EXPLORING INNOVATION AND BEHAVIORAL FLEXIBILITY IN CAPTIVE CARNIVORES

by

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To my family, who always encouraged me on this wild path.
To the animals, including my own two, who taught me more than I could ever put into words.

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ABSTRACT

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The highly specialized order Carnivora, while underrepresented in the comparative cognition literature, faces diverse ecological and social constraints. Thus, species and individuals should differ in behaviors associated with cognitive abilities, facilitating the successful navigation of these challenges. Behavioral flexibility was measured in 80 individuals of 17 species through personality assessments predicting success on a multi-access puzzle box (MAB) and behaviors associated with cognition on both a MAB and an Impossible Task. At the species level, social species were significantly more persistent on the MAB, and smaller body mass and higher encephalization was associated with persistence and latency to success on the MAB. Within species, on the individual level, there were several significant differences in behaviors between the sexes, ambassador versus exhibit animals, and wild versus captive-born species in the behavioral trait assessments, and on the MAB and Impossible Task. No significant differences existed between individuals of different ages or species rated differently on the IUCN scale or in brain volume on the MAB. This dissertation contributes to the growing field of animal cognition through the first use of personality

assessments predicting problem-solving success on an MAB, the largest and most inclusive sample of felids on an MAB, and the first use of an Impossible Task in non-domesticated felids.

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LIST OF ABBREVIATIONS

AIC	Akaike Information Criterion
BCZ	Bergen County Zoo
BZ	Bronx Zoo
CC	The Creature Conservancy
EQ	encephalization quotient
GLMM	generalized linear mixed model
HOI	human-oriented index
HLM	Hierarchical Linear and Nonlinear Modeling
IACUC	Institutional Animal Care and Use Committee
ICC	intraclass correlation coefficient
IT	Impossible Task
IUCN	International Union for Conservation of Nature
M	mean
MAB	multi-access box
MLMM	multilevel linear mixed model
MZ	Miami Zoo
OKC	Oklahoma City Zoo
PCA	principal components analysis
SD	standard deviation
SEM	standard error of the mean

SPSS	Statistical Package for the Social Sciences
TBZ	Turtle Back Zoo

CHAPTER 1

GENERAL INTRODUCTION

Cognition refers to how environmental information is acquired, processed, stored, and acted upon (Shettleworth, 2010). Within their natural environments, individuals face diverse social and ecological conditions, which are under increasing anthropogenic pressures and climate change. With millions of animals living in zoological settings, representing a nontrivial portion of the species populations, captive populations allow for relatively stable environments within which to measure animal cognition. In captivity, species can face unique environmental challenges associated with human proximity, limited abilities to express natural behaviors, altered climates and diets, and managed social dynamics. Their cognitive skills—perception, learning, memory, decision making, problem solving, and behavioral flexibility—provide measures of their overall intelligence. One such cognitive skill, behavioral flexibility, is defined in the comparative cognition literature as "a quality of trait that frees an animal from the constraints of instinct and allows it to adapt efficiently…it may also lead to different individuals finding different solutions to problems that all members of their species face" (Lea et al., 2020, p. 184). Cognition encompasses several components, including behavioral flexibility, which supports species in their abilities to apply knowledge to novel contexts.

Behavioral flexibility can be measured across species through the presence of problem solving (the process of overcoming an obstruction to obtain a reward; Rowell et al., 2021) and innovation (ability to create a new behavior or use a previously established behavior in a new situation; Griffin & Guez, 2014). In this dissertation, I measured

behavioral flexibility, problem solving, and innovation across three studies: (1) personality assessments, using keeper ratings to determine individual traits related to success on a multi-access puzzle box (MAB), which measures individuals' abilities to innovate and inhibit responses on a physical problem-solving task; (2) species' traits predicting performance of a larger sample on the same MAB task, and (3) an Impossible Task, highlighting the role that hand rearing and human presence has on persistence, behavioral diversity, and dependence on humans during problem solving. I studied cross-species variation of behavioral flexibility in carnivores to better understand the evolutionary and ontogenetic development of their cognitive abilities based on their diverse social and ecological challenges.

Behavioral Flexibility

The numerous and divergent conceptual and operational definitions of the term behavioral flexibility have led to some confusion (Audet & Lefebvre, 2017). Lea and colleagues (2020) identified more than 1,800 publications that used "behavioral flexibility" in the title, abstract, or keywords, with the number of publications growing rapidly in the last decade. Historically, the term has been used to mean simple variations in behavior (Poirier, 1969), which may be as nominal as choices for mates and resources; however, more recently, experiments on behavioral flexibility are used to measure complex cognitive abilities, such as problem solving, inhibition, and innovation (Griffin & Guez, 2014). Here, I follow Lea et al. (2020) in defining behavioral flexibility broadly as an individual's ability to make changes in behavior in response to environmental stimuli.

The concept of "behavioral flexibility" is a highly researched topic in the context of animal behavior and cognition and has been increasingly investigated in numerous species in both controlled and natural environments. For example, under laboratory conditions, pigeons (*Columba livia*) exhibited strategies to maximize rewards but changed the strategy once they were no longer being rewarded on reversal tasks (Randall & Zentall, 1997; Rayburn-Reeves et al., 2011). In the wild, where humans encroach on other species' habitats, baboons (*Papio ursinus*) raid human residential and commercial spaces for food (Hoffman & O'Riain, 2010), while African elephants (*Loxodonta africana*) have learned how to break electric fences with their tusks (Mutinda et al., 2014). Furthermore, animals in human-altered wild environments may exhibit more complex cognitive abilities in response to the increase in challenges (Barrett et al., 2019). For example, coyotes (*Canis latrans*) that exhibited behavioral flexibility by altering their activity levels reduced their risk of death from vehicle collisions (Murray & St. Clair, 2015). Populations of specific species have increased in urban landscapes based on individuals' abilities to utilize anthropogenic resources (e.g., coyote, Gehrt, 2011; red foxes, *Vulpes vulpes*, Soulsbury et al., 2011; spotted hyenas, *Crocuta crocuta*, Struller et al., 2022). However, the same species or closely related species in both natural and anthropogenically-affected environments may not exhibit the same degree of behavioral flexibility and are decreasing in population size. For example, northern raccoon (*Procyon lotor*) populations are increasing, with higher densities in urban landscapes than in rural landscapes (Prange et al., 2003; Timm et al., 2016), while pygmy raccoons (*Procyon pygmaeus*) have a suspected population size reduction of more than 80% since 2000 due to anthropogenic changes to their endemic environment (Cuarón et al., 2009, 2016).

These differences within and between species suggest that factors predicting adaptation to environments are complex and variation in the propensity for behavioral flexibility exists at both the individual and species levels (e.g., Dingemanse et al., 2010; Lea et al., 2020; Wright et al., 2010). It is the aim of this research to compare behavioral flexibility across individuals of a diverse group of species within the order Carnivora with a focus on felids to identify factors that may have been associated with the evolution of these traits in this understudied order.

Behavioral Flexibility Facets

Animals are not identical and do not behave at random. Behaviors vary in populations in the same environment and, as such, behavioral flexibility should be viewed through many lenses. For example, Price et al. (1991) demonstrated age and sex variation of Fathead minnows (*Pimephales promelas*) in their prey choice, habitat use, and activity patterns; Oliveria et al. (2018) detailed sex-specific habitat selection in European wildcats (*Felis silvestris silvestris*); and Ratcliffe et al. (2006) associated greater behavioral flexibility in foraging strategies in 59 predatory bat species (*Chiroptera*) with larger relative brain volume. Pertinent areas of focus for this research in carnivores include genetics, neural correlates/brain size, sex/age, personality, and human influence.

Genes are the largest contributor to variation in human intelligence (Haier, 2016). Whereas it is clear that intelligence is heritable in humans (Bouchard, 2004), the role of genetics in animal intelligence is less clear; in part, because studies on the heritability of intelligence in animals are scarce. There is some documentation that genetics play at least a moderate role in accounting for variation in cognitive abilities in several species

(Croston et al., 2015) including rats (*Rattus* spp*.,* Tolman, 1924), New Caledonian crows (*Corvus moneduloides*, Kenward et al., 2006), mice (*Mus musculus,* Galsworthy et al., 2005), dogs (*Canis lupus familiaris*, Gnanadesikan et al., 2020), orangutans (*Pongo abelii,* Damerius et al., 2019), chimpanzees (*Pan troglodytes,* Herrmann et al., 2010; Hopkins et al., 2014), and humans (Herrmann et al., 2010). In their analysis of data from 1,508 adult dogs, Gnanadesikan and colleagues (2020) found heritable variation in the cognitive traits of inhibitory control and communication among dog breeds.

In contrast, there is a plethora of information on brain properties and cognition in a variety of species. A combination of larger relative brain size (i.e., relative to body mass; Kotrschal et al., 2013; Marino, 2013; Reader & Laland, 2002; Sol et al., 2005; Triki et al., 2020), larger neocortex (Smaers et al., 2021), a greater number and size of neurons (Haug, 1987; van der Woude & Smid, 2017), and greater neuron packing density, intraneuronal distance, and axonal conduction velocity (Dicke & Roth, 2016) are associated with greater cognition. Yet, ample comparative data about animal cognition is rare; research has yet to determine the correct equation of neurobiological differences in nonhuman cognitive abilities.

The physical, ecological, and social pressures faced by males and females differ (e.g., mating strategy, offspring rearing); thus, divergent evolution of cognitive abilities between the sexes would be expected. There is evidence of sex differences in cognitive abilities in some species. Within guppies (*Poecilia reticulata*), females exhibit later exploratory diversity in a novel-object test (Lucon-Xiccato & Dadda, 2016), are less mobile, disperse more closely (Croft et al., 2003), and underperform relative to males in a spatial learning task. Female guppies exhibit more cautious behaviors than males—likely

due to the energy and protection required for bearing young (Lucon-Xiccato & Bisazza, 2017). In Jonasson's (2005) meta-analysis on spatial memory, both male rats and mice performed better than female rats and mice; however, for reference memory, male rats performed better than females whereas female mice perform better than male mice. This sexual dimorphism in spatial abilities, which is also exhibited in voles (*Microtus* spp., Jacobs et al., 1990), rhesus monkeys (*Macaca mulatta,* Lacreuse et al., 1999), deer mice (*Peromyscus maniculatus,* Kavaliers et al., 1996), and humans (Williams & Meck, 1991), may be a consequence of male competition for females through home range size, hunting success (Gaulin & FitzGerald, 1986), evolution of male navigational skills for foraging (Kolakowski & Malina, 1974), or risk-reduction benefits for females and their offspring to reduce mobility (Sherry & Hampson, 1997). In mammals, males tend to disperse further than females (Greenwood, 1980; Jones et al., 2003), as seen in Giant pandas (*Ailuropoda melanoleuca*) in which males inhabit larger home ranges than females (Perdue et al., 2011). The same is not true, however, for the monogamous Asian small-clawed otters (*Aonyx cinereus*), which demonstrate no sex differences in spatial abilities, likely due to sexual commonalities in ecology and sociality (Perdue et al., 2011). Sex differences often are species-specific and reflect ancestral ecological and social demands.

Cognitive abilities have evolved in response to selective pressures. Just as different behaviors are adaptive for males versus females, the adaptive value of a behavior may be dependent upon the age of the individual; behaviors may be more adaptive for males across their lifespan, but for only young females due to their differences in reproductive aging. Age-related differences in cognitive abilities can be addressed through Tinbergen's (1963) proximate and ultimate causes for behavior

framework, which provides a foundation for understanding species' behavioral flexibility. Proximate explanations of behavior, that is, the immediate reasons for why a behavior is expressed, contrast with ultimate explanations, which are concerned with reasons why a behavior evolved. In understanding why bears (*Ursus arctos* and *Ursus thibetanus*) settle near humans, proximate explanations to human habituation include bears having early experience with people and/or human-derived food (Elfström et al., 2014). Additionally, the higher presence of female, sub-adult bears near humans is explained by predation avoidance and reduced competition— ultimate drivers of behavior (Elfström et al., 2014). Older chimpanzees (Lacreuse et al., 2018) and coyotes (van Bourg et al., 2022) exhibited more cognitive declines in cognitive tasks than younger individuals of their species, required more trials and displayed more errors, and raptor juveniles (*Milvago chimango*) were more explorative and less neophobic in a multi-access puzzle box than older raptors (Biondi et al., 2010). Within zebrafish (*Danio rerio*), older age is associated with decreases in exploratory behavior, adaptive associations, and responses to altered environments (Yu et al., 2006). Aging thus may predict impaired cognition (Burke & Barnes, 2006), particularly in captivity where lifespans are extended. Whereas behavioral flexibility may assist species in responding appropriately to their environment, age differences in cognitive abilities may be due to the alleviation of sexual/social pressures.

Individuals often adjust their behaviors in different contexts (e.g., life-history traits, ecologies, climates, social groupings, human influence), producing individual variability in behavioral flexibility (Krebs & Davies, 2009). Individual traits predict behavioral flexibility in cognitive tests in a variety of species (African lions, *Panthera*

leo, and snow leopards, *Panthera uncia*, O'Connor et al., 2022; chimpanzees, Hopper et al., 2014; Fallow deer, *Dama dama*, Bergvall et al., 2011; spotted hyenas, Johnson-Ulrich et al., 2018; humans, Goldsmith, 1984; meerkats, *Suricata suricata*, Thornton & Samson, 2012; raccoons, Stanton et al., 2022; and zebra finches, *Taeniopygia guttata*, Brust et al., 2013). Better performance on a cognitive task can be associated with greater reproductive success. Female budgerigars (*Melopsittacus undulatus*) shift their preference to previously non-preferred males after witnessing these males successfully solve two extractive foraging problems (e.g., Petri dish and puzzle box, Chen et al., 2019). In theory, individuals that are more flexible in their behavior are more effective parents, more successful mates, and better at acclimating to environmental change; therefore, natural selection may promote the evolution of greater behavioral flexibility.

Phylogenetically related species diverge in behaviors and morphology when exposed to different environmental pressures. Recently, human urbanization and domestication/rearing of exotic species has required species to alter their behavior in relatively brief durations of time. Historically, "animal domestication proceeded along a continuum from anthropophily to commensalism" beginning with "control in the wild", and progressing "to control of captive animals, to extensive breeding, to intensive breeding, and finally to pets" (Larson & Fuller, 2014, p. 117). This human-directed selection now intentionally manipulates behaviors in animals in all captive settings (e.g., zoo, household, laboratory, farm) to ensure peaceful cohabitation. Whereas some animals have benefited from human care (e.g., companion animals), many species do not thrive in captivity. In enclosures, polar bears exhibit high levels of stereotypic behaviors (*Ursus maritimus*, Clubb & Mason, 2003), giraffes (*Giraffa camelopardalis,* Clauss et al., 2007),

and squid (*Sepioteuthis lessoniana*, Ikeda et al., 2009) have shorter life spans, and low fecundity persists in African elephants (Hartley, 2016) and cheetahs (*Acinonyx jubatus*, Clubb & Mason, 2007). With the presence of human visitors, jaguars (*Panthera onca*) displayed increased aggression and pacing behavior (Sellinger & Ha, 2005), chimpanzees were hurt more frequently (Lambeth et al., 1997), and orangutans hid from visitors while their infants clung more tightly to them (Birke, 2002).

Behaviors associated with human presence and disruption are also observed in the wild. Urbanization has caused species to change their activity levels (Murray & St. Clair, 2015), mating calls (Halfwerk et al., 2019), migration patterns (Møller et al., 2014), and avoidance behaviors to sound (Ulloa et al., 2021) and light (Swaddle et al., 2015). Carnivores are experiencing intense pressures on the plasticity of their behaviors in urban areas (Schell et al., 2021). Within Africa and Asia, African leopards (*Panthera pardus*, Bhatia et al., 2013), spotted hyenas (Abay et al., 2011; Young et al., 2020), and striped hyenas (*Hyaena hyaena,* Singh et al., 2010) coexist, and may even prosper (e.g., food, protection, etc.) in human landscapes. In North America, bobcats (*Lynx rufus,* Young et al., 2019a), cougars (*Puma concolor,* Benson et al., 2016), and coyotes (Gehrt et al., 2011; Young et al., 2019b) have adapted to and thrive in urban environments. Given the pressure of human socialization and environmental encroachment, it is not surprising that urban animals may look, sound, and behave differently than their non-urban, wild conspecifics.

Cognitive Evolutionary Theories

Studies with captive animals allow a more focused investigation of evolutionary factors that have selected for variations in animal cognition across species. Despite their

long-standing presence in captivity, few studies have experimentally assessed cognitive abilities in carnivores. I sought to measure the ability of carnivores to behave flexibly when faced with a foraging challenge presented in the form of a puzzle box to better understand how their cognitive abilities have been shaped both evolutionarily and ontogenetically. Behavioral flexibility is a domain-general skill; cognition may evolve because of the specific pressures on species but can generalize for adaptability. Species are not equally flexible due to their varied social and ecological pressures. Thus, species in this series of studies will differ in their ability to demonstrate behavioral flexibility. This research examines behavioral flexibility in 80 individuals of 17 species, which allows key comparisons to examine the associations between various socioecological factors and different measures of performance in problem-solving tasks. The subsequent chapters outline the exploration of the predictive validity of three non-mutually exclusive key hypotheses for the evolution of cognition in carnivores: the social complexity hypothesis, the cultural intelligence hypothesis, and the cognitive buffer hypothesis.

The Social Complexity Hypothesis

The social complexity hypothesis posits that advanced cognitive abilities evolved as a function of navigating the complexities of social living (Byrne & Whiten, 1988). Much of the evidence supporting the social complexity hypothesis comes from birds, primates, and cetaceans. Bond et al. (2003) compared two related species of birds on two cognitive tasks; the more social species, pinyon jays (*Gymnorhinus cyanocephalus*), outperformed the less social western scrub-jays (*Aphelocoma californica*) in social learning on an implicit ranking task and transitive inference in nonadjacent probe trials. As pinyon jays live in large, social groups, their social complexity facilitates social

learning and transitive inference capabilities (Bond et al., 2003). Support for this predisposition for capabilities related to social complexity is found in capuchins (*Cebus aequatorialis*, Harris & McGonigle, 1994) based on their performance on the five-term series problem looking at transitive choice and task transfer, in rhesus macaques (Chen et al., 1997) on serial tasks looking at ordinal position, and in geladas (*Theropithecus gelada*, Bergman, 2010) in playback experiments testing for individual recognition. Recent work has sought to expand the social complexity literature to additional mammalian species. In an analysis of 422 ungulates of 86 species, social ungulates, and those with longer gestation duration, had larger brains (Pérez-Barbería & Gordon, 2005). Social carnivores—African lions and spotted hyenas—were more persistent and more successful than asocial carnivores—African leopards and tigers (*Panthera tigris*)—on a puzzle box (Borrego & Gaines, 2016). It is important to note that the total sample size (n= 48) was relatively small and spotted hyenas are not felids like African lions, African leopards, and tigers. While this study is limited in its capacity to present carnivores as an example of the social complexity hypothesis, it highlights the importance of additional studies comparing social and asocial species within taxon. Evolutionary pressures on cognitive abilities may reflect the demands of social complexity; species that navigate ranks, complex relationships, and/or large group sizes will exhibit greater behavioral flexibility.

The Cultural Intelligence Hypothesis

The cultural intelligence hypothesis extends the social intelligence hypothesis; it proposes that the social learning afforded by social living confers benefits in cognitive evolution (van Schaik & Burkart, 2011). Support for this hypothesis depends heavily on

research with primates; when given a battery of cognitive tests, human children and adult chimpanzees have similar physical skills, but 2.5-year-old children outperformed adult chimpanzees and orangutans in social cognitive tasks (Herrmann et al., 2007) due to the specialized social-cognitive skills they evolved for living in complex groups that develop unique cultures, distinct languages, and social practices (Boyd & Richerson, 1996). However, it is important to note that the tests were constructed for humans, not apes, and there were a small number of tasks (e.g., 2-4) within each domain (Hermann et al., 2007). Through the results of this comparison of a small number of cognitive skills, it can be argued that primates, particularly humans, have evolved specialized cultural skills due to their complex social structures. Evidence for the cultural intelligence hypothesis has begun to accumulate outside of primates, in species for which learning may occur in mother-offspring dyads or in groups. Cetaceans communicate through unique vocalizations (sperm whale, *Physeter macrocephalus*, Cantor et al., 2015), cooperatively fish with humans (bottlenose dolphin, *Tursiops truncates*, Pryor & Lindbergh, 1990), and have community-specific greetings (orca, *Orcinus orca*, Hoyt, 1990) and modified, prey-specific feeding methods (i.e., humpback whale, *Megaptera novaeangliae*, lobtail feeding on sand lance, *Ammodytidae*, Weinrich et al., 1992). Within carnivores, social species, spotted hyenas (Benson-Amram et al., 2014), coyotes (Young et al., 2019c), and African lions (Borrego & Dowling, 2016), were significantly more successful on puzzle box trials when conspecifics were interacting with and/or opening the box compared to when they were tested in isolation. Cultural variation likely exists within species; diverse behaviors acquired by an individual will likely be passed to other individuals in that population but may not necessarily be present in the entire species as they are not due to genetics. As

such, the cultural intelligence hypothesis should be assessed within species—between locations in both captive and wild environments—and between closely-related species.

The Cognitive Buffer Hypothesis

The cognitive buffer hypothesis states that the evolution of large brains and cognition is driven by the benefits of behavioral flexibility in dynamic and unstable environments (Sol, 2009). According to Sol, "a large brain facilitates the construction of behavioural responses to unusual, novel or complex socioecological challenges" (2009, p. 130); both social and ecological components exert strong influence over adaptations. It builds on the theories that larger-brained individuals live longer (Deaner et al., 2003), allowing for more behavioral flexibility (Jerison, 1973) and adaptation to novel challenges (Ricklefs, 2004). Studies have examined brain size in odontocetes (Connor, 2007), ungulates (Shultz & Dunbar, 2006), birds (Lefebvre et al., 2002; 2004), and primates (Deaner et al., 2007; Reader & Laland, 2002), and found positive correlations with measures of cognition, including social learning, innovation, tool-use, and deception (reviewed by Lefebvre & Sol, 2008), social learning rate (Reader & Laland, 2002), cultural transmission (Bonnie et al., 2007), cooperation (Melis et al., 2006), general intelligence (Reader et al., 2011), problem solving (Lefebvre et al., 2004), and success in novel environments (Sol et al., 2008). Mammals have the largest brains of any taxonomic group (Sol et al., 2008) evolving because of body size and variation in encephalization (Jerison, 1973). In terrestrial carnivores, Swanson et al. (2012) found that carnivorous feeders had larger relative endocranial volumes and that body size was negatively associated with relative brain volume, suggesting that body size evolved first, and subsequently, brain size co-evolved. In captive environments, Benson-Amram and

colleagues (2016) found that larger brain size was predictive of problem-solving success across 39 species of carnivores on a puzzle box task. In the wild, larger-brained species outperform smaller-brained species when foraging in habitats that are more seasonally demanding and in establishing themselves when introduced to novel environments (Schuck-Paim et al., 2008; Sol et al., 2008; van Woerden et al., 2011). Urbanization affords important tests of this theory; according to the cognitive buffer hypothesis, urban species that exhibit high levels of behavioral flexibility should adapt well. Urban carnivores—raccoons and coyotes—exhibited high levels of success on a reversal learning paradigm (Stanton et al., 2021) and puzzle boxes (Daniels et al., 2019; Garcia et al., 2022). Barrett and colleagues (2019) suggested that species that encounter humans might exhibit higher levels of behavioral flexibility than their non-urban conspecifics and may be more likely to survive encounters with humans. Thus, in response to changing environments, species exhibit behavioral flexibility, serving as evidentiary support for the cognitive buffer hypothesis.

Carnivora

Carnivorans are particularly susceptible to population declines from anthropogenic pressures (MacDonald et al., 2010) and struggle in captivity (Bond & Lindburg, 1990; Clubb & Mason, 2003; Saragusty et al., 2014). Despite being underrepresented in cognitive studies, carnivorans make an excellent group to investigate the role of cognition. Carnivores are a highly specialized group whose behavior is influenced by several ecological constraints, and which face increasing pressure from human encroachment in their habitats (Watson et al., 2015; Woodroffe, 2000). These

species face ecological challenges and, presumably, benefit from cognitive abilities facilitating the successful navigation of these challenges.

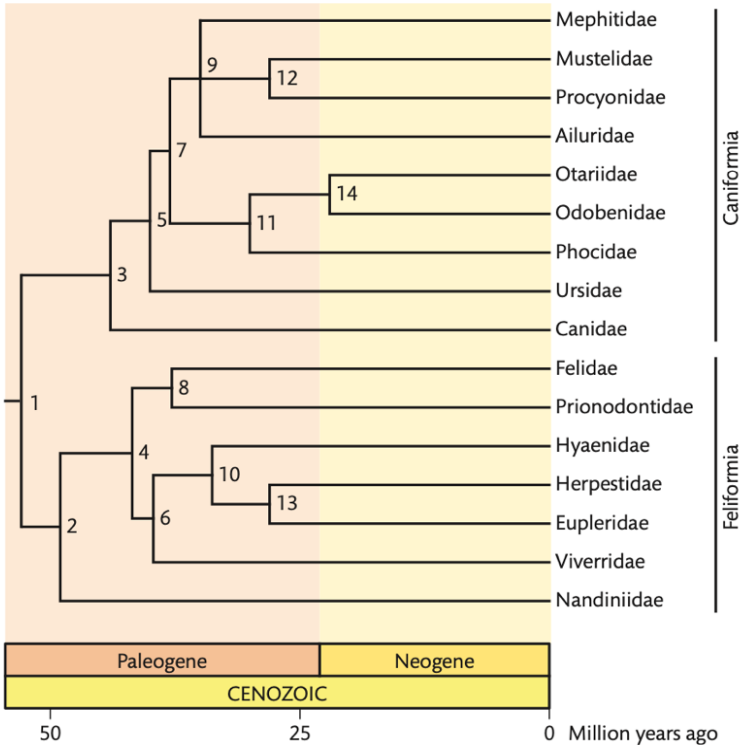
Exotic animals have lived in captivity for almost two centuries, with the first zoo established in 1828 in London (Hancocks, 1996). The intent of a zoo was to bring exotic species into a foreign area to satisfy human curiosity. However, challenges have persisted in how we care for the animals' physical and mental health. Stereotypic behaviors (McPhee, 2002), lack of enrichment and space (Lyons et al., 1997), inability to perform natural behaviors (Dawkins, 1988), reduced fecundity (Mason et al., 2009), and poor health and nutrition (Kenny, 1999) are some of the issues plaguing carnivores in captivity. Many carnivores do not adjust well to captivity and show signs of poor welfare, but there is a lack of research addressing these issues. Cognition has been linked to a species' ability to exploit novel resources and adapt to changing environments. Behaviorally flexible animals are more successful invaders (Sol & Lefebvre, 2000) and better at problem solving on behavioral tests (Audet et al., 2016), while boldness and neophobia influence engagement with novel objects and food in human habitats (Carter et al., 2012; Martin & Fitzgerald, 2005). By understanding how a species behaves, researchers can mitigate behavioral problems in captive environments.

The fifth largest order of mammals, Carnivora, includes more than 200 physically and behaviorally varied species inhabiting diverse habitats in every major landmass and, thus, serves as an ideal order in which to measure variation in behavioral flexibility. Carnivora are divided into two sub-clades based on bone structure, Feliformia and Caniformia, which diverged from each other approximately 55 million years ago (Eizirik & Murphy, 2009; see Figure 1). Feliformia consists of "cat-like" carnivorans including

the families Felidae and Hyaenidae. In contrast, Caniformia is a suborder consisting of "dog-like" carnivorans including the families Canidae and Procyonidae. Whereas there are other families in both Feliformia and Caniformia, only those families tested will be discussed.

Figure 1

Phylogenetic tree of Carnivora



Note. Reprinted from "Carnivores (Carnivora)," by Eizirik, E., and Murphy, W.J., 2009, from *The Timetree of Life* by Hedges, S.B., and Kumar, S. (Eds.), *Oxford University Press*, 504-507. A phylogenetic tree of carnivores (Carnivora) with time of divergence. Tree displays subclades (Caniformia and Feliformia) and families (Procyonidae, Canidae, Felidae, and Hyaenidae).

Felidae

The 37 species comprising the family Felidae are morphologically similar with rounded faces, facial whispers, and large ears, but have a wide range of body sizes from one kg (rusty-spotted cat, *Prionailurus rubiginosus*) to 300 kg (Amur tigers, MacDonald et al., 2010). There is some sexual dimorphism, with males generally 5-10% larger than females (Lamberski, 2015). Extant Felidae diverged approximately 11 million years ago (O'Brien & Johnson, 2007) into two subfamilies: Pantherinae, "big cats," and Felinae, "small cats." Pantherinae have longer, elastic vocal cords in their larynx that allow them to roar. Felinae vocal cords allow only purring, not roaring (Lamberski, 2015). Behaviorally, different felids are very similar (Estes, 2012). However, there are only two species of Felidae that have documented social systems, cheetahs and African lions. Whereas African lions live in groups called prides consisting of males, females, and young, only male cheetahs group together for female monopolization and predatory defense (Bradshaw, 2016). For those asocial Felidae, grouping may occur for hunting, breeding, or home range sharing (Gittleman, 1989). They are among the most threatened families with at least 29 of the 37 species having a decreasing population due to habitat loss, over-hunting/poaching, and loss of prey species (Nowell, 2009; Sunquist & Sunquist, 2009).

Hyaenidae

The four extant species of Hyaenidae are the spotted hyena, brown hyena (*Parahyaena brunnea*), aardwolf (*Proteles cristata*), and striped hyena (Mittermeier & Wilson, 2009). Individuals weigh between nine kg (aardwolf; Skinner & Chimimba, 2005) and 90 kg (spotted hyenas; Suedmeyer, 2015) with short torsos, low hind quarters,

and a sloping back (Heptner & Sludskii, 1992). Only in spotted hyenas are females larger than males; in the other three species, males are the larger sex (Mills & Hofer, 1998). Hyaenidae are phylogenetically closer to Felidae, but behaviorally and morphologically closer to Canidae (Kruuk, 1972). Brown hyenas are generally solitary but can live in small female-bonded and female-dominated clans like spotted hyenas, who live in large female clans; spotted hyena males live in smaller, nomadic clans (Suedmeyer, 2015). Aardwolves and striped hyenas are solitary and only group in the communal raising of offspring (Suedmeyer, 2015). While Hyaenidae face anthropomorphic threats such as hunting/poaching and human encroachment, none of the four species are currently endangered or threatened (Suedmeyer, 2015).

Canidae

The 35 species comprising the Canidae family represent the most geographically widespread Carnivoran family; they inhabit every continent but Antarctica and reside in a large geographic range across diverse habitats (Padilla & Hilton, 2015). Sociality may be the most diverse in Canidae compared to the other families included in this dissertation; Canidae families range from completely solitary, to seasonally paired, to large complex packs (Padilla & Hilton, 2015). Additionally, they are physically distinctive, with long legs and muzzles, upright ears, and bushy tails, weighing 0.6 kg (fennec fox, *Vulpes zerda*) to 79 kg (gray wolf, *Canis lupus*; Padilla & Hilton, 2015). They can exert great amounts of energy running at high speeds over long distances (Padilla & Hilton, 2015). While some Canidae thrive within human-developed landscapes, many risk extinction due to diseases, habitat disturbance, hunting/poaching, hybridization, and human encroachment; three taxa are critically endangered, three taxa are endangered, three taxa

are vulnerable, one taxon is near threatened, and six taxa are data deficient (Sillero-Zubiri et al., 2004).

Procyonidae

The smallest of the Carnivora families, Procyonidae consists of 14 species divided into six genuses: raccoons, coatimundis (*Nasua nasua*), kinkajous (*Potos flavus*), olingos (*Olingo gabbii*), ringtail cats (*Bassariscus astutus*), and red pandas (*Ailurus fulgens*; Ramsay, 2015). More closely related to Canidae than to Felidae, all species are omnivorous and native to temperate environments in North America and South America except the red panda, which is herbivorous and resides in Asia (Ramsay, 2015). Procyonidae weigh between two kg (kinkajou) and 20+ kg (raccoon; Ramsay, 2015), are arboreal, have long tails, and a short rostrum (Ramsay, 2015). Procyonidae face human disturbance, trapping/hunting, and habitat loss (Glatston, 1994) but are generally not threatened, except the red panda, which is endangered (Glatston & Roberts, 1988). Unfortunately, not much information exists on Procyonidae, especially outside of raccoons; ringtail cats (Richards, 1976), red pandas (Glatson & Roberts, 1988), and kinkajous (Ewer, 1973) are solitary, while olingos are thought to be either monogamous or solitary. Raccoons (Kaufmann, 1982) and coatimundis (Honacki et al., 1982) are incredibly flexible and can live solitarily (more commonly seen in males) or in large groups of up to 30 members (more commonly seen in females).

Summary

Whereas some species of carnivores have received conservation research attention (e.g., MacDonald et al., 2015), in relation to the number of species, carnivores are relatively understudied in zoos (Rose et al., 2019), particularly as relates to their

cognition (Benson-Amram et al., 2023), despite an increase in overall zoo studies (Escribano et al., 2021). An ideal order in which to measure cognitive abilities, Carnivora includes physically and behaviorally varied species inhabiting diverse environments and ranging in sociality with solitary species (e.g., cougars, Seidensticker et al., 1973), sex-dependent coalition groups (e.g., cheetahs, Bradshaw, 2016), and complex social groups (e.g., spotted hyenas, Drea & Frank, 2003). They span varied ecologies, including savanna, rainforest, grasslands, (e.g., African leopards, Bailey, 1993), alpine cliffs, rocky outcrops, ravines (e.g., snow leopards, Schaller, 1977), and lowland tropical rainforests and woodlands (e.g., clouded leopards, *Neofelis nebulosa,* Can et al., 2020). Their variance in ecological and social complexities make Carnivora an ideal taxonomic group with which to study the evolution of behavioral flexibility.

Cross-species differences in the following studies will provide information on the cognitive abilities of carnivores, providing data to increase the overall understanding of their cognition for both captive management and conservation purposes. In this dissertation, Chapters 2-4 present analyses of behavioral flexibility and problem solving in 17 species of Carnivorans. Chapter 2 is a published analysis of the association between behavioral trait facets and innovation on the MAB in felids with a focus on the individual level. Chapter 3 focuses on species level traits, such as conservation status (IUCN Red List), brain size and sociality as predictors of multiple measures of performance on the MAB. Chapter 4 presents a study using an Impossible Task to measure perseverance, behavioral diversity, and reliance on humans in captive carnivores' problem-solving and decision-making abilities.

CHAPTER 2

SCAREDY-CATS DON'T SUCCEED: BEHAVIORAL TRAITS PREDICT PROBLEM-SOLVING SUCCESS IN CAPTIVE FELIDAE

Personality generally refers to consistency in behavioral traits across time and situations. Applying the term to nonhuman animals has sometimes been considered controversial because of its anthropomorphic nature (Gosling & Vazire, 2002). Therefore, researchers often refer to behavioral traits, rather than personality, when working with nonhumans, and we will follow that convention. Behavioral traits will be used here to refer to individual differences in the expression of behavioral tendencies such as decision-making, risk taking, subjective wellbeing, and coping strategies (Dall et al., 2004) that are consistent across time and context. We explore the association between these traits and the ability of individuals of various felid species to solve a task designed to measure innovation.

Behavioral traits are influenced by natural selection through genetic and/or environmental effects (Moore et al., 1997, 1998). 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 (e.g., Carere et al., 2010; Dougherty & Guillette, 2018). Additional studies of behavioral traits have shown 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., individual differences suggest some may require more seclusion in enclosures; Wielebnowski, 1999), animal welfare (e.g., females score higher as tense-fearful than males; Wielebnowski, 1999), captive breeding (e.g., tense-fearful cheetahs are less likely to reproduce in captivity; Wielebnowski, 1999), enclosure grouping (e.g., age, number of individuals, and sex ratio are important for social housing; Stoinski et al., 2004), and conservation (e.g., bolder, less fearful individuals were less suitable for wild release; Bremner- Harrison et al., 2004). Therefore, knowledge of an individual's traits can predict how that individual may perform in a novel situation or task.

In captivity, individual behavioral traits affect animals' experiences and predict their adjustment and behaviors. Animal behavioral traits 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 the nature of interactions (positive or negative). Good HARs require the human and animal to have a history of positive interactions to allow successful behavioral predictions based on the caregiver's experience witnessing an animal's consistent likelihood to engage in different behaviors during the length of their relationship (Estep, 1992). In this manner, survey assessments also capture consistency in behavior across

time and situations, but 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, flexible is defined as "adapts comfortably to change," change can be defined as a shift in exhibits, conspecifics, and/or zookeepers. Keepers may use different experiences as reference points for their ratings based on their own interactions with the animal. 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, the use of keeper assessments is strengthened 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 behavioral trait descriptors from closely related species to fit the current subjects. Top-down assessments begin with an existing model of personality 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, akin to behavioral syndromes (Sih et al., 2004). Early research involving nonhuman animals focused on the popular five-factor model

derived from humans (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 behavioral syndromes in nonhumans may differ from that established in humans. For example, in primates, behavioral syndromes are 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 behavioral syndromes. 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 informative for predicting reproduction and overall welfare (Clubb & Mason, 2003). Most relevant 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 behavioral traits in five felid species. Keepers were asked to rate the cats on the same behavioral traits for each species. Although slightly 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, there were common facets that appeared to characterize Felidae in general (Gartner et al., 2014). This study lays the foundation for the current research, which 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 structure of behavioral traits in 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 individual 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 behavioral traits. 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 their physical characteristics (e.g., sex, origin, and age) and six behavioral traits (e.g., olfactory behaviors, chasing/stereotypy/ mouthing, fear, friendly to keeper, dominant, and patrolling). Similarly, Powell and Svoke (2008) evaluated giant pandas' (*Ailuroproda 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 behavioral trait 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 behavioral trait 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 behavioral trait assessments correlate with performance on novel object tests validating the use of behavioral trait ratings.

The current work extends the existing literature demonstrating that behaviors elicited by novel tasks are useful in validating zookeeper assessments of captive

carnivore behavioral traits. 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 in felids. 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. Behavioral trait 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. There have been numerous efforts to relate behavioral traits to individual differences in cognition. For example, the expression of particular traits can influence cognitive abilities such as success or failure (Carere & Locurto, 2011). However, there is, as of yet, no clear unifying theory about the expected association between personality and cognition in nonhumans (Griffin et al., 2015; Sih & Del Giudice, 2012).

Individual differences in behavioral traits are important for determining the best fit practices for captive husbandry (e.g., Goswami et al., 2020), well-being (e.g., Gartner et al., 2016), enrichment preference (e.g., Wang et al., 2019), health and reproduction (e.g., Wielebnowski, 1999), social compatibility (e.g., Bullock et al., 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. The current research extracts behavioral trait 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 and Methods

Species and Rater Information. Subjects included 52 individuals, 30 males and 22 females, from 14 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 37 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 City Zoo (OKC) in Oklahoma City, Oklahoma, and the Turtle Back Zoo (TBZ) in West Orange, New Jersey. Because keepers and subjects were housed at different institutions, the same keepers did not rate all subjects.

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; see Appendix B).

Table 1

Subjects for Behavior Surveys

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

Table 1- Continued

Name	Species	Sex	Age (yrs)	Rearing	Zoo
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
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
Bosco	Serval (*Leopardus serval*)	M	13	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

Carnivore Behavior Survey and Procedure. To properly compare the ability of behavioral traits to predict success in the MAB across all felids, individuals were not assigned species-unique traits. Instead, individuals were assessed on the same traits to determine whether individual or species level variation better predicts success in this task. Gosling and John (1999) reviewed 19 factor analytic studies across 12 nonhuman species verifying considerable generality in non-related species. In an effort to examine behavioral differences in captive Felidae, Stanton and colleagues (2015) analyzed

surveys of 30 species and 40 subfamilies to find that most behaviors identified in their study were similarly described and likely to apply to most felid species. In a similar review of 20 published studies, Gartner and Weiss (2013) found reasonable consistency of certain personality dimensions in felids. As such, we expected that the behaviors of the 13 species studied here would have similarly structured behavioral traits, Furthermore, all felids share morphological features such as binocular vision, flexible bodies with muscular limbs, protracting claws, and external ears with similar levels of hearing (Kitchener et al., 2010; Rothwell, 2003). However, it is important to note that it was not the goal of the current study to determine or compare the structure of behavioral syndromes in individual Felidae species.

The twenty-seven-item behavioral trait survey was developed based on previous surveys (Feaver et al., 1986; Gartner & Powell, 2012; Stanton et al., 2015; Wielebnowski, 1999), and included the trait "intelligent" (see Appendix A). However, we did not include scores on "intelligent" in our analyses as it is not clear that this should be considered a personality, rather than a cognitive trait, and, as such, the results predicting success on a problem-solving task could be circular. 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- overall, 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.*

Problem-Solving Task and Procedure. Upon completion of the surveys by the keepers, a problem-solving task, which involved retrieving a food reward from a custom

multi-access puzzle box (MAB) was presented. This task 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).

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
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

Table 2 - Continued

Adjective	Definition
With humans	
Aggressive	hostile or threatening reaction
Fearful	retreats from people
Friendly	initiates proximity
Uninterested	shows no interest

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 2); (2) Pull Rope Technique (see Figure 3); and (3) Pull Door Technique (see Figure 4). 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.

Figure 2

MAB Solution 1

Figure 3

MAB Solution 2

Figure 4

MAB Solution 3

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

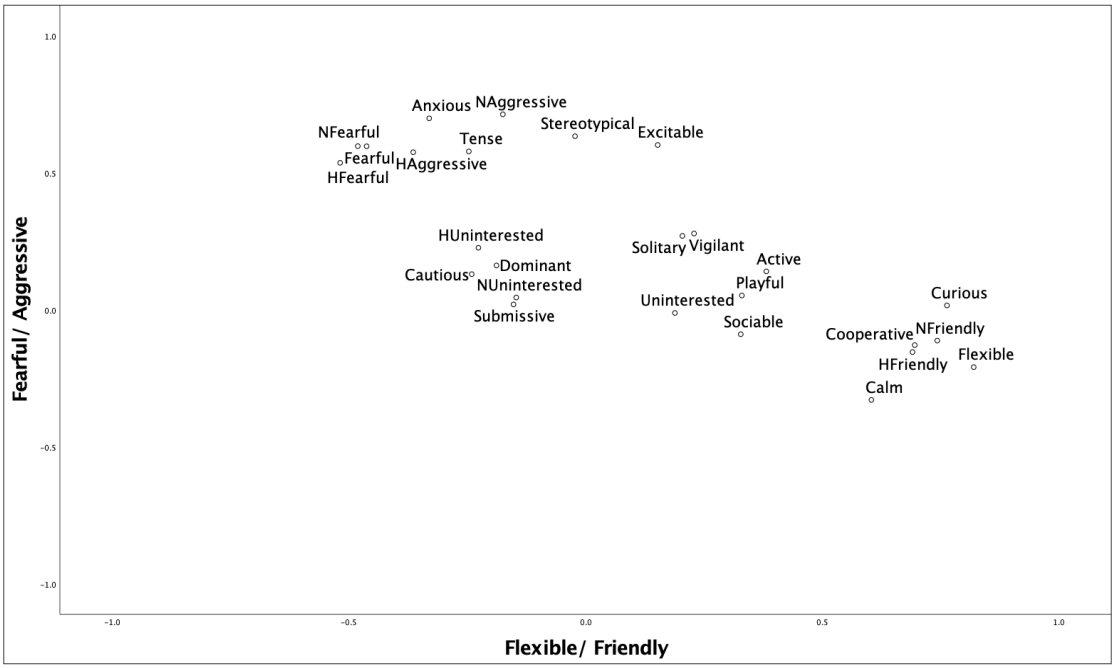
For individuals that had more than one keeper rating their behavioral trait, interrater reliabilities were calculated using the Intraclass Correlation Coefficients [ICC] where we examined consistency between multiple raters using the model for Case 1

described by Shrout and Fleiss (1979) where each subject was rated by a different set of randomly selected raters that did not rate all subjects. Subjects of the same species at the same facility may have been rated by the same raters but the raters differed by species and facility. Items deemed unreliable, defined as having an ICC of less than or equal to zero, were omitted from further analysis. The average of the keepers' ratings was then used when there were multiple raters for a subject.

Parallel analysis (Horn, 1965; O'Connor, 2000) was used as additional confirmation of the number of facets to be extracted from the survey data and both the mean and percentile estimations of model fit supported a five-component model to best fit the data. Subsequently, a principal components analysis (PCA) was conducted using a varimax rotation and five factors were extracted to combine the reliable behavioral traits into behavioral facets. Traits were assigned to the facet where they had the highest loading. Traits with negative loadings were reverse scored and composite variables taking the average ratings for each loaded trait were created. Only loadings of .40 or greater were considered. Figure 5 depicts the structure of the first three facets.

Figure 5

Principal Components Analysis (PCA) of Three Facets: Fearful/ Aggressive, Flexible/ Friendly, and Uninterested



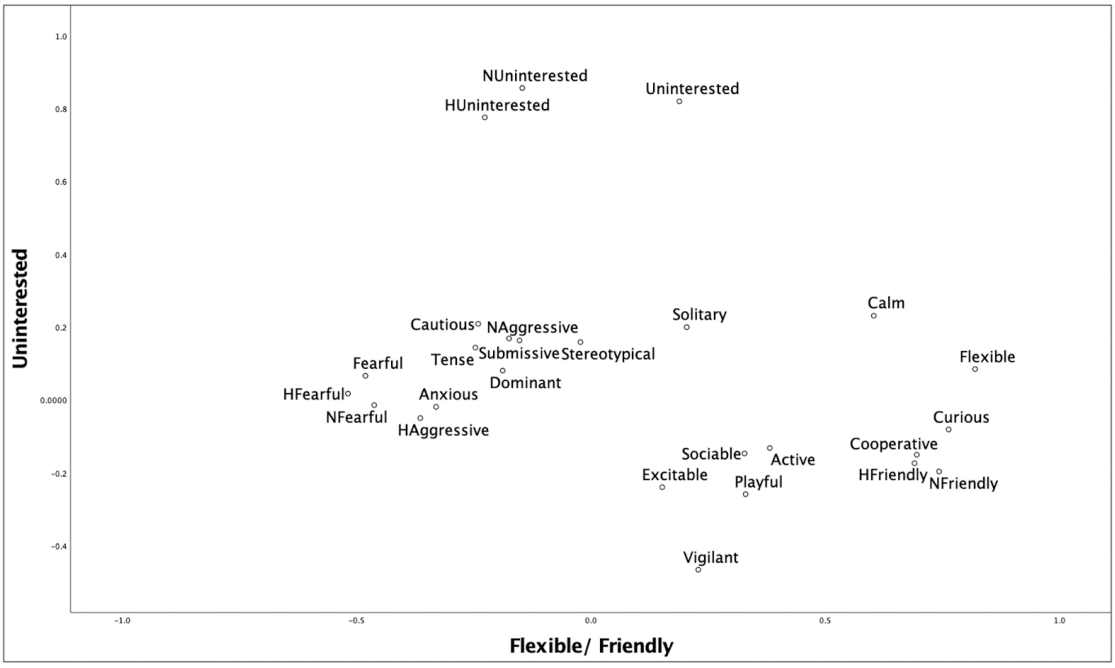
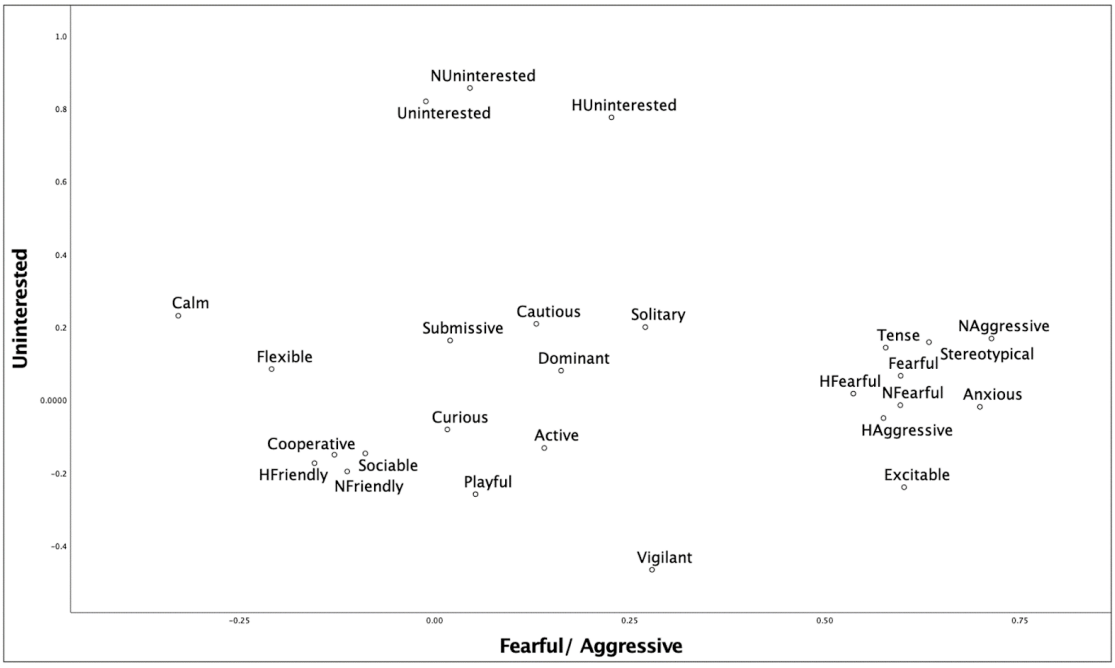


Figure 5 – Continued



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 Chapter 3. We regressed success on to sex, age, and subfamilies (1= *Pantherinae*, 2= *Felinae*) in the first step of a hierarchical logistic regression model using the Wald Chi-square test to determine whether any of the predictors significantly contributed to the outcome. We entered the five behavioral trait 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 five facets.

Results

Keeper Assessment Interrater Reliability. The reliabilities across raters, *ICC* were .37 (active), .41 (anxious), .39 (calm), .12 (cautious), .07 (cooperative), .44

(curious), .57 (dominant), .33 (excitable), .54 (fearful), .41 (flexible), .51 (playful), .23 (smart), .60 (sociable), .50 (solitary), .11 (stereotypical), .67 (submissive), .23 (tense), .05 (vigilant), .62 (uninterested), .18 (aggressive to novelty), .05 (fearful of novelty), .36 (friendly towards novelty), .63 (uninterested in novelty), .28 (aggressive to humans), .38 (fearful of humans), .14 (friendly to humans), and .36 (uninterested in humans). The reliabilities of mean ratings, *ICC* were .75 (active), .77 (anxious), .76 (calm), .40 (cautious), .26 (cooperative), .80 (curious), .87 (dominant), .71 (excitable), .85 (fearful), .78 (flexible), .84 (playful), .60 (smart), .88 (sociable), .83 (solitary), .39 (stereotypical), .91 (submissive), .60 (tense), .22 (vigilant), .89 (uninterested), .52 (aggressive to novelty), .21 (fearful of novelty), .74 (friendly towards novelty), .89 (uninterested in novelty), .66 (aggressive to humans), .75 (fearful of humans), .45 (friendly to humans), and .73 (uninterested in humans).

Reduction to Five Facets. The parallel analysis and PCA reduced twenty-six of the behavioral traits to five factors with factor loadings ≥ .40. For these five factors, all PCA values were greater than the eigenvalues derived from the parallel analysis, validating their use (Konečná et al., 2012). Upon examination of the extracted factors, we assigned all traits with values .40 or greater (e.g., Gartner & Weiss, 2013) to factors for which they had the highest factor loadings. Thus, we created composite facets representing the following five conceptually coherent facets- Flexible/Friendly, Fearful/Aggressive, Social/Playful, Uninterested and Cautious (see Table 3). The facets Flexible/Friendly, Fearful/Aggressive, and Social/Playful aligned well with previous research with felids (Gartner & Weiss, 2013). The facet Cautious might also be seen as

aligning well with Neurotic and Nervousness, which were extracted by prior studies (Gartner & Weiss, 2013; Phillips et al., 2017).

Table 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	

Table 3 - Continued

	Flexible/ Friendly	Fearful/ Aggressive	Uninterested	Social/Playful	Cautious
Submissive				.64	
Cautious					.73
Dominant					-.47
Active					-.46

Behavioral Traits Predict Success. Descriptive statistics and zero order correlations among the variables are shown in Table 4. Success was negatively correlated with Fearful/Aggressive (r =- .22, $p < .01$), and Cautious (r = -.24, $p < .01$). Sex was negatively correlated with Fearful/ Aggressive (r = -.18, $p < .05$). Age was positively correlated with Flexible/ Friendly (r = .19, $p < .05$), and negatively correlated with Social/Playful (r = -.45, $p < .01$) and Cautious (r = -.20, $p < .05$). Flexible/ Friendly was also positively correlated with Social/ Playful (r = .29, $p < .01$), and negatively correlated with Fearful/ Aggressive (r = -.54, $p < .01$), Uninterested (r = -.22, $p < .01$), and Cautious (r = -.29, $p < .01$). Social/Playful was negatively correlated with Fearful/ Aggressive (r = -.23, $p < .01$) and Uninterested (r = -.19, $p < .05$).

Sex, age, and subfamilies were entered into the first step of the logistic regression and the five behavioral facets were entered in the second step to predict success. Age (p = .63), sex (p = .21), and subfamilies (p = .13) did not significantly predict success. Fearful/Aggressive (B = -.37, SE =.16, $Wald$ = 5.48, p = .02) and Cautious (B = -.54, SE = .17, $Wald$ = 9.67, $p < .001$) significantly negatively predicted success. Individuals that were rated as more fearful or aggressive and individuals that were rated as more cautious were less likely to have success on the MAB. Flexible/ Friendly (B = .17, SE = .15, $Wald$

= 1.26, p = .26), Uninterested (B = -.09, SE = .15, $Wald$ = .348, p = .56), and Social/Playful (B = -.01, SE = .12, $Wald$ = .00, p = .97) were not significant predictors of success.

Table 4

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

The independent samples t-tests comparing subfamilies, Pantherinae and Felinae, for the five behavioral facets revealed no significant differences (all ps > .09).

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 behavioral traits that predict flexibility may facilitate captive husbandry strategies and especially conservation efforts. We examined whether captive carnivore behavioral traits predicted innovation, measured as success on a MAB. A twenty-seven-item keeper assessment survey reduced to five behavioral facets- Flexible/ Friendly, Fearful/Aggressive, Uninterested, Social/Playful, and Cautious.

Within felids, the most robust behavioral 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- our Social/Playful to their Sociable, our reverse-scored Cautious to their Dominant, and Fearful/Aggressive and Cautious to Curious. This consistency across studies suggests that felids may share similar trait structures. However, our study is important in suggesting that an individual's traits, rather than species differences, seem to predict success in the task. Evidence in other species supports this conclusion. Black rhinoceros individuals rated as more fearful also exhibited a longer latency to contact a novel object (Carlstead et al., 1999) and rainbow trout (*Onchorhyncus mykiss*) rated as shy but given emboldening experiences became bolder and exhibited reduced latencies to contact a novel object (Frost et al., 2007). In the current study, individuals that were rated as more fearful or aggressive and individuals that were rated as more cautious were less likely to have success on the MAB. However,

it is important to note that we tested success on only a single problem-solving task, so future research is needed to test the generalizability of these associations.

The behavioral traits assessed here were rated with reasonable reliability across keepers and predicted performance in the MAB, which measured innovation. Specifically, Fearful/Aggressive and Cautious predicted lack of success on the MAB. Highly fearful and cautious animals should be less likely to attempt solutions to novel problems, so these results were expected. Although most of the keepers completed the assessments with no knowledge of the subjects' performance, some keepers for ten subjects may have been influenced in their ratings by observing a subset of the experimental trials. Because we did not include the trait "intelligence" in our analyses, which was the trait that should be most influenced by the subject's performance, and because no keeper observed all trials, and each keeper had extensive experience of the subjects beyond observing them participate in these trials, we are not concerned that this biased our results. Ideally, 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 behavioral 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 behavioral 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 Flexible/Friendly and Social/Playful

to be predictive of success; however, this was not the case. We defined Flexible as "adapts comfortably to change," Friendly as "initiates proximity," and Curious as "readily explores new situations." Keeper ratings should be informed by knowledge of the animal's behavior in multiple contexts (e.g., shifting indoor and outdoor enclosures, proximity to zoo guests, etc.). Similarly, we defined Sociable as "seeks out companionship" and Playful as "initiates and easily joins in play." However, these terms may be related to age as younger cats were rated as more Social/Playful (r=-.45, p<.001), or to socially housed species, of which some of these subjects are not. It is possible that performance in a single problem-solving task is not a representative measure of the subject's more general abilities. Because neophobia may limit interaction with the novel puzzle box (e.g., coyotes; Young et al., 2019), the facets of fearful and cautious may have overshadowed other behavioral traits in predicting success. These results support previous findings suggesting that motivation and object exploration may be better predictors of success compared to cognitive ability or inhibitory skills (Johnson-Ulrich et al., 2018). This point is important given how frequently cognitive research is conducted to compare cognitive abilities between species (Vonk et al., 2021).

There are other nonsignificant 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 behavioral traits 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

Many studies of animal cognition have a low sample size (Shaw & Schmelz, 2017). To our knowledge, this study includes data from the largest and most inclusive sample of felids compared to previous studies of felid personality and cognition. Across the 14 Felidae species we assessed, a coherent behavioral trait structure was extracted involving five facets—Flexible/ Friendly, Fearful/Aggressive, Uninterested, Social/Playful, and Cautious. These facets are echoed in the Felidae literature as reviewed by Gartner and Weiss (2013). We report the first demonstration that these traits predicted problem-solving success on a test of innovation. Two facets—Fearful/Aggressive and Cautious—significantly negatively 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 behavioral traits measure. Felid behavioral trait research, in combination with cognitive testing, has practical applications for both captive welfare and wildlife conservation success.

CHAPTER 3

MULTI ACCESS PUZZLE BOX (MAB)

Puzzle boxes present a simple and efficient behavioral test for exploring cognition associated with problem solving and innovation (Chance, 1999). Developed in 1898 by E. L. Thorndike for his dissertation, *Animal Intelligence: An Experimental Study of the Associative Processes in Animals*, puzzle boxes contained the animal subjects, which then had to escape to access food that Thorndike placed in view outside of the box. He placed cats in 15 different wooden puzzle boxes that each required a different physical mechanism to escape (Thorndike, 1898). Thorndike noted the changes in the behaviors and timing of each cat's escape efforts; the cats learned that pressing a lever was the fastest way to escape the puzzle box and reach the fish reward. Based on this research, Thorndike proposed the "law of effect," the hypothesis that any behavior followed by pleasant consequences is repeated whereas any behavior followed by unpleasant consequences is stopped. Through this research, Thorndike laid the groundwork for the use of puzzle boxes to explore multiple facets of animal cognition, including exploratory behavior and persistence.

Benson-Amram, Weldele, and Holekamp (2013) presented a one-solution puzzle box to wild and captive spotted hyenas (*Crocuta crocuta*) and documented behavioral differences in exploratory behaviors, working behavior (persistence), and neophobia. These results suggest that behaviors associated with successful problem solving may differ in wild and captive populations of the same species; captive hyenas were more successful and more varied in their exploratory behaviors. Researchers speculate that

captivity shapes the expression of cognitive abilities (Laidre, 2008; Tomasello & Call, 2004), although the proposed mechanism varies. Bering (2004) has suggested that captivity may facilitate performance in some cognitive tasks through exposure to human artifacts. Other researchers have focused on the human/animal interaction. In a test battery with 103 orangutans (*Pongo spp.*), researchers predicted and found that individuals higher on the "human oriented index (HOI)," an assessment of comfortability with humans, would exhibit more exploratory behaviors, greater innovation, reduced neophobia, and success on a multi-step problem-solving task compared to those that scored lower on the HOI (honey tool-task; Damerius et al., 2017). Experiences with humans appear to affect species' cognitive abilities and behaviors associated with cognition.

Researchers have examined other factors that may predict problem-solving success. Benson-Amram et al. (2016) presented puzzle boxes to 39 captive species of the order Carnivora and determined that relative but not absolute brain size is related to better problem solving. They examined work time (persistence), behavioral (exploratory) diversity, and latency to approach (a measure of neophobia), but only work time was a significant predictor of success when brain volume and body mass were controlled (Benson-Amram et al., 2016). Borrego and Gaines (2016) presented spotted hyenas, African lions (*Panthera leo*), leopards (*Panthera pardus*), and tigers (*Panthera tigris*) with puzzle boxes. The social species, hyenas and lions, were more persistent in working on the puzzle box and were more successful than the asocial leopards and tigers (Borrego & Gaines, 2016). Puzzle box studies enable researchers to study problem-solving success

and its associated behaviors, but the results can be limited by the box's simplicity. In these studies, the box could be solved using only a single simple mechanism.

In contrast to single-solution puzzle boxes, multi-access puzzle boxes or 'MABs,' allow researchers to test innovation by requiring subjects to solve a novel problem and then use new solutions after past solutions become inaccessible. Auersperg and colleagues (2011) developed the original MAB to compare problem solving in keas (*Nestor notabilis*) and New Caledonian crows (*Corvus moneduloides*). The transparent box featured four mechanisms that each provided access to one food reward. Initially, the subjects could choose any of the four mechanisms, but after consistent success with a single option, that mechanism was blocked (Auersperg et al., 2011). Auersperg et al. (2011) examined differences in exploratory behaviors, learning, neophobia, innovation and inhibition using the MAB to compare cognitive traits at the individual-level and the species-level.

MAB studies assess whether individuals can produce new solutions to a task after old ones become obsolete, estimating the subjects' inhibition to refrain from using responses that no longer lead to success. Initially used almost exclusively with birds (*Corvidae*: Auersperg et al., 2011; *Estrilldidae:* Boogert et al., 2008; *Falconidae:* Biondi et al., 2008; *Paridae:* Griffin & Diquelou, 2015; Morand- Ferron & Quinn, 2011), use of the MAB has since been extended to mammals [monkeys (Golden-headed lion tamarin, *Leontopithecus chrysomelas,* Golden lion tamarin, *Leontopithecus rosalia,* Black lion tamarin*, Leontopithecus chrysopygus,* Emperor tamarin, *Saginua imperator,* Cottontop tamarin, *Saginua odepius,* Silvery marmoset, *Callithrix argentata,* White-headed marmoset*, Callithrix geoffroyi,* Day et al., 2003; Kendal et al., 2005), great apes

(chimpanzees, *Pan troglodytes*, Western lowland gorillas, *Gorilla gorilla gorilla*, bonobos, *Pan paniscus,* and orangutans, *Pongo abelii,* Manrique et al., 2013), meerkats (*Suricata suricatta,* Thornton & Samson, 2012), spotted hyenas (Johnson-Ulrich et al., 2018), raccoons (*Procyon lotor*, Daniels et al., 2019), coyotes (*Canis latrans,* Garcia et al., 2022), Asian elephants (*Elephas maximus,* Jacobson et al., 2022), African lions and snow leopards (*Panthera uncia,* O'Connor et al., 2022)].

MAB studies are limited even further in terms of use with carnivores as only eight published studies (two of the same data set) are available (Daniels et al., 2019; Garcia et al., 2022; Johnson-Ulrich et al., 2018, 2020, 2021; O'Connor et al., 2022; O'Connor & Vonk, 2022; Parsons et al., 2022). Whereas spotted hyenas have been documented as successful problem-solvers with one-solution puzzle boxes (Benson-Amram et al., 2013), Johnson-Ulrich et al. (2018, 2020) were the first to test hyenas with a MAB. Individuals demonstrated repeated innovation, opening the box with more than one solution. Successful individuals displayed behavioral repertoires of high persistence, high motor diversity (exploratory behavior), high activity, and low neophobia. Subsequently, Daniels et al. (2019) discovered that raccoons can learn to use more than one mechanism, exhibiting a range of behaviors directed towards the box (2019). Coyotes demonstrated changes to their behavioral budgets with increased boldness, persistence, and time resting (Parsons et al., 2022), and exploratory behaviors decreased when coyote pups reached the age of dispersal (Garcia et al., 2022). The performance of African lions and snow leopards (O'Connor et al., 2022) echoed the performance of raccoons (Daniels et al., 2019) and spotted hyenas (Johnson-Ulrich et al., 2018); cats that were successful on MABs were highly persistent, had high levels of exploratory diversity, and low

neophobia. Carnivores exhibit individual-level and species-level behavioral differences associated with success, and display evidence of learning and repeated innovation.

Higher Encephalization as a Predictor of Behavioral Flexibility

Comparative studies have examined neuroanatomical measures thought to be related to cognition. Mammals have brains that are significantly larger than expected for their body mass (González-Lagos, et al., 2010), which is metabolically expensive (Isler & van Schaik, 2006, 2009). It is theorized that larger brains evolved as an adaptation to their environment (Reader & Laland, 2003; Sol et al., 2005). In 1973, Jerison proposed the encephalization quotient, which is a measure of species' brain size relative to body mass (i.e., larger observed brain size than expected for body mass). Larger relative brain size has been linked to better problem solving in carnivores (Benson-Amram et al., 2016) and increased encephalization has been linked to greater behavioral flexibility in a variety of species (Finarelli & Flynn, 2007). Carnivore species with higher encephalization may exhibit greater behavioral flexibility on a problem-solving task than those with lower encephalization. Thus, to build on previous studies, I used brain volume, body mass, and encephalization quotient (EQ) measures (from Finarelli & Flynn, 2007) to investigate the problem-solving success and cognitive behaviors of different species.

Conservation Status as a Predictor of Behavioral Flexibility

Whereas the aforementioned studies (e.g., Benson-Amram et al., 2013; 2016; Borrego & Gaines, 2016; Daniels et al., 2019; Johnson-Ulrich et al., 2018; 2020; O'Connor et al., 2022) examined the cognitive behaviors associated with success using a puzzle box, this study seeks to use MABs to investigate carnivore cognition, specifically problem solving and innovation, through the lens of conservation status. The

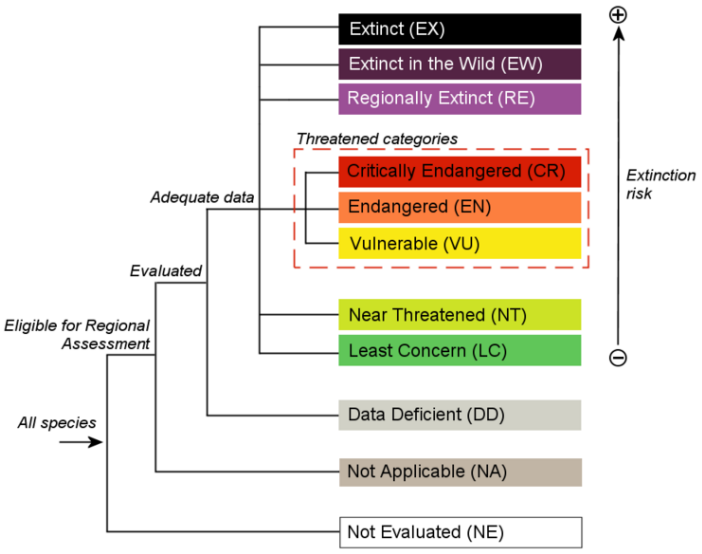
International Union for Conservation of Nature Red List of Threatened Species, hereafter the IUCN Red List, “is a clarion call to action in the drive to tackle the extinction crisis, providing essential information on the state of, and trend in, wild species” (Vié et al., 2009, p. 1). Since its inception in the 1950s by the Species Survival Commission of the World Conservation Unit (Rodrigues et al., 2006), the IUCN Red List has been recognized as the most comprehensive biodiversity categorization system that annually updates the conservation status of plant and animal species. It intends to identify and document species at risk to raise awareness and to direct conservation actions for species in need. The IUCN Red List has nine categories of decreasing biodiversity loss: not evaluated, data deficient, least concern, near threatened, vulnerable, endangered, critically endangered, extinct in the wild, and extinct (see Figure 6). Species may be considered “not evaluated” or “data deficient” until the IUCN has adequate data to support a label. To meet at-risk criteria, or to be labeled critically endangered, endangered, and vulnerable, the organization uses five independent criteria to rank species population loss: (1) high decline rate, (2) small range area and decline, (3) small population size and decline, (4) very small population size, and (5) unfavorable quantitative analysis (Mace et al., 2008). Those individuals at a higher risk of extinction, or higher on the IUCN Red List, may have poor behavioral flexibility, or an inability to adapt to changing environments. Thus, I analyzed how conservation status of each species tested using the IUCN Red List predicted multiple measures of performance of individuals of those species.

In 2008, researchers used IUCN data to estimate that the population of one in every two species are declining and one in four species is threatened with extinction

(Schipper et al., 2008). Twenty-five percent of all mammals with adequate data under the IUCN are threatened with extinction (*n*= 1139; Schipper et al., 2008); however, the status of 836 data deficient species is undetermined. Mammals are highly sensitive to anthropogenic changes as their conservation efforts tend to require unrestricted geographic ranges, uninhabited and untouched land, water and other resources, political power, and financial backing (Ceballos et al., 2005). Unfortunately for mammals, continents with higher biodiversity like South America and Africa are divided geographically into countries with different political systems, conservation goals, and that are financially and politically slower to develop (Ceballos et al., 2005). These areas are disproportionately affected by large mammal, particularly carnivore, harvesting (Schipper et al., 2008).

Figure 6

The International Union for Conservation of Nature Red List Categories and Criteria



Note. Reprinted from the International Union for Conservation of Nature Red List of Threatened Species (IUCN, 2023).

In the wild, carnivores are particularly susceptible to habitat loss, parasites, and diseases, hunted for sport, and victims of human-wildlife conflict (MacDonald, 2016; Valeix et al., 2012). Captivity, or the collection of animals, arose out of the human desire for entertainment (Koebner, 1994) but continues in part to provide institutional support for the preservation of biodiversity. Conservation programs depend upon decisions regarding captive individuals' adaptability. Empirical efforts seek to understand the cognitive abilities of the species; determining a good predictive test to properly measure adaptability is crucial for ensuring current protections in the wild and to plan for their futures. These species are socially, ecologically, and morphologically diverse, exhibit diverse behaviors, and as such, make an excellent model system for investigating cognition in species under a range of selective pressures (Bekoff et al., 1984; Borrego, 2017; Ewer, 1973). Studying carnivores in captivity allows us to better understand their behaviors and cognitive abilities.

Method

The materials, methodology, and some the subjects are those used in previously published work (O'Connor et al., 2022) and in Chapter 2 of this dissertation (O'Connor & Vonk, 2022).

Subjects. I tested 65 individuals representing 17 species of carnivores from four families- canids, felids, procyonids, and hyaenids (see Table 5) at five locations: the Bergen County Zoo (BCZ) in Paramus, NJ (n= 6), the Bronx Zoo (BZ) in Bronx, NY (n= 10), the Creature Conservancy (CC) in Ann Arbor, MI (n= 3), the Oklahoma City Zoo (OKC) in Oklahoma City, OK (n= 23), and the Turtle Back Zoo (TBZ) in West Orange, NJ (n= 25). The subjects' ages ranged from six months to 23 years old (M = 6.47, SD =

5.55). There were 38 males and 29 females in the sample. One subject was from the Canidae family, 61 subjects were from the Felidae family, three subjects were from the Hyaenidae family, and two subjects were from the Procyonidae family.

Three individuals not included in Table 5 were removed from testing prior to completing condition 1 due to safety concerns (i.e., ingesting pieces of the MAB). Although Sumatran tiger, "Bob," completed condition 1, he was removed from trials in condition 2 and only the first condition was scored. Similarly, spotted hyena, "Kiira," was scored on only her completed conditions 1 and 2 as she was removed from trials in condition 3. For Sumatran tiger, "Kami," she broke the box in the first trial of her third condition, successfully opening a previously solved solution; upon box repair and continuation, she had 10 (instead of nine) successful trials for coding. For coyote, "Cooper," and Siberian lynx, "Nanai," the first trials in the first conditions were not recorded due to technological issues; those trials were coded only for success.

Table 5

MAB Subjects and their Species, Sex, Age, and Zoo Location

Name	Species	Sex	Age (yrs)	Zoo Location
Amara	African lion	F	5	TBZ
Bahati	African lion	M	5	BZ
Demarcus	African lion	M	4	TBZ
Dunia	African lion	F	6	OKC
Huey	African lion	M	10	OKC
Ime	African lion	M	5	BZ
Moto	African lion	F	6	OKC
Sukari	African lion	F	15	TBZ
Thulani	African lion	M	5	BZ
Annika	Amur leopard	F	5	TBZ
Nadya	Amur leopard	F	0.5	TBZ
Valeri	Amur leopard	M	7	TBZ

Table 5 -- Continued

Name	Species	Sex	Age (yrs)	Zoo Location
Astrid	Bobcat	F	23	TBZ
Dodger	Bobcat	M	2	OKC
ZZ	Caracal	F	18	OKC
Alvin	Cheetah	M	1	TBZ
Boomer	Cheetah	M	5	OKC
Nandi	Cheetah	F	1	TBZ
Pete	Cheetah	M	5	OKC
Simon	Cheetah	M	1	TBZ
Theodore	Cheetah	M	1	TBZ
JD	Clouded leopard	M	3	OKC
Jye	Clouded leopard	M	1	TBZ
Madee	Clouded leopard	F	0.5	TBZ
Mali	Clouded leopard	F	1	TBZ
Rukai	Clouded leopard	F	3	OKC
Chinook	Cougar	M	4	BCZ
Harper	Cougar	F	5	TCC
Jane	Cougar	F	1	TBZ
Josey	Cougar	F	1	TBZ
Sage	Cougar	F	15	TBZ
Tacoma	Cougar	M	4	BCZ
Toho	Cougar	M	3	OKC
Tonka	Cougar	M	6	OKC
Wyatt	Cougar	M	1	TBZ
Cooper	Coyote	M	6	CC
Boon	Fishing cat	M	7	OKC
Chet	Fishing cat	M	12	OKC
Miri	Fishing cat	F	15	OKC
Puddles	Fishing cat	M	4	OKC
Rosa	Jaguar	F	9	TBZ
Tai	Jaguar	M	17	OKC
Arieta	Ocelot	F	8	OKC
Old Man	Ocelot	M	20	BCZ
Makusi	Ocelot	M	1	BCZ
Raif	Ocelot	M	8	OKC
Bosco	Serval	M	13	OKC
Nanai	Siberian lynx	M	½	TCC
Chameli	Snow leopard	F	6	TBZ
Gala	Snow leopard	M	4	TBZ
K2	Snow leopard	F	8	BZ
Khyber	Snow leopard	F	1	BZ

Table 5 -- Continued

Name	Species	Sex	Age (yrs)	Zoo Location
Leo	Snow leopard	M	13	BZ
Mike	Snow leopard	M	4	BZ
MJ	Snow leopard	M	2	BZ
Tanja	Snow leopard	F	18	BZ
Willie	Snow leopard	M	5	BZ
Kamaria	Spotted hyena	F	6	TBZ
Kiira	Spotted hyena	F	6	TBZ
Niru	Spotted hyena	M	3	TBZ
Bob	Sumatran tiger	M	0.5	OKC
Kami	Sumatran tiger	M	14	OKC
Lola	Sumatran tiger	F	10	OKC
Luna	Sumatran tiger	F	0.5	OKC
CoatiA	White-nosed coati	F	14	BZ
CoatiB	White-nosed coati	F	14	BZ

Note. Italicized subjects were not included in Chapter 2.

Species-level factors (see Table 6) included IUCN status, sociality, brain volume, body mass, and encephalization quotient. Brain volume, body mass, and encephalization quotient (EQ) for species were extracted from previously published data (Finarelli & Flynn, 2009), which has been applied to analyzing performance in a puzzle box experiment with carnivores (Benson-Amram et al., 2016).

Table 6

Species-level Measures for MAB

Species	Scientific Name	IUCN Status	Sociality	Brain Volume	Body Mass	EQ
African lion	*Panthera leo*	Vulnerable	social	223.63	161.5	2606.68
Amur leopard	*Panthera pardus orientalis*	Critically Endangered	asocial	125.21	52.04	1354.37
Bobcat	*Lynx rufus*	Least Concern	asocial	57.97	8.9	558.06
Caracal lynx	*Caracal caracal*	Least Concern	asocial	55.15	13.75	546.38
Cheetah	*Acinonyx jubatus*	Vulnerable	asocial	111.05	50	1198.03
Clouded leopard	*Neofelis nebulosa*	Vulnerable	asocial	68.71	19.68	697.02
Cougar	*Puma concolor*	Least Concern	asocial	125.21	51.6	1353.61
Coyote	*Canis latrans*	Least Concern	social	88.23	13.41	872.66
Eurasian lynx	*Lynx lynx*	Least Concern	asocial	70.11	17.95	706.91
Fishing cat	*Prionaliurus viverrinus*	Vulnerable	asocial	46.53	9.14	448.72
Jaguar	*Panthera onca*	Near Threatened	asocial	151.41	100	1709.91
Ocelot	*Leopardus pardalis mitis*	Least Concern	asocial	63.43	11.9	622.44
Serval	*Leptailurus serval*	Least Concern	asocial	56.8	12	557.69
Snow leopard	*Panthera uncia*	Vulnerable	asocial	101.49	44.17	1085.98
Spotted hyena	*Crocuta crocuta*	Least Concern	social	144.03	63	1577.71
Sumatran tiger	*Panthera tigris sumatrae*	Critically Endangered	asocial	70.11	17.95	3249.53
White-nosed coati	*Nasua nasua*	Least Concern	social	278.66	162.56	272.99

MAB Apparatus. I used two custom molded Starboard MABs with stainless-steel frames measuring 0.6m x 0.6m x 0.6m and 0.38m x 0.38m x 0.38m (see Figures 2-4 in Chapter 2). The larger MAB was used for large carnivores (i.e., African lion, Amur tiger, snow leopard), while the smaller MAB was used for small carnivores and juveniles (e.g., bobcats, clouded leopard, fishing cat). While Benson-Amram et al. (2016) used

measures of manual dexterity to ensure that physicality did not play a role in problem-solving success, no measure was used here as Benson-Amram et al. found their puzzle box to be equally difficult across a range of carnivores. Additionally, upon completion of trials, some individuals who did not solve all three solutions were randomly selected to receive the puzzle box. Their unsolved doors were either slightly opened (i.e. Solutions 2 and 3) or baited (i.e. smeared blood/ food on Solution 1) to ensure that species could physically open doors.

The contents of the boxes (i.e., food rewards from the subjects' regular diet) were accessible via three separate solutions:

Solution 1 (Push Door Technique). The box was opened by pushing on a spring-loaded door with hinges inside of the box. When pressure was applied to the door, the door swung down flat into the box (see Figure 2 in Chapter 2).

Solution 2 (Pull Rope Technique). A spring-loaded latch held a hinged door closed. A detachable rope was attached to the latch. To open the door, the subject grasped the rope and pulled away from the box at a 180º angle. Pulling the latch in the correct direction by the rope triggered the door to open (see Figure 3 in Chapter 2).

Solution 3 (Pull Door Technique). The box could be opened by pulling down a door on the side of the box. A lip at the top of the door was pulled down to open the entire side of the box. Hinges were attached along the base of the door to create resistance to open the door. The door was also held to the box frame with waterproof magnets. This encouraged the cats to apply a substantial amount of pressure to open the door (see Figure 4 in Chapter 2).

Procedure. Testing of these subjects was approved by the institutional IACUCs of Miami Zoo (2022-11), Oakland University (Protocol 19111), and Oklahoma City Zoo (see Appendix B). All subjects were tested individually in their home indoor, or outdoor, off-exhibit holding enclosures. Although the MAB could be left unbolted in enclosures, due to safety concerns, the box was bolted for certain species (e.g., tigers, lions, hyenas). Ultimately, this protocol was at the zoo's discretion, but I recommended a similar procedure for animals of similar sizes and strengths. The puzzle box was cleaned and disinfected between different species' trials. The camera was set up such that all interactions with the MAB and the entrance into the testing enclosure were documented. Filming started before the subject entered the enclosure and ended after trial completion with a maximum time of 15 minutes. See Chapter 2 for a more detailed procedure on the three conditions.

Data Coding. As with previous work (O'Connor et al., 2022), the following measures were coded by at least two trained student volunteers who were naïve to the hypotheses: (1) success, (2) repeated innovation, (3) persistence, (4) contact latency, (5) latency to success, and (6) exploration diversity (see Table 7). IUCN status, sociality, brain volume, body mass, and encephalization quotient were entered as predictors of these behavioral outcomes and number of successful solutions using multilevel linear mixed models. The presence or absence of all behaviors was coded and extracted using BORIS v8 software for behavioral coding (Friard & Gamba, 2016).

Table 7

MAB Behavioral Measures

Measure (level)	Definition
Success	Opening the MAB on a given trial (binary outcome- success or no success); the ratio of successful trials to total trials for each subject (ordinal outcome)
Repeated Innovation (subject)	Score of 0-3 indicating the number of solutions learned (Epstein, 1987)
Persistence (trial)	Ratio of time spent actively working on the MAB to total trial time (Borrego & Gaines, 2016); actively working on the MAB is spending time making physical contact with the MAB, or within 0.05 meters of the MAB; smaller on successful trials (less than 900 seconds) than on unsuccessful ones, where the denominator is always 900 seconds (O'Connor et al., 2022)
Contact Latency (trial)	Time from entering testing enclosure until the subject contacts or approaches within 0.05 meters of the MAB (Griffin & Guez, 2014; Johnson-Ulrich et al., 2018); used to measure Neophobia
Latency to Success (trial)	If successful, time taken to open the MAB from the contact latency start (Chow et al., 2016)
Exploration Diversity (trial)	Scored as sum of behaviors representing the level of exploration of a subject; the more behaviors present, the higher the score (Benson-Amram et al., 2013; Borrego & Gaines, 2016). Behaviors included: 'circling', 'pawing on top', 'pawing at sides', 'biting/licking', 'stalking', and 'standing on top'

Note. Definitions of important terms and summary of behavioral measures.

In addition to these outcomes, this study used IUCN conservation status (four levels: 2= least concern, 3= near threatened, 4= vulnerable, 6= critically endangered; no species were rated on levels 1= data deficient/ not evaluated, 5= endangered, 7= extinct in wild, or 8= extinct) as a predictor of innovation. Given the large number of species

represented in this data set, there is a unique opportunity to investigate conservation status as a predictor of variability in responding. I hypothesized that those species that the IUCN identified as "Least concern" will be better problem solvers on the MAB than those at higher risks of extinction. Conservation status as reported by the IUCN may be indicative of their cognitive processes in the wild. Individuals that represent species at risk of extinction will be unable to successfully exhibit repeated innovation, indicative of their poor survival rate in the wild due to their inability to innovate in the face of anthropogenic change. Specifically, species including but not limited to spotted hyenas (Least concern), coyotes (Least concern), and cougars (Least concern) will be better problem solvers and innovators than Sumatran tigers (Critically endangered) and Amur leopards (Critically endangered). Additionally, I utilized the species-level variables brain volume, body mass, and encephalization quotient as applied by Benson-Amram et al. (2016) to investigate whether larger relative brain size, controlling for body mass, was predictive of problem-solving success across 39 species of carnivores on a puzzle box task. Brain volume, body mass, and encephalization quotient values are as used by Benson-Amram et al. (2016), as reported by Finarelli and Flynn (2009). I hypothesized that species with higher encephalization would be more successful and exhibit more problem-solving behaviors than species with lower encephalization.

Results

Data were analyzed using IBM SPSS v. 28 software and HLM 6 Hierarchical Linear and Nonlinear Modeling (Raudenbush et al., 2000). A logistic regression was run to determine the association between sex (0 = male, 1= female) on success (0 = no trials solved, 1 = at least one trial was successful using any of the access points). Two chi-

square tests for independence were conducted to discover if there was an association between a) sex and b) species on repeated innovation (0-3= number of mechanisms solved). Four multilevel linear mixed models (MLMM) on the continuous outcomes of contact latency, latency to success, exploration diversity, and persistence for each trial were conducted to examine the association of factors at the level of the individual (sex), which were nested within the level of species. Species level factors included IUCN status (4 levels: 2 = least concern, 3= near threatened, 4 = vulnerable, 6= critically endangered), sociality (0 = not social, 1 = social), brain volume, body mass, and encephalization quotient. The first step of the model involved the estimation of a regression equation for each subject at level 1 to provide intercept and slope coefficients, which served as an index of the association between sex and the outcome variables. No interactions were included in the model because my hypotheses were centered around the main effects, primarily of the level 2 species variables. Fixed effects were estimated with robust standard errors.

Reliability and Correlations. The following reliabilities do not include data used in O'Connor et al. (2022), which reported high reliabilities on the same measures. High reliabilities are reported here using Intraclass Correlations (ICC) examining consistencies between raters for latency to success ($ICC(3, 61) = .97$, $p < .001$), contact latency ($ICC(3, 31) = .83$, $p < .001$), and persistence ($ICC(3, 61) = .78$, $p < .001$). Exploration diversity was not adequately reliable ($ICC(3, 61) = .41$, $p = .02$). Excellent reliability was obtained for success with Cohen's Kappa ($\kappa = 0.94$, $p < .001$).

Success Frequencies. On the puzzle box, 33 subjects (49.3%) solved zero conditions, 19 subjects (28.4%) solved one condition, six subjects (9.0%) solved two

conditions, and nine subjects (13.4%) solved all three conditions. African lions (n = 6/9), Amur leopards (n = ¼), bobcats (n = ½), caracal (n = 1/1), cougars (n = 8/9), coyote (n = 1/1), fishing cats (n = 3/4), jaguars (n = ½), ocelots (n = ¼), spotted hyenas (n = 2/3), Siberian lynx (n = 1/1), Sumatran tigers (n = 1/4), snow leopards (n = 4/9), and white-nosed coatis (n = 2/2) solved at least one solution of the MAB, with African lions (n = 2), Amur leopard (n = 1), bobcat (n = 1), cougars (n = 2), coyote (n = 1), jaguar (n = 1), spotted hyena (n = 1), Siberian lynx (n = 1), Sumatran tiger (n = 1), snow leopards (n = 3) solving multiple conditions. Cheetahs (n = 0/6), clouded leopards (n = 0/5), and serval (n = 0/1) did not succeed with any mechanism of the puzzle box.

Descriptives and Correlations. Descriptive statistics and zero-order correlations among the variables are shown in Table 8. Sex (1 = male, 2 = female) was positively correlated with success (r = .15, p < .01), persistence (r = .12, p < .05), and exploration diversity (r = .13, p < .01), and negatively correlated with latency to success (r = -.17, p < .01). Age was not significantly correlated with any other variables. Success (dichotomous) was positively correlated with persistence (r = .60, p < .01), and negatively correlated with latency to success (r = -.92, p < .01), contact latency (r = -.16, p < .01), and exploration diversity (r = -.11, p < .05). Latency to success was positively correlated with contact latency (r = .15, p < .01), persistence (r = .63, p < .01), and exploration diversity (r = .18, p < .01). Contact latency was negatively correlated with persistence (r = -.22, p < .01).

Success and Repeated Innovation. A logistic regression to determine the association between sex (0 = male, 1= female) on success (0 = no trials solved, 1 = at least one trial was successful using any of the access points) was not significant (χ^2 (1) =

0.79, $p = .36$). Two chi-square tests for independence were conducted to test for associations with the variables, species and sex with repeated innovation (0-3= number of solutions solved for each subject). There were no significant associations between sex and repeated innovation (χ^2 (3) = 4.31, $p = .23$). However, species significantly differed on the number of MAB solutions solved (χ^2 (48) = 71.04, $p < .05$) and success ratio (χ^2 (288) = 2.29, $p < .01$).

Table 8

Descriptive statistics and correlations among variables on the MAB

	1	2	3	4	5	6	7
1. Sex	-						
2. Age	.19	-					
2. Success	.15**	-.09	-				
3. Latency to Success	-.17**	.01	-.92**	-			
5. Contact Latency	-.06	.17	-.16**	.15**	-		
6. Persistence	.12*	-.09	.60**	.63**	-.22**	-	
7. Exploration Diversity	.13**	.04	-.11*	.18**	-.09	.09	-
Mean	1.51	6.47	0.49	545.59	31.37	0.39	10.06
Standard Deviation	0.50	5.55	0.50	388.54	122.09	0.34	17.41

Note. * $p < .05$; ** $p < .01$

Latency to Success. If the individual was not successful on a given trial, a value of 900s was assigned to indicate the maximum length of a trial; this ensured that lower latencies were representative of faster success. At level 1, sex ($b = -62.65$, $p = .27$) was

not a significant predictor of latency to success. At level 2, sociality (b = -117.72, p = .16), brain volume (b = 22.19, p = 0.30), and encephalization quotient (b = -2.37, p = .21) were not significant predictors of latency to success; IUCN status approached significance (b = 63.04, p = .06) with more endangered animals being slower to achieve success. Body mass (b = 6.72, p = .01) was a significant predictor of latency to success indicating that smaller individuals were faster to access a reward.

Contact Latency. If subjects were never within 0.05 meters of the MAB within a given trial, a value of 900s was assigned to indicate the maximum length a trial; this ensured that lower contact latencies were representative of less neophobia, and an absence of contact was representative of more neophobia. At level 1, sex (b = -21.48, p = .16) was not a significant predictor of contact latency. At level 2, IUCN status (b = -9.30, p = .51), sociality (b = -3.73, p = .86), brain volume (b = 3.16, p = 0.74), body mass (b = 0.08, p = .96), and encephalization quotient (b = -0.26, p = .77) were not significant predictors of contact latency.

Persistence. At level 1, sex (b = 0.05, p = .37) was not a significant predictor of persistence. At level 2, IUCN status (b = 0.03, p = .10), and brain volume (b = -.03, p = .09) were not significant predictors of persistence. Sociality (b = 0.19, p = 0.002), body mass (b = -0.01, p < .001), and encephalization quotient (b = 0.003, p = 0.05) were significant predictors of persistence. These results indicate that species that were social, had lower body mass and had a higher encephalization quotient were more persistent.

Exploration Diversity. At level 1, sex (b = 2.92, p = .25) was not a significant predictor of exploration diversity. At level 2, IUCN status (b = .14, p = .96), sociality (b = -3.77, p = .51), brain volume (b = -.26, p = .87), body mass (b = .10, p = .79), and

encephalization quotient (b = .02, p = .91) were not significant predictors of exploration diversity.

Discussion

As the largest multi-access puzzle box experiment in carnivores, this study incorporates data from O'Connor et al. (2022) for two species of carnivores (African lions and snow leopards) and builds upon both Benson-Amram et al.'s (2016) study involving single solution puzzle boxes for 39 carnivore species, and Borrego and Gaines' (2016) study using a single-solution puzzle box for four carnivore species using similar measures. The findings of this study contribute to the literature by providing evidence of species-level behavioral differences of innovative problem solving in captive carnivores. Fourteen species demonstrated innovation by initially opening the MAB, and 10 species exhibited repeated innovation by opening multiple solutions on the MAB. Three species (cheetahs, clouded leopards, and servals) did not successfully reach criterion for condition 1; however, individuals in all three species (2/6 cheetahs, 4/5 clouded leopards, and 1/1 serval) successfully opened solutions during initial trials on the MAB. In Benson-Amram et al. (2016), cheetahs were unsuccessful, whereas servals were successful in reaching criterion on the single solution MAB; no clouded leopards were tested. Evolutionary theories of cognition predict differences in abilities, such as innovation and problem solving, as a function of different ecological and social demands, but the extent to which these demands operate as selective pressures remain unclear.

In this experiment, sex was not a predictor of latency to success, contact latency, persistence, or exploration diversity. Some studies have documented males innovating more than females (e.g., Thornton & Samson, 2012), whereas other studies have

documented females innovating more than males (Reader & Laland, 2000). In a meta-analysis across non-human taxa, Amici et al. (2019) found that sexual dimorphism played a role in innovation; individuals were more innovative, neophilic, and explorative if they were of the larger sex rather than individuals of the smaller sex. However, there are several studies, in addition to the current experiment, that have found no effect of sex on innovation (Benson-Amram & Holekamp, 2012; Benson-Amram et al., 2013; Johnson-Ulrich et al., 2018; Johnson-Ulrich et al., 2020). The physical, ecological, and social pressures faced by males and females differ, and thus, I did expect differences between the sexes in their behaviors. Innovativeness may allow species to better exploit resources in their environments, which allows for better adaptation to captive environments and expansion in wild environments. Of importance to note, of the 17 species tested, four species had representatives of only one sex (caracal, coyote, serval, white-nosed coati) so I could not examine interactions of sex with species or species level variables. Future studies with larger sample sizes should include both sexual body size dimorphism, and whether species are ecological generalists or specialists in both diet and habitat; results could dismiss sexual dimorphism and purport generalists as better innovators, solidifying ecological pressures as having a significant role in shaping species' cognitive abilities.

Living with conspecifics results in challenges, potentially selecting for cognitive abilities that aid in successful navigation of these challenges (Byrne & Whiten, 1988). Here, sociality predicted persistence, with social species spending more time actively working on the MAB than asocial species. In addition, persistence was highly and positively correlated with success. Other research supports these results suggesting that persistence may assist in generating novel solutions to a problem (e.g., Johnson-Ulrich et

al., 2018; Thornton & Samson, 2012). Social species profit from the skills ascertained in maintaining relationships with conspecifics. With a MAB, dominant coyotes, which are presumably more successful in governing social dynamics, were more persistent than subordinate coyotes (Young et al., 2019b). Borrego and Gaines (2016) compared African lions, spotted hyenas, African leopards, and tigers on a single solution puzzle box finding that social species (African lions and spotted hyenas) were more persistent and more successful than asocial carnivores (African leopards and tigers). However, these studies are of the few providing evidentiary support in carnivores with much of the literature coming from more socially complex species (e.g., birds and primates). Thus, while they corroborate the finding that sociality predicts persistence, caution should be taken when generalizing these results. Additional evidence nullifying or supporting the role of sociality in the evolution of cognitive abilities would come with the inclusion of closely related species varying in their sociality, such as striped hyenas and aardwolves (asocial members of Hyaenidae), grey wolves, foxes, maned wolves (social pack, monogamous, asocial, respectively, members of Canidae), red pandas and kinkajous (asocial members of Procyonidae). As with previous studies (e.g., Borrego & Gaines, 2016), the social species here (with the exception of lions) came from different families than the rest of the subjects.

Whereas brain volume was not a significant predictor of any of the outcomes, individuals with a lower body mass had shorter latencies to success and were more persistent. These results support Benson-Amram et al.'s (2016) finding of individuals of smaller body-sized species to be more successful at opening the puzzle box than larger body-sized individuals. Larger animals are not more successful simply due to having a

larger brain; rather, it is the relation of brain size to body mass that likely plays a key role in the evolution of cognition abilities. Encephalization has been documented in carnivores with Felidae having increased encephalization among smaller taxa (Finarelli & Flynn, 2009). Increased encephalization has been linked to greater behavioral flexibility in a variety of species (Finarelli & Flynn, 2007; Lefebvre et al., 2004; Sol et al., 2005). Here, increased encephalization was a significant predictor of persistence, again paralleling research by Benson-Amram et al. (2016) establishing work time (persistence) as a significant predictor of carnivores' success on a MAB when brain volume and body mass were controlled for (Benson-Amram et al., 2016).

Contrary to predictions, IUCN status was not a predictor for measures related to innovative success on the MAB. I hypothesized that individuals at a higher risk of extinction, or higher on the IUCN Red List, would have poor behavioral flexibility, expressed as poor success on the MAB. It is likely that an inability to adapt to changing anthropomorphic environments results in a higher spot on the IUCN Red List. Further analyses should examine *why* individuals are on the IUCN Red List rather than *what* category they were ranked. For example, coyotes do incredibly well in urban environments (Gehrt, 2011), and are of least concern on the IUCN Red List with an increasing population, whereas red wolves (*Canis rufus*), although being closely related, socially parallel, and occupying comparable niches, are critically endangered on the IUCN Red List with less than 50 wild individuals (Hinton et al., 2017). Red wolf populations are in extreme danger because of hybridization with coyotes (Kelly et al., 1999), which was not detected until 1992 (Phillips et al., 1995), and as a result of human-wildlife conflict (Serenari & Taub, 2019). Here, American wildlife biologists were not

able to protect the species before realizing how critical the population level was, as they have been able to do with other populations (e.g., grey wolf reintroductions). Similarly, species hold different levels of significance between countries, affecting their conservation efforts.

While contact latency was negatively correlated with latency to success, there were no other effects on contact latency or exploration diversity. This is in contrast to findings from previous puzzle box tasks in carnivores (Benson-Amram & Holekamp, 2012; Borrego & Gaines, 2016; Daniels et al., 2019; Garcia et al., 2022; O'Connor et al., 2022), which found that neophobia significantly inhibited problem-solving success. All species exhibit neophobia to novelty in their environment (e.g., approaching potentially dangerous physical aspect or conspecific); thus, its insignificance here is puzzling. It is difficult to speculate why contact latency and exploration diversity were not significantly predicted by the factors I examined. Potentially, persistence was a more significant predictor as it incorporated species that did not interact much, if ever with the box. Regardless, these findings open up possibilities for future research for replicability and expansion. Additional subjects would ensure a more diverse genetic pool of species with subjects across ages representing both sexes. As IUCN status was not a clear predictor, further studies might examine the technical intelligence hypothesis (Bryne, 1997), which states that cognitive abilities evolved to assist species in adapting to their environments, using foraging factors such as territory size and hunting style. Additional measures such as rearing and other aspects of sociality might support other hypotheses such as the cognitive buffer hypothesis (Sol, 2009), which suggests that cognition evolved as a result of diverse social and ecological demands as part of changing environments. Additional

sample sizes with comparisons of carnivores that overlap ecologically, such as African lions, hyenas, and cheetahs, or Amur leopards and Amur tigers, can potentially shed light on why cognitive abilities evolved.

Overall, these findings contribute to the literature on cognitive abilities in carnivores. To summarize, persistence was predicted by sociality, smaller body size, and increased encephalization. A shorter latency to success was also predicted by a smaller body mass. This research provides support to previous studies in using a MAB as a means of measuring cognitive abilities (Daniels et al., 2019; Johnson-Ulrich et al., 2018, 2020, 2021; O'Connor et al., 2022), incorporating O'Connor et al.'s (2022) existing data and supporting Benson-Amram et al.'s (2016) theories related to the evolution of cognitive abilities. Whereas no single evolutionary theory explained species-level differences, variances in sociality, body mass, and encephalization quotient predicted carnivore problem-solving behavior suggesting fruitful directions for future research.

CHAPTER 4

IMPOSSIBLE TASK

Within captive-born species, there is information to support the powerful impact of ontogeny on behavior; captive-born species are less likely to succeed in the wild (Jule et al., 2008), displaying reductions in natural behaviors and an overall decrease in fitness (Willoughby & Christie, 2018). Specifically, captive-reared jaguars (Hunter & Rabinowitz, 2009), cougars (Ross & Jalkotzy, 1995), and cheetahs (Maruping, 2011) have failed to thrive in reintroductions to the wild (as reviewed in Jule et al., 2008). For example, captive-born carnivores have low survival rates if reintroduced to the wild; compared to wild-born carnivores, captive-born carnivores are habituated to humans and susceptible to starvation, unsuccessful predator/competitor avoidance, and disease (Jule et al., 2008). Studies documenting how poorly suited captive-born species are in adjusting to the wild (Beck et al., 1994; Mathews et al., 2005) reveal an inability to adapt to changing environments. Hand-rearing by humans occurs in captivity when animal mothers are unable, unwilling, or not permitted to rear their young (e.g., Kelling et al., 2013), or as the result of a choice to create captive animals amenable for educational use (Boyd et al., 2017). Hand-rearing involves intense bonding with humans and, thus, some natural behaviors, including those related to cognitive abilities, may be lost (Bloomsmith et al., 2006; Brent et al., 1995; Hirata & Celli, 2003; Ploj et al., 2003; Morimura & Mori, 2010). For example, hand-reared carnivores may become more dependent upon humans for the provision of food (e.g., Nájera et al., 2015) and may lose abilities to procure their own food (e.g., Huber, 2010). Decreases in persistence and requests for assistance during

a problem-solving test that is unsolvable can demonstrate these effects. I tested 14 hand-reared individuals of seven species of the Felidae family on an Impossible Task paradigm in which an apparatus is baited with food that is initially accessible but then becomes inaccessible (Miklósi et al., 2003). Studying human-directed (gaze, proximity) and apparatus-directed (interaction, behavioral diversity) behaviors allows for the examination of problem solving, perseverance, and dependence on humans. The felids tested here represent asocial, wild species, which theoretically, should persist on the problem-solving task without seeking human interaction. However, as hand-reared subjects, they likely have an increased dependency on humans, which might be associated with behavioral diversity. This dependency might be specific to humans that are familiar to the cats.

The effects of hand-rearing have been documented in some species in captivity (chimpanzees, *Pan troglodytes*, Freeman & Ross, 2014; gorillas, *Gorilla gorilla*, Meder, 1989; parrots, *Psittaciformes*, Fox, 2006; whooping cranes, *Grus americana*, Kreger et al., 2004), with evidence to suggest that hand-rearing induces positive and negative effects on the behavioral and physiological responses of captive species. Hand-rearing may result in an atypical reliance on human caregivers or a diminished natural fear of humans that can result in aggression. Although benefits of a human-animal relationship have been noted within zoo-housed exotic species (Bloomfield et al., 2015; Claxton, 2011; Hosey, 2008), domestic cats in manipulated rearing conditions meant to mimic zoo settings suggest that human hand-rearing of small exotic felids should be avoided due to negative behavioral and reproductive outcomes (Mellen, 1992). Hand-rearing can negatively impact behavior; natural behaviors may be suppressed (e.g., Meier, 1986) and

abnormal behaviors may be promoted (e.g., Bertocchi et al., 2015; Jones et al., 2011). Hand-rearing carnivores without proper conspecific socialization is associated with behavioral problems including fear and aggression around conspecifics, lack of conspecific play, difficulty with reproduction, and fixation on humans (Meier, 1986).

Research also suggests that hand-rearing affects behavioral interactions between animals and humans (e.g., Carlstead, 2009). Social referencing, the process of attending to others when facing ambiguous or unfamiliar situations (Feinman, 1982), extends to humans, and may be common in hand-reared individuals, especially those bonded to humans within their critical period (e.g., megachiropteran bats, *Pteropus pumilus, Pteropus rodricensis, Pteropus conspicillatus, Pteropus vampyrus,* Hall et al., 2011; chimpanzees, *Pan troglodytes,* Russell et al., 1997; dogs, *Canis lupus familiaris*, Merola et al., 2012; dolphins, *Tursiops truncates*, Pack & Herman, 2004; jackdaws, *Corvus monedula*, von Bayern & Emery, 2009; seals, *Arctocephalus pusillus*, Scheumann & Call, 2004; wolves, *Canis lupus lupus*, Udell et al., 2008). Social referencing is a learned behavior resulting in overreliance on humans due to early, unnatural, human-influenced experiences that may affect an individual's natural behaviors and appropriate integration into their environment. Although there is limited information, research on captive and hand-rearing of subjects suggests that an animal's status as an ambassador may similarly impact its behavior. As defined by the Association of Zoos and Aquariums (AZA), an ambassador animal is one that "is being presented to visitors and … visitors are intended to have direct contact (i.e., feeding, touching, swim (sic) with, etc.)" (AZA, 2022, p. 1). As such, hand-reared individuals, and more specifically, captive-born and ambassador individuals, often develop a bond with humans that can affect their behavioral repertoire

as demonstrated through attention to cues and differences in behavior from their mother-reared counterparts.

Hand-rearing may affect cognitive and behavioral development. Familiarity with humans likely facilitates nonhumans' successful performance on cognitive tasks involving reading human cues. For example, in object-choice experiments, more than 70 species, including domestic horses (Proops et al., 2010), domestic dogs (Hare & Tomasello, 1999), domestic goats (*Capra aegagrus hircus,* Kaminski et al., 2005), domestic pigs (*Sus scrofa domestica*, Nawroth et al., 2014), domestic cats (Miklósi et al., 2005; Scandurra et al., 2023), African gray parrots (*Psittacus erithacus*, Giret et al., 2009), sea lions (*Otaria byrona*, Highfill et al., 2007), silver foxes (*Vulpes vulpes*, Hare et al., 2005), bats (*Pteropus*, Hall et al., 2011), olive baboons (*Papio anubis*, Vick & Anderson, 2003), capuchin monkeys (*Cebus apella*, Anderson et al., 1995), gorillas (Byrnit, 2009), and chimpanzees (Barth et al., 2005) successfully retrieved a hidden reward using human cues (e.g., gaze, pointing, body orientation, etc.) in object choice tasks (Anderson et al., 1995). Corvids (*Corvus corax* and *Corvus corone,* Cibulski et al., 2014), domestic dogs (Scandurra et al., 2017), and humans (Ma & Han, 2010) performed better on cognitive tasks in the presence of familiar humans than unfamiliar humans. For example, corvids participated more and were more successful on two interactive cognitive tasks (exchange, object choice) with human experimenters with whom they had an established, long-term relationship compared to those human experimenters with whom they had a short relationship (Cibulski et al., 2014). Positive human-animal relationships can facilitate performance in cognitive tasks involving human experimenters.

However, over-reliance on humans may impact species' persistence, detracting from problem solving. For example, Topál and colleagues (1997) documented that domestic dogs kept with less human contact were more independent in a problem-solving task than dogs with more human contact. To create an experimental setting in which an animal might be motivated to communicate with or solicit attention from a human, Miklósi et al. (2003) observed dogs and wolves on an "impossible," sometimes referred to as the "unsolvable task." The Impossible Task was originally developed to study human communicative and/or cognitive behaviors in an insoluble version of a previously soluble problem. Miklósi et al. (2003) and Marshall-Pescini et al. (2017) found that, when presented to domestic dogs and wolves, wolves were most persistent and did not look for help, whereas dogs looked for human assistance relatively early in the trials (Marshall-Pescini et al., 2017). When comparing pet dogs to working dogs, working dogs behaved more similarly to the wolves and persisted until trials timed out (Byosiere & Essler, 2020). This difference in human-directed behavior both between and within species suggests that the nature of the relationship or amount of contact with humans during rearing, rather than species differences alone, may influence task persistence.

Researchers have tested several domesticated species, including horses (Alterisio et al., 2018; Malavasi & Huber, 2016; Ringhofer & Yamamoto, 2017), pigs (Pérez Fraga et al., 2020), cows (*Bos taurus linnaeus,* D'Aniello et al., 2022), goats (Di Lucrezia et al., 2023; Nawroth et al., 2016; Yoshida & Koda, 2020), and cats (Forman & Leavens, 2024; Miklósi et al., 2005; Scandurra et al., 2023; Zhang et al., 2021), on Impossible Tasks. Domestic cats initiated first gaze, gazed longer, and approached an attentive caregiver more frequently than an inattentive caregiver, and adjusted their attention-seeking

behaviors to both caregivers when the task became impossible (Zhang et al., 2021). Both horses (Malavasi & Huber, 2016) and goats (Nawroth et al., 2016) looked to humans; however, domestic cows (D'Aniello et al., 2022) did not show preferences for either the owner or a stranger, nor did they interact with humans more after success. In comparison to domestic dogs, domestic pigs did not look at humans on impossible trials and spent more time away from humans during trials when both a familiar and unfamiliar human were present, suggesting a species-specific heightened neophobia (Pérez Fraga et al., 2020). The pigs also interacted with the apparatus more than dogs, and at similar durations in possible and impossible trials; this persistence may reflect their natural predisposition to solve problems independently (Gieling et al., 2011, as cited in Pérez Fraga et al., 2020). Based on the previous research with domestic dogs (D'Aniello et al., 2015; Heberlein et al., 2016; Marshall-Pescini et al., 2009, 2013, 2017), domestic cats (Miklósi et al., 2005; Zhang et al., 2021), horses (Alterisio et al., 2018; Malavasi & Huber, 2016; Ringhofer & Yamamoto, 2017), pigs (Pérez Fraga et al., 2020), and goats (Nawroth et al., 2016; Yoshida & Koda, 2020), non-group living species may have greater levels of neophobia, and depend less on others for assistance during problem solving. Thus, it may be expected that captive, hand-reared exotic felids that are not highly social persist across possible and impossible trials and do not look for assistance from humans. Hand-reared felids are of interest because of their unique human-rearing experience.

Although there are several studies examining behavior during the Impossible Task in domestic species, no studies have examined performance on this task in hand-reared exotic species – in particular, felids. Felids comprise an important system to study as their

cognitive abilities are poorly understood (Benson-Amram et al., 2022), they are difficult to keep in captivity (Clubb & Mason, 2007), and the practice of hand-rearing felids is on the rise despite the consequences associated with their development (Meier, 1986) and behavior (Kelling et al., 2013). I have focused this research on captive, hand-reared, exotic felids that have become habituated to human care. Here, I measured behavioral diversity and interactions with humans and the apparatus to better understand felid reliance on humans in hand-reared exotic cats. In the context of the domestication hypotheses (Virányi & Range, 2014), hand-reared exotic felids will persist more than domesticated species due to a predisposition to solve problems independently (e.g., Brubaker et al., 2017; Marshall-Pescini et al., 2017; Pérez Fraga et al., 2020), but may seek human social support as a problem-solving strategy. In accordance with previous research with cats (e.g., Casey & Bradshaw, 2008; Crews et al., 2024; de Mouzon et al., 2022; Edwards et al., 2007; Leroux et al., 2018; Galvan & Vonk, 2016; Saito & Shinozuka, 2013), I hypothesized that subjects would respond differently to familiar versus less familiar humans. Specifically, hand-reared captive felids will persist independently on the apparatus, but may seek support by gazing more toward a familiar human keeper compared to an unfamiliar human researcher. This gaze behavior may emerge specifically on impossible trials.

Method

Subjects. Fourteen felids representing seven species were tested: one caracal (*Caracal caracal*), five cheetahs (*Acinonyx jubatus*), one clouded leopard (*Neofelis nebulosa*), three cougars (*Puma concolor*), one fishing cat (*Prionailurus viverrinus*), two ocelots (*Leopardus pardalis*), and one serval (*Leptailurus serval;* see Table 9).

Table 9

IT Subjects and their Location, Sex, Age, Housing, and Role

Name	Species	Location	Sex	Age	Housing	Zoo Role	Wild/ Captive Born
Karl	Caracal (*Caracal caracal)*	PRC	male	1	social	exhibit	captive
Kendi	Cheetah (*Acinonyx jubatus*)	PRC	male	1	social/ asocial	ambassador	captive
Nandi	Cheetah (*Acinonyx jubatus*)	TBZ	female	2	social/ asocial	ambassador	captive
Nyambe	Cheetah (*Acinonyx jubatus*)	PRC	male	1	social/ asocial	ambassador	captive
Diesal	Cheetah (*Acinonyx jubatus*)	MZ	male	11	social	ambassador	Captive
Koda	Cheetah (*Acinonyx jubatus*)	MZ	male	11	social	ambassador	captive
Drupata	Clouded leopard (*Neofelis nebulosa*)	PRC	male	9	social	exhibit	captive
Chinook	Cougar (*Puma concolor*)	BCZ	male	3	social	exhibit	wild
Meeka	Cougar (*Puma concolor*)	PRC	female	5	asocial	exhibit	captive
Tacoma	Cougar (*Puma concolor*)	BCZ	male	3	social	exhibit	wild
Minnow	Fishing cat (*Prionailurus viverrinus*)	PRC	male	3	social	exhibit	captive
Delilah	Ocelot (*Leopardus pardalis*)	PRC	female	18	asocial	exhibit	captive
Toltec	Ocelot (*Leopardus pardalis*)	PRC	male	15	asocial	exhibit	captive
Zeke	Serval (*Leptailurus serval*)	PRC	male	6	social	exhibit	captive

The subjects' ages ranged from one to 18 years (M = 6.36, SD = 5.37). All individuals were hand reared. Two of the individuals were wild-born (Chinook and Tacoma), six individuals were housed socially full-time, three were housed socially part-time, and three were housed individually. Five of the individuals were ambassador animals (Kendi, Nandi, Nyambe, Koda, and Diesal) and the other nine were exhibit animals. Two sets of subjects were related; cheetahs, Koda and Diesal, and cougars, Tacoma and Chinook, were full brothers. All subjects were tested individually in their off-exhibit home enclosures at four locations: the Bergen County Zoo (BCZ) in Paramus, NJ (n= 2), the Miami Zoo (MZ) in Miami, FL (n= 2), the Turtle Back Zoo (TBZ) in West Orange, NJ (n= 1), and the Panther Ridge Conservation Center (PRC) in Loxahatchee, FL (n= 9). All human assistants were female to avoid potential effects of sex (e.g., Kotrschal et al., 2009).

Impossible Task Apparatus. An apparatus like that used by Marshall- Pescini et al., (2009) was used (see Figure 7). A heavy AZEK® board laid flat as the bottom tray. On top, there were three raised rectangles of the same material that were hollow in the middle for food placement. The rectangles were covered by clear plexiglass sheets with small holes for ventilation of the food (see Figure 7, inset picture). The clear plexiglass, rectangular covers were attached with one screw for easy removal and retrieval of food. However, they were also made to lock to the raised rectangular food wells using screws, which allowed the food to be visible but not retrievable. Reward items were supplied by the zoos as part of the subjects' natural diet and they included beef cubes, shank bones, chicken breasts, and Nebraska Brand diet™.

Figure 7

Impossible Task Apparatus

Procedure. Testing of these subjects had been approved by the institutional IACUCs of Oakland University (Protocol 20102) (see Appendix B). Subjects were individually tested in their off-exhibit home enclosures. No more than one species at a time were tested at a given institution to allow disinfection of the apparatus between enclosures. Subjects were tested with five (one familiarization and four testing) sessions, which consisted of four 90-second trials (see Table 10).

The apparatus (see Figure 7) was baited with a food reward and placed in the subject's enclosure while the focal subject was physically and visually away from the testing area in a separate enclosure. A video camera was used to record the trials on video.

Familiarization Sessions. Each session consisted of four consecutive trials in which the apparatus was presented to the subjects. In the first two trials, the covers were completely open, exposing the food rewards inside. Upon (and contingent upon) completion of these initial two trials (defined as retrieving at least one reward), the coverings were placed over the holes halfway exposing the reward but encouraging comfort with the plexiglass and physical manipulation of the apparatus. If two consecutive trials were completed without success moving the half-covered plexiglass, testing trials were conducted with the food wells uncovered (see Table10).

Testing Sessions. Each subject participated in four sessions. Two of the sessions (Sessions 1 and 3) were conducted with familiar keepers and two sessions (Sessions 2 and 4) were conducted with an unfamiliar researcher (see Table 10). Session 1 was always conducted with the familiar keeper to decrease fear and encourage participation in the task while in close proximity to a human. In the familiar condition, a familiar zookeeper stood directly in front of the apparatus but out of the enclosure. In the unfamiliar condition, an unfamiliar individual stood directly in front of the apparatus but out of the enclosure. The familiar and unfamiliar individuals were the same person for each cat at each time they were tested. In both conditions, the subject was presented with two consecutive trials in which they could freely obtain food in the apparatus wells with no plexiglass cover, followed by a single trial in which the clear plexiglass covers were fixed to the board's three containers, thereby making the task unsolvable (Marshall-Pescini et al., 2009); an additional solvable trial completed the condition. This possible trial was the last experimental trial presented to encourage animals' interaction in subsequent trials. For the individuals that did not pass familiarization, the apparatus had

plexiglass partially covering the food wells; to retrieve the entirety of the food, the subject needed to slightly move the plexiglass with their face or paw.

Table 10

IT Procedure Flowchart

Trial Type	Session	Familiarity	Trial	Description
Familiarization	1	-	1	Covers completely open
			2	Covers completely open
	2	-	3	Covers halfway open
			4	Covers halfway open
Testing	1	Familiar	1	Possible task
			2	Possible task
			3	Impossible task
			4	Possible task
	2	Unfamiliar	1	Possible task
			2	Possible task
			3	Impossible task
			4	Possible task
	3	Familiar	1	Possible task
			2	Possible task
			3	Impossible task
			4	Possible task
	4	Unfamiliar	1	Possible task
			2	Possible task
			3	Impossible task
			4	Possible task

Data Coding. The trial began when the subject entered the enclosure with the apparatus. The first time the subject looked at the human in trials was coded as 'initial gaze.' The number of food wells that an individual opened was coded as 'number of successful solutions' (0-3). Whether the individual opened a food well during possible trials was coded as a dichotomous variable as 'success' (0-1). Success data were not

analyzed here because I was primarily interested in behavior on the impossible trial. The following total durations were quantified: (1) subject looking at human ('gaze at human'); (2) the subject within six inches of the fencing or door ('proximity to human); (3) the subject looking at apparatus but not interacting ('gaze at apparatus'); and (4) the subject's physical contact with any part of the apparatus ('interaction with apparatus'). For each trial, multiple behavioral measures were summed to examine 'behavioral diversity'; the behavioral measures include: (1) pawing/ scratching board; (2) sniffing board; (3) licking/ biting/ nibbling board; (4) pulling/ pushing board; (5) pacing; (6) self-grooming; and (7) vocalizing. The presence or absence of all behaviors was coded and extracted using BORIS v8 software for behavioral coding (Friard & Gamba, 2016).

Results

Reliability. All videos were double-coded by trained student volunteers resulting in acceptable reliabilities between coders as determined by Kendal's tau for non-parametric correlations. Adequate reliabilities are reported here for gaze at human duration ($\tau_b = .40$, $p < .001$), proximity to human ($\tau_b = .20$, $p < .01$), interaction with apparatus ($\tau_b = .72$, $p < .001$), number of successful solutions ($\tau_b = .78$, $p < .001$), and behavioral diversity ($\tau_b = .29$, $p < .001$). Gaze at apparatus was not reliable ($\tau_b = -.03$, $p = .75$) and this outcome will not be included in further analyses. Excellent reliability was obtained for the variable success (Cohen's Kappa, $\kappa = .92$, $p < .001$).

Data were analyzed using IBM SPSS v. 28 software. Four generalized linear mixed models (GLMM) were conducted on the outcomes of duration of interaction with apparatus, duration of gaze at human, duration of proximity to human, and behavioral diversity with subjects as a random effect and fixed factors of sex, ambassador status

(ambassador, exhibit animal), born (wild versus captive), human familiarity (familiar, unfamiliar), and trial type (i.e., whether the apparatus was locked or unlocked; that is possible versus impossible trials). All two-way and three-way interactions between ambassador status, born, familiarity, and trial type were also included in each model. Models were run with a normal probability distribution, an identity link function and Satterthwaite approximation, which is appropriate for small data sets.

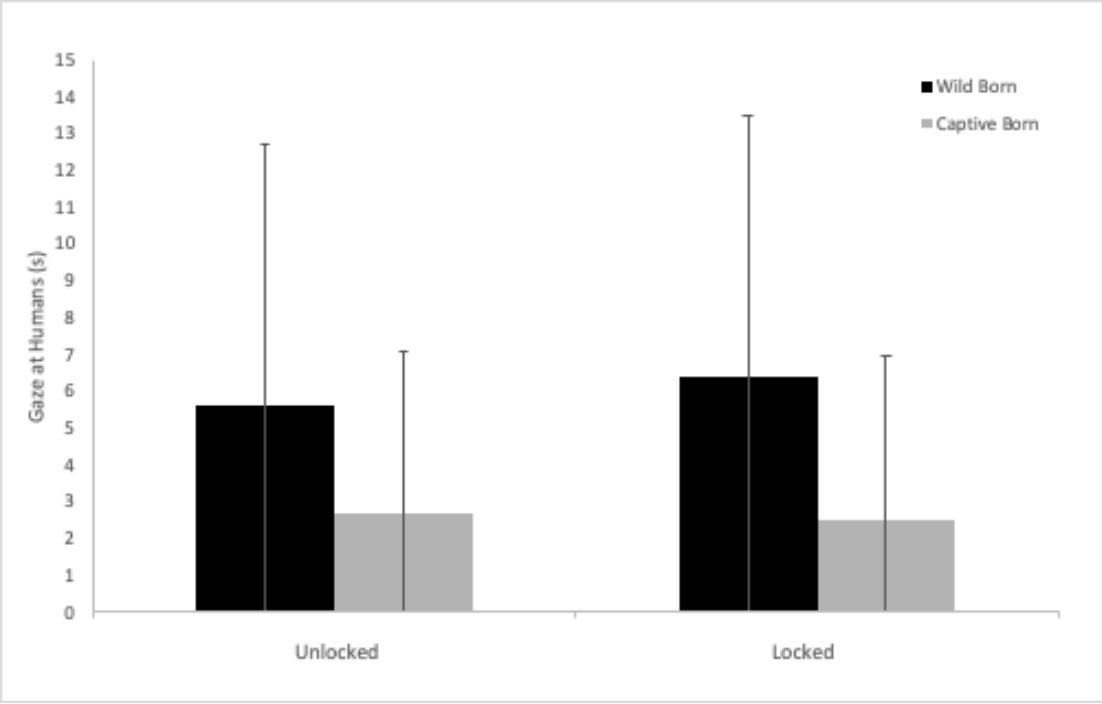
Interaction with Apparatus. Model fit was indicated by an AIC of 1885.15. There were no significant main effects of sex ($F(1, 209) = 0.72$, $p = .40$), ambassador status ($F(1, 209) = 0.00$, $p = 1.00$), or familiarity ($F(1, 55) = 2.17$, $p = .15$) on interaction with apparatus. However, there were significant main effects of born ($F(1, 209) = 10.67$, $p = .001$) and trial type $F(1, 55) = 6.37$, $p = .02$) on interaction with apparatus. Captive-born individuals ($M = 76.32$, $SE = 4.44$) interacted with the apparatus more than wild-born individuals did ($M = 35.06$, $SE = 11.06$). Subjects interacted with the apparatus more when it was unlocked ($M = 68.45$, $SE = 4.53$) than when it was locked ($M = 56.68$, $SE = 5.48$). There were no significant interactions.

Gaze at Human. Model fit for the duration of gaze at human was indicated by an AIC of 1265.46. There were no main effects for sex ($F(1, 8) = 0.58$, $p = .47$), ambassador status ($F(1, 9) = 0.71$, $p = .42$), or familiarity ($F(1, 15) = 0.63$, $p = .44$) on gaze at human. The effect of born ($F(1, 15) = 4.60$, $p = .06$) approached significance. There were main effects of trial type ($F(1, 15) = 4.91$, $p = .04$) on gaze at human; subjects gazed more during locked trials ($M = 4.92$, $SE = 1.23$) than during unlocked trials ($M = 3.84$, $SE = 1.56$). There was a two-way interaction with trial type and born ($F(1, 18) = 4.82$, $p = .04$). Wild-born cats looked for longer at the human compared to the captive born cats (see

Figure 8) with the difference between wild and captive cats approaching significance on unlocked trials (F (1, 9) = 4.06, p = .07), but not on locked trials (F (1, 47) = 2.59, p =.11).

Figure 8

Time Spent Gazing at Human for Wild-born and Captive-born Subjects



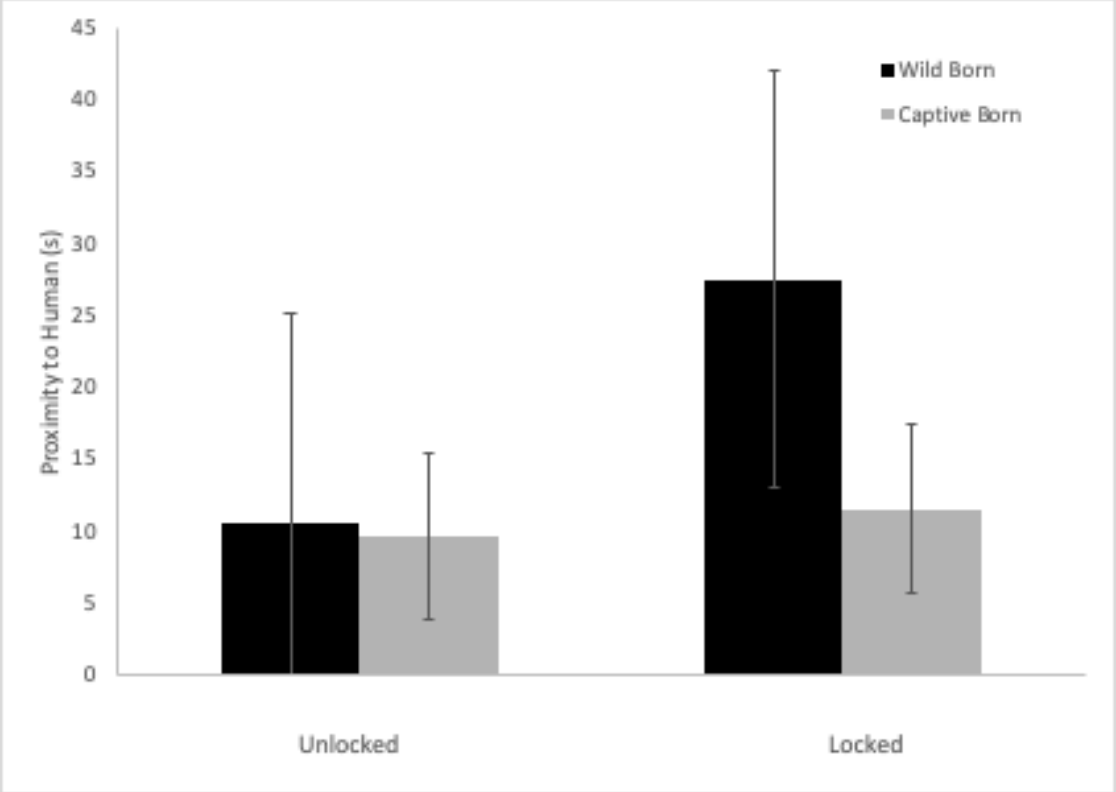
Note. Error bars represent standard deviations.

Proximity to Human. Model fit was indicated by an AIC of 1592.79. There were no significant main effects of ambassador status (F(1, 209) = 2.57, p = .11), born (F(1, 209) = 1.17, p = .28), or familiarity (F(1, 34) = 2.99, p = .09) on proximity to human. There were significant main effects for sex (F(1, 209) = 6.67, p = .01) and trial type (F(1, 35) = 14.03, p < .001). Females spent more time (M = 32.28, SE = 37.40) than males (M = 5.81, SE = 14.44) in proximity to humans and overall, subjects spent more time in

proximity to humans when the apparatus was locked (*M*= 16.86, *SD*= 6.38) than when it was unlocked (*M* = 9.93, *SD*= 6.13). There was also a significant two-way interaction with born and trial type ($F(1, 32) = 7.23$, $p = .01$). When the apparatus was locked, wild-born subjects spent more time in closer proximity to humans (*M* = 27.42, *SE* = 15.07) than when the apparatus was unlocked (*M* = 10.60, *SE* = 14.36; see Figure 9), but there was no difference in time spent near the caregiver for captive born cats. Wild born cats spent more time near humans on locked trials ($F (1, 12) = 9.62$, $p = .01$) but not on unlocked trials ($F (1, 155) = 0.77$, $p = .38$) compared to captive born cats.

Figure 9

Proximity to Human for Wild-born and Captive-born Subjects

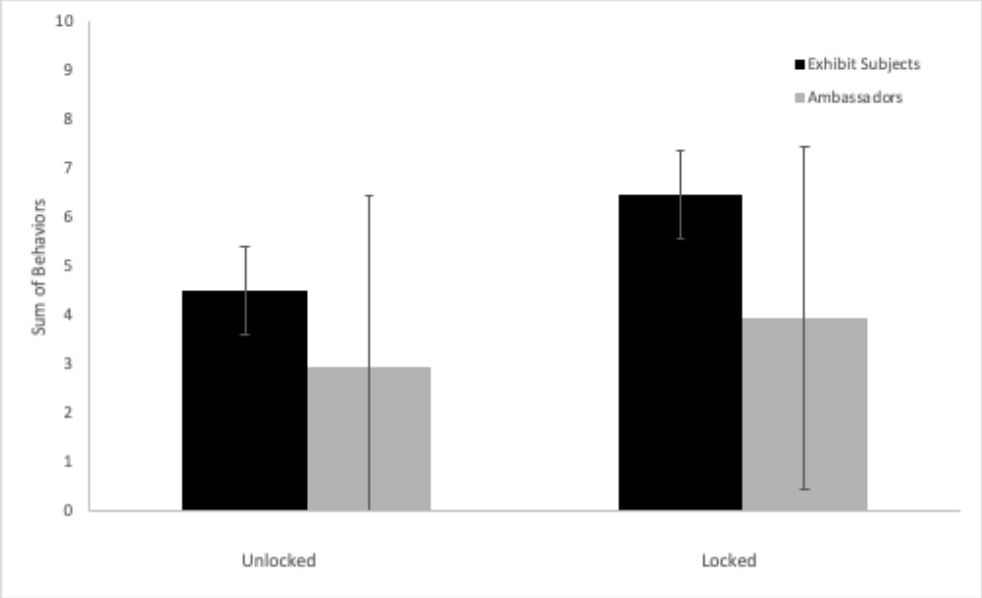


Note. Error bars represent standard deviations.

Behavioral Diversity. Model fit was indicated by an AIC of 985.38. There were no significant main effects of sex ($F(1, 209) = 0.35$, $p = .56$), born ($F(1, 209) = 0.95$, $p = .33$), familiarity ($F(1, 39) = 0.50$, $p = .49$), or trial type ($F(1, 39) = 2.29$, $p = .14$) on behavioral diversity. There were significant main effects of ambassador status ($F(1, 209) = 5.71$, $p = .02$); exhibit subjects ($M = 5.48$, $SE = 0.87$) showed greater behavioral diversity compared to ambassadors ($M = 3.45$, $SE = 0.88$). There was also a significant interaction between ambassador status and trial type ($F(1, 39) = 8.06$, $p = .01$). Exhibit subjects demonstrated a greater number of behaviors directed to the apparatus on locked ($M = 6.44$, $SE = 1.05$) versus unlocked trials ($M = 4.52$, $SE = 0.81$) whereas ambassador animals exhibited a similar number of behaviors directed to the apparatus on locked trials ($M = 3.95$, $SE = 0.89$) compared to unlocked trials ($M = 2.95$, $SE = 0.89$; see Figure 10). Ambassador and exhibit animals' diversity differed on locked ($F(1, 48) = 8.54$, $p = .01$) but not on unlocked trials ($F(1, 20) = 2.41$, $p = .14$) with exhibit cats showing greater diversity than ambassador cats on locked trials.

Figure 10

Sum of Behaviors Directed to Apparatus for Exhibit and Ambassador Subjects



Note. Error bars represent standard deviations.

Discussion

Hand-rearing can have negative consequences on the biology (e.g., Hampson & Schwitzer, 2016) and behavior (Mellen, 1992) of captive carnivores. I investigated hand-reared exotic cats' task persistence and social referencing to humans for guidance in an Impossible Task, which presents subjects with trials that can and cannot be solved. I examined associations with sex, ambassador status, whether the subject was wild, or captive born, and manipulated exposure to a familiar versus unfamiliar human. I measured duration of gaze and proximity to the human, persistence in the form of time spent with the apparatus, and behavioral diversity in the form of frequency of unique behaviors directed at the apparatus. Testing socialized, but non-domesticated, asocial species on problem-solving tasks provides clarity on whether dependence on familiar

human caregivers is likely to emerge, even in species that did not evolve to be highly social. It was expected that hand-reared captive felids would persist less on the apparatus when trials were impossible compared to when they were possible but would seek support by gazing more and spending more time in proximity to a familiar human compared to an unfamiliar human. Furthermore, it was expected that they would show fewer unique behaviors and interact with the apparatus for shorter periods of time when the apparatus was locked in the presence of a familiar versus an unfamiliar caregiver if they had developed dependencies on specific caregivers. It was expected that wild-born subjects may show greater behavioral diversity and persistence compared to captive-born cats, and that ambassador cats would show greater dependence (gaze and proximity to humans) on familiar humans compared to non-ambassador cats.

Sex differences were not expected due to the small sample size. Although sex differences do exist in novel object tasks (e.g., guppies, *Poecilia reticulata*, Lucon-Xiccato & Dadda, 2016; Burton's mouthbrooder cichlid, *Astatotilapia burtoni,* Wallace & Hofmann, 2021; Bagg Albino mice, Yamamoto et al., 2004) and in problem-solving tasks (e.g., domestic dogs, Duranton et al., 2014; guppies, Lucon-Xiccato et al., 2020; meerkats, *Suricata suricatta,* Thornton & Samson, 2012), in this experiment, there were no sex differences associated with problem-solving behaviors. However, surprisingly, females spent more time near humans than males. Cautiously interpreted, this may mean that hand-reared females may be more neophobic than males of the same species (e.g., Crane et al., 2020), choosing to spend more time near a more familiar human in the presence of an unfamiliar apparatus. Additional reasonings may include their probable higher association of humans with food (Udell et al., 2008), or they may perceive

themselves as dominant over (e.g., Mettler & Shivik, 2007), or cooperative with humans (e.g., Range et al., 2019; Range & Virányi, 2011). It is also possible that the sex differences observed here were in fact individual differences, due to the small sample size.

Individual differences in neophobia have been documented in captive felids (O'Connor et al., 2022) and likely exist not only between sexes, but also between wild and captive-born individuals, and between ambassador and exhibit individuals. In the present study, wild-born felids spent less time interacting with the apparatus than captive-born felids. Low levels of interaction with apparatuses may suggest greater neophobia to novelty (e.g., Griffin & Guez, 2014; Johnson-Ulrich et al., 2018). Although all subjects were hand-reared, wild-born subjects were initially mother-reared before being rescued as orphaned young cubs. Wild-born deer mice (*Peromyscus maniculatus*) were more cautious of novel objects than those bred in captivity for generations (Price, 1979), and two populations of wild-born guinea pigs (*Cavia aperea*), one first-generation and one born in captivity for thirty generations, were more alert to their physical environment than domesticated guinea pigs (Künzl et al., 2002). The wild-born subjects tested here are first-generation captive felids, and their hand-rearing began relatively later in life, potentially affecting their behaviors directed to humans and human-apparatuses.

Both captive-born and ambassador felids have presumed positive relationships with humans (e.g., Topál et al., 2005), likely resulting in less neophobia; for example, hand-reared European starlings (*Sturnus vulgaris,* Feenders & Bateson, 2013) were less neophobic and less impulsive than mother-reared starlings. Ambassador felids exhibited fewer unique behaviors directed to the apparatus compared to exhibit subjects, which

further suggests that there may be some level of reliance on humans as they are highly habituated to human presence and associate humans with their environment, problem solving, and food. However, differences in neophobia may be due in part to species; related species have different reactions to novel human apparatuses (e.g., bonobos, chimpanzees, and gorillas, Kalan et al., 2019). Hand-reared animals exhibit unique behaviors that could account for those seen in the present study; for example, hand-reared Rhesus monkeys (*Macaca mulatta*, Spencer-Booth & Hinde, 1971) exhibit less exploration in their environment than their mother-reared conspecifics. Thus, it might be presumed that, due to ambassador subjects' lifelong relationships with humans, these subjects may exhibit overall more reliance on humans, especially when it comes to a problem-solving task. In both a string-pulling task (Hiestand, 2011) and an Impossible Task (Rao et al., 2018), wolves exhibited more behavioral diversity and were more persistent than domestic dogs. When it comes to social support, like domestic dogs, ambassador subjects may rely on humans more than exhibit subjects would, which resemble wolves in their problem-solving behaviors. In a cooperative problem-solving task, human-raised wolves cooperated with humans and were more likely to initiate movement, whereas dogs were more likely to wait for humans to initiate action (Range et al., 2019). Like Range et al.'s highly socialized wolves (2019), this study's hand-reared, ambassador felids may have accepted humans as a partner to the task when insolvable on their own. The addition of mother-reared felids, and potentially wild felids, in additional Impossible Task studies would be integral in teasing out the effects of human presence on problem-solving efforts.

Of interest, subjects gazed at humans more, and interacted with the apparatus less, when the Impossible Task was locked, suggesting greater social referencing to humans and reduced persistence. Social referencing with humans may be predisposed in species that invest in the rearing of offspring, including domesticated (e.g., Nawroth et al., 2016) or social species (e.g., Miklósi et al., 2003), though there is some evidence in domesticated cats, which are an asocial species (e.g., Galvan & Vonk, 2016; Merola et al., 2015). Most of the data from the Impossible Task comes from social and/or domesticated species. Felids in the current study exhibited different gaze results to those social, non-domesticated (e.g., wolves, Miklósi et al., 2003) and asocial, domesticated species (e.g., cats, Miklósi et al., 2005), which did not gaze at humans; this study's gaze results more closely mirroring social, domesticated species (e.g., domestic dogs, Marshall-Pescini et al., 2017), which did look to humans, presumably for assistance. Additional support comes from results in hand-reared dingoes (*Canis lupus dingo,* Smith & Litchfield, 2013) and kangaroos (*Macropodidae*), both of which gazed at the experimenter during the Impossible Task (McElligott et al., 2020).

Of particular note, although unexpected, wild-born subjects spent longer looking at humans compared to captive subjects in all trials and spent more time in proximity to humans when the task was locked. These results, in combination with the result that wild-born subjects interacted with the apparatus less than captive-born subjects did, suggests that there may have been rapid learning of when the apparatus became impossible, thus leading the subjects to give up independent attempts to uncover the food and shift to a strategy of gazing to a human for assistance. As suggested by Marshall-Pescini et al. (2017), and supported by Lazzaroni et al., (2020), after a certain period of time in

impossible trials, animals give up and look around their environment for assistance. This is supported by the result that all subjects interacted with the apparatus more when it was unlocked than when it was locked, further corroborating my hypothesis that hand-reared individuals lack persistence and rely on human assistance.

All results presented challenges to the working hypotheses. It has been documented that both domestic cats (e.g., Galvan & Vonk, 2016; Saito & Shinozuka, 2013) and non-domesticated captive felids (e.g., Crews et al., 2024; Leroux et al., 2018) can discriminate and attend to familiar humans. However, I found no effects of human familiarity. This may be because of individual differences, or species differences. Individuals varied in their housing with conspecifics (social, asocial, combination of social/asocial), whether they were wild-born or captive-born, exhibit subjects (with minimal familiar keeper time, but maximum unfamiliar zoo visitors) or ambassadors (with constant familiar human contact). As such, a larger sample is needed to determine if a pattern exists among these variables. All subjects were solitary species, which engage in minimal social interactions over their lifespan (Jackson et al., 2019), and thus, may not find individual identity to be highly salient. This seems unlikely given that zoo animals are regularly exposed to both familiar and unfamiliar humans (and potentially conspecifics) and have been shown to respond differentially to familiar and unfamiliar individuals in other studies conducted in zoo environments (e.g., Crews et al., 2024; Leroux et al., 2018). It is more likely that captive cats are accustomed to receiving food from less familiar individuals as animal caretakers may shift areas; thus, they may look for assistance in a food-related context to any human that appears in a position to offer food.

It is important to note limitations of this study. For certain measures (e.g., gaze at apparatus), there was an excess of zero-inflated data, negatively affecting the distribution. Most likely, these results are in part due to the small sample of fourteen felids, with only three females. The current sample of only relatively asocial species (seven with four species represented by a single individual), and genetic relatedness may have reduced variability. Additionally, there was an uneven balance of ambassador subjects (who spend a majority of their day with keepers) and exhibit subjects (who were raised as cubs by keepers, but currently spend a majority of their day away from keepers). As two of the three cougars were wild-born, and all cheetahs were ambassadors, additional subjects of both species are important to better understand individual and species-level differences in human-directed behaviors. This is especially important as born type and ambassador were both confounded with species and thus, species differences may explain these effects. A larger and more representative sample of captive felids, that are both ambassadors and exhibit subjects, and are both mother and human-reared, will be needed to draw firm conclusions about the impact of rearing and familiarity of humans on behavior in the Impossible Task.

Whereas human-directed behavior during the Impossible Task has been examined in domesticated (Miklósi et al., 2005; Nawroth et al., 2016; Pérez Fraga et al., 2020; Ringhofer & Yamamoto, 2017; Zhang et al., 2021), and a few exotic species (McElligott et al., 2020; Rao et al., 2018), this was the first study in hand-reared exotic felids. These results stand alone in supporting hypotheses about the impact of human rearing on behaviors in an asocial and non-domesticated species on this task, suggesting that ontogenetic effects may serve as proximate causes for behavioral differences related to a

cognitive task. Considering the goals of accredited captive institutions to preserve populations and support their wild conservation, the results of this study add to the literature in both highlighting the potential weight of hand-rearing (Meier, 1986) and the effects of captivity on animal cognition (Horn et al., 2022). Hand-rearing is selected for in some facilities as it is credited with creating a more positive relationship with staff and serving to better educate the public (e.g., Boyd et al., 2017). Future research with an Impossible Task should include mother-reared captive carnivores and social felids (e.g., African lions) as human presence during early development and sociality likely shapes their view of all future human caregivers. A larger, more representative sample size is crucial to understanding the complex relationship between evolutionary pressures and generations of hand-rearing with humans on cognition and behavior.

CHAPTER 5

GENERAL CONCLUSIONS

Behavioral flexibility, the ability for individuals to adapt to novelty in their environment, serves as a proxy for advanced cognition. I examined behavioral flexibility in 80 individuals of 17 species to better understand the evolutionary development of carnivore cognition. Behavioral flexibility was measured through success (ratio of successful trials, repeated innovation, and latency to success) on a multi-access puzzle box (MAB) and behaviors (persistence, contact latency, exploration/ behavioral diversity) associated with cognition on both a MAB and an Impossible Task. Carnivores have evolved behavioral flexibility to adapt to challenges, but likely vary in their cognitive abilities due to their diversity in sociality and ecology. As such, I examined species-level traits that may predict behavioral flexibility including sociality, brain volume, body mass, encephalization quotient, and IUCN status, a measure of ability to adapt to changing environments. Additionally, within species, there is variation in performance which may be explained by individual differences such as sex, age, ambassador status (ambassador versus exhibit animal), born type (wild versus captive), rearing (human versus mother), and personality structure. Examining factors at the individual and species levels enabled me to examine possible selection pressures operating on their cognitive development.

There were three hypotheses through which I examined the findings: the social complexity hypothesis, the cultural intelligence hypothesis, and the cognitive buffer hypothesis. The social complexity hypothesis, in which cognition evolved as a result of social living (Byrne & Whiten, 1988) is evidenced by more advanced cognitive abilities

in social species relative to closely related asocial species (Borrego & Gaines, 2016). The cultural intelligence hypothesis, which builds on the social complexity hypothesis and states that social living imparts benefits in cognition from its complexity, derives support from research demonstrating differences between (Herrmann et al., 2007) and within species (Borrego & Dowling, 2016) related to sociality. The cognitive buffer hypothesis, which espouses the proposal that the evolution of larger brains is driven by benefits of behavioral flexibility and adaptation to dynamic environments (Sol, 2009), is supported by studies showing that higher encephalization, or a larger brain size related to body size (Jerison, 1973), is associated with measures of cognition (Benson-Amram et al., 2016; Lefebvre & Sol, 2008). I examined species and individuals that differed in some of these factors and used three methods; personality assessment, a MAB, and an Impossible Task- to measure aspects of behavioral flexibility to see which species-level and individual-level traits predicted various measures of performance supporting one hypothesis over the others regarding the evolution of cognitive abilities in carnivores.

All subjects in the Impossible Task were relatively asocial, and as such, sociality was examined only with regard to performance in the MAB. Here, sociality was only broadly defined as group-living or non-group living, although more nuanced assessments of sociality are possible in other groups (Vonk et al., 2021). Sociality significantly predicted only persistence, with social species spending more time actively working on the MAB than asocial species. Although these hypotheses are not mutually exclusive, with no other significant findings, there is not enough evidentiary support for the social complexity hypothesis. This contradicts the finding of Borrego and Gaines (2016) who found that social species outperform asocial species on a single solution puzzle box but

agrees with Benson-Amram- et al. (2016) who found no effects of sociality in a significantly larger sample tested on a puzzle box. In addition, as there was no evidence of social species exhibiting more behaviors directed towards the apparatus, or more problem-solving success, there was not enough evidence to examine the cultural intelligence hypothesis. Of note, the multi-access puzzle box was a physical problem-solving task, not a task measuring sociality, and therefore the extent to which sociality predicts success depends upon whether sociality confers benefits to cognition generally, or to sociocognitive abilities specifically (Vonk et al., 2021). As stated in Chapter 4, additional evidence nullifying or supporting the role of sociality in the evolution of cognitive abilities would come with the inclusion of additional species from various families differing in their sociality.

There is evidence to support heritable variation in cognitive traits; in 1508 adult dogs of 36 breeds, inhibitory control and communication control, two behaviors associated with cognition, were highly heritable cognitive traits (Gnanadesikan et al., 2020). Species with relatively large brains for their body size, or deemed as having higher encephalization, were associated with better problem-solving abilities; in 140 captive carnivores of 39 species, relative brain size predicted problem-solving success on a puzzle box (Benson-Amram et al., 2016). While not conclusive, the results of this dissertation support the cognitive buffer hypothesis as documented in previous studies (Benson-Amram et al., 2016; Finarelli & Flynn, 2007; Lefebvre et al., 2004; Lefebvre & Sol, 2008; Sol et al., 2005). Sociality, smaller body mass and higher encephalization was associated with persistence and latency to success, measures of cognition, on the MAB. As stated in Chapter 3, encephalization has been recognized in carnivores with Felidae

having increased encephalization among smaller taxa (Finarelli & Flynn, 2009), which is demonstrated through smaller carnivores having shorter latencies to success and being more persistent on the MAB. Additionally, a higher encephalization quotient was a significant predictor of persistence, again paralleling research by Benson-Amram et al. (2016) in establishing persistence as a significant predictor of carnivores' success on a MAB when controlling for relative brain size (Benson-Amram et al., 2016).

Applicable facets of focus for research in carnivores include both variables at the species level variables- genetics, sociality, and brain size- and at the individual level- genetics, sex/age, rearing history, and personality. I predicted that cognitive abilities across the three chapters would be associated with individual-level facets including sex, age, personality, and human-rearing of carnivore species. Cognitive abilities also likely evolve as a function of sexual differences; in 17 giant pandas, males outperformed females on a spatial memory task, whereas there were no sex differences seen in eight Asian small-clawed otters on the same task (Perdue et al., 2011). Giant pandas, a promiscuous species, exhibit sex differences as selected for by different range sizes between sexes, compared to the monogamous Asian small-clawed otters (Perdue et al., 2011). I expected females and males to differ in their cognitive abilities and behaviors due to the demands placed on them by their ecological and social environments (e.g., home range, mating strategy, offspring rearing), and thus, sexually divergent evolution of related cognitive abilities should exist. On the MAB, males had a shorter latency to success and scored higher with success, persistence, and exploration diversity. Additionally, males were rated as more Fearful/Aggressive in personality ratings, which likely influenced their performance on the MAB. Fearful/Aggressive personalities may

be more neophobic with novelty, which can influence their engagement (Martin & Fitzgerald, 2005), equating to poor performance on the MAB. On the Impossible Task, females spent significantly more time than males in proximity to humans. However, sex was not a predictor of success in either the MAB or the Impossible Task. While there was evidence of sexual dimorphism of behavioral and cognitive traits, sex was not a significant predictor of behaviors related to problem-solving on the MAB or the Impossible Task; most likely, sex differences are species-specific, as evidenced by (e.g., Perdue et al., 2011), according to that species' biological demands. I did not have enough males and females of each species to explore interactions between sex and species here.

Similarly, age plays a large role in the cognitive abilities and related behaviors in species; raptor juveniles were more explorative and less neophobic than older raptors on a multi-access puzzle box (Biondi et al., 2010), and behavioral flexibility decreased with age in adult coyotes in a spatial serial reversal test and a color discrimination task due to age-related cognitive declines (van Bourg et al., 2022). I hypothesized that younger individuals would be more successful and exhibit more behaviors on the MAB, but age did not predict success on the MAB. However, in Chapter 2, age was positively correlated with the personality trait Flexible/Friendly, and negatively correlated with Social/Playful and Cautious. The small sample on the Impossible Task in Chapter 4 (n = 14) ranged in age from one year to 18 years (M = 6.36) but there were uneven distributions of sex and age within species because of small sample size, which prohibited analysis of age effects. Nonetheless, as with sex, there were behavioral differences related to age, as demonstrated in other research (e.g., Benson-Amram & Holekamp, 2012).

Personality traits evolve through natural selection (Moore et al., 1998), and numerous studies have documented differing personality traits within species including a variety of captive (e.g., Gartner et al., 2014) and wild (e.g., Myers & Young, 2018) carnivores, which may affect their behaviors and outcomes in cognitive studies. Based on prior literature (e.g., Carlstead et al., 1999; Gartner & Powell, 2012; Gartner & Weiss, 2013; Powell & Svoke, 2008; Razal et al., 2016), I expected variation in personality traits that would affect the behavior of the carnivores tested here – many of whom belonged to species for whom personality traits had not yet been established. Chapter 2 established a personality structure in Felidae involving five facets- Flexible/ Friendly, Fearful/Aggressive, Uninterested, Social/Playful, and Cautious. Additionally, I measured the ability of carnivore personality facets to predict success on the MAB; two facets- Fearful/Aggressive and Cautious- significantly predicted failure in the MAB. No other behavioral measures related to the MAB, as documented in Chapter 3, were explored in combination with personality traits. The presence of a consistent personality structure across species, which predicted success on an MAB, allowed for the examination of personality as a potential factor that selects for cognitive abilities across species. Because personality structure had not been previously established in many of the species examined in this dissertation, the personality structuring, and its use to predict behavioral flexibility, are novel contributions to the animal cognition literature.

Contextual factors may also influence later behavior and cognition. Hand-rearing requires intense-bonding with humans that may affect behaviors towards conspecifics and humans (e.g., Bloomsmith et al., 2006; Nájera et al., 2015). Hand-rearing alters several aspects of early life experience that may play a role in cognitive abilities and behaviors.

Based on their inclusion of humans in their physical and social environments, I expected that all subjects would seek support by gazing towards humans in the Impossible Task, specifically on the impossible trials (Chapter 4). Subjects gazed at humans more, and interacted with the apparatus less when the apparatus was locked, and ambassador subjects exhibited fewer unique behaviors directed to the apparatus compared to exhibit subjects, suggesting greater social referencing to humans. As there were no mother-reared subjects for comparison, I can only suggest that the behaviors directed towards humans, and away from a cognitive task, are due to a greater reliance on humans for support in hand-reared cats. However, further subjects, including those that are mother reared, are needed to make any substantial claims on the role of hand-rearing in behaviors associated with cognition. This is particularly true as I did not find an increase in carnivore behaviors towards familiar humans rather than unfamiliar humans as I expected.

In combination, there is evidence in the two experiments, that individual differences in sex, age, personality, and potentially hand-rearing, play a role in the behaviors associated with cognitive tasks in captive carnivores. Future research building upon these experiments may find interest in expanding the sample size to include more individuals in varied species, levels of sociality, rearing differences, and additional locations. Although the overall sample size was large relative to other comparative studies, analyses, and the ability to draw conclusions for hypotheses, was limited by sample size within each species. As such, additional testing on both the MAB and the Impossible Task might produce different results. Of significant interest, and at great difficulty, would be to place this MAB in the wild. Benson-Amram, Weldele, and

Holekamp (2013) compared an identical puzzle box in both wild and captive populations of hyenas and found that captive hyenas were better problem solvers than wild hyenas. Johnson-Ulrich, Holekamp, and Hambrick (2020) and Johnson-Ulrich, Johnson-Ulrich, and Holekamp (2018) also used an identical multi-access box paradigm in both wild and captive spotted hyenas, respectively, determining that problem-solving was more generalizable across populations. However, captivity may have an 'enculturation effect' (Tomasello & Call, 2004), or greater cognitive abilities due to their interactions with humans; captive species are less neophobic as they are more accustomed to human-made objects and can be more persistent as they have more concentrated work time. Although performance on both the MAB and Impossible Task represent examples of relatively low levels of neophobia to human-made apparatuses, hand-reared felids reduced their persistence on the task when the Impossible Task was locked. Here, felids may have relied on humans due to being hand-reared in captivity. Based on both the literature and this dissertation, captivity limits the generalizability of the results; to properly understand behavioral flexibility, studies should examine innovative problem solving in an animal's natural habitat.

Even with limitations, the two experiments conducted here present the first use of personality assessments predicting problem-solving success on an MAB, the largest and most inclusive sample of carnivores on an MAB, and the first use of an Impossible Task in non-domesticated felids. In both the wild and captivity, carnivores remain an excellent group to investigate cognition as they are a highly specialized group facing diverse pressures and differing in their abilities to adapt to environmental stimuli. All species face increasing anthropogenic changes in their natural environments (Watson et al., 2015;

Woodroffe, 2000). However, some carnivore species are better able to adapt both in the wild (e.g., Gehrt, 2011) and in captivity (e.g., McPhee, 2002). As such, to understand the evolution of advanced cognition, we should try to understand selection pressures. Behavioral flexibility is a proxy for advanced cognition; greater behavioral flexibility should be demonstrated in species that face both ecological and social challenges. Additional studies are needed to examine individuals' and species abilities to make changes in behavior in response to environmental variations to better understand their evolution.

APPENDIX A

CARNIVORE BEHAVIOR SURVEY

Carnivore Behavior Survey for Zookeepers (for individual carnivores)

*A graduate student at Oakland University, Victoria O'Connor, in conjunction with _____ **Zoo**, is conducting a survey on carnivore temperament. We would like you to share your observations of the behavior of each particular animal so that we can compare it to others within and outside of the Zoo. We are interested in your independent impressions; therefore, please do not consult with other keepers on your answers.*

Date:_____ Location: _____

Carnivore's Name:_____ Age:_____ Sex: _____

Rater's Name:_____ Age:_____ Sex: _____

Instructions:

Consider each item according to its definition and independently of any other item. Your impressions are based on this subject compared to your experience with other individuals of its species. Rate each adjective in order and independently of the other items. There are no right or wrong answers. For each adjective, circle the appropriate rating: (0) the adjective does not describe at all to (7) the adjective describes very well.

General	*Doesn't apply*	*Does not Describe at all*			*Neutral*			*Describes very well*
Active: moves about a lot	0	1	2	3	4	5	6	7
Anxious uneasy, easily startled	0	1	2	3	4	5	6	7
Calm: not easily disturbed by changes within or outside environment	0	1	2	3	4	5	6	7
Cautious: exhibits care in actions	0	1	2	3	4	5	6	7
Cooperative: easily compliant	0	1	2	3	4	5	6	7
Curious: readily explores new situations	0	1	2	3	4	5	6	7
Dominant: displaces/ overpowers others	0	1	2	3	4	5	6	7
Excitable: strong reaction to changes	0	1	2	3	4	5	6	7
Fearful: easily shaken; avoids changes and assumes protective or aggressive body postures	0	1	2	3	4	5	6	7
Flexible: adapts comfortably to change	0	1	2	3	4	5	6	7
Playful: initiates and easily joins in play	0	1	2	3	4	5	6	7
Smart: learns quickly, associates situations and people well, good memory	0	1	2	3	4	5	6	7
Sociable: seeks out companionship	0	1	2	3	4	5	6	7
Solitary: chooses to spend time alone	0	1	2	3	4	5	6	7
Stereotypical: fixed and oversimplified in behaviors	0	1	2	3	4	5	6	7
Submissive: gives in easily to others	0	1	2	3	4	5	6	7
Tense: shows restraint in posture and movement; carries the body stiffly and tries to pull back and be less noticeable	0	1	2	3	4	5	6	7
Vigilant: alert, attentive, notices all changes	0	1	2	3	4	5	6	7
Uninterested: no care in changes in environment, or conspecifics	0	1	2	3	4	5	6	7

	Doesn't apply	*Does not Describe at all*			*Neutral*			*Describes very well*
With novelties or environmental changes								
Aggressive: approaches with threat expression and posture	0	1	2	3	4	5	6	7
Fearful: avoids/retreats from others	0	1	2	3	4	5	6	7
Friendly: approaches readily	0	1	2	3	4	5	6	7
Uninterested: indifferent response	0	1	2	3	4	5	6	7
With humans								
Aggressive: approaches negatively	0	1	2	3	4	5	6	7
Fearful: avoids/retreats from people	0	1	2	3	4	5	6	7
Friendly: approaches readily	0	1	2	3	4	5	6	7
Uninterested: indifferent response	0	1	2	3	4	5	6	7

1. How many days per week are you responsible for the care of this animal? _____
2. How many hours per day do you spend where you and this animal can see each other? _____
3. How many years have you worked with/at:

   Big Cats:_____ This species:_____

   The Zoo:_____ This individual:_____

	Not well						*Very well*
4. How well do you know this individual?	0	1	2	3	4	5	6

5. What activities do you engage in with this individual? (Please circle all that apply)

   Direct Contact Indirect Contact Feeding Vet Appts/ Medication Dispersal Training

   Enrichment Zookeeper Talks/ Education Breeding

6. Please circle how often you give this animal any of the following enrichment possibilities:

	Never	*Occasionally*	*1/month*	*1/week*	*1+/week*	*Daily*	*Daily+*
Toys or objects	0	1	2	3	4	5	6
Toys made from animal products (hides, bones, etc.)	0	1	2	3	4	5	6
Live prey	0	1	2	3	4	5	6
Boxes or cardboard	0	1	2	3	4	5	6
Puzzles/ items to solve	0	1	2	3	4	5	6
Snacks or treats (in addition to regular diet)	0	1	2	3	4	5	6
Other	0	1	2	3	4	5	6

Comments:_____

_____

APPENDIX B

IACUC APPROVAL LETTERS

IACUC Approval Form for Project 19111 Behavioral Flexibility in Carnivores (MAB)

Oakland University
Institutional Animal Care and Use Committee
Committee Action Record

November 19, 2019	4525
Committee Review Date	**RAM Number**

PROJECT TITLE

Behavioral Flexibility in Captive Carnivores

Approved [X] Withhold Approval [ ]

NEW PROJECT

[X] 19111 — Jennifer Vonk, Ph.D.

IACUC Project Approval Number — **Principal Investigator**

REVISED PROJECT

Your Request for Revision of your Application for Use of Vertebrate Animals has been reviewed by IACUC and given full approval.

[ ] _____ _____

New IACUC Project Approval Number* **Principal Investigator**

* Please use this new approval number, with the revision number indicated, in all future activities.
A Cover Letter, similar to that used when addressing manuscript publications, needs to be attached to the application in RAM when submitting revisions to a previously approved IACUC application, or when submitting required modifications (in order to secure approval). Address required modifications in the same chronological order as they are listed in the Committee Action Record. Strike through the parts of the application that are being revised. **(Do not use the Track Changes option to do the strike through or to make required modifications or revisions. Use the Strike Through option [~~abc~~] under the font tool bar.)** The revisions need to be made in a readable typeface and of a different color of type so that anyone reviewing the modifications can easily identify where they are within the application.

Authorization for Project Commencement

Keith Williams — 11/21/2019

IACUC Chairperson: Keith Williams, PhD **Date**

Approval Period: December 1, 2019 through November 30, 2022

Annual Review Dates: December 1, 2020 and December 1, 2021

November 30, 2022

IACUC Approval Form for Project 20102 Behavioral Flexibility Using an Impossible Task in Captive Carnivores

Oakland University
Institutional Animal Care and Use Committee
Committee Action Record

October 15, 2020	4576
Committee Review Date	**RAM Number**

PROJECT TITLE

Behavioral Flexibility Using an Impossible Task in Captive Carnivores

Approved [X] Withhold Approval [ ]

NEW PROJECT

[X] 20102 — Jennifer Vonk, Ph.D.

IACUC Project Approval Number — **Principal Investigator**

REVISED PROJECT

Your Request for Revision of your Application for Use of Vertebrate Animals has been reviewed by IACUC and given full approval.

[ ] _____ _____

New IACUC Project Approval Number* **Principal Investigator**

* Please use this new approval number, with the revision number indicated, in all future activities.

A Cover Letter, similar to that used when addressing manuscript publications, needs to be attached to the application in RAM when submitting revisions to a previously approved IACUC application, or when submitting required modifications (in order to secure approval). Address required modifications in the same chronological order as they are listed in the Committee Action Record. Strike through the parts of the application that are being revised. (Do not use the Track Changes option to do the strike through or to make required modifications or revisions. Use the Strike Through option [~~abc~~] under the font tool bar.) The revisions need to be made in a readable typeface and of a different color of type so that anyone reviewing the modifications can easily identify where they are within the application.

Authorization for Project Commencement

10/16/2020

IACUC Chairperson: Keith Williams, PhD **Date**

Approval Period: October 15, 2020 through October 14, 2023

Annual Review Dates: October 15, 2021 and October 15, 2022

October 15, 2023

IACUC Approval Form for Project SC-Captive 4/21 Exploring Innovation in Captive Carnivores

HUNTER
The City University of New York
Office of Research Administration/695 Park Avenue/Room E1424/New York, NY 10021
Telephone: 212 772-4020 FAX: 212 772-4941
Institutional Animal Care and Use Committee

Memorandum

TO: Sheila Chase

CC: Barbara Wolin, Patricia Glennon, and Annmarie Rivera

FROM: Paul Feinstein, Chair

DATE: May 11th, 2018

RE: Protocol Approval

The IACUC reviewed and approved your protocol entitled "Exploring Innovation in Captive Carnivores" at the meeting of May 9th, 2018.

Subject to annual updates, this protocol "SC-Captive 4/21" (valid for 5/2018-4/2021) will expire April, 2021.

Good luck with this project!

IACUC Approval Form for WCS Project 18:01 Measuring Problem-Solving in Social and Asocial Carnivores

Paul. P. Calle, VMD, Dipl. ACZM
Chair, WCS IACUC
Chief Veterinarian
Director, Zoological Health

8 March 2018

Ms. Victoria O'Connor
The City University of New York – Hunter College
695 Park Avenue
New York, NY

RE: Submission Date: 2/24/18
IACUC Tracking #: 18:01
Title of Project: Measuring problem solving in social and asocial carnivores

Dear Ms. O'Connor:

Thank you for submitting the above-referenced Vertebrate & Invertebrate Research Application to the Wildlife Conservation Society's Institutional Animal Care and Use Committee ("WCS IACUC") for review. The WCS IACUC has reviewed your Application and determined that:

☒ The research project is **approved.**

If approved, the research project is subject to the terms and conditions contained in Section H of the Vertebrate & Invertebrate Research Application Form, which you signed and submitted with your application. The Terms & Conditions are included with this letter for your reference.

If approved, the WCS IACUC's approval of the research project expires three (3) years from the approval date, unless the WCS IACUC indicates otherwise.

We look forward to receiving project updates (one page or less) before each WCS IACUC meeting, and a final report upon conclusion of the study.

Thank you again for your submission, and good luck with your research.

Sincerely,

Paul P. Calle. VMD, Dipl ACZM, Dipl ECZM (zhm)
WCS Vice President for Health Programs
Chief Veterinarian & Director, Zoological Health Program
Chair, WCS IACUC

Encl.

2300 Southern Boulevard, Bronx, NY 10460, USA t 718.220.7100 f 718.220.7126 e pcalle@wcs.org

VERTEBRATE & INVERTEBRATE RESEARCH
APPROVAL TERMS & CONDITIONS

Approval by the WCS IACUC of your Vertebrate & Invertebrate Research Application is subject to following Terms & Conditions, which are contained in Section H of the Vertebrate & Invertebrate Research Application Form that you signed and submitted with your application. They are repeated here for your reference.

1. In submitting a proposal each scientific investigator acknowledges, agrees and certifies that:

   a. he/she has read, understands and accepts the policies and procedures outlined in this WCS IACUC **Vertebrate & Invertebrate Research Application Form**;

   b. he/she agrees to conduct the proposed research in accordance with those policies and procedures and in accordance with any other requirements of the WCS IACUC imposed in connection with its approval of the proposed research, including procedures which to the greatest extent possible minimize stress and discomfort to the animal(s) involved;

   c. in the event of any proposed changes in animal species or procedures or any adverse impact on any animal(s) in the study, he/she immediately will stop the research and verbally report to the WCS IACUC regarding same (with a written follow-up report);

   d. the information he/she has provided in the proposal is accurate and complete as of the date of submission, and in the event of any change in circumstances affecting the accuracy and completeness of the information provided, he/she will provide additional information as necessary to make the information provided accurate and complete;

   e. he/she will provide reports or updates **(one page or less unless otherwise requested or required)** to the WCS IACUC for each subsequent WCS IACUC Committee meeting or as otherwise requested by the WCS IACUC, regarding the progress of the research, and a final report upon conclusion of the study;

   f. he/she acknowledges and agrees that if the research proposal is not approved by the WCS IACUC, the research cannot proceed;

   g. he/she acknowledges and agrees that any WCS IACUC approval has a maximum duration of three years, unless the WCS IACUC indicates otherwise.

2. In addition to the provisions set forth above in section H.1, each scientific investigator who is an external applicant (i.e. not a WCS employee) agrees and certifies that:

   a. any and all information provided by WCS to investigator, which concerns WCS and

its operations, animal collections, research, projects or finances, or its trustees, officers, employees or contractors, or to which Investigator obtains access in connection with the research project for which WCS IACUC approval is requested, constitutes "Confidential Information." Confidential Information shall be treated confidentially and with the same standard of care that investigator and his/her institution use in maintaining their own Confidential Information, provided that that standard is not negligent. He/she shall not disclose such Confidential Information to any third party or use such information for any purpose other than the research purposes for which WCS IACUC approval is requested, without prior written consent of WCS. Confidential Information does not include any information which, evidenced with written proof, (i) is already publicly available or known through lawful means to the investigator before WCS's disclosure, (ii) after disclosure, becomes generally known to the public through no breach or fault of investigator, (iii) is received by investigator from a third party who is free to make such disclosure without breaching any legal obligation to WCS, (iv) investigator develops independently as evidenced by his/her own written records, or (v) is required to be disclosed by judicial or administrative process, in which case investigator will notify WCS of the obligation and cooperate reasonably with any efforts by WCS to bar or seek a modification of the order;

b. any new invention, development or discovery resulting from research involving collection or free-ranging animals at WCS's facilities, conducted by investigator pursuant to the WCS IACUC's approval, shall be promptly and confidentially disclosed in writing to WCS. Inventorship shall be determined in accordance with applicable patent law (if patentable) or by mutual agreement between the parties (if not patentable), taking into account the role and contributions of individuals involved in the development of the invention;

c. upon request by WCS, he/she will provide WCS with copies of all data collected or obtained, and all moving or still visual records with or without sound, or audio records, developed or created by investigator in any media, in connection with research involving collection or free-ranging animals at WCS's facilities, conducted pursuant to the WCS IACUC's approval. He/she irrevocably grants WCS a perpetual, royalty-free, non-exclusive right and license to use such data and records and prepare derivative works there from, for any non-commercial purposes, in any media, and in any territory;

d. he/she will have the right to publish and disclose results of research involving collection or free-ranging animals at WCS's facilities, conducted by investigator pursuant to the WCS IACUC's approval. He/she will submit the proposed publication or other disclosure (including of moving or still visual records with or without sound, or audio records, developed or created by investigator) to WCS for its review at least thirty (30) days prior to the scheduled submission of the results to any third party (including, without limitation, to any journal publisher). WCS may request that the proposed publication or other disclosure be delayed for up to sixty

(60) additional days as necessary to file a patent application or so that WCS's Confidential Information may be removed before publication. In all publications, authorship shall be determined on a case-by-case basis in accordance with scientific principle. If a WCS scientist is a co-author, the manuscript for the publication shall be made available through discussion between investigator and the WCS scientist. If there is no WCS scientist co-author, then investigator shall provide a copy of each publication arising out of investigator's research to WCS at the time that the manuscript is accepted for publication. Investigator agrees to acknowledge WCS for its assistance, in all publications resulting from research involving collection or free-ranging animals at WCS's facilities, conducted by investigator pursuant to the WCS IACUC's approval, when appropriate and subject in each instance to WCS's prior consent;

e. if, in connection with his/her proposed research, he/she intends to request the transfer of Biomaterials from WCS, he/she will complete and sign a **Biomaterials Agreement and Release**, which shall be submitted to the WCS IACUC together with his/her **Vertebrate & Invertebrate Research Application Form**;

3. In addition to the provisions set forth above in section H.1, each scientific investigator who is a WCS employee agrees and certifies that:

a. he/she shall treat Confidential Information (as defined in section H.2.a above) confidentially and with the same standard of care that WCS uses in maintaining its own Confidential Information. He/she shall not disclose such Confidential Information to any third party or use such information for any purpose other than the research purposes for which WCS IACUC approval is requested, without prior written consent of WCS.

b. he/she is an "Included Person" within the meaning of the WCS Intellectual Property Policy, as adopted October 26, 2010 and as may be amended from time to time ("WCS IP Policy") and as such, is subject to the WCS IP Policy and its provisions, including provisions concerning ownership and use of IP created by Included Persons in the course of WCS activities.

APPENDIX C

ZOO APPROVAL LETTERS

Approval Letter for Research Conducted at Bergen County Zoo

August 10, 2021

To whom this may concern,

On behalf of the Bergen County Zoo, this letter confirms our support of research at the zoo and will provide Victoria O'Connor with access to test our animals. We are very excited to partner on the research projects and are looking forward to the findings.

Sincerely,

Cindy Norton

Cindy Norton, Zoo Curator
Bergen County Zoo
216 Forest Avenue
Paramus, NJ 07652
201-634-3114

Approval Letter for Research Conducted at Creature Conservancy

Dec. 26, 2021

Oakland University IACUC
Meadow Brook Road
Rochester, Michigan 48309

Dear IACUC Committee Members:

This letter is written in support of Dr. Jennifer Vonk, and the students under her supervision, performing cognitive-behavioral research with the cats housed at the Creature Conservancy in Ann Arbor Saline, MI. Dr. Vonk and her students will, under my watch, have access to the general public area to conduct the playback trials for the proposed study.

We look forward to having Dr. Vonk and her students test our cats to further their animal cognition research; and I believe the cats will benefit from the time and attention her students bring to their work.

Sincerely,

Sign here

Insert your name and title here, Sruti Jamalapuram, Mammal Curator
The Creature Conservancy

Approval Letter for Research Conducted at Panther Ridge Conservation Center

September 1, 2021

To whom this may concern,

On behalf of the Panther Ridge Conservation Center, this letter confirms our support of research at the facility. We have reviewed and approved the experimental protocol of Dr. Jennifer Vonk and her student, Victoria O'Connor for the Impossible Task for use with our cats and are happy to provide access to animal staff and the cats for testing

Sincerely,

Judy Berens, Executive Director
Panther Ridge Conservation Center
2143 D. Road
Loxahatchee, FL 33470
561-795-8914

Approval Letter for Research Conducted at Turtle Back Zoo

November 14th, 2019

Victoria O'Connor
Oakland University
318 Meadow Brook Road
Rochester, MI 48309

Dear Victoria,

On behalf of the Essex County's Turtle Back Zoo, I am writing to confirm our support of your research at the zoo. Since the Turtle Back Zoo does not have an IACUC, we are agreeing to Oakland University's IACUC.

We are very excited to partner with you on your research and are looking forward to your findings. Please let me know if you need any additional information, or if I can assist in any other way.

Sincerely,

Erin Mowatt
Director of Animal Operations
Turtle Back Zoo
560 Northfield Avenue
West Orange, NJ 07052
973-731-5800 x 292
emowatt@parks.essexcountynj.org

IACUC Approval for Projects 2022-11 Exploring Innovation and Behavioral Flexibility in Captive Carnivores and 2022-10 "Impossible Task" with Hand-reared and Mother-reared Carnivores Conducted at Miami Zoo

Re: Zoo Miami Animal Care and Use Committee

Jennifer Vonk <vonk@oakland.edu> Thu, Feb 8, 2024 at 9:53 AM
To: Victoria Oconnor <voconnor@oakland.edu>

We have this from Miami. They had their own IACUC so we didn't need approval letters or an MOU.

---------- Forwarded message ---------
From: **Ridgley, Frank (MDPR)** <Frank.Ridgley@miamidade.gov>
Date: Tue, Jun 7, 2022 at 1:31 PM
Subject: Zoo Miami Animal Care and Use Committee
To: McGuire, Molly (MDPR) <Molly.McGuire@miamidade.gov>, vonk@oakland.edu <vonk@oakland.edu>

Drs. McGuire and Vonk,

The two studies submitted by Dr. McGuire, on behalf of Dr. Vonk, Exploring Innovation and Behavioral Flexibility in Captive Carnivores has been approved by the ZMACUC and has the number 2022-11 and "Impossible Task" with Hand-reared and Mother-reared Carnivores has also been approved by the ZMACUC and has the number 2022-10. There is a renewal date of 6/7/2023 for both studies. Should the studies go beyond this date, the PIs are responsible for resubmitting the IACUC application for review and renewal at least three weeks before the renewal date in order to continue the study. Thank you for your patience during the review process and your interest in doing research at Zoo Miami.

Thanks,

Frank

Frank Ridgley DVM, Zoo Conservation and Veterinary Services Manager

Conservation and Research Department

Zoo Miami

Miami-Dade Co. Parks, Recreation & Open Spaces Dept.

12400 SW 152nd St. Miami, FL 33177

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IACUC Approval for Project *Exploring Innovation, Behavioral Flexibility, and Conservation Status in Captive Carnivores* Conducted at Oklahoma City Zoo

4 December 2020

Dear Dr. Barrett:

The Oklahoma City Zoo and Botanical Garden's Scientific Review Committee (Committee) has reviewed your research application entitled "Exploring Innovation, Behavioral Flexibility, and Conservation Status in Captive Carnivores". I am pleased to inform you that the Committee has approved your application.

This study is approved for a three-year period effective from the date of this letter. If the study is not completed within three years, you must submit an application to extend the approval period. In addition, if any changes are made to the procedures or subjects, you must inform the Director of Conservation and Science in writing.

Your primary contacts to facilitate implementation of your study are:
Dr. Rebecca Snyder, Director of Conservation and Science, rsnyder@okczoo.org, 405-425-0256
Tyler Boyd, Curator of Carnivores, tboyd@okczoo.org, 405-425-0657

I look forward to working with you on this project!

Sincerely,

Rebecca J. Snyder, Ph.D.
Director of Conservation and Science
Oklahoma City Zoo and Botanical Garden
2000 Remington Place
Oklahoma City, OK 73111

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