to Blumstein's (2002) thoughts, it might be that visual and olfactory predator recognition in tamarins are more "hard-wired"

traits while auditory predator recognition may have to be learned. This would be interesting to further investigate with a study that combines predator recognition by all senses and compare them.

5.3 Behavioral differences between pre- and post-period

When looking at differences in the observed behaviors between pre- and post-exposure period some significant results were revealed in both tamarin groups. "Touching mesh" was more common in pre-exposure period than in post-exposure period when presented to the fox in both species. "Touching mesh" might be increased during time before feeding since the tamarins are trying to get close to the food. The Brazilian bare-faced group also performed more "Vocalization" in pre-exposure period. The reason for this is probably that the upcoming feeding event at the end of this period excites vocalizations. "Locomotion" and "Social interaction" were more common in pre-exposure period than in post-exposure period for the cotton-headed tamarin group. This could be because the response from exposures to the fox lasted into post-exposure period and thereby suppressed the calm behaviors. "Locomotion" could be part of calm behaviors in this context. When "Locomotion" was performed without the anti-predator behaviors, it was perceived as a sign of the tamarins being relaxed and moving more freely. "Foraging" was more common in the post-than in the pre-exposure period within both tamarin groups during sessions with the fox. This is likely because being fed with new food increases the will to eat.

No differences between pre- and post-exposure periods from sessions with the snake were discovered in the cotton-headed tamarins. But the Brazilian bare-faced tamarins displayed more "Foraging" before than after exposure, which probably is due to the reasons mentioned before, that being fed with new food increases the will to eat. The behaviors "Scratching" and "Investigating" were more common in pre-exposure period than in post-exposure period as well which implies that this group might have had a lasting effect of fear response into post-exposure period. "In box" were more common in post-exposure period than pre-exposure period which might as well be a sign of fear response lasting into post-exposure period where the tamarins entered the box to feel protected.

With all these results in mind, it does appear that the fearful reactions discovered in both species last into post-exposure period as well. In agreement to these results, other researchers have found that reactions towards predators indeed last into post-exposure period. Barros et al. (2002) saw that vocalizations connected to predators were given for the different predator models hawk, rattlesnake and oncilla in captive marmosets, where the reactions lasted during post-period for the oncilla. Thus, also in Barros' study the carnivore elicited the strongest

responses suggesting that maybe a carnivore predator model is the most effective one to use in captive environments with these species.

5.4 Behavioral differences between before and after movement

From results of the initial reactions in the Brazilian bare-faced tamarin group, speculations of a moving fox perhaps being more effective than a still one were raised, but this could not be confirmed when testing frequencies of anti-predator behaviors from before and after movement of the predator models against each other.

As opposed to the other tamarin group, differences in anti-predator behaviors could be found between the period before and after movement of the predator models in the cotton-headed tamarins. During both presentations of the fox and the snake, "Vocalization" was more common before movement than after. So in this tamarin group the movement did not increase the fear response. The reason for more vocalizations being performed before movement could simply be that the most fear response is expressed directly after the predator is revealed due to surprise.

5.5 Behavioral differences between presentations with the different predator models

On the whole, presentations with the fox were perceived as the more effective ones in producing anti-predator responses. This was further confirmed when results from testing behavioral differences between the two predator models were analyzed. "Gazing" were more common during sessions with the fox than sessions with the snake in both species. "Vocalization" was more common towards the fox in the cotton-headed tamarins and "Moving closer" was more common towards the fox in the Brazilian bare-faced tamarins. These anti-predator behaviors (as "Moving closer" can be interpreted as tendency to mobbing behavior in the Brazilian bare-faced tamarin group) being more common towards the fox than the snake, suggests that the fox is the most effective predator model. When putting anti-predator behaviors as well as exposure periods together, significant differences for the fox eliciting higher responses than the snake was found in both species. The reason for the fox being more effective to use as a predator model could be due to the theory formed by Blumstein (2002), that predator recognition of mammals have been preserved under relaxed selection since the morphology are convergent in mammalian predators.

It is difficult to discuss if a fox or a snake is the more effective predator model of the two to use in these species, since they were presented so differently. However, a conclusion of the fox presented in this particular way being more

effective than the snake presented in this particular way can still be made. As captive tamarins species are hold in very different ways, and as groups and even individuals of tamarins are different, it is not possible to extend the conclusions to the species as a whole. But it can provide information about how to design the best predator model for these two tamarin groups and maybe also give an indication of how to design environmental enrichments that deal with anti-predator behaviors in other captive Callitrichidae.

5.6 Contact with stimuli

During the sessions in this study, contact with stimuli was noted as well. Making contact with the stimuli was quite more frequent in the Brazilian bare-faced group than in the cotton-headed tamarin group. The Brazilian bare-faced tamarin group made most contact with the plant, again indicating that they did not fear the plant. They made contact a few times with the other stimuli as well but almost half of the times they made contact with the plant. It should be mentioned that 17 of 19 times it was the same individual that approached the stimuli. It was the female Sabine that was perceived as more bold and curious than the others, which might have had an effect on these results. The other tamarin group, the cotton-headed tamarins, did not make as much contact with the stimuli. Only a few times they did and these times it was with the snake and the plant. Since there are so few occasions it is hard to draw any conclusions from the data but with the behavioral studies in mind, it is not surprising that the two groups show different results also in this aspect.

5.7 Behavioral changes over time

In the cotton-headed tamarins, some relationships between behavior frequency and day of study were revealed. When presented with a moving snake, this group had a slight increase in "Locomotion" over time. This might be a sign of an escalating fear towards the snake. But from what was observed during the sessions, this group did not seem to perceive the snake as fearful consistently nor did they react by moving around a lot the few times they did seem scared. So the reason could instead be the opposite. As mentioned before more movement in this group might be a sign of the tamarins feeling more relaxed and moving freely to a larger extent. Possibly, therefore also this result is a sign of habituation. A change over time for "Foraging" when presented to the moving plant was also found, where "Foraging" decreased slightly over time. It might be an escalating anxiety for the moving plant that is the reason since the plant, as has been explained before, actually induced more fearful responses than the snake did.

When testing for behavioral changes over time in the Brazilian bare-faced group, interesting results were discovered. Both "Vocalization" and "Moving closer" had a slight, but still significant decrease over time in the before movement period with the fox. Also when looking at data from the presentations of the snake after movement, a small decline over time was found for "Gazing" and "Vocalization". These results might be a sign of a habituation happening within the group when the stimulus is not varied.

When fusing anti-predator behaviors and exposure periods together, a decrease with day of study was confirmed with both predator models, further implying that there might be a habituation effect towards the predator models in the Brazilian bare-faced tamarin group. Possible interventions to prevent habituation could be varying the placement, movement or duration of the stimuli. However, additional research would be needed to clarify if a predator model varied in these ways would maintain anti-predator behaviors in the long run.

Habituation towards predator models has been confirmed in studies of other taxa. Hemmi & Merkle (2009) saw a clear habituation towards a dummy fish predator in fiddler crabs (*Uca vomeris*) even though they encountered real predators during the time of habituation process. They also saw that just a small change in approaching distance of the dummy led to a regain of their initial responses. Also in barn swallows (*Hirundo rustica*), evidence for habituation have been found. The swallows habituated rapidly regardless of type of model or distance to them (Smith & Graves 1978). Even within Callitrichidae habituation towards predator models has been seen. Dacier et al. (2006) saw that captive marmosets rapidly habituated towards a taxidermic oncilla and reduced scan behavior. So is the habituation discovered in the present study a sign of the tamarins understanding that the models are not dangerous? It could be that some sort of negative consequence is needed in order for them not to habituate. This kind of thought that some sort of consequence is needed to truly learn prey animals to react fearfully towards predators is present among researchers within the field of ethology. There is evidence of animals that have learnt to react to real predators rapidly when some sort of negative consequence has been the outcome. Berger et al. (2001) found that moose mothers that had their calf killed by a wolf, increased vigilance when presented with wolf calls with 500% compared to before. This study shows that a direct consequence such as the death of an offspring is an event that can affect the behavior of the mothers strongly. With this in mind it can be argued that maybe some consequence is necessary also in the tamarins to affect anti-predator behaviors in the long run.

There are, however, also previous studies that have found a long lasting effect of using predator exposures. Shier & Owings (2006) found that predator exposures had an immediate and lasting effect on captive black-tailed prairie dogs

(*Cynomys ludovicianus*). The authors also state that it appeared to promote survival after release. Further evidence for effective predator exposures, this time towards a predator model, was discovered by De Azevedo & Young (2006) that showed that rheas learn to recognize predators and retain predator recognition for almost three months. Contradictory results was reported by Mineka et al. (1980) where only three out of eight rhesus monkeys behaving fearfully towards real and model snakes showed systematic behavioral changes across seven sessions, indicating that exposures to predators were not successful.

If this study would have shown an increase in anti-predator behaviors over time, it could be argued that maybe the tamarins learned to react fearfully towards the models to some degree. If that was the case it would be very interesting to repeat the same study after some time to see if that effect was long lasting. But even if that was done, this would not show that they had learned to react fearfully towards real predators. In order to show that, you would have to release the tamarins into the wild and monitor how they react to predators there.

5.8 Conclusions

Anti-predator response was expressed towards both the fox and the snake within the Brazilian bare-faced group. In the cotton-headed tamarin group, higher frequencies of anti-predator responses were shown towards the fox compared to the control but not towards the snake, this group instead showed more anti-predator responses to the control plant. There were some signs of the fear response lasting even into post-exposure period when the predator model was removed. The fox was the most effective predator model of the two in both species. There even seemed to be a tendency for mobbing behavior directed towards it. No evidence for a moving object being more effective than a still was found. Possible habituation effects to both the fox and the snake were found.

To conclude, using a stuffed fox as a predator model is an effective way of inducing anti-predator responses in these tamarin groups, although a habituation effect should be alerted for. Hopefully, a predator model designed with the results from this study in mind can be used at Parken Zoo as an environmental enrichment. This study has begun to fill a gap in the field of conservation biology and will hopefully inspire further research in the same area.

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