Captive-born collared peccary (*Pecari tajacu*, Tayassuidae) fails to discriminate between predator and non-predator models

Carlos Magno de Faria[1], Fernanda de Souza Sá[1], Dhiordan Deon Lovenstain Costa[1], Mariane Mendes da Silva[1], Beatriz Cristiana da Silva[1], Robert John Young[2], Cristiano Schetini de Azevedo[1]

1: Departamento de Evolução, Biodiversidade e Meio Ambiente, Instituto de Ciências Exatas e Biológicas, Universidade Federal de Ouro Preto, Minas Gerais, Brasil. Campus Morro do Cruzeiro, s/n, Bauxita. Cep: 35400-000. Ouro Preto, Minas Gerais, Brasil. Phone: 55 31 3559-1598. E-mails: carlosmagno.ufop@gmail.com; fernandasouzasa@gmail.com; dhiordan_deon@live.com; marianemendessilva@hotmail.com; beatrizcriss@gmail.com

2: University of Salford Manchester, Peel Building - Room G51, Salford, M5 4WT, United Kingdom. E-mail: r.j.young@salford.ac.uk

[*]Corresponding author: C.S. Azevedo, Departamento de Evolução, Biodiversidade e Meio Ambiente, Instituto de Ciências Exatas e Biológicas, Campus Morro do Cruzeiro, s/n, Bauxita, CEP: 35400-000, Ouro Preto, MG, Brasil. Phone: +55 31 3559-1598. E-mails: cristianoroxette@yahoo.com

Abstract

Captive animals may lose the ability to recognize their natural predators, making conservation programs more susceptible to failure if such animals are released into the wild. Collared peccaries are American tayassuids that are vulnerable to local extinction in certain areas, and conservation programs are being conducted. Captive-born peccaries are intended for release into the wild in Minas Gerais state, southeastern Brazil. In this study, we tested the ability of two groups of captive-born collared peccaries to recognize their predators and if they were habituated to humans. Recognition tests were performed using models of predators (canids and felids) and non-predators animals, as well as control objects, such as a plastic chair; a human was also presented to the peccaries, and tested as a separate stimulus. Anti-predator defensive responses such as fleeing and threatening displays were not observed in response to predator models. Predator detection behaviors both from visual and olfactory cues were displayed, although they were not specifically targeted at predator models. These results indicate that collared peccaries were unable to recognize model predators. Habituation effects, particularly on anti-predator behaviors, were observed both with a one-hour model presentation and across testing days. Behavioral responses to humans did not differ from those to other models. Thus, if these animals were to be released into the wild, they should undergo anti-predator training sessions to enhance their chances of survival.

Keywords: behavior, captivity, conservation, predation, recognition.

Introduction

Captive-born animals that do not suffer from predatory pressures may lose their ability to recognize their natural predators after a few generations in captivity (Yorzinski 2010). This is because the skills required for predator recognition do not develop, saving energy that is directed to other activities, such as feeding and reproduction (McPhee 2003; Adams et al. 2006; Blumstein 2006). The recognition of predators and non-predators by a captive animal can be tested using stuffed models, audio playbacks or predator odors, feces, urine (Griffin et al. 2001; 2002; Azevedo et al. 2012) or by the comparison of the anti-predator behaviors exhibited by captive-born and wild conspecifics (Jackson & Brown 2011). When responses from these tests fail, then anti-predator training sessions can be applied, so that the animals regain their ability to discriminate between predators and non-predators (Griffin et al. 2000; Shier & Owings 2007; Crane & Mathis 2011; Moseby et al. 2012).

The ability to recognize predators may be reflected in the ability to detect them, escape from them, and ultimately in the individual's fitness (Moseby et al. 2016). However, alien, invasive predators can be a conservation problem because the expressed anti-predator behaviors can be inappropriate, facilitating their capture by the predators, consequently diminishing the individual's fitness (Sih et al. 2009; Lehtonen et al. 2012; Carthey & Blumstein 2017). Furthermore, since predators normally avoid areas under human interference, prey species could live in closer proximity to humans to reduce predation risk. However this may increase their risk of individuals being captured or killed by humans (Muhly et al. 2011).

Anti-predator recognition tests show that captive-born animals can present an innate response to predators, exhibiting correct anti-predator responses in the very first predator encounter (Tammar wallabies – *Macropus eugenii*, Blumstein et al. 2000; Vancouver Island marmots – *Marmota vancouverensis*, Blumstein et al. 2006; Meerkat – *Suricata suricatta*, Hollén & Manser 2007; Gray mouse lemur – *Microcebus murinus*, Sündermann et al. 2008; Rainbow trout – *Oncorhynchus mykiss*, Kopack et al. 2015; Leopard gecko – *Eublepharis macularius*, Landová et al. 2016) or that captive-born animals can fail in predator discrimination, showing no anti-predator responses when facing predators (Cotton-top tamarins – *Saguinus oedipus*, Friant et al. 2008; Greater rheas – *Rhea americana*, Azevedo et al. 2012). A long co-evolutionary history of prey and their predators, a genetically fixed mechanisms of olfactory predator recognition, or a period of relaxed selection, where functional components in other contexts are sufficient for the maintenance of anti-predator behaviors are suggested as mechanisms for the innate responses (Blumstein et al. 2000, 2006; Hollén & Manser 2007; Sündermann et al. 2008). Effects of domestication, the complete lack of predator encounter or predation events and the similarity of sound frequencies between predators and non-predators are suggested as reasons for the lack of discrimination (Friant et al. 2008; Azevedo et al. 2012).

Anti-predator training sessions have been applied to Tamar wallabies (Griffin 2003), greater rheas (Azevedo & Young 2006), Nile tilapia (*Oreochromis niloticus*, Mesquita & Young 2007), red-legged partridges (*Alectoris rufa*, Gaudioso et al. 2011), Amazon parrots (*Amazona aestiva*, Azevedo et al. 2017) among others, and all species acquired adequate anti-predator responses after few training sessions. Anti-predator training, thus, may be an important tool for animal conservation programs (van Heezik et al, 1999; Griffin et al. 2000; Alonso et al. 2011); however, more recently *in situ* exposure to predators is being claimed as more important for captive-born animals' survival after release than pre-release anti-predator training (Moseby et al. 2016). No study has evaluated if the anti-predator behaviors exhibited by collared peccaries are innate or learned.

Prey species can use some characteristics of their predators to evaluate predation risk: body size, eye position and eye-gaze, olfactory cues and sounds cues (Carter et al. 2008; Hettena et al. 2014, Schmitz 2017; Tang et al. 2017). For example, the larger the predator, the greater the risk of predation (Cohen et al. 1993; Preisser & Orrock 2012). Thus, it is expected that the captive-born collared peccaries present a strong anti-predator response when large predators are in sight. Olfactory cues can be associated with visual cues to enhance anti-predatory responses (Kiesecker et al. 1996; Ward & Mehner 2010). For species with an acute sense of smell, such as collared peccaries and aquatic species, the use of olfactory cues is suggested for use during predator recognition tests (Fischer et al. 2017; Mitchell et al. 2017). It has been suggested that prey species present a genetically fixed olfactory recognition mechanism that allows innate predator discrimination (Sündermann et al. 2008). This predator recognition system is based on olfactory molecules, originating from meat metabolism, present in the predators' feces and urine (Arnould et al. 1998; Ferrero et al. 2011).

In addition, to the loss of the ability to recognize predators, captive animals may also become habituated to humans (Abramson & Kieson 2016). Habituation to humans may have deleterious effects on animals when reintroduced into nature, since reduced fear of humans can be generalized to predators (Jones & Waddington 1992; Coleman et al. 2008; St Clair et al. 2010; Blumstein 2016). Therefore, it is important to evaluate whether this response of habituation to humans is being generalized, potentially, influencing the animals' anti-predator responses before their release.

The collared peccary, *Pecari tajacu* Linnaeus, 1758 (Cetartiodactyla, Tayassuidae), occurs from the south of the United States to the north of Argentina (Desbiez et al. 2012), and it has been recorded in all Brazilian terrestrial Biomes (Chiarello et al. 2008; Desbiez et al. 2012). Although not present on the Brazilian Red List of Threatened Species (Desbiez et al. 2012), the collared peccary is considered endangered to local extinction in Minas Gerais state, southeastern Brazil, mainly due to habitat fragmentation, hunting and illegal trade (Chiarello et al. 2008). In this Brazilian state, efforts are being made to reintroduce captive-born individuals into a protected wild area (Project Cateto, funded by Vallourec, in partnership with Federal University of Ouro Preto, Federal University of Minas Gerais, and Instituto Estadual de Florestas in Minas Gerais – Brazil, and with University of Salford – United Kingdom). However, the reintroduction process is complex, and different behavioral, genetic, parasitological, and ethnozoological studies are being conducted with this captive population.

The complexity of the reintroduction process depends on the pre-release procedures, such as: foraging and anti-predator training; the choice of the ideal area to release the animals; their monitoring after release; environmental education activities in the release area; and on ecological and health studies conducted before and after release. All of these activities imply the need for financial expenditure and specialized personnel (Sarrazin & Barbaut 1996). The aim being to better prepare the animals for survive after release, since the peccaries have been kept in captivity since 2005. In this context, it is important to conduct predator discrimination studies with these captive-born peccaries.

The main predators of collared peccaries in the wild are the puma (*Puma concolor*), the jaguar (*Panthera onca*), the domestic/feral dog (*Canis lupus familiaris*), the ocelot (*Leopardus pardalis*), the common boa (*Boa constrictor*), and some bird of prey species (Sowls 1984). The most common anti-predatory behaviors of collared peccaries when intimidated by predators are to escape by running away, and tooth chattering to produce a loud and threatening sound, which can be emitted by the peccaries as a defensive threat; tooth chattering can be associated with other behaviors, such as running escapes (Sowls 1997; Nogueira et al. 2017). Alert and inspecting behaviors (such as flehmen) also increase with the increase of the predation risk (Sowls 1997; Nogueira et al. 2017).

The aims of this study were to evaluate the behavioral responses of captive-born collared peccaries to different models of predators and non-predators, and also evaluate if peccaries were habituated to humans. We hypothesized that captive-born collared peccaries have lost their ability to recognize/respond to their natural predators and have become habituated to humans. We predict that when exposed to predator and non-predators models, these animals will react similarly, exhibiting no classical anti-predator responses (escape running and tooth chattering), indicating their inability to discriminate between predators and non-predators. We also predicted that peccaries will respond to humans in the same way as they respond to non-predator models, indicating habituation to humans. The evaluation of predator recognition by the collared peccaries would be important in taking the decision to apply or not anti-predator training before release.

Materials and methods

Study site, animals and maintenance

The present study was conducted at the Engenho D'Água farm, located in São Bartolomeu district (20º15'41" S, 43º36'34" W), Ouro Preto municipality, Minas Gerais, southeastern Brazil. The study area's vegetation is classified as semideciduous seasonal forest within the Atlantic Forest domain (Messias et al. 2017). The mean annual temperature varies between 14°C and 28°C, with an annual pluviometric mean of

1,552mm and two distinct seasons: a dry season from March to September and a rainy season from October to February, the climate being classified as Cwb in the Köeppen system (Pedreira & Sousa, 2011).

Twenty captive-born collared peccaries (*P. tajacu*, Tayassuidae) were studied. The studied animals represent the 11th generation of captive-born animals. Individuals were separated into two groups, each composed of eight females and two males, all adults [weight (kg) mean ± SD: 17.47 ± 4.85] and none were wild-caught or belonged to the founder group. Each group was housed in a 625 m^2 enclosure each, separated by 10 m and delimited by wire mesh fence. Animals in one enclosure were not able to see the animals of the other enclosure because of the vegetation in between enclosures and due to a black curtain covering the wire mesh. The ground substrate was composed of clay with a few clumps of grass, some small-sized trees, and five large diameter concrete pipes, used as hiding places by the animals. Peccaries were fed once a day, always at 07:00h, with a mixture of dry food for pigs (CCPR®: a mixture of cotton bran, soybean meal, corn, molasses, and vitamins and minerals) and soybean meal (10kg per enclosure).

Experimental protocol

Predator (canids and felids), non-predator animals, as well as control objects, such as a plastic chair; also, a human were presented to the peccaries. The models used were: (A) predators: stuffed ocelot (*Leopardus pardalis* – medium size), life size PVC model in natural standing position of a Rottweiler dog (*Canis lupus familiaris* – large size), and life size PVC model in natural standing position of a jaguar (*Panthera onca* – large size); (B) Non-predator animals: stuffed crab-eating raccoon (*Procyon cancrivorus* – medium size), stuffed domestic chicken (*Gallus gallus domesticus* – small size), and a stuffed coati (*Nasua nasua* – small size); (C) Control objects: plastic chair (large size), garbage basket (medium size) and a ball inside a bag (small size). A live human (*Homo sapiens* – large size) were also presented to the peccaries. Predator and non-predator models were associated with odor signatures of their own species, such as feces and urine. Fecal and urine samples were collected at Belo Horizonte Zoo (Minas Gerais, Brazil) in the days immediately before each test. This procedure was adopted because collared peccaries use both olfactory and visual cues to identify predators (Sowls 1997) and because both visual and olfactory cues together can elicit stronger reactions to predators (Fischer et al. 2017).

Model presentation order was defined by Latin square (Table 1) and the same order was adopted for both groups of peccaries. This order was chosen due to logistical reasons (transportation of feces and urine from BH Zoo to the study area). The models were presented to the peccaries always on the same side outside of the enclosure, near the wire mesh fence in a place highly visible to the animals. A pulley system was created so that the models would appear in movement; the peccaries did not see the placement of the models, because this occurred behind a black curtain. Exposition time was one hour per model. Each model was presented five times for each group of peccaries; only one model per day was presented and never repeated the next day, and each model was presented to each peccary group separately. Behavioral data collection during the daily one-hour model presentation, occurred between 8:00h and 15:00h (each day, the one-hour testing period was chosen randomly). We collected 50 hours of behavioral data in each enclosure, totaling 100 hours. All behavioral data were collected using scan sampling, with instantaneous recording of behavior every minute (Martin & Bateson 2007). Behavioral data collection occurred from a hide; therefore, peccaries were not able to see the researcher.

______________________Insert Table 1_________________________________

An ethogram for the collared peccaries was constructed based on 30 hours of preliminary observations and on the study of Byers & Bekoff (1981) (Table 2). Behaviors described in Table 2 were recorded individually and then pooled into similar categories before analysis. Peccaries were able to flee from predators using the entire 625m^2 of their enclosures or hide in concrete pipes, although peccaries were never observed running to the pipes to seek cover (but pipes were used for resting).

________________________Insert Table 2____________________________

This study was approved by the Animal Ethics Committee of the Federal University of Ouro Preto, under protocol number 2015/26.

Statistical analyses

The daily number of occurrences of each behavior was used in the analyses. We compared the behavioral responses of the collared peccaries to predator, non-predator, human and control objects using generalized linear mixed models (GLMMs), where the behaviors were the response variables; the treatment (predator, non-predator, control objects, human), type of model (ocelot, jaguar, dog, etc.), and the size of the model (small, medium and large size) were the explanatory variables; groups (group 1 and group 2) entered the models as random variables; potential habituation effects across observations were accounted for by adding the day of test (1 to 50) as a covariate in the GLMM models. The Tukey test was applied for *post-hoc* comparisons. We also evaluated habituation to the models (temporal behavioral modification) by comparing the first five minutes to the last five minutes of behavioral data in each one-hour session using the Wilcoxon signed-rank test. All analyses were performed in the statistical program Minitab 18, using the level of significance of 95%, except for the Wilcoxon tests to measure habituation, where the Bonferroni correction was applied and the results were considered statistically significant if $\alpha \leq 0.01$ (Zar 2010).

Results

The most expressed behaviors in number of recordings were: inactive (45.87%), foraging (20.24%), locomotor activity (12.98%), anti-predator behaviors (5.65%; alert: 4.16%; inspecting: 1.49%) and social interactions (2.87%). Peccaries were not visible in 12.39% of the observations due to hiding in the shelters; this category was not included in the analyses. Classic peccary anti-predator behaviors, such as tooth chattering and escaping, were not recorded during the anti-predator recognition tests, thus, only the behaviors alert and inspecting (flehmen) entered in the analysis of this category.

Only two behaviors were displayed differently between predator, non-predator, human and control models. Locomotor activity and alert were more expressed when the human model was exhibited to the peccaries (locomotor activity: $F = 5.84$, $DF = 3$, $p = 0.001$; alert: $F = 4.39$, $DF = 3$, $p = 0.006$) (Figure 1). All other behaviors were exhibited in the same proportion, regardless of the treatment. Locomotor activity was also affected by model-size: peccaries moved significantly more when presented with large than with medium sized models ($F = 4.62$, $DF = 2$, $p = 0.012$), whilst locomotor activity with small models was intermediate when compared with control models.

______________________Insert Figure 1______________________________________

Alert and inspecting, the observed anti-predator behaviors, declined throughout the 50-day testing period (Alert: $F = 28.84$, $p < 0.001$; Inspecting: $F = 32.01$, $p < 0.001$; Inactivity: $F = 3.81$, $p = 0.05$). Anti-predator behaviors were mostly expressed in the first 15 days of testing, and then remained low, which suggests a habituation effect. Inactivity presented an inverse response, increasing in frequency after 15 days of testing (Figure 2).

__________________________________Insert Figure 2_____________________________

Habituation effects with the one hour model presentation were visible for most behaviors. In particular, both anti-predator behaviors decreased in the last five minutes with the predator, non-predator and objects (Figure 3). With the human, inspecting increased in the last five minutes, but alert decreased (Figure 3). Inactivity always increased in the last five minutes, except with the human, where it remained stable (Figure 3). Foraging and social interactions showed more varied patterns between model types (Figure 3), whereas locomotor activity was never affected.

_________________________Insert Figure 3______________________________

Discussion

Neither of the two anti-predator behaviors observed were affected by model predator type; inspecting and alert, the only anti-predator behaviors expressed by the peccaries in this study, were exhibited equally when confronted with predator and non-predator model, and highly when confronted with a human. Classic peccary anti-predator behaviors, such as escaping or tooth chattering, were never registered during the tests, showing that the peccaries did not identify the models as predators. Collared peccaries did not show significant changes in their behaviors when confronted with a predator models or a human. Our subjects' isolation from predators promoted by the captive environment and the consequent lack of predator encounters may have led to the loss of the ability of these individuals to recognize the dangers of predators. This was also observed by Azevedo et al. (2012) studying greater rheas (*Rhea americana*) and Martin (2014) studying crayfishes. Furthermore, other anti-predator behaviors (alert and flehmen) were exhibited by the peccaries in the same manner when exposed to the different predator and non-predator models, which suggests the loss of predator recognition. Other studies show that captive animals may not totally lose their anti-predatory defense capabilities, demonstrating the persistence of some innate responses (Gall & Mathi 2009; Du et al. 2012).

The behavioral responses of the peccaries to the models were in agreement with the relaxed selection hypothesis of predator recognition, where prey is unable to recognize predators after multiple prey generations without predation pressure (Lahti et al. 2009; Carthey & Blumstein 2017). The studied peccaries have been maintained in captivity since 2005, and this time period seemed to be sufficient for relaxed selection to have occurred (11 generations in captivity). The collared peccaries showed no classic anti-predatory responses to the predator models (i.e. escape running, tooth chattering); peccaries were relaxed in front of the predator and non-predator models, supporting the hypothesis of no predator recognition by our subjects (Creel et al. 2014).

The behavior of the collared peccaries was different when confronted with a human. Locomotor activity and alert were more exhibited in the presence of a human than in the presence of other models. This result was not expected because the peccaries were used to receiving their food and care from humans (keepers). Captive animals are commonly habituated to humans because of their frequent contact with their caretakers (Abramson & Kieson 2016); thus, not associating this contact with any danger (Knight 2009; McGowan et al. 2014; Samia et al. 2015). In the present study, peccaries were held in semi-natural enclosures, with minimum contact with the keeper (contact only occurred during food delivery or during capture for medical procedures). Since the human used as a model was not the peccaries' keeper, probably, they showed some fear to the strange human. For animals destined to be reintroduced back to the wild, this is a good situation, since habituated animals may take more risks, approaching more frequently to humans, facilitating their hunting and capture (Lopes 2016); that is, they display boldness syndrome (Geffroy et al. 2015).

Generalized habituation (habituation to humans being transferred to other species) could be a problem in conservation programs and should be avoided (Blumstein 2016). The differences observed between the first and last five minutes of the discrimination tests involving predator and non-predator models are indicative of habituation. Peccaries only increased inspecting, one of the anti-predator behaviors expressed, when confronted by the human model. Besides this, inactivity increased in the last five minutes for all models, except the human. This result corroborates the lack of predator recognition by the collared peccaries. Habituation to predators has been reported in mosquito larvae (Roberts 2014), in lizards (Rodrigues-Prieto et al. 2010), and in a theoretical modeling study (Oosten et al. 2010).

The behavioral responses shown by the peccaries indicated that the animals modified their movements according to the size of the models; the peccaries showed more locomotion in the presence of the smallest and the largest models, but they do not exhibited any classic peccary anti-predator behaviors. The size of the predator may be related to the intensity of the predatory responses exhibited by the prey; larger predators require faster responses by the prey than to smaller predators (Templeton et al. 2005; Preisser & Orrock 2012). Collared peccaries in the present study responded equally to larger and smaller predators and non-predator, again demonstrating their lack of discrimination between models.

Predator detection or discrimination is the first step in the anti-predator response, but is not sufficient if it is not followed by defensive behaviors (e.g. fleeing, tooth chattering in the case of peccaries). The results in this study showed that the peccaries did not display any defensive behaviors when confronted with predator models. This contrasts with Nogueira et al. (2017) who showed that peccaries presented anti-predator defensive behaviors when chased by a human with a capture net in their enclosure, suggesting that these behaviors were still present in the captive animal's behavioral repertoire. Our results suggest that peccaries did not evaluate the threat as being significant enough to display anti-predatory behaviors, either because the models were outside the enclosure and no aversive stimulus was linked to the models, or because the peccaries did not identify the models as predators. Thus, these collared peccaries are candidates for anti-predator training.

Conclusion

From the present study, we conclude that the captive-born collared peccaries were not able to recognize their predators. The peccaries were not habituated to humans. These animals should undergo anti-predator training and fear of humans training if they are to be released into the wild.

Acknowledgments

We would like to thank Vallourec for their financial support, CAPES (Brazilian Research Agency) for research grants (process nº 88881.064952/2014-01), Fazenda Engenho D´água for supporting the research and the transport section of the Federal University of Ouro Preto. Science without Borders supported RJY with a special visiting professor scholarship. We also would like to thank Dr. Sérgio Nogueira-Filho, Dr. Myllene Mariette, and an anonymous reviewer for their valuable suggestions on this paper.

References

Abramson CI, Kieson E (2016) Conditioning methods for animals in agriculture: a review. Ciência Animal Brasileira 17:359-375. doi: http://dx.doi.org/10.1590/1089-6891v17i341981

Adams JL, Camelio KW, Orique MJ, Blumstein DT (2006) Does information of predators influence general wariness? Behavioural Ecololy and Sociobiology 60:742-747. doi: 10.1007/s00265-013-1556-z

Alonso R, Orejas P, Lopes F, Sanz C (2011) Pre-release training of juvenile little ows *Athene noctua* to avoid predation. Animal Biodiversity and Conservation 34.2: 389-393.

Arnould C, Malosse C, Signoreti JC, Descoins C (1998) Which chemical constituents from dog feces are involved in its food repellent effect in sheep? Journal of Chemical Ecology 24: 559-576.

Azevedo CS, Young RJ (2006) Behavioural responses of captive-born greater rheas *Rhea americana* Linnaeus (Rheiformes, Rheidae) submitted to antipredator training. Revista Brasileira de Zoologia 13:186-193. doi: 10.1590/S0101-81752006000100010

Azevedo CS, Young RJ, Rodrigues M (2012) Failure of captive-born greater rheas (*Rhea americana*, Rheidae, Aves) to discriminate between predators and nonpredator models. Acta Ethologica 15:179-185. doi: 10.1007/s10211-012-0124-2

Azevedo CS, Rodrigues LSF, Fontenelle JCR (2017) Important tools for Amazon parrots reintroduction programs. Revista Brasileira de Ornitologia 25:1-11.

Blumstein DT, Daniel JC, Griffin AS, Evans CS (2000) Insular tammar wallabies (*Macropus eugenii*) respond to visual but not acoustic cues from predators. Behavioral Ecology 11:528-535. doi: 10.1093/beheco/11.5.528

Blumstein DT (2006) The multipredator hypothesis and the evolutionary persistence of antipredator behavior. Ethology 112:209-217. doi: 10.1111/j.1439-0310.2006.01209.x

Blumstein DT, Holland BD, Daniel JC (2006) Predator discrimination and ‘personality’ in captive Vancouver Island marmots (*Marmota vancouverensis*). Animal Conservation 9:274-282. doi: 10.1111/j.1469-1795.2006.00033.x

Blumstein DT (2016) Habituation and sensitization: new thoughts about old ideas. Animal Behaviour 120:255-262. doi: 10.1016/j.anbehav.2016.05.012

Byers JA, Bekoff M (1981) Social, spacing, and cooperative behaviour of the collared peccary, *Tayassu tajacu*. Journal of Mammalogy 62:767-785

Carter J, Lyons NJ, Cole HL, Goldsmith AR (2008) Subtle cues of predation risk: starlings respond to a predator’s direction of eye-gaze. Proceedings of the Royal Society B 275:1709-1715. doi: 10.1098/rspb.2008.0095

Carthey AJR, Blumstein DT (2017) Predicting predator recognition in a changing world. Trends in Ecology and Evolution 2324. doi: 10.1016/j.tree.2017.10.009

Chiarello AG, Aguiar LMS, Cerqueira R, Melo FR, Rodrigues FHG, Silva VM (2008) Livro vermelho da fauna brasileira ameaçada de extinção: mamíferos ameaçados de extinção do Brasil. Belo Horizonte. MG: Fundação Biodiversitas

Cohen JE, Pimm SL, Yodzis P, Saldaña J (1993) Body sizes of animal predators and animal prey in food webs. Journal of Animal Ecology 62:67-78. doi: 10.2307/5483

Coleman A, Richardson D, Schechter R, Blumstein DT (2008) Does habituation to humans influence predator discrimination in Gunther’s dik-diks (*Madoqua guenteri*)? Biology Letters 4:250-252. doi:10.1098/rsbl.2008.0078

Crane AL, Mathis A (2011) Predator-recognition training: a conservation strategy to increase postrelease survival of hellbenders in head-starting programs. Zoo Biology 30:611-622. doi: 10.1002/zoo.20358

Creel S, Schuette P, Christianson D (2014) Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. Behavioral Ecology 25:773-784. doi: 10.1093/beheco/aru050

Desbiez ALJ, Keuroghlian A, Beisiegel BM, Medici EP, Gatti A, Mendes Pontes AR, Campos CB, Tófoli CF, Moraes Junior EA, Azevedo FC, Pinho GM, Cordeiro JLP, Júnior TSS, Morais AA, Mangini PR, Flesher K, Rodrigues LF, Almeida LB (2012) Avaliação do risco de extinção do cateto *Pecari tajacu* Linnaeus, no Brasil. Biodiversidade Brasileira 3:74–83

Du Y, Huang Y, Zhang H, Li D, Yang B, Wei M, Zhou Y, Liu Y (2012) Innate predator recognition in giant pandas. Zoological Science 29:67-70. doi: 10.2108/zsj.29.67

Fischer S, Oberhummer E, Cunha-Saraiva F, Gerber N, Taborsky B (2017) Smell or vision? The use of different sensory modalities in predator discrimination. Behavioral Ecoloy and Sociobiology 71:143. doi: 10.1007/s00265-017-2371-8

Friant SC, Campbell MW, Snowdon CT (2008) Captive-born cotton-top tamarins (*Saguinus oedipus*) respond similarly to vocalizations of predators and sympatric nonpredators. American Journal of Primatology 70:707-710. doi: 10.1002/ajp.20552

Gall BG, Mathis A (2009) Innate predator recognition and the problem of introduced trout. Ethology 116:47-58. doi: 10.1111/j.1439-0310.2009.01718.x

Gaudioso VR, Sánchez-Garcia C, Pérez JA, Rodríguez PL, Armenteros JA, Alonso ME (2011) Does early antipredator training increase the suitability of captive red-legged partridges (*Alectoris rufa*) for releasing? Poultry Science 90:1900-1908. doi: 10.3382/ps.2011-01430

Geffroy B, Samia DSM, Bessa E, Blumstein DT (2015) How nature-based tourism might increase prey vulnerability to predators. Trends in Ecology and Evolution 30:755-765. doi: 10.1016/j.tree.2015.09.010

Griffin AS, Blumstein DT, Evans CS (2000) Training captive bred and translocated animals to avoid predators. Conservation Biology 14:1317-1326. doi: 10.1111/j.1439-0310.2009.01718.x

Griffin AS, Blumstein DT, Evans CS (2001) Learning specificity in acquired predator recognition. Animal Behaviour 62:577-589. doi: 10.1006/anbe.2001.1781

Griffin AS, Blumstein DT, Evans CS (2002) Selective learning in a marsupial. Ethology 108:103-114. doi: 10.1046/j.1439-0310.2002.00840.x

Griffin AS (2003) Training tammar wallabies (*Macropus eugenii*) to respond to predators: a review linking experimental psychology to conservation. International Journal of Comparative Psychology 16:111-129.

Hettena AM, Munoz N, Blumstein DT (2014) Prey responses to predator's sounds: a review and empirical study. Ethology 120:427-452. doi: 10.1111/eth.12219

Hollén LI, Manser MB (2007) Persistence of alarm-call behaviour in the absence of predators: a comparison between wild and captive-born meerkats (*Suricata suricatta*). Ethology 113:1038-1047. doi: 10.1111/j.1439-0310.2007.01409.x

Jackson CD, Brown GE (2011) Differences in antipredator behaviour between wild and hatchery-reared juvenile Atlantica salmon (*Salmo salar*) under seminatural conditions.

Canadian Journal of Fisheries and Aquatic Sciences 68:2157-2165. doi: 10.1139/F2011-129

Jones RB, Waddington D (1992) Modification of fear in domestic chicks, *Gallus gallus domesticus*, via regular handling and early environmental enrichment. Animal Behaviour 43:1021-1033. doi: 10.1016/S0003-3472(06)80015-1

Kiesecker JM, Chivers DP, Blaustein AR (1996) The use of chemical cues in predator recognition by western toad tadpoles. Animal Behaviour 52:1237-1245. doi: 10.1006/anbe.1996.0271

Knight J (2009) Making wildlife viewable: habituation and attraction. Society and Animals 17:167-184. doi: 10.1163/156853009X418091

Kopack CJ, Broder ED, Lepak JM, Fetherman ER, Angeloni LM (2015) Behavioral responses of a highly domesticated, predator naïve rainbow trout to chemical cues of predation. Fisheries Research 169:1-7. doi: 10.1016/j.fishres.2015.04.005

Lahti DC, Johnson NA, Ajie BC, Otto SP, Hendry AP, Blumstein DT, Coss RG, Donohue K, Foster SA (2009) Relaxed selection in the wild. Trends in Ecology and Evolution 24:487-496. doi: 10.1016/j.tree.2009.03.010

Landová E, Musilová V, Polák J, Sedlácková K, Frynta D (2016) Antipredatory reaction of the leopard gecko *Eublepharis macularius* to snake predators. Current Zoology 62:439-450. doi: 10.1093/cz/zow050

Lehtonen TK, McCrary JK, Meyer A (2012) Introduced predator elicits deficient brood defence behaviour in a crater lake fish. Plos One 7:e30064. doi: 10.1371/journal.pone.0030064

Lopes ARS (2016) Avaliação de técnicas de reabilitação na sobrevivência e comportamento de papagaios-verdadeiros (*Amazona aestiva*, Psittacidae) translocados. Dissertation, Universidade Federal de Ouro Preto

Martin CW (2014) Naïve prey exhibit reduced antipredator behavior and survivorship. PeerJ 2:e665. doi: 10.7717/peerj.665

Martin P, Bateson P (2007) Measuring Behaviour: an introductory guide. 2nd ed. Cambridge: Cambridge University Press, Cambridge

McGowan MM, Patel PD, Stroh JD, Blumstein DT (2014) The effect of human presence and human activity on risk assessment and flight initiation distance in skinks. Ethology 120:1-9. doi: 10.1111/eth.12281

McPhee ME (2003) Generations in captivity increases behavioral variance: considerations for captive breeding and reintroduction programs. Biological Conservation 115:71-77. doi: 10.1016/S0006-3207(03)00095-8

Mesquita FO, Young RJ (2007) The behavioural responses of Nile tilapia (*Oreochromis niloticus*) to anti-predator training. Applied Animal Behaviour Science 106:144-154. doi: 10.1016/j.applanim.2006.06.013

Messias MCTB, Sousa HC, Scalon VR, Roschel MB, Candido ES, Fujaco MA (2017) Phanerogamic flora and vegetation of Itacolomi State Park, Minas Gerais, Brazil. Biota Neotropica 17:e20160236. doi: http:// dx.doi.org/10.1590/1676-0611-BN-2016-0236

Mitchell MD, Bairos-Novak KR, Ferrari MCO (2017) Mechanisms underlying the control of responses to predator odours in aquatic prey. Journal of Experimental Biology 220:1937-1946. doi: 10.1242/jeb.135137

Moseby KE, Cameron A, Crisp HA (2012) Can predator avoidance training improve reintroduction outcomes for the greater bilby in arid Australia? Animal Behaviour 83:1011-1021. Doi: 10.1016/j.anbehav.2012.01.023

Moseby KE, Blumstein DT, Letnic M (2016) Harnessing natural selection to tackle the problem of prey naiveté. Evolutionary Applications 9:334-343. doi: 10.1111/eva.12332

Muhly TB, Semeniuk C, Massolo A, Hickman L, Musiani M (2011) Human activity helps prey win the predator-prey space race. PlosOne 6:e17050. doi: 10.1371/journal.pone.0017050

Nogueira SSC, Reis AM, Marsaro SG, Duarte JMB, Moreto V, Lima SGC, Costa TSO, Nogueira-Filho SLG (2017) The defensive behavioral patterns of captive white-lipped and collared peccary (Mammalia, Tayassuidae): an approach for conservation of the species. Acta Ethologica 20:127-136. doi: 10.1007/s10211-017-0256-5

Oosten JE, Magnhagen C, Hemelrijk CK (2010) Boldness by habituation and social interactions: a model. Behavioural Ecology and Sociobiology 64:793-802. doi: 10.1007/s00265-009-0896-1

Pedreira G, Sousa HC (2011) Comunidade arbórea de uma mancha florestal permanentemente alagada e de sua vegetação adjacente em Ouro Preto-MG, Brasil. Ciência Florestal 21:663-675. doi: 10.5902/198050984511

Preisser EL, Orrock JL (2012) The allometry of fear: interspecific relationships between body size and response to predation risk. Ecosphere 3:1-27. doi: org/10.1890/ES12-00084.1

Roberts D (2014) Rapid habituation by mosquito larvae to predator kairomones. Journal of Vector Ecology 39:355-360. doi: https://doi.org/10.1111/jvec.12111

Rodriguez-Prieto I, Martin J, Fernandez-Juricic E (2010) Habituation to low-risk predators improves body condition in lizards. Behavioural Ecology and Sociobiology 64:1937-1945. doi: 10.1007/s00265-010-1004-2

Samia DSM, Nakagawa S, Nomura F, Rangel TF, Blumstein DT (2015) Increased tolerance to humans among disturbed wildlife. Nature Communications 6:1-8. doi: 10.1038/ncomms9877

Sarrazin F, Barbaunt R (1996) Reintroduction: challenges and lessons for basic ecology. Trends in Ecology and Evolution 11:474-478.

Schmitz O (2017) Predator and prey functional traits: understanding the adaptive machinery driving predator-prey interactions. F1000Research 6:1767. Doi: 10.12688/f1000research.11813.1

Shier DM, Owings DH (2007) Effects of social learning on predator training and postrelease survival in juvenile black-tailed prairie dogs, *Cynomys ludovicianus*. Animal Behaviour 73:567-577. doi: 10.1016/j.anbehav.2006.09.009

Sih A, Bolnick DI, Luttbeg B, Orrock JL, Peacor SD, Pintor LM, Preisser E, Rehage JS, Vonesh JR (2009) Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos 119:610-621. doi: 10.1111/j.1600-0706.2009.18039.x

Sowls LK (1984) The Peccaries. Tucson: The University of Arizona Press. Texas

Sowls LK (1997) Javelinas and other peccaries: their biology, management and use. Tucson: Texas AeM University Press. Texas

St Clair JJH, García-Peña GE, Woods RW, Székely T (2010) Presence of mammalian predators decreases tolerance to human disturbance in a breeding shorebird. Behavioral Ecology 21:1285-1292. doi:10.1093/beheco/arq144

Sündermann D, Scheumann M, Zimmermann E (2008) Olfactory predator recognition in predator-naïve gray mouse lemurs (*Microcebus murinus*). Journal of Compartive Psychology 122:146-155. doi: 10.1037/0735-7036.122.2.146

Tang ZH, Huang Q, Wu H, Kuang L, Fu SJ (2017) The behavioral response of prey fish to predators: the role of predator size. PeerJ 5:e3222. doi: 10.7717/peerj.3222

Templeton CN, Greene E, Davis K (2005) Allometry of alarm calls: black-capped chickadees encode information about predator size. Science 308:1934-1937. doi: 10.1126/science.1108841

Van Heezik Y, Seddon PJ, Maloney RF (1999) Helping reintroduced houbara avoid predation: effective antipredator training and the predictive value of pre-release behaviour. Animal Conservation 2:155-163. doi: 10.1111/j.1469-1795.1999.tb00061.x

Ward AJW, Mehner T (2010) Multimodal mixed messages: the use of multiple cues allows greater accuracy in social recognition and predator detection decisions in the mosquitofish, *Gambusia holbrooki*. Behavioral Ecology 21:1315-1320. doi: 10.1093/beheco/arq152

Yorzinski JL (2010) Predator recognition in the absence of selection. In: Gursky-Doyen S, Supriatna J (eds) Indonesian Primates. Springer-Verlag, New York, pp 181-197

Zar JH. 2010. Biostatistical Analysis. 5th ed. New Jersey: Prentice Hall

Table 1: Predator model, non-predator model, human, and control objects presentation order (Latin square design) to collared peccaries (*Pecari tajacu*) during a predator discrimination experiment.

		Model		
1- Jaguar	11- Ocelot	21- Dog	31- Jaguar	41- Ocelot
2- Chicken	12- Garbage basket	22- Ball	32- Chicken	42- Garbage basket
3- Chair	13- Coati	23- Raccoon	33- Chair	43- Coati
4- Human	14- Dog	24- Jaguar	34- Human	44- Dog
5- Ocelot	15- Ball	25- Chicken	35- Ocelot	45- Ball
6- Garbage basket	16- Raccoon	26- Chair	36- Garbage basket	46- Raccoon
7- Coati	17- Jaguar	27- Human	37- Coati	47- Jaguar
8- Dog	18- Chicken	28- Ocelot	38- Dog	48- Chicken
9- Ball	19- Chair	29- Garbage basket	39- Ball	49- Chair
10- Raccoon	20- Human	30- Coati	40- Raccoon	50- Human

Table 2: Ethogram used for collared peccaries (*Pecari tajacu*) based on 30 hours of preliminary observations, and on the study of Byers & Bekoff (1981), used in the predator recognition experiments.

Behavior	Description
Locomotor activity	The collared peccary walked in the enclosure calmly, with low speed (less than 1m/s), trotted in the enclosure (intermediate speed between walking and running – between 1 and 3 m/s) or ran through the enclosure (more than 3m/s).
Foraging	The collared peccary ate food from the feeders or from the ground, rooted the ground with its nose or sniffed the ground with its nose.
Inactive	The collared peccary remained inactive in the enclosure for at least 1 minute.
Social interactions (positive or negative)	The collared peccary sniffed and rubbed its nose at other individuals' body, gave gently bites on other individuals' body, scratched on different parts of the body with its legs or pawed the ground with the front paws and/or muzzle. The collared peccary bit another individual or fought with violent bites and persecution another individual.
Alert	The collared peccary remained alert (stood, with head raised, ears upright, facing forward, watching intensively the surroundings)**.
Inspecting (flehmen)	The collared peccary lifted its nose and smelled the air**.
Escaping	The collared peccary escaped/ran from some model/object*.
Tooth chattering	The collared peccary produced loud clacking sounds made by rapid movements of the mandible*.
Not Visible	The collared peccary were out of sight, inside the concrete pipes.

*: Classical anti-predator behaviors of collared peccaries. **: Behaviors that increase in frequency with the increase of predation risk.

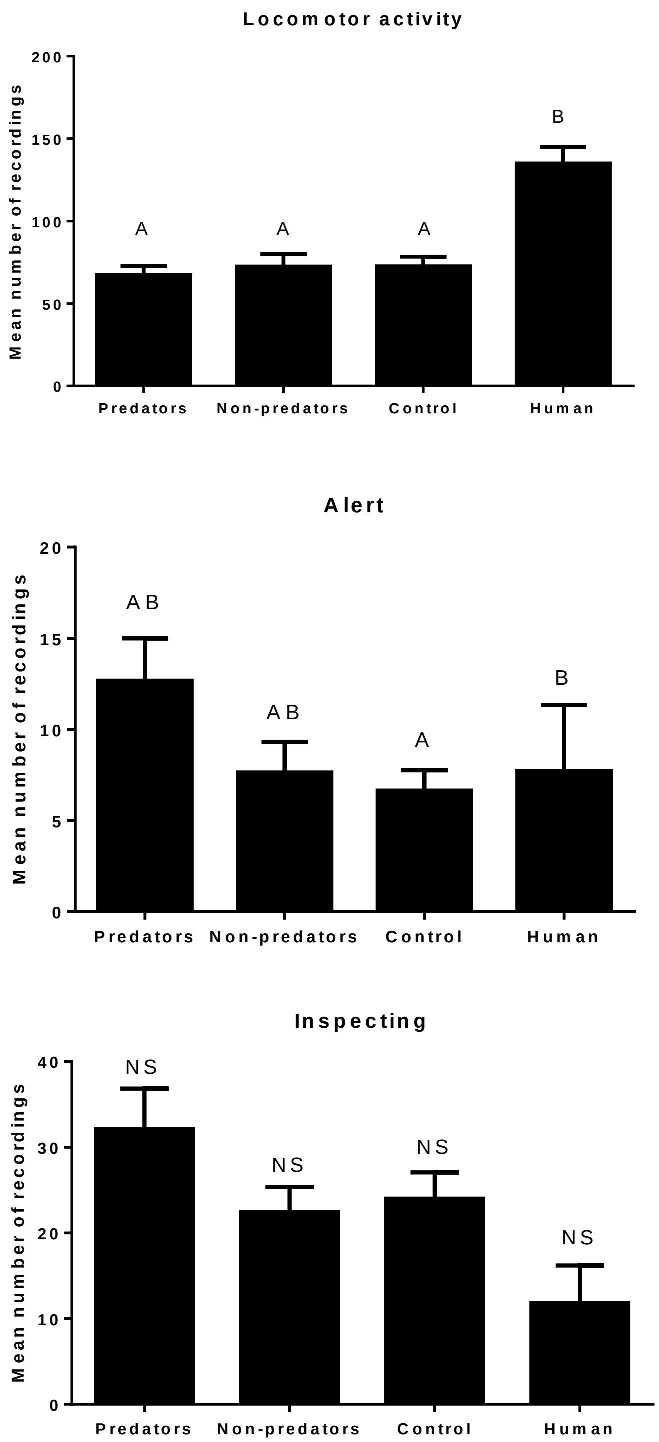

Figure 1: Means and standard deviations of the behaviors “locomotor activity”, “alert” and “inspecting” registered during the predator discrimination experiment (predator and non-predator models, a human and control objects were displayed to the collared peccaries). Different letters represent statistical significant differences.

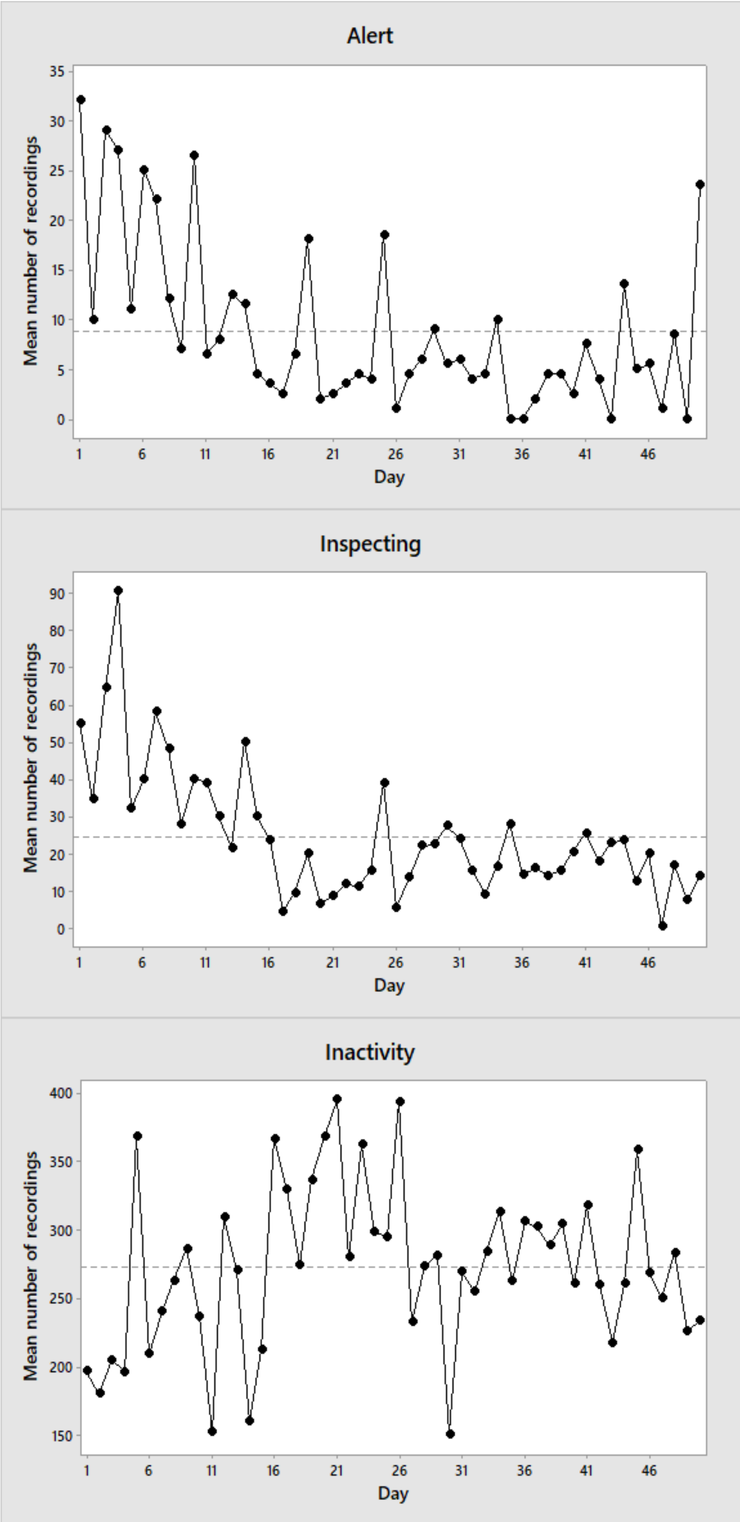

Figure 2: Means of the behaviors registered during 50 days of predator discrimination experiment undertaken by collared peccaries (*Pecari tajacu*; predator, non-predator, human and control objects were displayed to the collared peccaries.

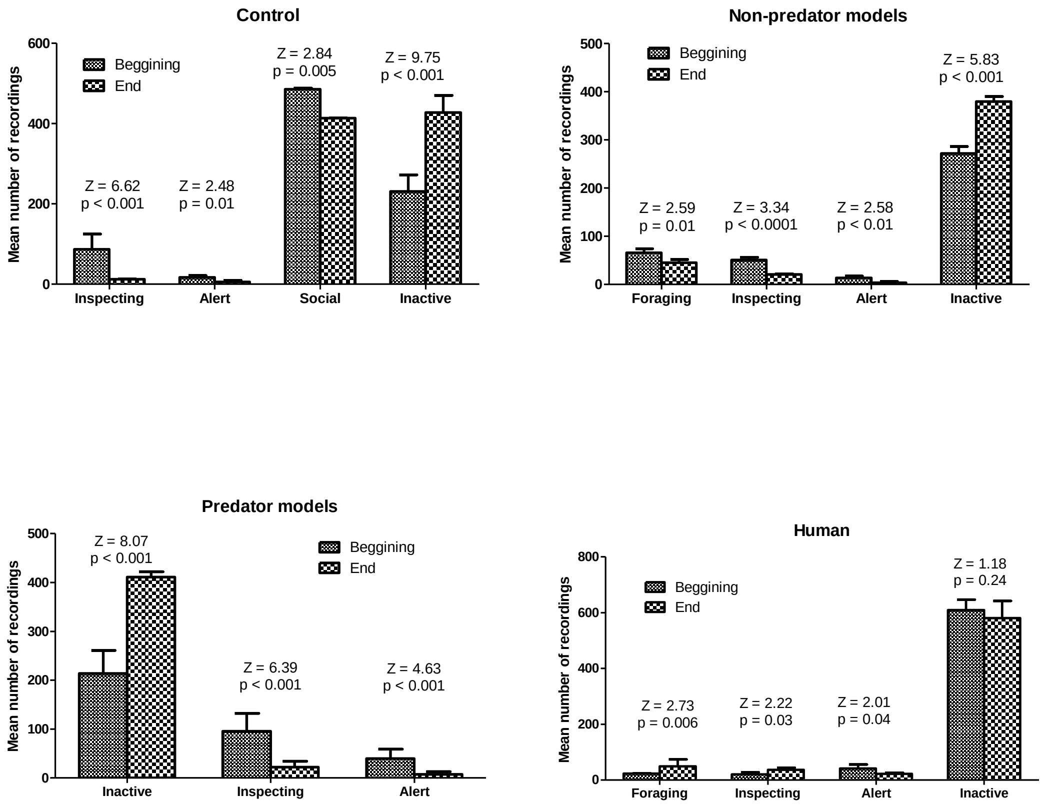

Figure 3: Means and standard deviations of the behaviors registered during the first and last five minutes (i.e. “beginning” and “end”) of the one-hour model presentation sessions, using control objects, non-predator models, predator models and humans. Z = Wilcoxon signed-rank result.