Scaredy- Cats don't succeed: Behavioral traits predict problem-solving success in captive Felidae

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Animal behavioral traits 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 these traits 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 five facets (Flexible/Friendly, Fearful/Aggressive, Uninterested, Social/Playful, and Cautious) from behavioral trait assessments based on zookeeper surveys in 52 *Felidae* individuals representing thirteen species. We analyzed whether age, sex, species, and these facets predicted success in a multi access puzzle box – a measure of innovation. We found that Fearful/Aggressive and Cautious facets were negatively associated with success. This research provides the first test of the association between behavioral trait facets and innovation in a diverse group of captive felidae. Understanding the connection between behavioral traits and problem-solving can assist in ensuring the protection of diverse species in their natural habitats and ethical treatment in captivity.

1 **Scaredy-Cats don't succeed: Behavioral Traits Predict**
2 **Problem-Solving Success in Captive Felidae**
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Abstract

Behavioral traits can be determined from the consistency in an animal's behaviors across time

and situations. These behavioral traits may have been differentially selected in closely related

species. Studying the structure of these traits 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 five facets (Flexible/Friendly,

Fearful/Aggressive, Uninterested, Social/Playful, and Cautious) from behavioral trait

assessments based on zookeeper surveys in 52 *Felidae* individuals representing thirteen species.

We analyzed whether age, sex, species, and these facets predicted success in a multi access

puzzle box – a measure of innovation. We found that Fearful/Aggressive and Cautious facets

were negatively associated with success. This research provides the first test of the association

between behavioral trait facets and innovation in a diverse group of captive felidae.

Understanding the connection between behavioral traits and problem-solving can assist in

ensuring the protection of diverse species in their natural habitats and ethical treatment in

captivity.

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

Introduction

33   Personality generally refers to consistency in behavioral traits across time and situations.

34 Applying the term to nonhuman animals has sometimes been considered controversial because of

35 its anthropomorphic nature (Gosling & Vazire, 2002). Therefore, researchers often refer to

36 behavioral traits, rather than personality, when working with nonhumans, and we will follow that

37 convention. Behavioral traits will be used here to refer to individual differences in the expression

38 of behavioral tendencies such as decision-making, risk taking, subjective wellbeing, and coping

39 strategies (Dall et al., 2004) that are consistent across time and context. We explore the

40 association between these traits and the ability of individuals of various felid species to solve a

41 task designed to measure innovation.

42   Behavioral traits are influenced by natural selection through genetic and/or

43 environmental effects (Moore et al., 1998). Studies have found that, in more than 100 species

44 ranging from insects to mammals, conspecifics, independent from sex or age, differ profoundly

45 in their behavior (e.g., Carere et al., 2010; Dougherty & Guillette, 2018). Additional studies of

46 behavioral traits have shown varied effects on health and longevity, including immune function

47 (e.g., Capitanio et al., 2008), morbidity (e.g., Natoli et al., 2005), chronic stress (e.g.,

48 Wielebnowski et al., 2002), and mortality (e.g., Weiss et al., 2013). In addition to heritability and

49 fitness (e.g., Sinn et al., 2006), social foraging and collective behavior (e.g., Aplin et al., 2014),

50 swarm intelligence for defense, resource exploitation and hunting (e.g., Krause et al., 2010),

51 well-being (e.g., King & Landau, 2003; Weiss et al., 2009; Weiss et al., 2006), and predator

52 avoidance (e.g., Handegard et al., 2012) have also been linked to these individual differences.

53 Personality is relevant for improving zoo management (e.g., individual differences suggest some

54 may require more seclusion in enclosures; Wielebnowski, 1999), animal welfare (e.g., females

55 score higher as tense-fearful than males; Wielebnowski, 1999), captive breeding (e.g., tense-

56 fearful cheetahs are less likely to reproduce in captivity; Wielebnowski, 1999), enclosure

57 grouping (e.g., age, number of individuals, and sex ratio are important for social housing;

58 Stoinski et al., 2004), and conservation (e.g., bolder, less fearful individuals were less suitable

59 for wild release; Bremner- Harrison et al., 2004). Therefore, knowledge of an individual's traits

60 can predict how that individual may perform in a novel situation or task.

61 In captivity, individual behavioral traits affect animals' experiences and predict their

62 adjustment and behaviors. Animal behavioral traits are primarily assessed in three ways: keeper

63 assessments, behavioral coding, and preference tests (Watters & Powell, 2012). Keeper

64 assessments involve familiar individuals rating the predefined traits of each subject on a scale

65 based on their human-animal relationships (HAR), knowledge of the subject accumulated across

66 time, mutual recognition between the human and animal, and the nature of interactions (positive

67 or negative). Good HARs require the human and animal to have a history of positive interactions

68 to allow successful behavioral predictions based on the caregiver's experience witnessing an

69 animal's consistent likelihood to engage in different behaviors during the length of their

70 relationship (Estep & Hetts, 1992). In this manner, survey assessments also capture consistency

71 in behavior across time and situations, but these assessments are subjective. First, raters can

72 interpret trait definitions differently. For example, raters may define "flexible" differently based

73 on their own experiences and biases. Whereas in the survey used here, flexible is defined as

74 "adapts comfortably to change," change can be defined as a shift in exhibits, conspecifics, and/or

75 zookeepers. Keepers may use different experiences as reference points for their ratings based on

76 their own interactions with the animal. Similarly, one keeper may define "bold" as reacting

77 aggressively to novelty, while another may see that as acting fearfully and score the individual

78 low on boldness. In addition, keepers may allow their own biases to color their ratings; for

79   example, they may be more likely to rate male animals high and to rate female animals low on

80   boldness even when the animals behave similarly. Thus, the use of keeper assessments is

81   strengthened when multiple keepers have built a relationship with the subject and reliability can

82   be determined.

83   Another potential issue with keeper assessments is that the traits animals are rated for are

84   often derived from top-down models that may not fit the target species. Thus, it is important to

85   first understand the traits that best describe the variability in the behavior of members of the

86   study species (Vonk & Eaton, 2018). Of the various possible forms of keeper assessment

87   identified by Uher (2011), we adopted a lexical top-down approach, using behavioral trait

88   descriptors from closely related species to fit the current subjects. Top-down assessments begin

89   with an existing model of personality and attempt to assess the extent to which a given species

90   exhibits traits derived from that model. These assessments seek to identify facets- sets of

91   definable traits that correlate and can be grouped together under an umbrella term, akin to

92   behavioral syndromes (Sih et al., 2004) . Early research involving nonhuman animals focused on

93   the popular five-factor model derived from humans (McCrae & Costa, 1987; Tupes & Christal,

94   1992), which includes the facets of openness, conscientiousness, neuroticism, extraversion, and

95   agreeableness.

96   Factor analytic approaches have revealed that the structure of behavioral syndromes in

97   nonhumans may differ from that established in humans. For example, in primates, behavioral

98   syndromes are described by the combination of two or more of the following six facets:

99   dominance, extraversion, dependability, emotional stability, agreeableness, and openness (Weiss

100   et al., 2000). In canids, there is less agreement regarding which key traits compose the structure

101   of canid behavioral syndromes. Domestic dogs exhibit a variety of traits that include

102   extraversion, neuroticism, agreeableness, openness/conscientiousness (Gosling & John, 1999),

103   playfulness, curiosity/ fearlessness, chase-proneness, sociability, and aggressiveness (Svartberg

104   & Forkman, 2002).

105   Of particular relevance to the current study, Stanton, Sullivan, and Fazio (2015)

106   conducted an in-depth meta-analysis on the current Felidae literature, ultimately creating a

107   standardized Felidae ethogram. Ethograms include the documentation of species-exhibited

108   behaviors by knowledgeable individuals (Stanton et al., 2015) and allow behavioral tracking of

109   captive populations that can be informative for predicting reproduction and overall welfare

110   (Clubb & Mason, 2003). Most relevant studies on felids have derived models consisting of the

111   following six facets: active, aggressive, curious, dominant, sociable, and timid/fearful/tense

112   (Gartner & Weiss, 2013). For instance, in cheetahs (*Acinonyx jubatus*), Wielebnowski (1999)

113   documented three major behavioral facets- tense-fearful, excitable-vocal, and aggressive whereas

114   Phillips and colleagues (2017) identified three facets- nervousness, adventurousness, and

115   aggression using keeper observations. Thus, similar facets emerged in both samples of cheetahs

116   from studies conducted eighteen years apart. Gartner, Powell and Weiss (2014) measured

117   behavioral traits in five felid species. Keepers were asked to rate the cats on the same behavioral

118   traits for each species. Although slightly different facets emerged from a factor analysis

119   including neuroticism, dominance, and impulsiveness in African lions, neuroticism,

120   agreeableness/openness, and dominance/ impulsiveness in clouded leopards, neuroticism,

121   impulsiveness/ openness, and dominance in snow leopards, dominance, impulsiveness, and

122   neuroticism in domestic cats, and dominance, agreeableness, and self-control in Scottish

123   wildcats, there were common facets that appeared to characterize Felidae in general (Gartner et

124   al., 2014). This study lays the foundation for the current research, which examines variability

125   within and between felid species. The current research drew upon several previously used keeper

126   assessments (Carlstead et al., 1999; Gartner & Weiss, 2013; Gold & Maple, 1994; Martin-Wintle

127   et al., 2017; Phillips & Peck, 2007; Wielebnowski, 1999; Wielebnowski et al., 2002) to

128   incorporate the traits: active, anxious, calm, cautious, cooperative, curious, dominant, excitable,

129   fearful, flexible, playful, smart, sociable, solitary, stereotypical, submissive, tense, vigilant, and

130   uninterested.

131   Having established the structure of behavioral traits in a taxa like felids, one can then

132   examine whether the derived traits usefully predict behaviors in various contexts. Testing

133   contexts, as defined by Freeman, Gosling and Schapiro (1993), incorporate the subjects'

134   responses to a novel stimulus to elicit differing reactions from the subjects to document

135   individual differences. The initial studies of Carlstead, Mellen and Kleiman (1999) and Powell

136   and Svoke (2008) introduced the idea that observations of subjects' interactions with novel

137   enrichment provides insight into their behavioral traits. Carlstead and colleagues (1999) paired

138   keeper assessments with a novel object test and a novel conspecific scent test. Using a 52-trait

139   and behavior assessment that they developed, keepers from different zoos were able to reliably

140   differentiate black rhinoceros individuals (*Diceros bicornis*) based on their physical

141   characteristics (e.g., sex, origin, and age) and six behavioral traits (e.g., olfactory behaviors,

142   chasing/stereotypy/ mouthing, fear, friendly to keeper, dominant, and patrolling). Similarly,

143   Powell and Svoke (2008) evaluated giant pandas' (*Ailuroproda melanoleuca*) responses to ten

144   novel enrichment items and their 23 trait and behavior assessment using keeper responses,

145   allowing them to create individual behavioral profiles.

146   Studies have demonstrated that the novel- object test can be a reliable and valid

147   behavioral trait tool in *Felidae*. Gartner and Powell (2012) used keeper assessments and coded

148   behaviors in response to six novel objects to identify five dimensions- active/vigilant,

149   curious/playful, calm/self-assured, timid/anxious, and friendly to humans- differentiating snow

150   leopards (*Panthera uncia*) based on age and sex. Similarly, Phillips et al. (2017) examined four

151   behavioral trait states in tigers (*Panthera tigris*), including aggression, fear, vigilance, and

152   obedience; this time, using both keeper assessments and behaviors towards olfactory and

153   physical enrichment. Ratings from behavioral trait assessments correlate with performance on

154   novel object tests validating the use of behavioral trait ratings.

155   The current work extends the existing literature demonstrating that behaviors elicited by

156   novel tasks are useful in validating zookeeper assessments of captive carnivore behavioral traits.

157   However, this work extends the current literature by assessing whether keeper assessments can

158   predict performance on a novel problem-solving task for environmental and cognitive

159   enrichment. Here, the multi-access puzzle box (MAB) as described in O'Connor et al. (2022) is

160   used as a test of innovation in felids. Various authors (Benson-Amram et al., 2013; 2016; Daniels

161   et al., 2019; Johnson-Ulrich et al., 2018; O'Connor et al., 2022), found that behavioral measures

162   of high persistence, high motor diversity/ exploration diversity, high activity/ working time, and

163   low neophobia are associated with success on a MAB in carnivores. Behavioral trait facets

164   similar to these behaviors are expected to predict performance in a task designed to measure

165   behavioral flexibility. For example, traits such as '*Cautious*' and '*Anxious*' might relate to

166   neophobia, whereas '*Playful'* and '*Curious*' might relate to exploration. There have been

167   numerous efforts to relate behavioral traits to individual differences in cognition. For example,

168   the expression of particular traits can influence cognitive abilities such as success or failure

169   (Carere & Locurto, 20110). However, there is, as of yet, no clear unifying theory about the

170 expected association between personality and cognition in nonhumans (Griffin et al., 2015; Sih

171 & Del Giudice, 2012).

172   Individual differences in behavioral traits are important for determining the best fit

173 practices for captive husbandry (e.g., Goswami et al., 2019), well-being (e.g., Gartner et al.,

174 2016), enrichment preference (e.g., Wang et al., 2019), health and reproduction (e.g.,

175 Wielebnowski, 1999), social compatibility (e.g., Bullock et al., 2021), social group dynamic

176 roles (e.g., Dunston et al., 2016), and environmental/ management changes (e.g., Quintavalle

177 Pastorino et al., 2017). Additionally, activity/stress levels (e.g., Torgerson-White & Bennett,

178 2014) have been shown to predict behavioral responses across a variety of taxa, including

179 carnivores. The current research extracts behavioral trait facets from keeper assessments to

180 explore whether these facets predict success on a MAB box, which measures innovation, in 52

181 individuals representing 13 species of felids.

182 **Materials & Methods**

183   **Species and Rater Information.** Subjects included 52 individuals, 30 males and 22

184 females, from 13 species (see Table 1). The age of the subjects ranged from six months to

185 twenty-three-years-old (M=6.68, SD=5.96). Raters include thirty-seven keepers who spent, on

186 average, 2.2 years with subjects (SD= 2.19) from five locations: the Bergen County Zoo (BCZ)

187 in Paramus, New Jersey, the Bronx Zoo (BZ) in Bronx, New York, The Creature Conservancy

188 (TCC) in Ann Arbor, Michigan, the Oklahoma Zoo (OKC) in Oklahoma City, Oklahoma, and

189 the Turtle Back Zoo (TBZ) in West Orange, New Jersey. Because keepers and subjects were

190 housed at different institutions, the same keepers did not rate all subjects.

191   Testing was approved by the IACUCs at Oakland University (# 19111), The City

192 University of New York: Hunter College (#SC-Captive 4/21), and The Wildlife Conservation

193 Society (#18:01).

194   **Carnivore Behavior Survey and Procedure.** To properly compare the ability of

195   behavioral traits to predict success in the MAB across all felids, individuals were not assigned

196   species-unique traits. Instead, individuals were assessed on the same traits to determine whether

197   individual or species level variation better predicts success in this task. Gosling and John (1999)

198   reviewed 19 factor analytic studies across 12 nonhuman species verifying considerable

199   generality in non-related species. In an effort to examine behavioral differences in captive

200   Felidae, Stanton and colleagues (2015) analyzed surveys of 30 species and 40 subfamilies to find

201   that most behaviors identified in their study were similarly described and likely to apply to most

202   felid species. In a similar review of 20 published studies, Gartner and Weiss (2013) found

203   reasonable consistency of certain personality dimensions in felids. As such, we expected that the

204   behaviors of the 13 species studied here would have similarly structured behavioral traits,

205   Furthermore, all felids share morphological features such as binocular vision, flexible bodies

206   with muscular limbs, protracting claws, and external ears with similar levels of hearing

207   (Kitchener et al., 2010; Rothwell, 2003). However, it is important to note that it was not the goal

208   of the current study to determine or compare the structure of behavioral syndromes in individual

209   Felidae species.

210   The twenty-seven-item behavioral trait survey was developed based on previous surveys

211   (Feaver et al., 1986; Gartner & Powell, 2012; Stanton et al., 2015; Wielebnowski, 1999), and

212   included the trait "intelligent." However, we did not include scores on "intelligent" in our

213   analyses as it is not clear that this should be considered a personality, rather than a cognitive

214   trait, and, as such, the results predicting success on a problem-solving task could be circular.

215   Each item in the survey included a specific description. For example, *Active*, was described as

216   "moves about a lot" (see Table 2). Four traits, *Aggressive, Fearful, Friendly, and Uninterested*,

217   were rated with regard to three contexts- overall, with novelties or environmental changes, and

218   with humans. All traits were rated on an eight-point Likert scale, where 0= *Doesn't apply*,

219   1=*Does not describe at all*, 4=*Neutral*, and 7=*Describes very well*.

220   Each keeper was given the questionnaire individually and instructed not to consult others,

221   so that their responses reflected their independent ratings of the individual subjects. Keepers

222   were asked to provide the following information about themselves: age, sex, and years of

223   experience with big cats, the species, the individual, and their zoo. In most cases, keepers

224   completed the questionnaires without knowledge of how individuals performed in the MAB

225   although this was not the case for a subset of the cats tested at OKC (n = 10). Given their long-

226   term experience with the individuals, zookeepers' ratings of felid traits are unlikely to have been

227   impacted by the individual's performance in the small number of experimental trials in a single

228   task that were observed by any given keeper. Furthermore, any bias resulting from witnessing

229   test sessions was expected to be limited to intelligence and we opted not to include intelligence

230   in our model. Therefore, to retain the largest and most inclusive sample, we opted not to remove

231   data from these subjects.

232   **Problem-Solving Task and Procedure.** Upon completion of the surveys by the keepers,

233   a problem-solving task, which involved retrieving a food reward from a custom multi-access

234   puzzle box (MAB) was presented. This task presents a simple and effective behavioral test for

235   exploring innovation and has been used successfully in a variety of carnivores (O'Connor et al.,

236   2022).

237   All subjects were tested individually in their indoor, or outdoor, off-exhibit holding

238   enclosures. The custom multi-access puzzle boxes were two molded Starboard boxes with

239   stainless-steel frames measuring 0.6m x 0.6m x 0.6m and 0.38m x 0.38m x 0.38m. A food

240   reward placed inside the box was accessible via three separate solutions: (1) Push Door

241   Technique (see Figure 1); (2) Pull Rope Technique (see Figure 2); and (3) Pull Door Technique

242   (see Figure 3). Each solution was presented on a different side of the box. The puzzle box was

243   cleaned and disinfected between different species' trials and subjects could not see each other

244   during trials.

245   Subjects underwent one trial per day. The trial began when the subject made physical

246   contact with the puzzle box. Trials ended when the subject opened the puzzle box (a successful

247   trial) or after 15 minutes elapsed without the subject opening the puzzle box (a failed trial). At

248   the end of each trial, the subject was shifted to an adjacent enclosure according to the zoos'

249   procedures. A subject either failed a condition, which was defined as failing to open the box in

250   three out of five trials, or succeeded in a condition, which was defined as opening the box in

251   three out of five trials. Subjects that succeeded moved on to the next condition. Subjects that

252   failed did not advance to the next condition and testing was discontinued.

253   Condition 1 (5 trials): The reward was retrievable via any of the solutions; all three doors

254   were unlocked at the start of the first trial. Once a subject achieved their first successful trial, the

255   door that they opened remained unlocked and the other two doors were locked for the remainder

256   of the first condition. Three successful trials out of a possible five advanced the subject to the

257   next condition. Condition 2 (5 trials): The remaining two unsolved doors were unlocked at the

258   start of the first trial. Once a subject succeeded in opening an unlocked door, that door remained

259   unlocked and the other two doors were locked for the remainder of the second condition. Three

260   successful trials out of a possible five advanced the subject to the final condition. Condition 3 (5

261   trials): Only the remaining unsolved door was unlocked, and the subject was given five trials in

262   which to open it three times, ending testing.

263   **Statistical Analysis.** Data were analyzed using SPSS v. 28 software for Macintosh.

264   Results were considered significant at alpha level $p < .05$.

265   For individuals that had more than one keeper rating their behavioral trait, interrater

266   reliabilities were calculated using the Intraclass Correlation Coefficients [ICC] where we

267   examined consistency between multiple raters using the model for Case 1 described by Shrout

268   and Fleiss (1979) where each subject was rated by a different set of randomly selected raters that

269   did not rate all subjects. Subjects of the same species at the same facility may have been rated by

270   the same raters but the raters differed by species and facility. Items deemed unreliable, defined as

271   having an ICC of less than or equal to zero, were omitted from further analysis. The average of

272   the keepers' ratings was then used when there were multiple raters for a subject.

273   Parallel analysis (Horn, 1965; O'Connor, 2000) was used as additional confirmation of

274   the number of facets to be extracted from the survey data and both the mean and percentile

275   estimations of model fit supported a five-component model to best fit the data. Subsequently, a

276   principal components analysis (PCA) was conducted using a varimax rotation and five factors

277   were extracted to combine the reliable behavioral traits into behavioral facets. Traits were

278   assigned to the facet where they had the highest loading. Traits with negative loadings were

279   reverse scored and composite variables taking the average ratings for each loaded trait were

280   created. Only loadings of .40 or greater were considered. Figure 4 depicts the structure of the

281   first three facets.

282   In their interactions with the MAB, individual carnivores were coded on their *Success* (0=

283   no solutions opened, 1=success on at least one condition). At least two independent observers

284   verified the classification of trials as successful. Additional data from this task will be reported

285   elsewhere. We regressed success on to sex, age, and subfamilies (1= *Pantherinae*, 2= *Felinae*) in

286   the first step of a hierarchical logistic regression model using the Wald Chi-square test to

287   determine whether any of the predictors significantly contributed to the outcome. We entered

288   the five behavioral trait facets derived from the PCA in the second step of the model.

289   Independent samples t-tests were conducted to determine whether the subfamilies differed on

290   any of the five facets.

291   **Results**

292   **Keeper Assessment Interrater Reliability.** The reliabilities across raters, *ICC* were .37

293   (active), .41 (anxious), .39 (calm), .12 (cautious), .07 (cooperative), .44 (curious), .57

294   (dominant), .33 (excitable), .54 (fearful), .41 (flexible), .51 (playful), .23 (smart), .60 (sociable),

295   .50 (solitary), .11 (stereotypical), .67 (submissive), .23 (tense), .05 (vigilant), .62 (uninterested),

296   .18 (aggressive to novelty), .05 (fearful of novelty), .36 (friendly towards novelty), .63

297   (uninterested in novelty), .28 (aggressive to humans), .38 (fearful of humans), .14 (friendly to

298   humans), and .36 (uninterested in humans). The reliabilities of mean ratings, *ICC* were .75

299   (active), .77 (anxious), .76 (calm), .40 (cautious), .26 (cooperative), .80 (curious), .87

300   (dominant), .71 (excitable), .85 (fearful), .78 (flexible), .84 (playful), .60 (smart), .88 (sociable),

301   .83 (solitary), .39 (stereotypical), .91 (submissive), .60 (tense), .22 (vigilant), .89 (uninterested),

302   .52 (aggressive to novelty), .21 (fearful of novelty), .74 (friendly towards novelty), .89

303   (uninterested in novelty), .66 (aggressive to humans), .75 (fearful of humans), .45 (friendly to

304   humans), and .73 (uninterested in humans).

305   **Reduction to Five Facets.** The parallel analysis and PCA reduced twenty-six of the

306   behavioral traits to five factors with factor loadings ≥ .40. For these five factors, all PCA values

307   were greater than the eigenvalues derived from the parallel analysis, validating their use

308   (Konečná et al., 2012). Upon examination of the extracted factors, we assigned all traits with

309   values .40 or greater (e.g., Gartner & Weiss, 2013) to factors for which they had the highest

310   factor loadings. Thus, we created composite facets representing the following five conceptually

311   coherent facets- Flexible/Friendly, Fearful/Aggressive, Social/Playful, Uninterested and Cautious

312   (see Table 3). The facets Flexible/Friendly, Fearful/Aggressive, and Social/Playful aligned well

313   with previous research with felids (Gartner & Weiss, 2013). The facet Cautious might also be

314   seen as aligning well with Neurotic and Nervousness, which were extracted by prior studies

315   (Gartner & Weiss, 2013; Phillips et al., 2017).

316   **Behavioral Traits Predict Success.** Descriptive statistics and zero order correlations

317   among the variables are shown in Table 4. Success was negatively correlated with

318   Fearful/Aggressive (r=-.22, p<.01), and Cautious (r=-.24, p<.01). Sex was negatively correlated

319   with Fearful/ Aggressive (r=-.18, p<.05). Age was positively correlated with Flexible/ Friendly

320   (r=.19, p<.05), and negatively correlated with Social/Playful (r=-.45, p<.01) and Cautious (r=-

321   .20, p<.05). Flexible/ Friendly was also positively correlated with Social/ Playful (r=.29, p<.01),

322   and negatively correlated with Fearful/ Aggressive (r=-.54, p<.01), Uninterested (r=-.22, p<.01),

323   and Cautious (r=-.29, p<.01). Social/Playful was negatively correlated with Fearful/ Aggressive

324   (r=-.23, p<.01) and Uninterested (r=-.19, p<.05).

325   Sex, age, and subfamilies were entered into the first step of the logistic regression and the

326   five behavioral facets were entered in the second step to predict success. Age (p=.63), sex

327   (p=.21), and subfamilies (p=.13) did not significantly predict success. Fearful/Aggressive (B=-

328   .37, SE=.16, $Wald$=5.48, p=.02) and Cautious (B=-.54, SE=.17, $Wald$=9.67, p<.001) significantly

329   negatively predicted success. Individuals that were rated as more fearful or aggressive and

330   individuals that were rated as more cautious were less likely to have success on the MAB.

331   Flexible/ Friendly (B=.17, SE=.15, $Wald$=1.26, p=.26), Uninterested (B=-.09, SE=.15,

332   *Wald*=.348, *p*=.56), and Social/Playful (*B*=-.01, *SE*=.12, *Wald*=.00, *p*=.97) were not significant

333   predictors of success.

334   The independent samples t-tests comparing subfamilies, Pantherinae and Felinae, for the

335   five behavioral facets revealed no significant differences (all *p*s >.09).

Discussion

337   Innovation, as a component of behavioral flexibility, is critical for enabling animals to

338   adapt to changing environments. Species and individuals differ in the extent to which they

339   exhibit behavioral flexibility. Identifying behavioral traits that predict flexibility may facilitate

340   captive husbandry strategies and especially conservation efforts. We examined whether captive

341   carnivore behavioral traits predicted innovation, measured as success on a MAB. A twenty-

342   seven-item keeper assessment survey reduced to five behavioral facets- Flexible/ Friendly,

343   Fearful/Aggressive, Uninterested, Social/Playful, and Cautious.

344   Within felids, the most robust behavioral facets from prior research are Sociable,

345   Dominant, and Curious (Gartner and Weiss, 2013). Our PCA analysis with a greater diversity of

346   species identified similar facets- our Social/Playful to their Sociable, our reverse-scored Cautious

347   to their Dominant, and Fearful/Aggressive and Cautious to Curious. This consistency across

348   studies suggests that felids may share similar trait structures. However, our study is important in

349   suggesting that an individual's traits, rather than species differences, seem to predict success in

350   the task. Evidence in other species supports this conclusion. Black rhinoceros individuals rated

351   as more fearful also exhibited a longer latency to contact a novel object (Carlstead et al., 1999)

352   and rainbow trout (*Onchorhyncus mykiss*) rated as shy but given emboldening experiences

353   became bolder and exhibited reduced latencies to contact a novel object (Frost et al., 2007). In

354   the current study, individuals that were rated as more fearful or aggressive and individuals that

355   were rated as more cautious were less likely to have success on the MAB. However, it is

356 important to note that we tested success on only a single problem-solving task so future research

357 is needed to test the generalizability of these associations.

358   The behavioral traits assessed here were rated with reasonable reliability across keepers

359 and predicted performance in the MAB, which measured innovation. Specifically,

360 Fearful/Aggressive and Cautious predicted lack of success on the MAB. Highly fearful and

361 cautious animals should be less likely to attempt solutions to novel problems, so these results

362 were expected. Although most of the keepers completed the assessments with no knowledge of

363 the subjects' performance, some keepers for ten subjects may have been influenced in their

364 ratings by observing a subset of the experimental trials. Because we did not include the trait

365 "intelligence" in our analyses, which was the trait that should be most influenced by the subject's

366 performance, and because no keeper observed all trials, and each keeper had extensive

367 experience of the subjects beyond observing them participate in these trials, we are not

368 concerned that this biased our results. Ideally, studies should have all raters complete their

369 ratings before any of the tests are conducted. This was not always possible here based on the

370 complications of arranging testing at multiple locations during a global pandemic.

371   Previous studies have identified behavioral traits and facets in felids, some in conjunction

372 with a novel object test (Carlstead et al., 1999; Gartner & Powell, 2012; Powell & Svoke, 2008;

373 Razal et al., 2016). This is the first study to report an association of behavioral traits with success

374 on a test of innovation. Diverse behaviors have been associated with problem-solving success in

375 carnivores (Benson-Amram et al., 2013; Benson-Amram et al., 2016; Daniels et al., 2019;

376 Johnson-Ulrich et al., 2018; O'Connor et al., 2022). Based on these findings, we expected

377 Flexible/Friendly and Social/Playful to be predictive of success; however, this was not the case.

378 We defined Flexible as "adapts comfortably to change," Friendly as "initiates proximity," and

379   Curious as "readily explores new situations." Keeper ratings should be informed by knowledge

380   of the animal's behavior in multiple contexts (e.g., shifting indoor and outdoor enclosures,

381   proximity to zoo guests, etc.). Similarly, we defined Sociable as "seeks out companionship" and

382   Playful as "initiates and easily joins in play." However, these terms may be related to age as

383   younger cats were rated as more Social/Playful (r=-.45, p<.001), or to socially housed species, of

384   which some of these subjects are not. It is possible that performance in a single problem-solving

385   task is not a representative measure of the subject's more general abilities. Because neophobia

386   may limit interaction with the novel puzzle box (e.g., coyotes; Young et al., 2019), the facets of

387   fearful and cautious may have overshadowed other behavioral traits in predicting success. These

388   results support previous findings suggesting that motivation and object exploration may be better

389   predictors of success compared to cognitive ability or inhibitory skills (Johnson-Ulrich et al.,

390   2018). This point is important given how frequently cognitive research is conducted to compare

391   cognitive abilities between species (Vonk et al., 2021).

392   There are other nonsignificant results to note. Our research does not corroborate previous

393   findings that age (e.g., Benson-Amram & Holekamp, 2012) or sex (e.g., Amici et al., 2019)

394   predicted problem-solving. It is important to note that our measure of success was only a very

395   cursory measure of performance in this task. The MAB allows for examination of multiple

396   measures of cognition (e.g., trials to success, number of successful trials, number of solutions

397   learned, latency to learn new solution) and behavior (e.g., number of behaviors performed,

398   perseveration), but we examined only the simplest outcome here as a pilot test of how well

399   behavioral traits could predict problem-solving success, which might be associated with

400   adaptability and flexibility to change in novel environments. Thus, we would encourage future

401 researchers to examine how individual differences predict variable success in tasks that might

402 assess traits relevant for species' survival in the wild or ability to adapt in captivity.

403 **Conclusions**

404   Many studies of animal cognition have a low sample size, (Shaw & Schmelz, 2017). To

405 our knowledge, this study includes data from the largest and most inclusive sample of felids

406 compared to previous studies of felid personality and cognition. Across the thirteen Felidae

407 species we assessed, a coherent behavioral trait structure was extracted involving five facets-

408 Flexible/ Friendly, Fearful/Aggressive, Uninterested, Social/Playful, and Cautious. These facets

409 are echoed in the Felidae literature as reviewed by Gartner and Weiss (2013). We report the first

410 demonstration that these traits predicted problem-solving success on a test of innovation. Two

411 facets- Fearful/Aggressive and Cautious significantly negatively predicted success in this task.

412 This work should be considered preliminary, but we hope the promising results encourage future

413 studies with larger sample sizes and further refinement of the behavioral traits measure. Felid

414 behavioral trait research, in combination with cognitive testing, has practical applications for

415 both captive welfare and wildlife conservation success.

416

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Descriptive information for all subjects

1 **Table 1:**
2 **Descriptive information for all subjects.**

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

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

Definitions of traits used in the keeper assessment survey.

1 **Table 2:**
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
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
With novelties or environmental changes	
Aggressive	hostile or threatening reaction
Fearful	retreats from others
Friendly	initiates proximity
Uninterested	shows no interest
With humans	
Aggressive	hostile or threatening rection
Fearful	retreats from people
Friendly	initiates proximity
Uninterested	shows no interest

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

1 **Table 3:**
2
3 **Component Matrix of Five Facets Reduced from Twenty-Six Behavioral Traits**

	Flexible/ Friendly	Fearful/ Aggressive	Uninterested	Social/Playful	Cautious
Flexible	.82				
Curious	.76				
Friendly to Novelty	.74				
Cooperative	.70				
Friendly to Humans	.69				
Calm	.60				
Aggressive to Novelty		.71			
Anxious		.70			
Stereotypical		.63			
Excitable		.60			
Fearful		.60			
Fearful to Novelty		.60			
Tense		.58			
Aggressive to Humans		.58			
Fearful of Humans		.54			
Uninterested in Novelty			.86		
Uninterested			.82		
Uninterested in Humans			.78		
Vigilant			-.47		
Sociable				.79	

Playful	.68	
Submissive	.64	
Cautious		.73
Dominant		-.47
Active		-.46

Descriptive Statistics and Correlations Among the Variables.

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

	1	2	3	4	5	6	7	8	9
1. Success	-								
2. Sex	.10	-							
3. Age	.05	.07	-						
4. Subspecies	.12	-.11	-.01	-					
5. Flexible/ Friendly	.12	.01	.19*	.15	-				
6. Fearful/ Aggressive	-.22**	-.18*	-.10	.00	-.54**	-			
7. Uninterested	-.06	-.01	.07	-.07	-.22**	.13	-		
8. Social/ Playful	-.02	.01	-.45**	.01	.29**	-.23**	-.19*	-	
9. Cautious	-.24**	.12	-.20*	.03	-.29**	.17*	.11	-.16	-
Mean	.44	1.48	6.3	1.56	4.28	3.06	3.12	3.51	3.86
Standard Deviation	.50	.50	5.89	.50	1.17	1.17	1.15	1.69	1.13

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.
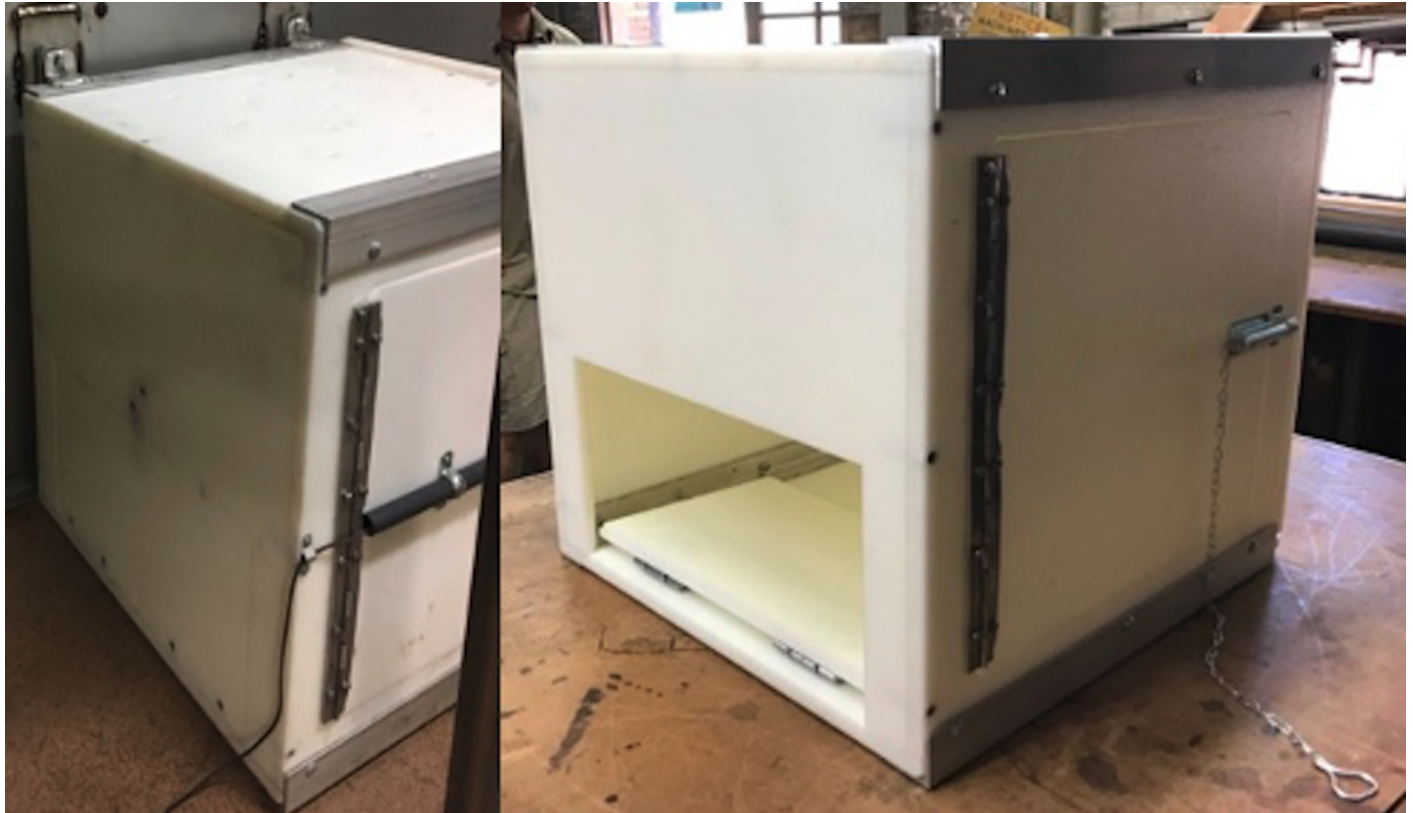
Figure 2

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.

Figure 4

Structure of the first three facets extracted from the PCA