Determining the effects of neophobia and exploration on problem-solving abilities in a social ground squirrel

By

Autumn Neufeld

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Abstract

Animals adapt to overcome novel environmental challenges and can do so by using cognitive abilities to problem solve, ultimately increasing their ability to survive and thus their fitness. Neophobia and exploration are both novelty-related cognitive factors and can affect problem-solving, although there is a gap in the literature regarding granivores' problem-solving abilities. Cape ground squirrels (*Xerus inauris*) are a non-hibernating species that live in southern Africa in large family groups with no dominance hierarchy. A plexiglass puzzle box with a hinge lid was used to test their problem-solving abilities, with latency to approach, and location, used as a measure for neophobia, and trap diversity (the number of different burrow clusters visited) used as a measure of exploration (a measurement only possible for females). We found the more explorative squirrels to be less efficient at solving the puzzle box, as shown by having more failed attempts to open the puzzle box. We found no difference in the latency to approach the box and the efficiency with which an individual completed the puzzle, nor was there any significance regarding location and problem-solving efficiency. A sex difference in problem-solving abilities was expected but not found, as males disperse and encounter novel environments during their lifetime while females remain at their natal burrows. The time to approach the puzzle box did not predict puzzle completion. Neophobia did not affect problem-solving abilities, while exploration had a negative effect on problem-solving abilities in females. Exploration cannot be measured in males due to their large home range; further investigation into other cognitive factors is warranted.

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Introduction

Cognition, the process by which animals acquire, process, store, and use information from their surroundings, can vary in its degree of flexibility (Shettleworth 2010). Higher cognitive abilities can help organisms overcome challenges that are present in their environment (Reader and Laland 2002; Thornton and Samson 2012) as they allow individuals to innovate and exploit new or old resources differently (Reader 2003; Sol 2003). Innovation, the process that results in a novel learned behaviour in an individual that was not a result of social or environmental learning, can be limited by cognitive capacity (Ramsey et al. 2007; Overington et al. 2009). In addition, individual variation in innovation can cause some individuals to have higher cognitive abilities than others (Chow et al. 2016). Many different cognitive factors affect innovation, including exploration, the amount of novel space an individual covers (Overington et al. 2011), and neophobia, the fear of novelty (Barnett 1958). Evidence supporting the influence of these factors on cognitive abilities, and therefore fitness, remains inconclusive, as an individual's behaviour is also shaped by variables such as social group dynamics, age, and anthropogenic disturbances (Kummer and Goodall 1985; Thornton and Samson 2012; Benson-Amram and Holekamp 2012).

Problem-solving, the process of overcoming an obstacle to access a resource (Rowell et al. 2021), can be used to easily examine the influence of exploration and neophobia (Chow et al. 2016), and can give us insight into the most influential cognitive factors on animal innovation. While these cognitive factors have been well studied, there are inconsistencies in how previous studies were designed. For example, the relationship between neophobia and problem-solving has mixed results when tested in different

habitats and under different conditions, such as urbanized vs non-urbanized areas (Sol et al. 2002; Overington et al. 2011; Benson-Amram and Holekamp 2012; Young et al. 2019). More studies on free-ranging animals in urbanized and non-urbanized environments are needed to understand the influence of neophobia on cognitive abilities. Additionally, in most studies, exploration often has a positive relationship with problem-solving success (Overington et al. 2011; Benson-Amram and Holekamp 2012), but this factor is thought to be connected to age, with juveniles predicted to be more explorative than adults (Kummer and Goodall 1985). Exploration may be more closely tied to the amount of free time an individual has rather than their age, as the spare time hypothesis suggests that because juveniles receive care from other conspecifics, they spend less time vigilant compared to their adult conspecifics, resulting in more free time and more investment in innovation (Kummer and Goodall 1985; Thornton and Samson 2012). Thus, it is the free time an individual has that should determine exploration. We would expect to see a sex difference if, for example, one sex disperses and the dispersing sex has less free time due to more locomotion (Thornton and Samson 2012). In this case, we could expect to see more efficient problem-solving abilities in the non-dispersing sex (Thornton and Samson 2012), but if neophobia has a stronger influence than exploration, we might find the opposite. We may see a sex-based difference in problem-solving abilities regarding neophobia, as previous findings predict a change in neophobic levels once an individual reaches dispersal age, as less neophobic individuals tend to disperse rather than more neophobic conspecifics (Debeffe et al. 2014). Being bolder could lead to being a more successful problem solver, as dispersed individuals need to acquire the skills to face challenges of the novel environments they will move to during and after dispersal

(Thornton and Samson 2012). The effect of dispersal on an individual's problem-solving ability is not fully understood, as there are conflicting results across multiple studies, and more studies of individuals pre- and post-dispersal age are needed (Thornton and Samson 2012; Benson-Amram and Holekamp 2012; Garcia et al. 2022; Müller and Pillay 2023).

Problem-solving abilities can be assessed using puzzle boxes designed to be opened using a novel behaviour by an animal (Auersperg et al. 2011; Johnson-Ulrich et al. 2021). The majority of animal problem-solving research to date has focused on carnivores and primates, and few studies have focused on social granivores (Reinhardt 1994; Reader and Laland 2002; Drea and Carter 2009; Young et al. 2019; Garcia et al. 2022; Petelle et al. 2023), leaving other social systems and life histories untested. These gaps could be addressed by studying a species like the Cape ground squirrel (*Xerus inauris*), as adult males disperse and spend more time in locomotion looking for females in estrus, while female squirrels spend the majority of their time feeding within their small home range, resulting in more free time for females than males (Waterman 1995).

Cape ground squirrels (*Xerus inauris*) are a highly social species living across the arid areas of southern Africa. Females and their offspring live in family groups and exhibit cooperative behaviours, and have no dominance hierarchy (Waterman 1995). At maturity, males may delay dispersal to stay with their family group (natal males) or disperse from their family group and join other dispersed males to form an all-male group (band males) (Waterman 1995; Scantlebury et al. 2008). Cape ground squirrels are a non-hibernating species that breeds throughout the year, suggesting that seasonal differences in cognitive abilities would not be expected. However, natal and band tactics have different susceptibilities to environmental conditions, as band males spend more time

moving and less time foraging compared to natal males (Scantlebury et al. 2008; O'Brien et al. 2021). This difference in exploration tendencies could mean that a difference in problem-solving ability is also present, and so, separating this species by reproductive tactic in addition to sex (categories being band males, natal males, and females) could lead to a better understanding of the cognitive factors that drive problem-solving in these animals. Cape ground squirrels are also known to inhabit both semi-urban areas with frequent anthropogenic disturbances and rural sites (Unck et al. 2009). This difference in exposure to humans could affect neophobic levels and result in a difference in problem-solving abilities.

The goal of my study is to determine how cognitive factors such as neophobia and exploration contribute to problem-solving in Cape ground squirrels. In addition, I will examine how these cognitive factors are associated with intrinsic factors, such as sex. I hypothesized that neophobia will negatively affect problem-solving abilities, as animals that are more exposed to new objects/anthropogenic activity will be less cautious when contacting a puzzle box, have higher cognitive abilities and be more efficient problem-solvers (H1, Table 1). This hypothesis led to four predictions: 1) Squirrels living in the semi-urban area will be more efficient at solving a puzzle box as they will be less neophobic because of their exposure to human activity and objects (P1). 2) Squirrels with lower neophobia that approach and interact with the puzzle box more quickly (lower latency) will be more efficient problem-solvers (P2) (Benson-Amram and Holekamp 2012). 3) Female squirrels will be less neophobic than males, as they spend all their time in their natal habitat and are therefore more familiar with their surroundings, leading to more efficient problem-solving (P3) (Waterman 1995). 4) Males will be less neophobic

than females, as a change in neophobic levels around dispersal can benefit males encountering novel challenges in novel environments, as bolder individuals are more likely to problem-solve (P4) (Thornton and Samson 2012; Debeffe et al. 2014).

Higher exploratory behaviour may also improve an individual's problem-solving abilities (H2), as greater exploration increases exposure to novel situations where novel behaviours could be learned. I predicted that females with higher exploration tendencies will be more efficient problem-solvers compared to females with lower exploration tendencies (P1) (Kummer and Goodall 1985), as the energetic costs of gestation and lactation of females require efficient foraging skills, and therefore higher cognitive abilities to access the high-value resources (Cole et al. 2012).

Methods

Study area, trapping, and handling

My study took place on S.A. Lombard Nature Reserve (27°350S, 25°350E) in South Africa, where squirrels have been studied since 2002 (Waterman and Archibald 2019). The reserve consists of 3359 ha of Cymbopogon-Themeda grassland with small bush patches (Van Zyl 1965), with an average annual temperature of 17.6 °C. Summer temperatures reach as high as 40 °C and winter temperatures as low as -8.7 °C (Unck et al. 2009). My experiment was conducted during the austral winter of 2025, which is also the dry season (May-July).

I trapped squirrels using live traps (15 x 15 x 50 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin), baited with a mixture of peanut butter and bird seed (Waterman 1995). Traps were placed in burrow clusters (an aggregation of burrow systems, usually occupied by a single family group) (Waterman 1995). The squirrels were handled using

cone-shaped cloth handling bags, which allowed mass, reproductive condition, and sex to be determined (Koprowski 2002). The age of the squirrels was assessed by mass and reproductive condition. Squirrels less than 500 g were considered juveniles, squirrels over 500 g with no mature reproductive characteristics were considered subadults, and squirrels over 500 g with reproductive characteristics were considered adults. Adult females have elongated nipples, as nipples swell permanently after their first estrus, at around eight months, while adult males have a descended scrotum (Waterman 1995). Squirrels were permanently identified with the passive integrated transponder tags (Shenzhen XCC RFID Technology Co., Ltd., China) inserted under their skin and given unique dye marks on their back (Rodol D, Jos. H. Lowenstein & Sons, Inc., Brooklyn, New York; Melchior and Iwen 1965) so they could be identified during behavioural observations. These dye marks allowed me to identify the age and sex of the squirrels that were attempting the puzzle box.

Determining male reproductive tactic (natal vs band)

I determined the reproductive tactic of a male using three methods: 1) I used our long-term dataset to look at the age of males if they were caught over multiple years. If they were born on the site and still lived with their family, they were natal males. 2) I observed the sleeping arrangements of the males, as a natal male will sleep with his family group, and the band males will sleep with other dispersed males, or alone (Waterman 1995). I recorded the morning emergence of squirrels from their burrows from an observation tower and/or hides on top of vehicles using 10 x 50 binoculars and 15-45 x 60 spotting scopes (O'Brien et al. 2021; Warrington et al. 2022). The unique dye marks painted on the squirrels were used to distinguish among individuals (O'Brien et al. 2021). I categorized

adult males who emerged alone or with other males as band males, and adult males that consistently emerged with females as natal males. 3) Finally, I used the location of trapping to determine reproductive tactic if observations were not clear (Warrington et al. 2022). Since band males change burrows almost daily and natal males remain in the same location with their family group (Waterman 1995), the location of trapping can also be used (Warrington et al. 2022). If a male was consistently trapped at their natal burrow (site where they were born), then they were assigned a natal tactic, while males who were trapped at various burrows across the study site were assigned a band tactic (Warrington et al. 2022).

Exploration measurement (H2)

I used trap diversity to determine the exploration tendency of individuals (Santicchia et al. 2021). Trap diversity is the number of different burrow clusters where an individual was trapped, and it allowed me to examine an animal's movement patterns (Vanden Broecke et al. 2021). I could calculate the exploration tendency for females due to their smaller home ranges, while band males and natal males can have larger home ranges and cannot be guaranteed to be in the area where traps are set, and so male exploration was not calculated. I measured the total number of burrow clusters visited by females and standardized this measurement by dividing it by the total hours that traps were set near their burrow clusters and within their foraging range (Warrington et al. 2025). Distances between burrows were calculated using the distance matrix tool in QGIS (version 3.40.3). Distances were then filtered for burrows that had traps set within 125 metres, which is within the size of a female's home burrow (Lem 2020).

Puzzle box trials (H1, H2)

My experiment included both areas of high (house area) and low (floodplain) anthropogenic use. The house area is a fenced area with high human and vehicle activity, while the floodplain is away from human occupation with low human contact other than squirrel researchers (Unck et al. 2009). Squirrels in the house area are less neophobic than floodplain squirrels, as there are fewer threats from natural predators, and they are more habituated to humans due to the frequent activity of reserve personnel (Unck et al. 2009). Four puzzle boxes (15.8 x 22.9 x 8.3 cm) constructed of 0.32 cm thick clear polycarbonate material, and held together by 1.27 x 1.91 cm corner braces, machine bolts, and nuts (see Appendix; Müller and Pillay 2024) were used. Each box had two 1.91 x 7.62 cm corner brackets attached to the side, allowing them to be staked to the ground using tent pegs. These pegs ensured the boxes stayed in place for the duration of a trial. Part of the lid (10.1 cm) was attached to the main box with hinges and had a 3/8 cm lip over the end of the box, allowing the squirrels to open the boxes with their nose or paws. Red electrical tape was wrapped around the hinges to prevent the screws from being loosened by squirrels or vervet monkeys (*Chlorocebus pygerythrus*) in the area. The puzzle boxes had six holes, each three mm wide, drilled into the main part of the lid to allow the scent of bait to guide the squirrels to the lip of the lid (see Appendix). To successfully solve the puzzle, the squirrels had to open the box by lifting the lid with their paws or their nose.

The squirrels were habituated to the boxes by placing them with their lids open and baited with five grams of peanut butter two to four days before trials commenced. The box was rebaited when empty, up to four times a day. This timing allowed individuals

many opportunities to take the bait, as well as multiple days to interact with the box. Habituation ended once at least one individual had interacted with the box at least six times, and the bait had been taken at least three times, and once I observed normal foraging and play behaviours near the puzzle boxes. Habituation and trials were recorded using two different types of camcorders, Sony DCR-SR68 (Sony Electronics Inc., San Diego) and JVC Everio GZ-MG130 (JVCKenwood Corporation, Japan), mounted on tripods 45 cm off the ground that were set near the puzzle boxes during habituation (see Appendix). The box was placed one meter from the edge of a burrow cluster on ground that was not rocky, to allow tent pegs to be inserted into the ground. The boxes were oriented the same way during habituation and all trials. The camcorders were set up five meters from a puzzle box, and their zoom lenses were set at 3X on the JVC camcorders and at 15X on the Sony camcorders. At these zoom settings, the frame size of the videos was standardized for all cameras, and at these tripod heights, the dye marks and behaviours of the squirrels were clear. I tested these distances and camera settings in preliminary trials and found them to be sufficient to record detailed behavioural data. The puzzle boxes were cleaned with a mix of vinegar and water and air dried in the sun between each use to remove any scents (Waterman and Archibald 2019).

For my experiments, I baited the boxes with 5 g of peanut butter and set the box with the lid closed. I attempted to run three trials per individual, one a day for three days. By having a three-day trial period, I was able to record multiple attempts from the same individual and increase the sample size of successful puzzle completions. During preliminary trials, we observed only one squirrel from each social group eating the peanut butter during habituation, and only this same individual attempted the puzzle box. If two

squirrels solved the puzzle from one social group, the trials continued at that group until both individuals completed three trials, or until the second individual did not appear on the last three videos (I assumed they had moved to a different burrow cluster). The timeline of three trials per individual allowed me to record more successful trials, as some individuals took more than one trial to solve the puzzle.

Data I collected from the videos included the number of attempts, time to approach the puzzle box, and time spent attempting to open the box (Table 2). Attempts at the box included any movement the squirrel made to manipulate the box, like scratching or biting. Failed attempts included any attempt that was unsuccessful at opening the box. Time to complete was the time from the first attempt until the peanut butter was eaten. If a squirrel took more than one trial to solve the puzzle box, the number of attempts and their time to complete were cumulative. Before each trial, I recorded the average wind speed using a Kestrel 3000 Pocket Weather Meter (Nielsen Kellerman, Chester, PA, USA) over a 1-min period to ensure trials were not performed during high-wind periods (wind speed gusting to over 18 km per hour [kph]), which can affect squirrel behaviour (Fairbanks and Dobson 2007; Waterman and Archibald 2019).

Trials started at 0700 h before the squirrels emerged in the morning and stopped after the puzzle box had been solved or when the squirrels immerge into the burrows at 1700 h local time. The cameras recorded a maximum of 10 hours of video, including any failed trials that occurred in that time. Once the puzzle was solved, the trial was completed, and the next trial occurred at 0700 h the following morning at the same location until three trials were completed. I targeted 15 family groups, intending to have one individual from each group complete three trials. This design allowed both males and

females to complete the puzzle box, as the family groups chosen had both males and females. The order of social groups tested was randomized using a random number generator to avoid temporal autocorrelation.

Data analysis

I performed all analyses using R (version 4.5.0), and the significance of each relationship was determined using an alpha value of 0.05. I only included adult individuals in my analysis. For models 1 and 3, only individuals that successfully completed the puzzle box were included, and two outliers were removed: one female squirrel who was tested during preliminary trials in the previous year, and the one natal male who was successful.

I investigated H1 using a mixed linear regression with time to complete as my response variable. Location (veldt or house area) (H1P1), and time to approach the puzzle box on the first encounter (H1P2), and sex (H1P3, H1P4) were included as fixed effects, and burrow cluster as a random effect (Table 3). Model assumptions were checked by using a Shapiro-Wilks test to test residual normality.

I also assessed H1 by using a logistic regression, with a puzzle completion on the first encounter with the puzzle box (yes, the puzzle was completed, or no, the puzzle was not solved) as my binary response variable. Location (H1P1), time to approach (H1P2) and reproductive tactic (H1P3, H1P4) were included as fixed effects. Reproductive tactic was divided into 3 levels: females, natal males, and band males to separate males based on reproductive tactic. I included burrow cluster as a random effect to account for repeated measures.

A linear mixed model with a negative binomial distribution was used to assess H1, with the total number of attempts used on the puzzle box before completion as my

response variable. I included location (H1P1), time to approach (H1P2), and sex (H1P3, H1P4) as fixed effects. Burrow cluster was added as a random effect. Model assumptions were examined and met by looking at dispersion.

Models 4 and 5 include only female squirrels that successfully completed the puzzle box, as exploration cannot be measured on male squirrels due to home range size. H2P1 was assessed using a mixed linear regression with time to complete as the response variable and exploration score (calculated from trap diversity) as the fixed effect, with burrow cluster as a random effect. In addition, I ran another model with a Poisson distribution, with the number of attempts as the response variable and exploration score as the fixed effect. I added burrow cluster as a random effect. Model assumptions were examined and met.

Results

A total of 52 adult squirrels that could be identified attempted to solve the puzzle box. These 52 individuals were from 15 different family groups. Of these 52 individuals, 20 were from the house area, and 32 were from the floodplain area. This sample included 27 females, 8 band males, and 17 natal males.

Of the total 52 adult squirrels that attempted the box, 14 solved it at some point during their 3-trial exposure. Of these 14 adult squirrels that successfully solved the puzzle, 10 were female, 3 were band males, and 1 was a natal male (37% of females were successful, 37.5% of band males were successful, and 6% of natal males were successful). Only 7 individuals solved the puzzle during their first trial, with 4 more individuals solving the puzzle during their second trial, and 3 individuals solving the puzzle during

their third trial. Time to complete and number of attempts were cumulative across trials, and so all prior interactions contributed to the final values used in the models below.

For my first model, I removed two outliers, as one was a female squirrel who was tested during preliminary trials, and the other was the only natal male in this model. When comparing the time to complete the puzzle box of those who successfully solved the puzzle (n = 12), none of our predictors were significant. There was no difference in the time to complete the puzzle box between floodplain and house squirrels (Fig. 1, β = 216.85 ± 204.47 SE, t = 1.06, df = 6.7, p = 0.33). There was also no difference in time to complete based on a squirrel's neophobia when measured as time to approach the box (Fig. 2, β = 10.30 ± 12.91 SE, t = 0.80, df = 8.0, p = 0.45). There were no sex differences in time to complete the puzzle box (Fig. 3, β = -202.66 ± 241.94 SE, t = -0.84, df = 6.13, p = 0.44).

I conducted a power analysis using GPower software to uncover whether the lack of significance regarding the time to approach the puzzle box was due to a small sample size, which indicated that approximately 395 observations would be required to detect a small effect (f^2 = 0.02) with 80% power at α = 0.05.

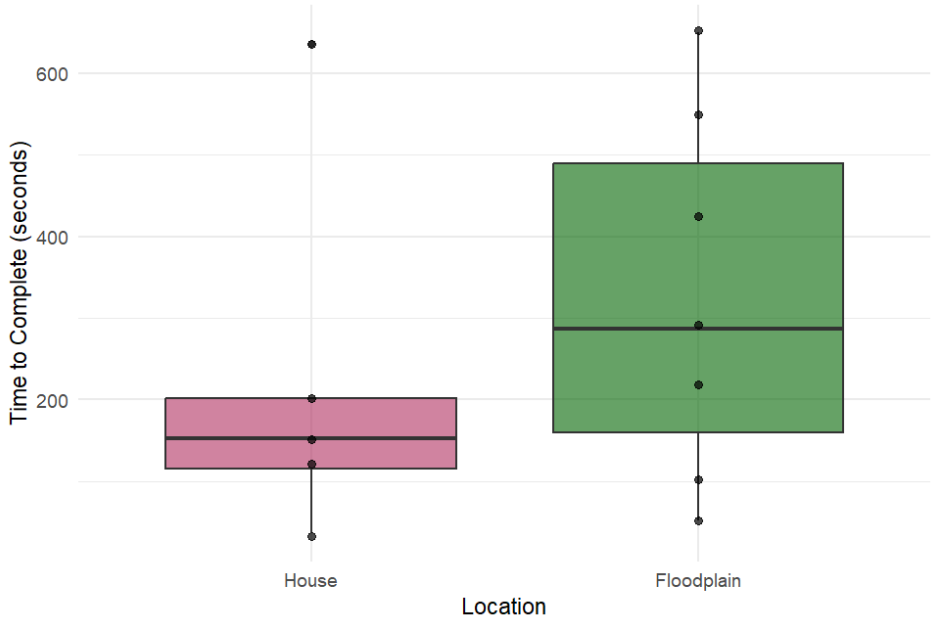


Figure 1. The effect of location (a semi-urban house area and a rural floodplain area) on the total time to complete the puzzle box (seconds) of the Cape ground squirrel (n = 12).

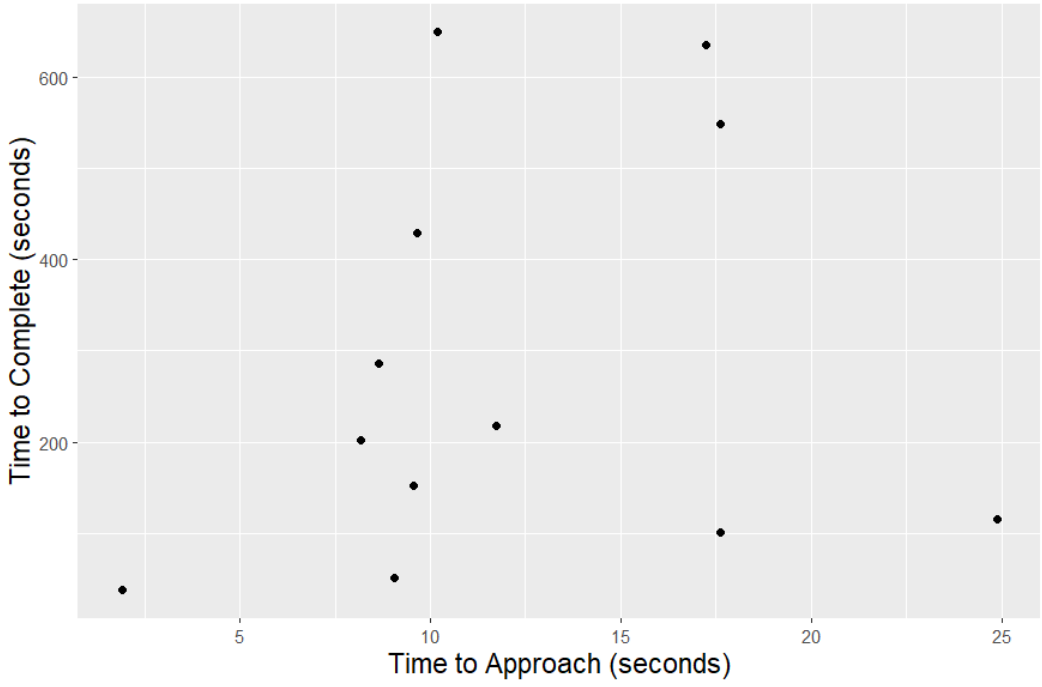


Figure 2. The relationship between time to approach the puzzle box on the first encounter during problem-solving trials and the total time to complete the puzzle box (seconds) of the Cape ground squirrel (n = 12).

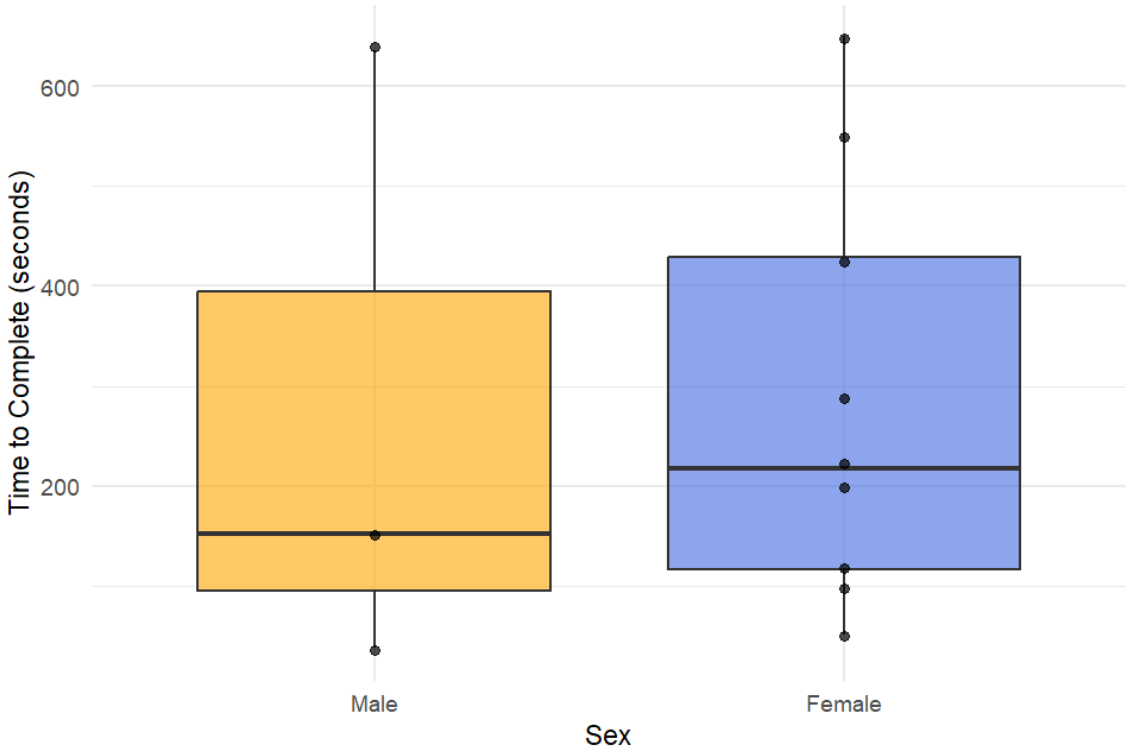


Figure 3. The relationship between sex and the total time to complete the puzzle box (seconds) of the Cape ground squirrel (n = 12).

There was no difference in success rate on first encounter with the puzzle box (n = 52) between the floodplain squirrels and the house area squirrels (Fig. 4, β = -0.52 ± 0.94 SE, z = -0.56, p = 0.58). There was also no difference in the time an individual took to approach the puzzle box and success rate during their first encounter (Fig. 5, β = 0.01 ± 0.02 SE, z = 0.41, p = 0.68). Neither reproductive tactic nor sex had a significant effect on the success rate of individuals (Fig. 6, females n = 27 vs band males n = 8: β = -0.46 ± 1.1 SE, z = -0.43, p = 0.67; natal males n = 17 vs band males n =8: β = -1.44 ± 1.5, z = -0.96, p = 0.34).

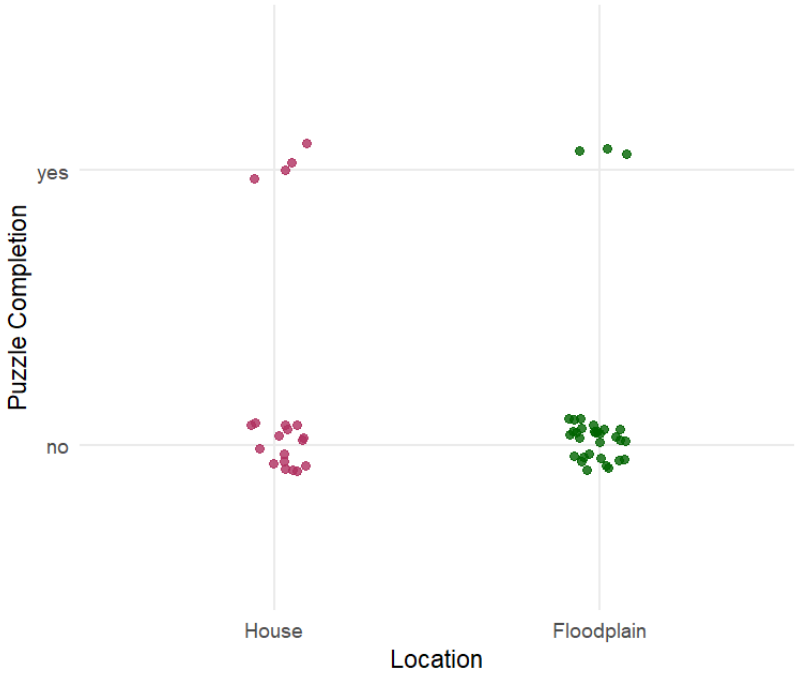


Figure 4. The effect of location (a house area and a floodplain area) on completion of the puzzle box (seconds) of the Cape ground squirrel (n = 52).

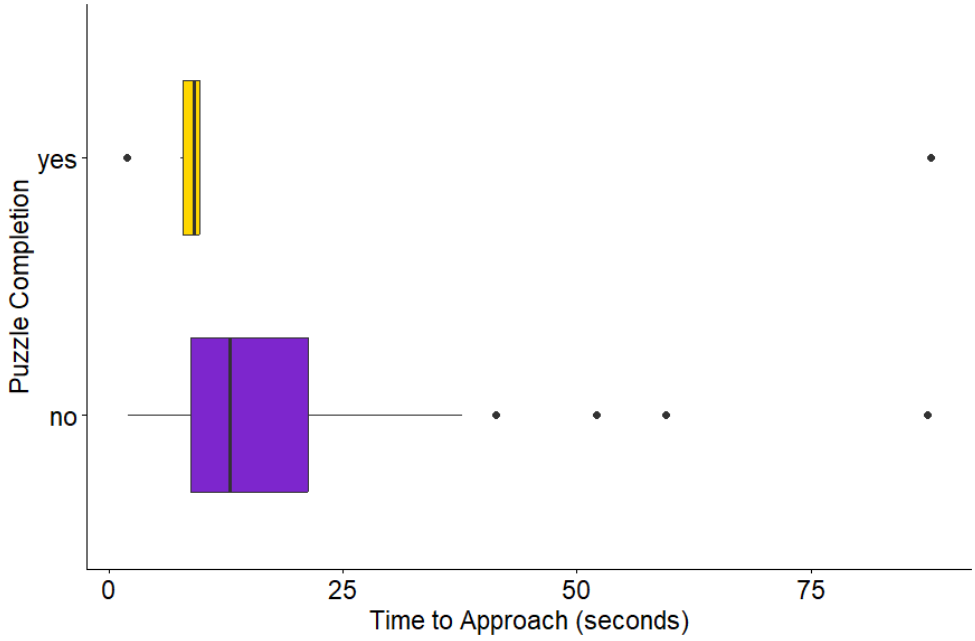


Figure 5. The relationship between time to approach the puzzle box on the first encounter during trials (seconds) and completion of the puzzle box of the Cape ground squirrel (n = 52).

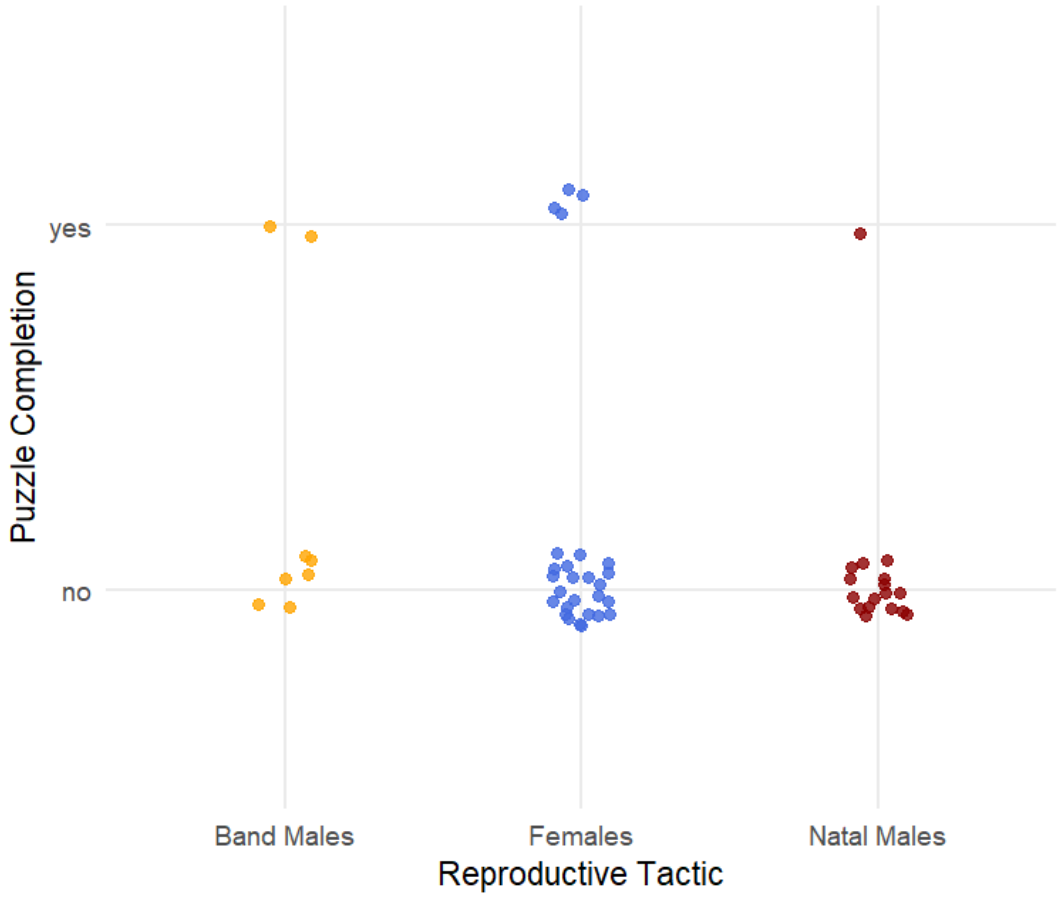


Figure 6. The effect of sex and reproductive tactic (females n = 27, band males n = 8, natal males n = 17) on completion of the puzzle box of the Cape ground squirrel.

The two outliers mentioned previously were excluded from my third model for the same reasons. The total number of attempts used on the puzzle box before completion (n = 12) did not significantly differ between the floodplain and the house area (Fig. 7, $\beta = 0.57 \pm 0.66$, $z = 0.86$, $p = 0.39$). Time to approach did not significantly affect the total number of attempts used on the puzzle box before completion (Fig. 8, $\beta = 0.01 \pm 0.05$, $z = 0.26$, $p = 0.80$). Sex did not significantly affect the total number of attempts used on the puzzle box before completion (Fig. 9, $\beta = 0.19 \pm 0.74$, $z = 0.26$, $p = 0.79$).

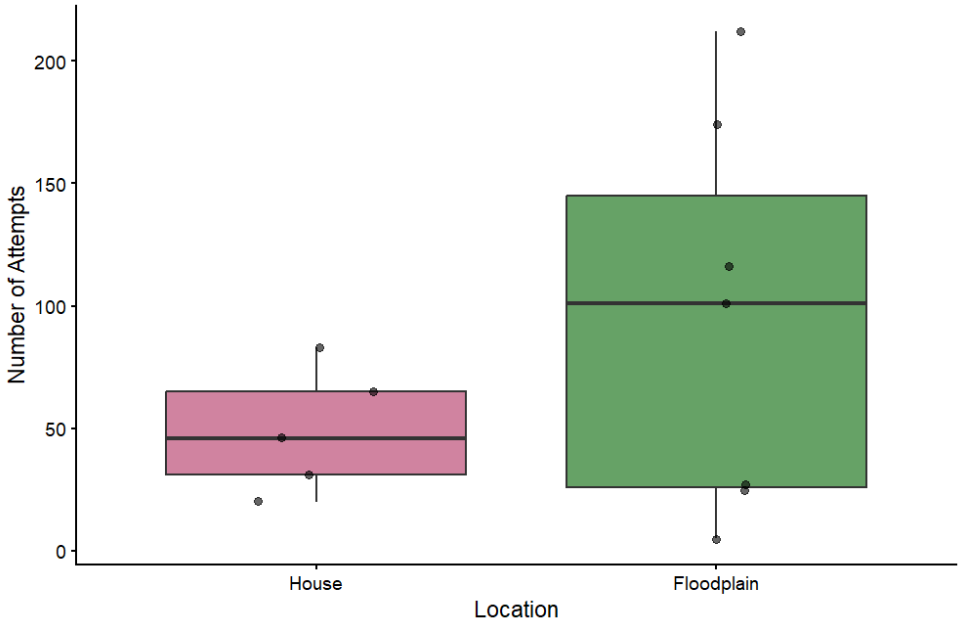


Figure 7. The effect of location (a house area and a floodplain area) on the number of attempts to complete the puzzle box of the Cape ground squirrel (n = 12).

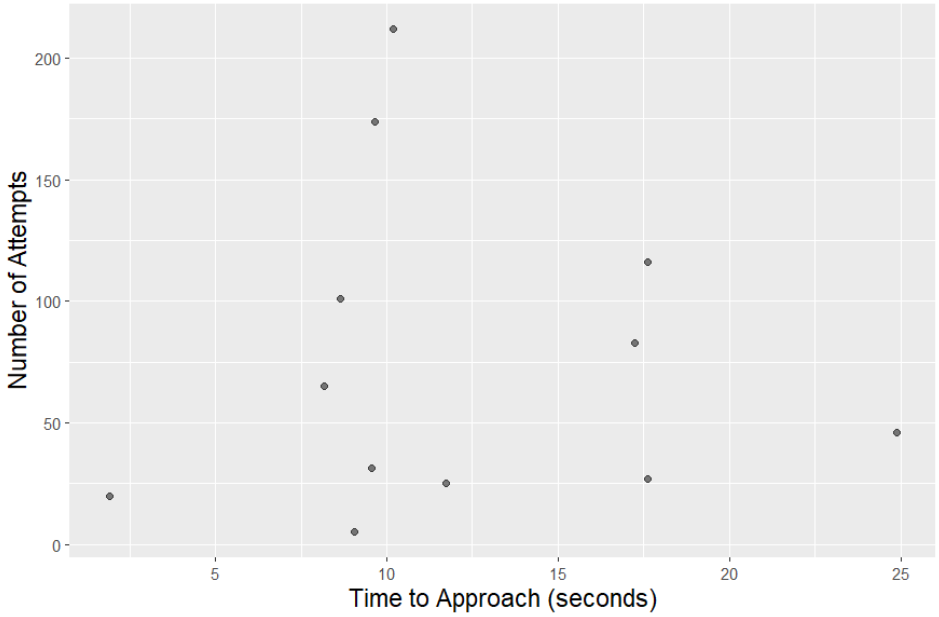


Figure 8. The relationship between time to approach the puzzle box on the first encounter during problem-solving trials and the number of attempts to solve the puzzle of the Cape ground squirrel (n = 12).

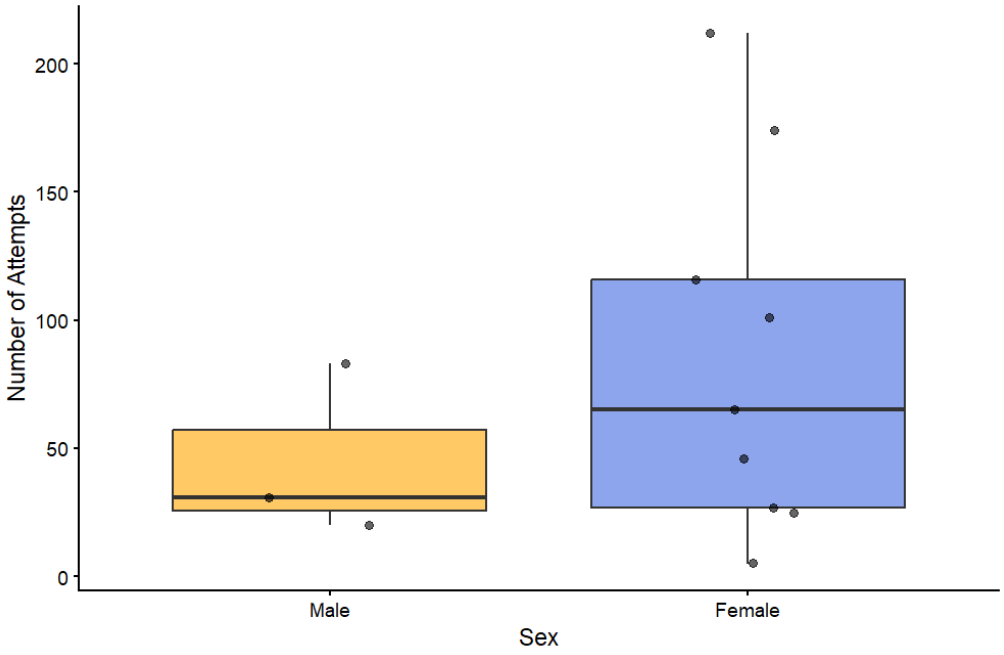


Figure 9. The relationship between sex and the number of attempts to complete the puzzle box of the Cape ground squirrel (males n = 3, females n = 9).

In addition, to see if males and females differed in neophobic levels, I ran another linear mixed-effects model with sex as a fixed effect, time to approach as the response variable, and burrow cluster as a random effect. There was no significant difference between males and females in their time to approach the puzzle box (Fig. 10, $\beta = -4.30 \pm 5.25$, $t = -0.82$, $p = 0.42$).

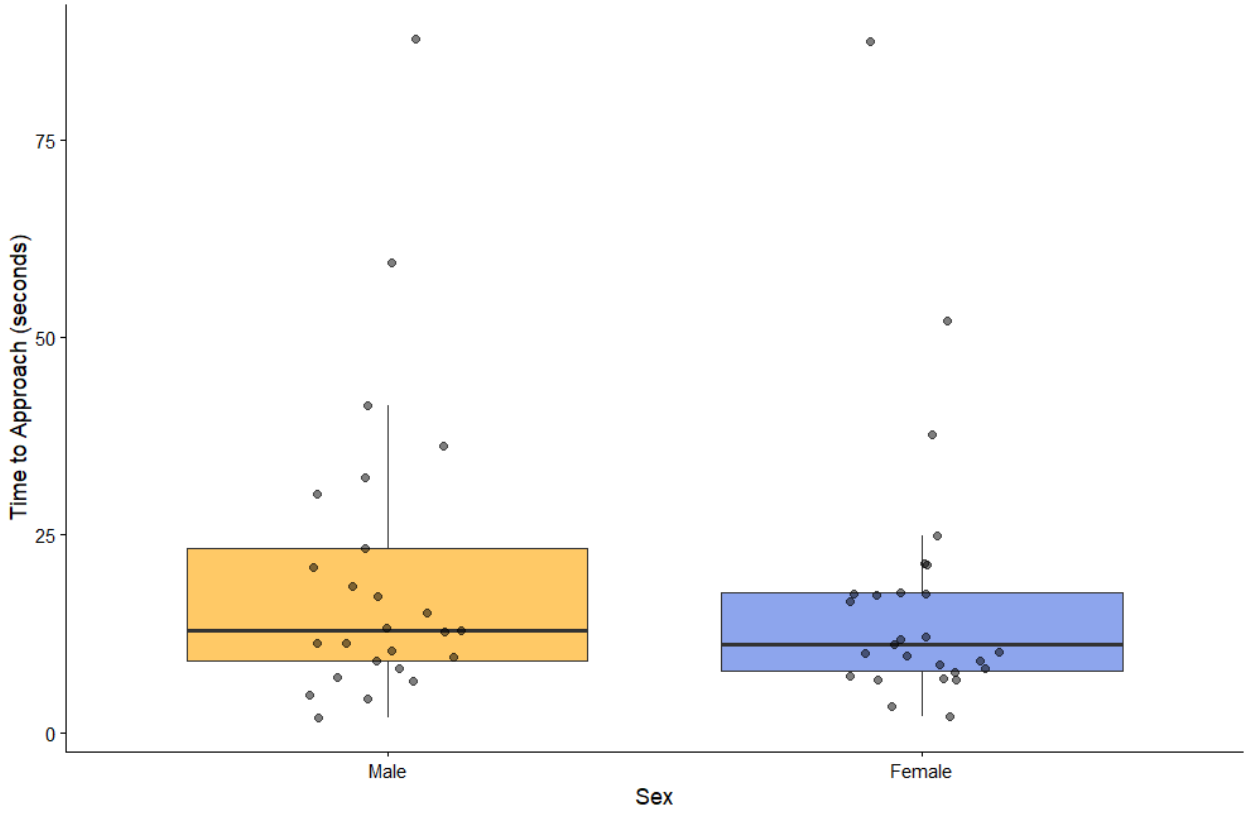


Figure 10. The relationship between sex and the time to approach the puzzle box during the first interaction of Cape ground squirrels (n = 52).

Exploration score did not significantly affect the time to complete the puzzle by female squirrels (Fig. 11, $\beta = 165.20 \pm 1381.50$, $z = 0.12$, $p = 0.91$). Exploration score did significantly affect the number of attempts made by female squirrels up until an individual's first successful completion of the puzzle box (Fig. 12, $\beta = 18.56 \pm 2.07$, $z = 8.97$, $p < 0.001$).

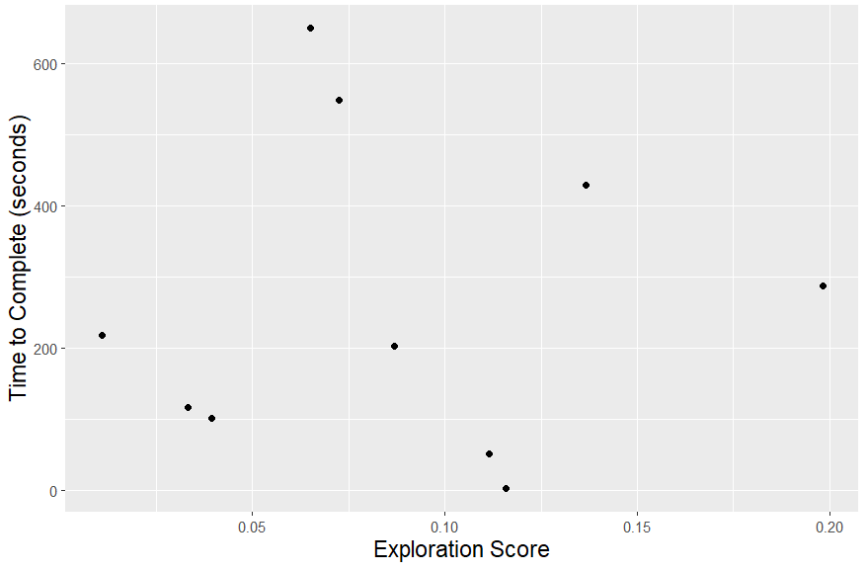


Figure 11. The relationship between exploration scores of female Cape ground squirrels and the total time to complete the puzzle box (seconds) (n = 10).

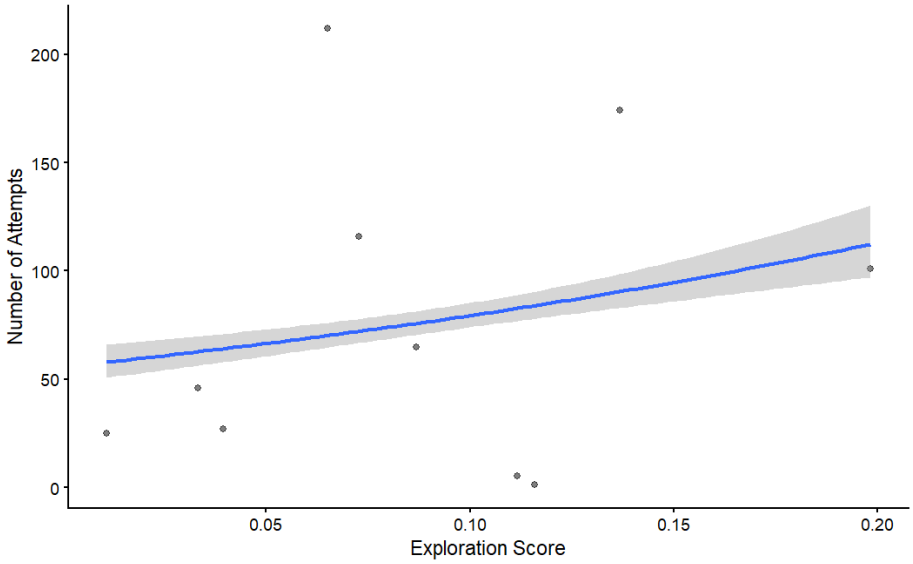


Figure 12. The relationship between exploration score and the number of attempts used to solve the puzzle box, of female (n = 10) Cape ground squirrels, with the gray shaded area 95% confidence interval.

Discussion

In this study, I examined the effects of neophobia and exploration, both novelty-related cognitive factors, on problem-solving abilities in Cape ground squirrels. Exploration significantly affects the number of attempts to complete the puzzle box but does not significantly affect the total time to complete. These results suggest that exploration inhibits problem-solving abilities. I found no relationship between neophobia and problem-solving efficiency.

Interestingly, Cape ground squirrel problem-solving was not statistically affected by neophobia in either of the measures that we tested (location and time to approach). Although there are a few conflicting results regarding neophobia and problem-solving in the literature (Bremner-Harrison et al. 2004; Debeffe et al. 2014), many studies find that neophobia negatively affects problem-solving. Neophobia inhibited spotted hyena (*Crocuta crocuta*) and raccoon (*Procyon lotor*) problem-solving (Benson-Amram and Holekamp 2012; Daniels et al. 2019). Neophobia had no statistical significance on Cape ground squirrels' puzzle abilities, and there could be several different reasons to explain this lack of a relationship. As in other studies, testing free-ranging animals with a puzzle box relies on the animal's willingness to approach a novel object and to interact with it (Petelle et al. 2023). Thus, my study may have been biased towards neophiliac individuals. Although I tried to reduce this possibility by habituating not by a set number of days but by a set number of interactions, this bias may still have influenced which individuals attempted the puzzle. It is also possible that a larger sample size was needed, as for models 1 and 3, only 12 individuals were used, and the majority were female. An extended study targeting male bands would be beneficial to understand more about male

cognition. As seen in my additional test, there was no difference between males and females and their neophobic levels, which is interesting, as the sexes in Cape ground squirrels have differing lifestyles. A future study targeting natal males and band males with a larger sample size would allow an investigation of reproductive tactic in addition to sex, and may allow for clearer results, since natal males and band males differ in home ranges, and possibly neophobia (Waterman 1995; Scantlebury et al. 2008).

In female Cape ground squirrels, higher exploration was associated with more failed attempts, indicating inhibiting problem-solving abilities with increased exploration. Exploration is most often seen as increasing problem-solving abilities across a variety of animals (Biondi et al. 2010; Benson-Amram and Holekamp 2012; Jacobson et al. 2023). This trend is possibly due to the small sample size, and conducting another study with a larger sample size could help understand this relationship. The statistical significance for only one measure of problem-solving efficiency (number of attempts) and not the other (time to complete) could indicate that other cognitive factors are influencing the problem-solving abilities of these squirrels.

Despite some squirrels successfully completing the puzzle, there were no relationships found between neophobia or sex and problem-solving abilities. While these findings confirm that individuals possess the cognitive capacity to complete the task, there is now a gap in identifying the cognitive factors that lead to interindividual variation in problem-solving. In other studies, another cognitive factor linked to problem-solving was behavioural diversity, defined as the number of different behaviours an individual employs. In spotted hyenas, exploration contributed to successful problem-solving, and a positive relationship was also found between success and behavioural diversity (Benson-

Amram and Holekamp 2012). Behavioural diversity has also been known to affect problem-solving abilities of other species, including grey squirrels (*Sciurus carolinensis*), raccoons, bat-eared foxes (*Otocyon megalotis*), and Indian mynas (*Sturnus tristis*) (Benson-Amram and Holekamp 2012; Griffin et al. 2014; Chow et al. 2016; Daniels et al. 2019; Petelle et al. 2023). Behavioural flexibility is thought to be greater in species that experience inconsistent resources, as it may allow them to be more adaptable in how much time they invest in foraging, and so looking at food availability during this study could allow a greater insight into some of the environmental influences on problem-solving (Shettleworth 2010; Davey 2018).

Many cognitive factors are also influenced by intrinsic factors, such as age. According to the spare time hypothesis, exploration is predicted to be closely connected to age (Kummer and Goodall 1985). In spotted hyenas and some primates, including several different species of callitrichid monkeys, younger individuals are more exploratory and less neophobic than adults (Kendal et al. 2005; Benson-Amram and Holekamp 2012). This pattern might have arisen because they have more free time to explore their surroundings due to the supervision and protection they receive from conspecifics (Kummer and Goodall 1985; Benson-Amram and Holekamp 2012). In Chimango Caracara *(Milvago chimango)*, juveniles were more exploratory and less neophobic as well, but they were not more successful problem-solvers (Biondi et al. 2010). Exploration was not associated with problem-solving ability in either juvenile or adult individuals in Chimango Caracara. However, neophobia was significantly associated with problem-solving in juvenile caracara, but not in adults, again supporting the spare time hypothesis (Biondi et al. 2010). While age could not be tested in my study,

because there were too few younger squirrels, I was able to compare the exploration scores of females through trap diversity. This analysis suggested that exploration plays at least some role in problem-solving abilities in Cape ground squirrels, but other cognitive factors must also have an influence. Another study using a different measurement for exploration, such as measuring the distance travelled from a female's home burrow cluster, could lead to clearer results. In addition, a larger sample size with younger squirrels, which could allow us to evaluate the influence of intrinsic factors, like age, on cognitive factors and problem-solving abilities.

Problem-solving in Asian elephants (*Elephas maximus*) was unaffected by neophobia, and there were no observed sex differences (Jacobson et al. 2023), similar to our results with Cape ground squirrels. This lack of a sex difference was not due to differences in neophobia in Cape ground squirrels, meaning if these sexes differ in problem-solving abilities, it is due to another cognitive factor that was not tested during this study. Further research on other cognitive factors could determine if differences between male and female cognitive abilities exist in this social ground squirrel.

I did observe innovative behaviour in the squirrels, as they had to employ a novel behaviour to solve the puzzle box. However, the absence of clear differences in innovation between the sexes or reproductive tactics may be due to the lack of a dominance hierarchy in this social ground squirrel. In meerkats, the inability to physically outcompete other members of a group for access to a resource leads to innovation (Thornton and Samson 2012). The lack of dominance hierarchy in Cape ground squirrels negates the need for a physically-lacking subordinate individual to outcompete dominant

individuals through cognitive abilities, which could explain our lack of differences between sexes or reproductive tactics.

Trial and error rather than innovation may also explain puzzle completion, and as a result, could obscure the relationship between different cognitive factors and puzzle box success. Individuals may solve the puzzle accidentally, simply by making more attempts or spending more time at the box (Petelle et al. 2023). To better determine which cognitive factors influence problem-solving, future studies could examine repeated successful trials. Reinforcement with food after a successful attempt should encourage the behaviour that solved the puzzle box, leading to a shorter time to complete the puzzle, and a clearer determination of innovation (Chow et al. 2016).

Future studies focused on the exact effects of neophobia and exploration on Cape ground squirrels are needed to understand problem-solving abilities and innovation. Although this study is a start to filling in the gap in the literature regarding social granivores and their cognitive abilities, specifically regarding novelty, more research is needed to determine the factors influencing the problem-solving abilities of these squirrels.

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Tables

Table 1. Hypotheses and predictions

	Hypotheses	Predictions
1	Neophobia hinders problem-solving abilities, and so those who are less neophobic are better problem-solvers	**P1:** House squirrels will have higher completion, fewer attempts on successful trials, and lower time to complete on successful trials **P2**: Individuals who have lower latency to approach the puzzle box will have higher completion, fewer attempts on successful trials, and lower time to complete on successful trials **P3**: Females who stay in their natal burrow area and are familiar with the area will be less neophobic and have higher completion, fewer attempts on successful trials, and lower time to complete on successful trials **P4**: Males, who will eventually disperse, and have lower neophobia to increase problem-solving abilities to overcome challenges in their novel environment, will have fewer attempts on successful trials, and a shorter time to complete successful trials
2	Being more explorative increases problem-solving abilities	**P1**: Females, who have more free time than band males, will have higher explorative scores, fewer attempts on successful trials, and lower time to complete on successful trials

Table 2. Data collected during puzzle box trials

Data Collected	Description	Hypotheses tested
# of attempts	Any movement to manipulate the box. This data will only be calculated on completed trials.	H1, H2
time to approach the puzzle box	Time (seconds) since the squirrel touched the box until the first attempt	H1
time to complete the puzzle box	Time (seconds) spent from the first attempt until the peanut butter is eaten. This data will only be calculated on completed trials.	H1, H2

Table 3. Models and associated predictions for examining the relationship between neophobia and exploration on problem-solving in the Cape ground squirrel *Xerus inauris*.

Model	**Hypotheses**	**Response variable**	**Fixed effects**	**Random effects**	**Reproductive tactic or Sex?**
Model 1: Mixed linear regression	H1	Time to complete (seconds)	Location (P1) Time to approach (seconds) (P2) Sex (P3, P4)	Burrow cluster	Sex
Model 2: Logistic regression	H1	Puzzle completion (yes or no)	Location (P1) Time to approach (seconds) (P2) Sex (P3, P4)	Burrow cluster	Reproductive tactic (males sorted into natal or band male)
Model 3: Mixed linear model with negative binomial distribution	H1	Number of attempts (count)	Location (P1) Time to approach (seconds) (P2) Sex (P3, P4)	Burrow cluster	Sex
Model 4: Mixed	H2	Time to complete (seconds)	Exploration score (P1)	Burrow cluster	Males excluded

linear regression					
Model 5: Mixed linear model with Poisson distribution	H2	Number of attempts (count)	Exploration score (P1)	Burrow cluster	Males excluded

Appendix

