

Curiosity might not kill the cat: Personality predictors of problem-solving success in captive carnivores

Victoria L. O'Connor¹, Jennifer M Vonk^{Corresp. 2}

¹ Psychology, Oakland University, Rochester, MI, United States

² Psychology, Oakland University, Rochester, Michigan, United States

Corresponding Author: Jennifer M Vonk
Email address: vonk@oakland.edu

Animal personalities can be determined from the consistency in their behaviors across time and situations. These behavioral traits may have been differentially selected in closely related species. Studying the structure of personality across species within an order can inform a better understanding of the selection pressures under which behavior evolves. These adaptive traits are still expected to vary within individuals and might predict general cognitive capacities that facilitate survival, such as behavioral flexibility. We derived six facets (Fearful/Aggressive, Sociable/Active, Solitary/Vigilant, Curious, Stereotypical, and Intelligent) from personality assessments based on zookeeper surveys in 52 *Felidae* individuals representing thirteen species. We analyzed whether age, sex, species, and these personality facets predicted success in a multi access puzzle box – a measure of innovation. We found that Stereotypical and Intelligent facets predicted success, with Curious and Fearful/Aggressive approaching significance. This research provides the first test of the association between personality facets and innovation in a diverse group of captive carnivores. Understanding the connection between personality traits and problem-solving success can assist in ensuring the protection of diverse species in their natural habitats and ethical treatment in captivity.

Curiosity Might Not Kill the Cat: Personality Predictors of Problem-Solving Success in Captive Carnivores

Victoria L. O'Connor^{1*}, Jennifer Vonk¹

¹ Department of Psychology, Oakland University, Rochester Hills, Michigan, USA

Corresponding Author:

Victoria L. O'Connor¹

654 Pioneer Drive, Rochester, MI, 48309, USA

Email address: voconnor@oakland.edu

Abstract

Animal personalities can be determined from the consistency in their behaviors across time and situations. These behavioral traits may have been differentially selected in closely related species. Studying the structure of personality across species within an order can inform a better understanding of the selection pressures under which behavior evolves. These adaptive traits are still expected to vary within individuals and might predict general cognitive capacities that facilitate survival, such as behavioral flexibility. We derived six facets (Fearful/Aggressive, Sociable/Active, Solitary/Vigilant, Curious, Stereotypical, and Intelligent) from personality assessments based on zookeeper surveys in 52 *Felidae* individuals representing thirteen species. We analyzed whether age, sex, species, and these personality facets predicted success in a multi access puzzle box – a measure of innovation. We found that Stereotypical and Intelligent facets predicted success, with Curious and Fearful/Aggressive approaching significance. This research provides the first test of the association between personality facets and innovation in a diverse group of captive carnivores. Understanding the connection between personality traits and problem-solving success can assist in ensuring the protection of diverse species in their natural habitats and ethical treatment in captivity.

Keywords: Felidae, individual differences, keeper assessment, innovation, behavioral flexibility

Introduction

Personality, also known as behavioral syndrome (Sih et al., 2004), or coping style (Coppens et al., 2010), is a somewhat controversial topic as applied to nonhuman animals because of its anthropomorphic nature. All three terms refer to individual differences in social decision-making, performance on cognitive and learning tasks, risk taking, subjective wellbeing, and coping strategies (Dall et al., 2004) that are consistent across time and context. Personality is the consistent expression of behavioral tendencies by an animal; it encapsulates individual differences in behavior within a species.

Personality is influenced by natural selection through genetic and/or environmental effects (Moore et al., 1998). Recent studies have found that, in more than 100 species ranging from insects to mammals, conspecifics, independent from sex or age, differ profoundly in their behavior (Carere et al., 2010). Recent studies of personality show varied effects on health and longevity, including immune function (e.g., Capitanio et al., 2008), morbidity (e.g., Natoli et al., 2005), chronic stress (e.g., Wielebnowski et al., 2002), and mortality (e.g., Weiss et al., 2013). In addition to heritability and fitness (e.g., Sinn et al., 2006), social foraging and collective behavior (e.g., Aplin et al., 2014), swarm intelligence for defense, resource exploitation and hunting (e.g., Krause et al., 2010), well-being (e.g., King & Landau, 2003; Weiss et al., 2009; Weiss et al., 2006), and predator avoidance (e.g., Handegard et al., 2012) have also been linked to these individual differences. Personality is relevant for improving zoo management (e.g., Wielebnowski, 1999), animal welfare (e.g., Wielebnowski, 1999), captive breeding (e.g., Wielebnowski, 1999), enclosure grouping (e.g., Stoinski et al., 2004), and conservation (e.g., Bremner- Harrison et al., 2004).

In captivity, individual personalities affect animals' experiences and predict their adjustment and behaviors. Animal personalities are primarily assessed in three ways: keeper

assessments, behavioral coding, and preference tests (Watters & Powell, 2012). Keeper assessments involve familiar individuals rating the predefined traits of each subject on a scale based on their human-animal relationships (HAR), knowledge of the subject accumulated across time, mutual recognition between the human and animal, and types of interactions, specifically more positive interactions than negative. Good HARs require the human and animal to have a history of positive interactions to allow successful predictions based on their experience witnessing an animal's consistent likelihood to engage in different behaviors during the length of their relationship (Estep & Hetts, 1992). Yet, these assessments are subjective. First, raters can interpret trait definitions differently. For example, raters may define "flexible" differently based on their own experiences and biases. Whereas in the survey used here it is defined as "adapts comfortably to change," change can be defined as a shift in exhibits, conspecifics, and/or zookeepers. Similarly, one keeper may define "bold" as reacting aggressively to novelty, while another may see that as acting fearfully and score the individual low on boldness. In addition, keepers may allow their own biases to color their ratings; for example, they may be more likely to rate male animals high and to rate female animals low on boldness even when the animals behave similarly. Thus, keeper assessments must be used only when multiple keepers have built a relationship with the subject and reliability can be determined.

Another potential issue with keeper assessments is that the traits animals are rated for are often derived from top-down models that may not fit the target species. Thus, it is important to first understand the traits that best describe the variability in the behavior of members of the study species (Vonk & Eaton, 2018). Of the various possible forms of keeper assessment identified by Uher (2011), we adopted a lexical top-down approach, using personality descriptors from other species to fit the current subjects. Top-down assessments begin with an existing

model of personality (usually designed for humans) and attempt to assess the extent to which a given species exhibits traits derived from that model. These assessments seek to identify facets- sets of definable traits that correlate and can be grouped together under an umbrella term. Early research involving nonhuman animals focused on the popular five-factor model (McCrae & Costa, 1987; Tupes & Christal, 1992), which includes the facets of openness, conscientiousness, neuroticism, extraversion, and agreeableness.

Factor analytic approaches have revealed that the structure of personality in nonhumans may differ from that established in humans. For example, in primates, personality is described by the combination of two or more of the following six facets: dominance, extraversion, dependability, emotional stability, agreeableness, and openness (Weiss et al., 2000). In canids, there is less agreement regarding which key traits compose the structure of canid personality. Domestic dogs exhibit a variety of traits that include extraversion, neuroticism, agreeableness, openness/conscientiousness (Gosling & John, 1999), playfulness, curiosity/ fearlessness, chase-proneness, sociability, and aggressiveness (Svartberg & Forkman, 2002).

Of particular relevance to the current study, Stanton, Sullivan, and Fazio (2015) conducted an in-depth meta-analysis on the current Felidae literature, ultimately creating a standardized Felidae ethogram. Ethograms include the documentation of species-exhibited behaviors by knowledgeable individuals (Stanton et al., 2015) and allow behavioral tracking of captive populations that can be problematic for reproduction and overall welfare (Clubb & Mason, 2003). Most personality studies on felids have derived models consisting of the following six facets: active, aggressive, curious, dominant, sociable, and timid/fearful/tense (Gartner & Weiss, 2013). For instance, in cheetahs (*Acinonyx jubatus*), Wielebnowski (1999) documented three major behavioral facets- tense-fearful, excitable-vocal, and aggressive whereas

Phillips and colleagues (2017) identified three facets- nervousness, adventurousness, and aggression using keeper observations. Thus, similar facets emerged in both samples of cheetahs from studies conducted eighteen years apart. Gartner, Powell and Weiss (2014) measured personality in five felid species. Keepers were asked to rate the cats on the same personality traits for each species; different facets emerged from a factor analysis including neuroticism, dominance, and impulsiveness in African lions, neuroticism, agreeableness/openness, and dominance/ impulsiveness in clouded leopards, neuroticism, impulsiveness/ openness, and dominance in snow leopards, dominance, impulsiveness, and neuroticism in domestic cats, and dominance, agreeableness, and self-control in Scottish wildcats (Gartner et al., 2014). This study lays the foundation for the current research; it examines variability within and between felid species. The current research drew upon several previously used keeper assessments (Carlstead et al., 1999; Gartner & Weiss, 2013; Gold & Maple, 1994; Martin-Wintle et al., 2017; Phillips & Peck, 2007; Wielebnowski, 1999; Wielebnowski et al., 2002) to incorporate the traits: active, anxious, calm, cautious, cooperative, curious, dominant, excitable, fearful, flexible, playful, smart, sociable, solitary, stereotypical, submissive, tense, vigilant, and uninterested.

Having established the personality structure of a taxa, like felids, one can then examine whether the derived traits usefully predict behaviors in various contexts. Testing contexts, as defined by Freeman, Gosling and Schapiro (1993), incorporate the subjects' responses to a novel stimulus to elicit differing reactions from the subjects to document personality differences. The initial studies of Carlstead, Mellen and Kleiman (1999) and Powell and Svoke (2008) introduced the idea that observations of subjects' interactions with novel enrichment provides insight into their personality differences. Carlstead and colleagues (1999) paired keeper assessments with a novel object test and a novel conspecific scent test. Using a 52-trait and behavior assessment that

they developed, keepers from different zoos were able to reliably differentiate black rhinoceros individuals (*Diceros bicornis*) based on sex, origin, and age and to rate them on six behaviors: olfactory behaviors, chasing/stereotypy/ mouthing, fear, friendly to keeper, dominant, and patrolling (Carlstead et al., 1999). Similarly, Powell and Svoke (2008) evaluated giant pandas' (*Ailuropoda melanoleuca*) responses to ten novel enrichment items and their 23 trait and behavior assessment using keeper responses, allowing them to create individual behavioral profiles.

Studies have demonstrated that the novel- object test can be a reliable and valid personality tool in *Felidae*. Gartner and Powell (2012) used keeper assessments and coded behaviors in response to six novel objects to identify five dimensions- active/vigilant, curious/playful, calm/self-assured, timid/anxious, and friendly to humans- differentiating snow leopards (*Panthera uncia*) based on age and sex. Similarly, Phillips et al. (2017) examined four personality states in tigers (*Panthera tigris*) including aggression, fear, vigilance, and obedience; this time, using both keeper assessments and behaviors towards olfactory and physical enrichment. Ratings from personality assessments correlate with novel object tests validating the use of personality ratings.

The current work extends the existing literature demonstrating that behaviors elicited by novel tasks are useful in validating zookeeper assessments of captive carnivore personalities. However, this work extends the current literature by assessing whether keeper assessments can predict performance on a novel problem-solving task for environmental and cognitive enrichment. Here, the multi-access puzzle box (MAB) as described in O'Connor et al. (2022) is used as a test of innovation. Various authors (Benson-Amram, et al., 2013; 2016; Daniels et al., 2019; Johnson-Ulrich et al., 2018; O'Connor et al., 2022), found that behavioral measures of

high persistence, high motor diversity/ exploration diversity, high activity/ working time, and low neophobia are associated with success on a MAB in carnivores. Personality facets similar to these behaviors are expected to predict performance in a task designed to measure behavioral flexibility. For example, traits such as ‘*Cautious*’ and ‘*Anxious*’ might relate to neophobia, whereas ‘*Playful*’ and ‘*Curious*’ might relate to exploration diversity.

Individual differences in animal personality are important for determining the best fit practices for captive husbandry (e.g., Goswami et al., 2019), well-being (e.g., Gartner, Powell & Weiss, 2016), enrichment preference (e.g., Wang et al., 2019), health and reproduction (e.g., Wielebnowski, 1999), social compatibility (e.g., Bullock, James & Williams, 2021), social group dynamic roles (e.g., Dunston et al., 2016), and environmental/ management changes (e.g., Quintavalle Pastorino et al., 2017). Additionally, activity/stress levels (e.g., Torgerson-White & Bennett, 2014) have been shown to predict behavioral responses across a variety of taxa, including carnivores. This research extracts personality facets from keeper assessments to explore whether these facets predict success on a MAB box, which measures innovation, in 52 individuals representing 13 species of felids.

Materials & Methods

Species and Rater Information. Subjects included 52 individuals, 30 males and 22 females, from 13 species (see Table 1). The age of the subjects ranged from six months to twenty-three-years-old ($M=6.68$, $SD=5.96$). Raters include thirty-seven keepers who spent on average 2.2 years with subjects ($SD= 2.19$) from five locations: the Bergen County Zoo (BCZ) in Paramus, New Jersey, the Bronx Zoo (BZ) in Bronx, New York, The Creature Conservancy (TCC) in Ann Arbor, Michigan, the Oklahoma Zoo (OKC) in Oklahoma City, Oklahoma, and the Turtle Back Zoo (TBZ) in West Orange, New Jersey.

Testing was approved by the IACUCs at Oakland University (# 19111), The City University of New York: Hunter College (#SC-Captive 4/21), and The Wildlife Conservation Society (#18:01).

Carnivore Behavior Survey and Procedure. To properly compare personality types across all felids, individual species were not assigned species-unique traits. The twenty-seven-item personality survey was developed based on previous personality surveys (Feaver et al., 1986; Gartner & Powell, 2012; Stanton et al., 2015; Wielebnowski, 1999). Each item in the survey included a specific description. For example, *Active*, was described as “moves about a lot” (see Table 2). Four traits, *Aggressive*, *Fearful*, *Friendly*, and *Uninterested*, were rated with regard to three contexts- general, with novelties or environmental changes, and with humans. All traits were rated on an eight-point Likert scale, where 0= *Doesn't apply*, 1=*Does not describe at all*, 4=*Neutral*, and 7=*Describes very well*.

Each keeper was given the questionnaire individually and instructed not to consult others, so that their responses reflected their independent ratings of the individual subjects. Keepers were asked to provide the following information about themselves: age, sex, and years of experience with big cats, the species, the individual, and their zoo. In most cases, keepers completed the questionnaires without knowledge of how individuals performed in the MAB although this was not the case for cats tested at OKC.

Problem-Solving Task and Procedure. Upon completion of the surveys by the keepers, a problem-solving task was presented to each subject. The problem-solving task, which involved retrieving a food reward from a custom multi-access puzzle box (MAB), presents a simple and effective behavioral test for exploring innovation and has been used successfully in a variety of carnivores (O'Connor et al., 2022).

All subjects were tested individually in their indoor, or outdoor, off-exhibit holding enclosures. The custom multi-access puzzle boxes were two molded Starboard boxes with stainless-steel frames measuring 0.6m x 0.6m x 0.6m and 0.38m x 0.38m x 0.38m. A food reward placed inside the box was accessible via three separate solutions: (1) Push Door Technique (see Figure 1); (2) Pull Rope Technique (see Figure 2); and (3) Pull Door Technique (see Figure 3). Each solution was presented on a different side of the box. The puzzle box was cleaned and disinfected between different species' trials and subjects could not see each other during trials.

Subjects underwent one trial per day. The trial began when the subject made physical contact with the puzzle box. Trials ended when the subject opened the puzzle box (a successful trial) or after 15 minutes elapsed without the subject opening the puzzle box (a failed trial). At the end of each trial, the subject was shifted to an adjacent enclosure according to the zoos' procedures. A subject either failed a condition, which was defined as failing to open the box in three out of five trials, or succeeded in a condition, which was defined as opening the box in three out of five trials. Subjects that succeeded moved on to the next condition. Subjects that failed did not advance to the next condition and testing was discontinued.

Condition 1 (5 trials): The reward was retrievable via any of the solutions; all three doors were unlocked at the start of the first trial. Once a subject achieved their first successful trial, the door that they opened remained unlocked and the other two doors were locked for the remainder of the first condition. Three successful trials out of a possible five advanced the subject to the next condition. Condition 2 (5 trials): The remaining two unsolved doors were unlocked at the start of the first trial. Once a subject succeeded in opening an unlocked door, that door remained unlocked and the other two doors were locked for the remainder of the second condition. Three

successful trials out of a possible five advanced the subject to the final condition. Condition 3 (5 trials): Only the remaining unsolved door was unlocked, and the subject was given five trials in which to open it three times, ending testing.

Statistical Analysis. Data were analyzed using SPSS v. 28 software for Macintosh. Results were considered significant at alpha level $p < .05$.

For individuals that had more than one keeper rating their personality, interrater reliabilities were calculated using Kendall's correlation coefficient (W), a nonparametric measure, for each individual's personality traits used in other similar studies (e.g., Lloyd et al, 2007; Gartner & Powell, 2012).

A principal components analysis (PCA) was conducted using a varimax rotation and eigenvalues > 0.8 were extracted to combine the reliable personality traits into personality facets. Some items were cross-loaded on more than a single facet. Such traits were typically assigned to the facet where they had the highest positive loading. Some exceptions were made if a factor with multiple cross-loadings was a better conceptual fit for a different factor, as discussed below. Only loadings of .30 or greater were considered. Traits with negative loadings were reverse scored and composite variables taking the average ratings for each loaded trait were created. Cronbach's α was calculated for internal consistency within each facet that contained more than one item.

In their interactions with the MAB, individual carnivores were coded on their *Success* (0= no solutions opened, 1=success on at least one condition). At least two independent observers verified the classification of trials as successful. Additional data from this task will be reported in another manuscript. With a hierarchical logistic regression, we regressed success on to sex, age, and subspecies (1= *Pantherinae*, 2= *Felinae*) in the first step of the model and the six personality

facets derived from the PCA in the second step of the model. Independent samples t-tests were conducted to determine whether the subfamilies differed on any of the six facets.

Results

Keeper Assessment Interrater Reliability. Kendall's correlation coefficients (W) tests were calculated for each subject that was rated by more than one keeper to assess inter-rater reliability ($M= 2.69$, $SD= 1.31$). Subjects' coefficients (W) ranged from 0.34 to 0.93, with p values from $<.001$ to $.42$; ratings for the majority of subjects showing high correspondence among raters.

Reduction to Six Facets. The PCA reduced twenty-six of the personality traits to seven factors with factor loadings $>.30$. Upon examination of the extracted factors, we assigned traits to factors for which they had the highest positive factor loadings, with a few exceptions. For parsimony, we included the trait cautious, which comprised its own factor, in Factor 1 (Fearful/Aggressive), on which it also loaded. We included Dominance in Factor 2 (Sociable/Active) even though it loaded more strongly with Stereotypical. Thus, although the PCA extracted seven factors, we created composite facets representing the following six conceptually coherent facets- Fearful/Aggressive, Sociable/Active, Solitary/Vigilant, Curious, Stereotypical, and Intelligent (see Table 3). The facets Fearful/Aggressive, Sociable/Active and Curious aligned well with previous research with felids (Gartner & Weiss, 2013). The facets, Stereotypical and Intelligent were created from singular traits. The Cronbach's α reliabilities for the facets with multiple items were $.90$ for Fearful/Aggressive, $.63$ for Sociable/Active, $.32$ for Solitary/Vigilant, and $.82$ for Curious.

Personality Predicts Success. Descriptive statistics and zero order correlations among the variables are shown in Table 4. Sex, age, and subspecies were entered into the first step of the logistic regression and the six personality facets were entered in the second step to predict

success. Age ($p=.63$), sex ($p=.21$) and subspecies ($p=.13$) did not significantly predict success. Stereotypical ($B=.46$, $SE=.16$, $Wald=7.89$, $p=.01$) and Intelligent ($B=.42$, $SE=.18$, $Wald=5.33$, $p=.02$) significantly predicted success ($R^2_{\text{Nagelkerke}}=.22$) Individuals that were rated as more stereotypical and individuals that were rated as more intelligent were more likely to have success on the MAB. Two facets- Fearful/ Aggressive ($B=-.42$, $SE=.24$, $Wald=3.05$, $p=.08$) and Curious ($B=.41$, $SE=.23$, $Wald=3.36$, $p=.07$) approached significance in predicting success. The facets Sociable/Active ($B=-.29$, $SE=.21$, $Wald=1.96$, $p=.16$), and Solitary/Vigilant ($B=-.15$, $SE=.16$, $Wald=.89$, $p=.35$) were not significant predictors of success ($R^2_{\text{Nagelkerke}}=.22$).

The independent samples t-tests comparing subspecies, Pantherinae and Felidae, for the six personality facets revealed no significant differences (all $ps > .16$), although Sociable/ Active ($t(138)=-.32$, $p=.07$, 95% CI [-.49, .35],) and Curious ($t(138)=-.46$, $p=.056$, 95% CI [-.42, .26]) approached significance.

Discussion

Innovation, as a component of behavioral flexibility, is critical for enabling animals to adapt to changing environments. Species and individuals differ in the extent to which they exhibit behavioral flexibility. Identifying personality traits that predict flexibility may facilitate captive husbandry strategies and especially conservation efforts. We examined whether captive carnivore personality traits predicted innovation, measured as success on a MAB. A twenty-seven-item keeper assessment survey reduced to six personality facets- Fearful/Aggressive, Sociable/Active, Solitary/Vigilant, Curious, Stereotypical, and Intelligent. Within felids, the most robust personality facets from prior research are Sociable, Dominant, and Curious (Gartner and Weiss, 2013). Our PCA analysis with a greater diversity of species identified similar facets- Sociable/Active, Fearful/Aggressive, and Curious. However, it is important to note that our PCA analysis extracted seven facets with several items cross-loading on more than one facet, so the

results regarding a model of feline personality should be taken with caution. Some facets had lower than adequate reliability so, as with any ratings, it is important to consider how biases and inconsistent interpretations may have impacted the trait ratings.

There were some other surprising findings from the PCA. For example, scores for the item, curious were not inversely related to scores on the uninterested items, and dominant was not inversely related to submissive. These surprising findings suggest that keepers may not have defined the terms as expected when completing their ratings. Dominance is a term that has negative connotations for many animal caretakers and trainers (Bradshaw et al., 2009), which could bias the way keepers rate subjects on these traits. Some keepers may confuse fear-based aggression with dominance, for example. This suggests the need to further refine our questionnaires to accurately capture personalities of the family Felidae. Nonetheless, it is reassuring that the facets emerging from our analyses are reasonably consistent with results from previous studies of felids (Gartner & Weiss, 2013).

Despite some concerns, some of our facets were rated with high reliability across keepers and predicted performance in the MAB, which measured innovation. Specifically, Stereotypical, and Intelligent predicted success on the multi-access puzzle box, with the effects of Curious and Fearful/Aggressive approaching significance. More curious and less fearful animals should be more likely to attempt solutions to novel problems, so these results were expected. The sample size may have reduced our ability to observe significant results. It is also important to note that some keepers at a single test site (OKC) may have completed the questionnaires rating intelligence with knowledge of how the subjects performed in the tests. Future studies should have all raters complete their ratings before any of the tests are conducted. This was not always

possible here based on the complications of arranging testing at multiple locations during a global pandemic.

Previous studies have identified personality traits and facets in felids, some in conjunction with a novel object test (Carlstead et al., 1999; Gartner & Powell, 2012; Powell & Svoke, 2008; Razal et al., 2016). This is the first study to report an association of personality traits with success on a test of innovation. Diverse behaviors have been associated with problem-solving success in carnivores (Benson-Amram et al., 2013; Benson-Amram et al., 2016; Daniels et al., 2019; Johnson-Ulrich et al., 2018; O'Connor et al., 2022). Based on these findings, we expected Stereotypical to be negatively related with success; however, here, Stereotypical positively related to success. We defined Stereotypical as “fixed and oversimplified in behavior.” Historically, stereotypes have been used as indicators of poor welfare in captivity, greatly exemplified by captive carnivore pacing. More recent research suggests that stereotypes are unreliable indicators of welfare (Mason & Latham, 2004); they may be copied from a conspecific, just an individual’s unique behavior, or have been established early in that animal’s history and persist regardless of changing environments. However, knowledge of what this term implies may have led to inaccurate reporting of stereotypes by keepers.

There are several insignificant results to note. Our research does not corroborate previous findings that age (e.g., Benson-Amram & Holekamp, 2012) or sex (e.g., Amici et al., 2019) predicted problem-solving. It is important to note that our measure of success was only a very cursory measure of performance in this task. The MAB allows for examination of multiple measures of cognition (e.g., trials to success, number of successful trials, number of solutions learned, latency to learn new solution) and behavior (e.g., number of behaviors performed, perseveration), but we examined only the simplest outcome here as a pilot test of how well

personality could predict problem-solving success, which might be associated with adaptability and flexibility to change in novel environments. Thus, we would encourage future researchers to examine how individual differences predict variable success in tasks that might assess traits relevant for species' survival in the wild or ability to adapt in captivity.

Conclusions

Across the thirteen Felidae species we assessed, a coherent personality structure was extracted involving six facets- Fearful/Aggressive, Sociable/Active, Solitary/Vigilant, Curious, Stereotypical, and Intelligent. These facets are echoed in the Felidae literature as reviewed by Gartner and Weiss (2013). For the first time, these traits predicted problem-solving success on a test of innovation. Four facets- Stereotypical, Intelligent, Curious, and Fearful/Aggressive significantly or almost significantly predicted success in this task. This work should be considered preliminary, but we hope the promising results encourage future studies with larger sample sizes and further refinement of the personality measure. Felid personality research, in combination with cognitive testing, has practical applications for both captive welfare and wildlife conservation success.

Acknowledgements

The authors wish to thank all who provided assessments and/or puzzle box testing assistance for this research: L. Barrett, P. Thomas, R. Snyder, T. Scarberry, R. Aversa, T. Teegan, T. Sinclair, E. White, R. Meo-Henry, L. Harney, B. Albert, N. Turner, C. Hood, S. Jamalapuram, A. Birk, P. Billette, K. Ellis, K. Wilson, S. Fantuzzi, A. Blanco, J. Kleoudis, V. Hussey, J. Neiss, B. O'Meara, E. Mowatt, C. Walsh, T. Gunther, S. Nelson, C. Norton, S. Spillman, R. Orens, T.L. Rossit, J. Jeffords, A. Cook, Kelly, M. Townten, R. Miyajima, L. Hayes, K. Templeton, K. Flatley, N. Borrego and R. Sides.

References

- Amici, F., Widdig, A., Lehmann, J., & Majolo, B. (2019). A meta-analysis of interindividual differences in innovation. *Animal Behaviour*, 155, 257-268.
- Aplin, L. M., Farine, D. R., Mann, R. P., & Sheldon, B. C. (2014). Individual-level personality influences social foraging and collective behavior in wild birds. *Proceedings of The Royal Society*, 281(1789).
- Benson-Amram, S., Dantzer, B., Stricker, G., Swanson, E. M., & Holekamp, K. E. (2016). Brain size predicts problem-solving ability in mammalian carnivores. *Proceedings of the National Academy of Science, USA*, 113(9), 2532-2537.
- Benson-Amram, S., Weldele, M. L., & Holekamp, K. E. (2013). A comparison of innovative problem-solving abilities between wild and captive spotted hyaenas, *Crocuta crocuta*. *Animal Behaviour*, 85(2), 349-356.
- Borrego, N. & Gaines, M. (2016). Social carnivores outperform social carnivores on an innovative problem. *Animal Behaviour* 1(14), 21-26.
- Bradshaw, J. W., Blackwell, E. J., & Casey, R. A. (2009). Dominance in domestic dogs—useful construct or bad habit?. *Journal of Veterinary Behavior*, 4(3), 135-144.
- Bremner-Harrison, S., Prodhhl, P. A., & Elwood, R. W. (2004). Behavioral trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). *Animal Conservation*, 7(3), 313-320.
- Bullock, N., James, C., & Williams, E. (2021). Using keeper questionnaires to capture zoo-housed tiger (*Panthera tigris*) personality: considerations for animal management. *Journal of Zoological and Botanical Gardens*, 2(4), 650-663.
- Capitanio, J. P., Abel, K., Mendoza, S. P., Blozis, S. A., McChesney, M. B., Cole, S. W., & Mason, W. A. (2008). Personality and serotonin transporter genotype interact with social context to affect immunity and viral set-point in simian immunodeficiency virus disease. *Brain, Behavior, and Immunity*, 22(5), 676-689.
- Carere C., Caramaschi, D., & Fawcett, T. (2010). Covariation between personalities and individual differences in coping with stress: converging evidence and hypotheses. *Current Zoology*, 56(6), 728-740.
- Carlstead, K., Mellen, J., & Kleiman, D. G. (1999). Black rhinoceros (*Diceros bicornis*) in US zoos: I. Individual behavior profiles and their relationship to breeding success. *Zoo Biology*, 18(1), 17-34.
- Clubb, R., & Mason, G. (2003). Captivity effects on wide-ranging carnivores. *Nature*, 425(6957), 473-474.
- Coppens, C. M. de Boer, S. F., & Koolhaas, J. M. (2010). Coping styles and behavioral flexibility: towards underlying mechanisms. *Proceedings of The Royal Society*, 385(1560).
- Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioral ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, 7(8), 734-739.
- Daniels, S. E., Fanelli, R. E., Gilbert, A., & Benson-Amram, S. (2019). Behavioral flexibility of a generalist carnivore. *Animal Cognition* 22(3), 387-396.
- Dunston, E. J., Abell, J., Doyle, R. E., Evershed, M., & Freire, R. (2016). Exploring African lion (*Panthera leo*) behavioural phenotypes: individual differences and correlations between sociality, boldness and behaviour. *Journal of Ethology*, 34(3), 277-290.

- Estep, D. Q. (1992). Interactions, relationships and bonds: The conceptual basis for scientist-animal relation. *The Inevitable Bond: Examining Scientist-Animal Interactions*, 6-26.
- Feaver, J., Mendl, M., & Bateson, P. (1986). A method for rating the individual distinctiveness of domestic cats. *Animal Behaviour*, 34(4), 1016-1025.
- Freeman, H., Gosling, S. D., & Schapiro, S. J. (2011). Comparison of methods for assessing personality in nonhuman primates. In A. Weiss, J.E. King, & L. Murray (Eds.), *Personality and Temperament in Nonhuman Primates* (pp. 17-40). Springer, New York, NY.
- Gartner, M. C., & Powell, D. (2012). Personality assessment in snow leopards (*Uncia uncia*). *Zoo Biology*, 31(2), 151-165.
- Gartner, M. C., Powell, D. M., & Weiss, A. (2014). Personality structure in the domestic cat (*Felis silvestris catus*), Scottish wildcat (*Felis silvestris grampia*), clouded leopard (*Neofelis nebulosa*), snow leopard (*Panthera uncia*), and African lion (*Panthera leo*): a comparative study. *Journal of Comparative Psychology*, 128(4), 414.
- Gartner, M. C., Powell, D. M., & Weiss, A. (2016). Comparison of subjective well-being and personality assessments in the clouded leopard (*Neofelis nebulosa*), snow leopard (*Panthera uncia*), and African lion (*Panthera leo*). *Journal of Applied Animal Welfare Science*, 19(3), 294-302.
- Gartner, M. C., & Weiss, A. (2013). Scottish wildcat (*Felis silvestris grampia*) personality and subjective well-being: Implications for captive management. *Applied Animal Behaviour Science*, 147(3-4), 261-267.
- Gold, K. C., & Maple, T. L. (1994). Personality assessment in the gorilla and its utility as a management tool. *Zoo Biology*, 13(5), 509-522.
- Gosling, S. D., & John, O. P. (1999). Personality dimensions in nonhuman animals: A cross-species review. *Current Directions in Psychological Science*, 8(3), 69-75.
- Goswami, S., Tyagi, P. C., Malik, P. K., Pandit, S. J., Kadivar, R. F., Fitzpatrick, M., & Mondol, S. (2020). Effects of personality and rearing-history on the welfare of captive Asiatic lions (*Panthera leo persica*). *PeerJ*, 8, e8425.
- Handegard, N. O., Boswell, K. M., Ioannou, C. C., Leblanc, S. P., Tjostheim, G. B., & Couzin, I. D. (2012). The dynamics of coordinated group hunting and collective information transfer among schooling prey. *Current Biology*, 22(13), 1213-1217.
- Johnson-Ulrich, L., Johnson-Ulrich, Z. & Holekamp, K. (2018). Proactive behavior, but not inhibitory control, predicts repeated innovation by Spotted hyenas tested with a multi-access box. *Animal Cognition*, 21(3), 379-392.
- King, J. E., & Landau, V. I. (2003). Can chimpanzee (*Pan troglodytes*) happiness be estimated by human raters? *Journal of Research in Personality*, 37(1), 1-15.
- Krause, J., Ruxton, G. D., & Krause, S. (2010). Swarm intelligence in animals and humans. *Trends in Ecology and Evolution*, 25(1), 28-34.
- Lloyd, A. S., Martin, J. E., Bornett-Gauci, H. L. I., & Wilkinson, R. G. (2007). Evaluation of a novel method of horse personality assessment: Rater-agreement and links to behaviour. *Applied Animal Behaviour Science*, 105(1-3), 205-222.
- Martin-Wintle, M. S., Shepherdson, D., Zhang, G., Huang, Y., Luo, B., & Swaisgood, R. R. (2017). Do opposites attract? Effects of personality matching in breeding pairs of captive giant pandas on reproductive success. *Biological Conservation*, 207, 27-37.
- McCrae, R. R., & Costa, P. T. (1987). Validation of the five-factor model of personality across instruments and observers. *Journal of Personality and Social Psychology*, 52(1), 81.

- Moore, A. J., Brodie III, E. D., & Wolf, J. B. (1997). Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. *Evolution*, 51(5), 1352-1362.
- Natoli, E., Say, L., Cafazzo, S., Bonanni, R., Schmid, M., & Pontier, D. (2005). Bold attitude makes male urban feral domestic cats more vulnerable to Feline Immunodeficiency Virus. *Neuroscience & Biobehavioral Reviews*, 29(1), 151-157.
- O'Connor, V.L., Thomas, P., Chodorow, M., & Borrego, N. (2022). Exploring innovative problem-solving in African lions (*Panthera leo*) and snow leopards (*Panthera uncia*). *Behavioural Processes* [in press].
- Phillips, C., & Peck, D. (2007). The effects of personality of keepers and tigers (*Panthera tigris tigris*) on their behaviour in an interactive zoo exhibit. *Applied Animal Behaviour Science*, 106(4), 244-258.
- Phillips, C. J., Tribe, A., Lisle, A., Galloway, T. K., & Hansen, K. (2017). Keepers' rating of emotions in captive big cats, and their use in determining responses to different types of enrichment. *Journal of Veterinary Behavior*, 20, 22-30.
- Powell, D. M., & Svoke, J. T. (2008). Novel environmental enrichment may provide a tool for rapid assessment of animal personality: A case study with giant pandas (*Ailuropoda melanoleuca*). *Journal of Applied Animal Welfare Science*, 11(4), 301-318.
- Quintavalle Pastorino, G., Viau, A., Curone, G., Pearce-Kelly, P., Faustini, M., Vigo, D., ... & Preziosi, R. (2017). Role of personality in behavioral responses to new environments in captive Asiatic lions (*Panthera leo persica*). *Veterinary Medicine International*, 2017.
- Razal, C. B., Pisacane, C. B., & Miller, L. J. (2016). Multifaceted approach to personality assessment in cheetahs (*Acinonyx jubatus*). *Animal Behavior and Cognition*, 3(1), 22-31.
- Sih, S., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: An integrative overview. *The Quarterly Review of Biology*, 79(3), 241-277.
- Sinn, D. L., Apiolaza, L. A., & Moltschaniwskyj, N. A. (2006). Heritability and fitness-related consequences of squid personality traits. *Journal of Evolutionary Biology*, 19(5), 1437-1447.
- Stanton, L. A., Sullivan, M. S., & Fazio, J. M. (2015). A standardized ethogram for the *felidae*: A tool for behavioral researchers. *Applied Animal Behaviour Science*, 173, 3-16.
- Stoinski, T. S., Lukas, K. E., Kuhar, C. W., & Maple, T. L. (2004). Factors influencing the formation and maintenance of all-male gorilla groups in captivity. *Zoo Biology*, 23(3), 189-203.
- Svartberg, K., & Forkman, B. (2002). Personality traits in the domestic dog (*Canis familiaris*). *Applied Animal Behaviour Science*, 79(2), 133-155.
- Torgerson-White, L. L., & Bennett, C. (2014). Rating methodology, personality axes, and behavioral plasticity: A case study in African lions. *Animal Behavior and Cognition*, 1(3), 23-248.
- Tupes, E. C., & Christal, R. E. (1992). Recurrent personality factors based on trait ratings. *Journal of Personality*, 60(2), 225-251.
- Uher, J. (2011). Personality in nonhuman primates: What can we learn from human personality psychology?. In A. Weiss, J.E.King, & L. Murray (Eds.), *Personality and temperament in nonhuman primates* (pp. 41-76). Springer, New York, NY.
- Vonk, J., & Eaton, T. (2018). Personality in nonhuman animals: Comparative perspectives and applications. In V. Zeigler-Hill & T. Shackelford (Eds.). *The Sage Handbook of Personality and Individual Differences*, [pp. 23-51]. Sage Publishers.

- Wang, Q., Liu, D., Holyoak, M., Jia, T., Yang, S., Liu, X., ... & Jiang, G. (2019). Innate preference for native prey and personality implications in captive Amur tigers. *Applied Animal Behaviour Science*, 210, 95-102.
- Watters, J. V., & Powell, D. M. (2012). Measuring animal personality for use in population management in zoos: suggested methods and rationale. *Zoo Biology*, 31(1), 1-12.
- Weiss, A., Gartner, M. C., Gold, K. C., & Stoinski, T. S. (2013). Extraversion predicts longer survival in gorillas: an 18-year longitudinal study. *Proceedings of the Royal Society of London B: Biological Sciences*, 280(1752), 20122231.
- Weiss, A., King, J. E., & Figueredo, A. J. (2000). The heritability of personality factors in chimpanzees (*Pan troglodytes*). *Behavior Genetics*, 30(3), 213-221.
- Weiss, A., King, J.E., & Perkins, L. (2006). Personality and subjective well-being in orangutans (*Pongo pygmaeus* and *Pongo abelii*). *Journal of Personality and Social Psychology*, 90(3), 501-511.
- Weiss, A., Inoue-Murayama, M., Hong, K., Inoue, E., Udono, T., Ochiai, T., Matsuzama, T. Hirata, S., & King, J. E. (2009). Assessing chimpanzee personality and subjective well-being in Japan. *American Journal of Primatology*, 71(4), 283-292.
- Wielebnowski, N. C. (1999). Behavioral differences as predictors of breeding status in captive cheetahs. *Zoo Biology*, 18(4), 335-349.
- Wielebnowski, N. C., Fletchall, N., Carlstead, K., Busso, J. M., & Brown, J. L. (2002). Noninvasive assessment of adrenal activity associated with husbandry and behavioral factors in the North American clouded leopard population. *Zoo Biology*, 21(1), 77-9.

Table 1(on next page)

Descriptive information for all subjects

Table 1:
Descriptive information for all subjects.

Name	Species	Sex	Age (yrs)	Rearing	Zoo
Amara	African lion (<i>Panthera leo</i>)	F	5	Captive	TBZ
Bahati	African lion (<i>Panthera leo</i>)	M	5	Captive	BZ
Demarcus	African lion (<i>Panthera leo</i>)	M	4	Captive	TBZ
Huey	African lion (<i>Panthera leo</i>)	M	10	Captive	OKC
Ime	African lion (<i>Panthera leo</i>)	M	5	Captive	BZ
Sukari	African lion (<i>Panthera leo</i>)	F	15	Captive	TBZ
Thulani	African lion (<i>Panthera leo</i>)	M	5	Captive	BZ
Annika	Amur leopard (<i>Panthera pardus orientalis</i>)	F	5	Captive	TBZ
Nadya	Amur leopard (<i>Panthera pardus orientalis</i>)	F	½	Captive	TBZ
Valeri	Amur leopard (<i>Panthera pardus orientalis</i>)	M	7	Captive	TBZ
Astrid	Bobcat (<i>Lynx rufus</i>)	F	23	Captive	TBZ
Dodger	Bobcat (<i>Lynx rufus</i>)	M	2	Wild	OKC
ZZ	Caracal (<i>Caracal caracal</i>)	F	18	Captive	OKC
Alvin	Cheetah (<i>Acinonyx jubatus</i>)	M	1	Captive	TBZ
Nandi	Cheetah (<i>Acinonyx jubatus</i>)	F	1	Captive	TBZ
Simon	Cheetah (<i>Acinonyx jubatus</i>)	M	1	Captive	TBZ
Theodore	Cheetah (<i>Acinonyx jubatus</i>)	M	1	Captive	TBZ
JD	Clouded leopard (<i>Neofelis nebulosa</i>)	M	3	Captive	OKC
Jye	Clouded leopard (<i>Neofelis nebulosa</i>)	M	1	Captive	TBZ
Madee	Clouded leopard (<i>Neofelis nebulosa</i>)	F	½	Captive	TBZ
Mali	Clouded leopard (<i>Neofelis nebulosa</i>)	F	1	Captive	TBZ
Rukai	Clouded leopard (<i>Neofelis nebulosa</i>)	F	3	Captive	OKC
Chinook	Cougar (<i>Puma concolor</i>)	M	4	Wild	BCZ
Harper	Cougar (<i>Puma concolor</i>)	F	5	Wild	TCC
Jane	Cougar (<i>Puma concolor</i>)	F	1	Wild	TBZ
Josey	Cougar (<i>Puma concolor</i>)	F	1	Wild	TBZ
Sage	Cougar (<i>Puma concolor</i>)	F	15	Captive	TBZ
Tacoma	Cougar (<i>Puma concolor</i>)	M	4	Wild	BCZ
Wyatt	Cougar (<i>Puma concolor</i>)	M	1	Wild	TBZ
Boon	Fishing cat (<i>Prionailurus viverrinus</i>)	M	7	Captive	OKC
Chet	Fishing cat (<i>Prionailurus viverrinus</i>)	M	12	Captive	OKC
Miri	Fishing cat (<i>Prionailurus viverrinus</i>)	F	15	Captive	OKC
Puddles	Fishing cat (<i>Prionailurus viverrinus</i>)	M	4	Captive	OKC
Rosa	Jaguar (<i>Panthera onca</i>)	F	9	Captive	TBZ
Tai	Jaguar (<i>Panthera onca</i>)	M	17	Captive	OKC
Arieta	Ocelot (<i>Leopardus pardalis</i>)	F	8	Captive	OKC
Bosco	Ocelot (<i>Leopardus pardalis</i>)	M	13	Captive	OKC

Old Man	Ocelot (<i>Leopardus pardalis</i>)	M	20	Captive	BCZ
Makusi	Ocelot (<i>Leopardus pardalis</i>)	M	1	Captive	BCZ
Raif	Ocelot (<i>Leopardus pardalis</i>)	M	8	Captive	OKC
Nanai	Siberian lynx (<i>Lynx lynx wrangeli</i>)	M	½	Wild	TCC
Chameli	Snow leopard (<i>Panthera uncia</i>)	F	6	Captive	TBZ
Gala	Snow leopard (<i>Panthera uncia</i>)	M	4	Captive	TBZ
K2	Snow leopard (<i>Panthera uncia</i>)	F	8	Captive	BZ
Khyber	Snow leopard (<i>Panthera uncia</i>)	F	1	Captive	BZ
Leo	Snow leopard (<i>Panthera uncia</i>)	M	13	Wild	BZ
Mike	Snow leopard (<i>Panthera uncia</i>)	M	4	Captive	BZ
MJ	Snow leopard (<i>Panthera uncia</i>)	M	2	Captive	BZ
Tanja	Snow leopard (<i>Panthera uncia</i>)	F	18	Captive	BZ
Willie	Snow leopard (<i>Panthera uncia</i>)	M	5	Captive	BZ
Kami	Sumatran tiger (<i>Panthera tigris sumatrae</i>)	M	14	Captive	OKC
Lola	Sumatran tiger (<i>Panthera tigris sumatrae</i>)	F	10	Captive	OKC

Table 2(on next page)

Definitions of traits used in the keeper assessment survey.

Table 2:
Definitions of traits used in the keeper assessment survey.

Adjective	Definition
Active	moves about a lot
Anxious	uneasy, easily startled
Calm	not easily disturbed by changes within or outside environment
Cautious	exhibits care in actions
Cooperative	easily compliant
Curious	readily explores new situations
Dominant	displaces/ overpowers others
Excitable	strong reaction to changes
Fearful	easily shaken; avoids changes and assumes protective or aggressive body postures
Flexible	adapts comfortably to change
Playful	initiates and easily joins in play
Smart	learns quickly, associates situations and people well, good memory
Sociable	seeks out companionship
Solitary	chooses to spend time alone
Stereotypical	fixed and oversimplified in behaviors
Submissive	gives in easily to others
Tense	shows restraint in posture and movement; carries the body stiffly and tries to pull back and be less noticeable
Vigilant	alert, attentive, notices all changes
Uninterested	no care in changes in environment, or conspecifics
<i>With novelties or environmental changes</i>	
Aggressive	hostile or threatening reaction
Fearful	retreats from others
Friendly	initiates proximity
Uninterested	shows no interest
<i>With humans</i>	
Aggressive	hostile or threatening reaction
Fearful	retreats from people
Friendly	initiates proximity
Uninterested	shows no interest

Table 3(on next page)

Component Matrix of Six Facets Reduced from Twenty-Six Behavioral Traits.

Table 3:
Component Matrix of Six Facets Reduced from Twenty-Six Behavioral Traits.

	Fearful/ Aggression	Sociable/ Active	Solitary/ Vigilant	Curious	Stereotypical	Intelligence
Fearful	.721					
Fearful of Novelty	.742					
Fearful of Humans	.776					
Cautious	.444					
Tense	.647					
Anxious	.652					
Aggressive to Humans	.585					
Aggressive to Novelty	.525					
Calm	-.552					
Cooperative	-.649					
Curious	-.651					
Flexible	-.714					
Friendly to Humans	-.645					
Friendly to Novelty	-.703					
Sociable		.472				
Playful		.575				
Active		.395				
Excitable		.535				
Dominant		.335				
Solitary			.474			
Vigilant			.500			

Uninterested	.553	
Uninterested in Humans	.523	
Uninterested in Novelty	.553	
Stereotypical		.453
Smart		.551

Table 4(on next page)

Descriptive Statistics and Correlations Among the Variables.

1 **Table 4:**
2 **Descriptive Statistics and Correlations Among the Variables.**
3

	1	2	3	4	5	6	7	8	9	10
Success	-									
Sex	.096	-								
Age	.064	.028	-							
Subspecies	.116	-.110	-.079	-						
Fearful/ Aggressive	-.208*	-.066	-.055	-.084	-					
Sociable/ Active	.027	-.045	-.602**	.049	-.248**	-				
Solitary/ Vigilant	-.030	-.182*	.276**	.074	.115	-.271**	-			
Curious	-.165	-.222**	.014	.084	.319**	-.066	.203*	-		
Stereotypical	.066	-.191*	.040	.015	.388**	.072	.122	.346**	-	
Intelligent	.214*	.072	-.107	.127	-.433**	.231**	.064	-.164	-	-
									.249**	
<i>Mean</i>	.443	1.48	6.30	1.56	3.38	3.85	4.11	3.32	2.80	4.96
<i>Standard Deviation</i>	.499	.501	5.89	.498	1.06	1.25	1.31	.998	1.52	1.26

4

Figure 1

The multi-access puzzle box showing the open push door technique, or solution 1 which is opened by pushing the door allowing for access to the food reward.

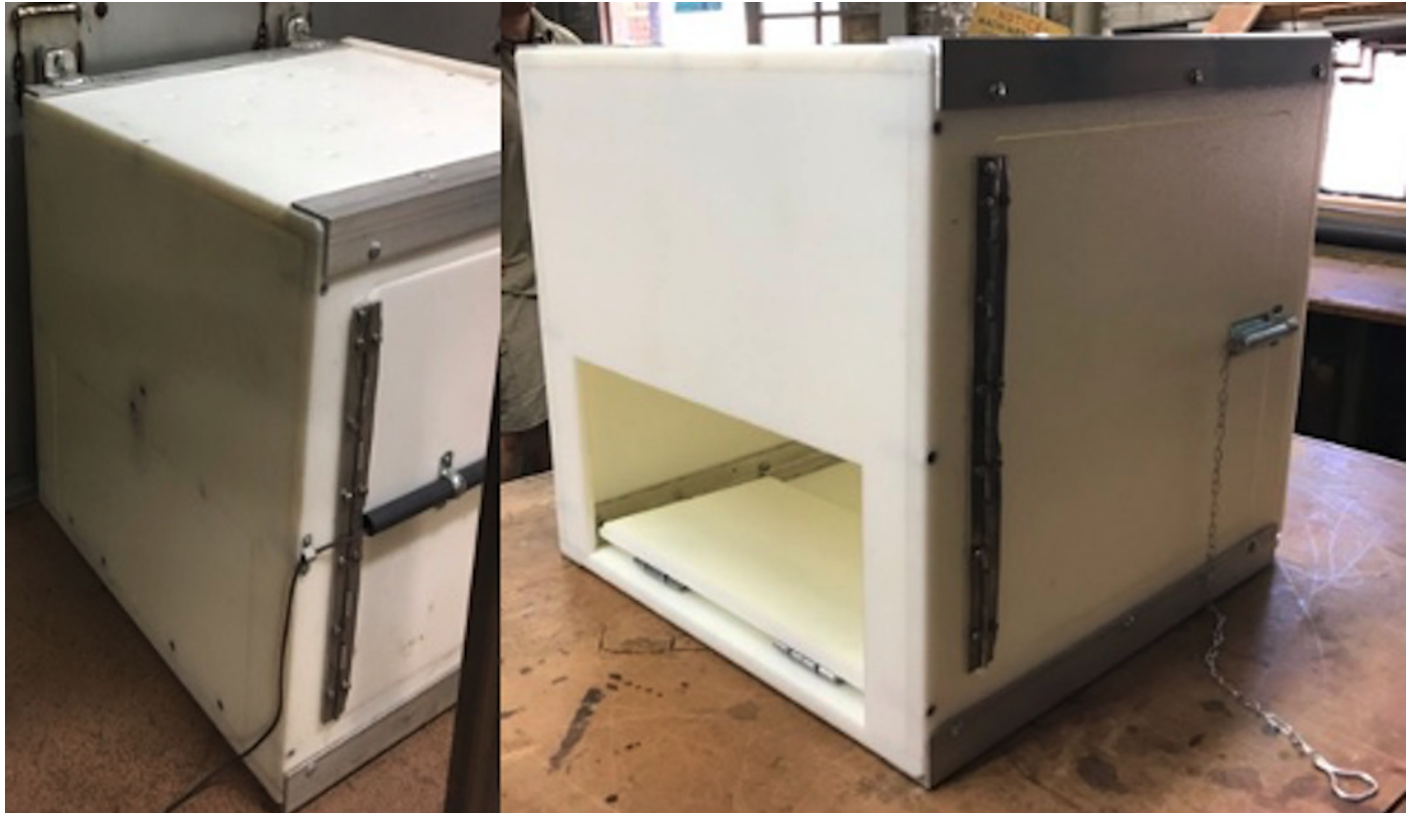


Figure 2

The multi-access puzzle box showing the pull rope technique, or solution 2 which swings open by pulling the rope exposing the inside of the box.



Figure 3

The multi-access puzzle box showing the open pull door technique, or solution 3 which pulls down flush to the ground, exposing the entire inside of the box.

