J Ethol (2015) 33:137–144
DOI 10.1007/s10164-015-0422-z

ARTICLE

Evaluating behavioral syndromes in coyotes (*Canis latrans*)

Julie K. Young · Marion Mahe · Stewart Breck

Received: 1 July 2014 / Accepted: 15 January 2015 / Published online: 4 February 2015

Abstract As more research focuses on behavioral syndromes and their role in ecological and evolutionary processes, it is imperative that methods to test behavior are valid. The objectives of this study were to (1) assess behavior in captive coyotes (*Canis latrans*) using three methods [agitation scores, novel object test, and flight-initiation distance (FID)] and (2) to determine whether the three tests were correlated within individuals to describe behavioral syndromes. Female coyotes had higher agitation scores during handling (2.6 ± 0.5) than males (1.5 ± 0.3; $t = 1.90$, $p = 0.06$): scores ranged from 0 to 8 on a 0–11 scale. The most common behavior observed was biting at y-stick. Only 27 % of males and 10 % of females approached a novel object within 1 m, with females (37.3 ± 18.6 s) taking less time than males (136.7 ± 50.4 s; $p = 0.09$). There was no difference in the distance at which males (17.5 ± 4.0 m) and females fled during FID tests (20.7 ± 5.4 m; $p = 0.64$, $n = 30$). We found no relationships between FID and agitation scores ($r^2 = 0.13$, $p = 0.12$) or time to approach a novel object and agitation scores ($r^2 = 0.001$, $p = 0.89$). There was a slightly positive relationship between FID and time to approach a novel object ($r^2 = 0.15$, $p = 0.03$), but no relationship among all three tests ($r^2 = 0.15$, $p = 0.45$). Our results suggest a behavioral syndrome for boldness and explorations, but these traits are unlikely to be coupled with aggression in coyotes. While these three tests may not be ideally combined to create a behavioral syndrome in individual coyotes, using FID and novel object testing may elucidate a type of behavioral syndrome.

Keywords Aggression · *Canis latrans* · Flight-initiation distance · Novel object · Personality

J. K. Young (✉)
USDA-Wildlife Services-National Wildlife Research Center-Predator Research Facility, Department of Wildland Resources, Utah State University, BNR 163, Logan, UT 84322-5295, USA
e-mail: julie.young@usu.edu; julie.k.young@aphis.usda.gov

M. Mahe
Department of Agronomy, Agrocampus Ouest Rennes, 65 Rue de Saint-Brieuc, 35042 Rennes, France
e-mail: mmahe@agrocampus-ouest.fr

S. Breck
USDA-Wildlife Services-National Wildlife Research Center-Predator Research Facility, 4101 LaPorte Avenue, Fort Collins, CO 80521, USA
e-mail: stewart.w.breck@aphis.usda.gov

Introduction

Understanding differences in animal personalities and their ecological and evolutionary consequences is an emerging topic with important management ramifications. Central to this topic is the concept of behavioral syndromes, in which individual animals exhibit consistent behaviors (Sih et al. 2004a, b; Réale et al. 2010; Stamps and Groothuis 2010a). Behavioral syndromes are also called personality (Cockrem 2007; Ruis et al. 2000), coping style (Koolhaas et al. 1999), and individual temperament (Adams et al. 2011). Behavioral syndromes are thought to be expressed consistently across different contexts (e.g., Carrete and Tella 2010). However, recent studies indicate behavioral syndromes may be contextual within individuals (Nyqvist et al. 2013), suggesting multiple sources of behavioral information are needed to determine whether a given species demonstrates consistent or contextual behavioral syndromes. The most common consistent behavioral syndromes reveal associations among

boldness, exploration, and aggression (Bremner-Harrison et al. 2004; Sih et al. 2004a, b; Bell 2007; Smith and Blumstein 2010; Conrad et al. 2011; Stamps and Groothuis 2010b). However, because some populations and species contradict this pattern, either behavioral syndromes do not exist in all species or the tests used to measure behavioral syndromes are not appropriate (Burns 2008; Nyqvist et al. 2013).

It is not always clear which behavioral characteristics are best suited for identifying behavioral syndromes within a given species. For example, animals in areas such as national parks or in cities, where persecution by humans is negligible, may appear bold towards humans, yet this boldness may simply be an artifact of habituation, the gradual decrease in response to repeated stimuli (Metcalf et al. 2002; Baudains and Lloyd 2007; Stankowich 2008). It is possible that captive animals may also habituate to humans and appear bold. Protected animals may also exhibit more exploratory behaviors near humans because it is relatively low risk. These environments could lead to the development of bolder or more aggressive animals if there is a fitness gain for individuals exhibiting bolder behavior (Diamond 1986). In this context, bolder individuals would be over-represented in animal populations that colonize and live in urban and protected areas. Boldness may improve fitness by increasing attractiveness to mates (Godin and Dugatkin 1996) or competitive ability for obtaining territories (Both et al. 2005). Alternatively, fitness may be reduced if boldness and aggression lead to human conflict.

Flight-initiation distance (FID), novel object test, and agitation scores during human handling measure boldness, exploration, and aggression, respectively. One of the standard tests of risk behavior is to measure FID, the distance between the animal and a potential predator at which the animal starts to flee (Stankowich and Blumstein 2005; Blumstein 2006). For many species, humans can be used in FID tests to study risk behavior of animals. Animals appear to perceive humans as predators and variation in boldness to human observers has been shown across species (Fernandez-Juricic et al. 2002; Frid and Dill 2002; Blumstein 2003, 2006; Blumstein et al. 2005; Evans et al. 2010). FID has been correlated to the habitat within which a predator approaches (Carrete and Tella 2010), the threat posed by the predator (Ydenberg and Dill 1986), and fitness gains or losses (Ydenberg and Dill 1986; Broom and Ruxton 2005; Cooper and Frederick 2007). Although FID is correlated to boldness, it has rarely been used to measure behavioral syndromes in populations (Evans et al. 2010) or among individuals (Carrete and Tella 2010). Exploration evaluates a different type of risk behavior that may be measured through novel object tests (Burns 2008). Unlike FID, where risk is associated directly with predation threat, the risk in novel object tests is unknown and unfamiliar. Novel object testing may provide a rapid assessment of the degree of exploratory behaviors within behavioral syndromes. Animals may fear or avoid a novel object when in familiar environments. Exploration is measured as latency to approach, frequency and duration of contact, or time spent investigating (Forkman et al. 2007). Finally, aggression may be assessed by how an animal responds to handling by humans and provide an important contribution to defining behavioral syndromes (Réale et al. 2000; Möeller and Nielson 2010; Möeller and Garamszegi 2012). Because behavioral syndrome by default involves a suite of behaviors, there is the need to understand whether individuals exhibit correlated measures across these behavioral tests.

As more research focuses on behavioral syndromes and their role in ecological and evolutionary processes, it becomes imperative that testing methods are valid and comparable. Determining whether results of the tests are correlated for the focal species will help researchers compare results across and within studies that use different measures. The objective of this study is to determine whether there are correlates in the outcome of three discrete tests that measure boldness (FID), exploration (novel object test), and aggression (handling scores), so that they can be used to define behavioral syndromes. We used coyotes (*Canis latrans*) as our model species.

Coyotes are an excellent model species for this study because they express variation in behavior among and within populations and live in wilderness, rural, and urban environments. Coyotes were originally restricted to western North American prairies (Young and Jackson 1951; Nowak 1978), but rapidly expanded their distribution from Alaska to Central America (Bekoff 1977; Hall 1981). This expansion is partially explained by their wide dietary breadth and variation in habitat and space use (e.g., Andelt 1985; Rose and Polis 1998; Mills and Knowlton 1991; Crooks and Soulé 1999; Atwood et al. 2004). Coyotes typically are found as territorial, mated pairs with offspring that both parents provide care to, but may also be found in packs with additional non-breeding adults or alone as transients (Bowen 1981; Gese et al. 1996; Patterson and Messier 2001). Coyotes demonstrate a wide range of behavioral traits (Mettler and Shivik 2007; Darrow and Shivik 2009).

Materials and methods

We conducted experiments from November 2012 through January 2013 at the USDA Wildlife Services, National Wildlife Research Center, Predator Research Facility in Millville, Utah, USA. The facility maintains a captive population of coyotes for research purposes, with most

born at the facility but some pups (<2 months old) brought in from the wild every 3–5 years to maintain genetic diversity. Captive coyotes had similar experiences in interactions with humans, housing, and feeding throughout their lives and were cared for to maximize humane standards and similarities with wild coyotes (Shivik et al. 2009). All captive coyotes are handled annually to obtain blood samples for heartworm testing. Adult and juvenile captive coyotes were housed in various pens throughout the facility, ranging in size from 0.10 to 0.60 ha. Each pen contained 1–2 sun shelters, a water nozzle or bucket, at least one den box, and an individual coyote or a breeding pair of coyotes. We attempted to score 76 coyotes on capture and handling, novel objects, and FID tests; however, sample sizes differ among tests because some animals were not handled, did not approach the novel object, or could not be approached while at rest for FID tests. Coyotes were first tested on handling scores because of timing of the blood draws for heartworm testing but other behavioral tests were randomized in order. The study was approved by USDA-NWRC IACUC (QA-2074).

Capture and handling scores

We scored coyote behavior related to aggression for 54 coyotes, 27 of each sex, being handled for annual heartworm testing over a 5-day period in November 2012. We used two teams of people but they were often mixed such that teams were not consistently the same discreet group of people. All coyote handlers received the same training prior to this experiment. One observer was assigned to each team to record coyote behaviors. The two observers standardized their scoring methodology by first simultaneously scoring behaviors of 10 coyotes not included in the study to ensure consistency between observers. The observers had no previous information about the coyote's behaviors during previous captures.

The time it took to capture each coyote and handling time were recorded, along with behaviors that were exhibited by the coyote while being handled. Coyotes were restrained within their den box, which limited the ability of the recorder to determine exact start and end times of each observed behavior. Therefore, we used a binary response (yes/no) to code for observed behaviors and create an agitation index for each coyote (Verdolin and Harper 2013). Eleven behaviors were recorded during handling and each coyote was given an agitation score equaling the sum of behaviors they performed (Table 1). An individual coyote could therefore have a minimum agitation score of 0, where no behaviors were observed, and a maximum of 11, where all agitation behaviors were observed. While some behaviors are commonly recognized as aggressive (e.g., growling) in wild coyotes, others were specific to facility procedures for captive coyotes. For example, handlers may opt to use a broom as a visual barrier when coyotes act aggressively and the situation is deemed unsafe to handlers. The broom is typically placed to obstruct the coyote's head from the rest of the body and provide a visual barrier and something for the coyote to safely bite instead of biting the y-stick being used as a restraining tool. A y-stick is a pole, shaped like a 'y' at one end that can be used to pin an animal to the ground. Capture and restraint in the den box also limited each coyote's ability to move and display behavioral postures. Therefore, posture was not recorded. All coyotes were captured and handled once.

Table 1 Definitions for aggressive behaviors observed during handling of captive coyotes at the NWRC Predator Research Facility, Millville, Utah, USA

Behavior	Definition
Bite y-stick	Coyote attempts to or succeeds at biting a y-stick
Bite person	Coyote attempts to or succeeds at biting a person
Broom	Coyote behavior suggests risk to handler: a broom is placed in front of face to block view and/or provide something safe for the coyote to bite
Gaped mouth	Coyote's mouth is open and directed toward handler, y-stick, or broom; this excludes open mouth observed during quick breathing
Lunge out	Coyote attempts to propel self/escape from den box when handling crew is pinning
Lunge at y-stick	Coyote lunges towards y-stick
Raised hackles	Coyote's hair on nape is raised
Roll and pop	Coyote rolls and pops out from under y-stick
Show teeth	Coyote raises lips to show teeth
Time out	Coyote is actively fighting restraint and handling crew need a 'time out' to set up again
Vocalize	Coyote growls or barks

Flight-initiation-distance test

We selected at random among those coyotes found at rest for FID tests. Nineteen males and 11 females were tested for FID. Of these, 20 (12 males and 8 females) also had handling scores and 29 (18 males, 11 females) completed novel object tests. One of two researchers, both of whom were relatively unfamiliar to the coyotes (e.g., did not assist with daily care), walked at a normal pace directly towards the coyote until the coyote stood up and walked away. Both researchers were of similar height and weight and walked at the same pace. Within each test, the researcher continued to walk toward the coyote if it stood but did not otherwise move. When the coyote moved away from the researcher, the researcher stopped walking and marked the spot with spray paint. The researcher then

marked the spot where the coyote had been resting. Spots where the coyote had been at rest were easy to identify because of snow on the ground at the time of testing. For coyotes housed as pairs ($n = 9$ pairs), data was recorded for the location of each coyote and distance at which each fled. Multiple coyotes were typically tested before measurements were taken to avoid disturbing other coyotes at rest. Once no resting coyotes were available, we used a metric tape to measure to the nearest centimeter and record the direct-line distance at which each coyote fled. Tests were run over a 3-week period in January 2013.

Novel object test

A novel object was selected that was a shape unfamiliar to the captive coyotes. We used a wooden stool. The stool was 0.8 m tall and was placed in the pen, approximately 5 m from the entrance. One person placed the stool in a randomly selected pen and left the pen immediately while a second person observed the coyote in the pen. The novel object was presented to 35 males and 30 females housed alone during the trial. Of these 65 coyotes, 45 (25 males and 20 females) also had handling scores. We recorded the time until the coyote made any approach toward the novel object, approached within 5 m of the object, approached within 1 m of the object, and touched the object. Approach was defined as any movement towards the object. The object was removed once contact was made or 15 min had passed. A previous novel object study with captive coyotes was used to determine the length of the observation period (Heffernan et al. 2007). We elected to use latency to approach for analysis because it may be more heavily affected by fear of the object (Burns 2008). If the novel object was not approached, individuals were given a score of 15 min. All coyotes were tested once over a 10-day period in December 2012.

Statistical analysis

We tested whether males and females differed in their handling scores, latency to approach a novel object, and the FID test by using an F test for approach and t tests for handling and FID. We used linear regressions to identify relationships between age and sex, age and handling score, and combinations of the three tests (e.g., FID and handling score). We used multiple regression analysis to combine data from all three tests. When we evaluated only those coyotes with at least two of the three data sources ($n = 30$), data for time to approach a novel object and FID data were not normally distributed so we log-transformed these data for further analyses. Statistical significance was set at $p = 0.05$ for all tests.

Results

Capture and handling scores

Coyotes scored for handling ranged in age from 1–8 years old (3.7 ± 0.3). There was no difference in age of coyotes handled by sex ($t = -0.65$; $p = 0.52$) nor was there a relationship between coyote age and handling score ($r^2 = 0.03$; $p = 0.24$). Age was therefore excluded from further analysis. Agitation scores ranged from 0 to 8, with females (2.6 ± 0.5) scoring higher than males (1.5 ± 0.3; $t = 1.90$, $p = 0.06$). Agitation score was not related to the time it took to handle the coyote ($r^2 = 0.006$, $p = 0.57$).

The most common behavior observed during handling was biting at y-stick, which we observed in 72.2 % of coyotes (Table 1). All other behaviors were observed in less than half the coyotes. Gaping mouth (40.7 %), lunging at y-stick (29.6 %), and use of broom (24.1 %) were observed in more than twice as many coyotes as lunging out of box (9.3 %), raised hackles (9.3 %), taking a time out (5.6 %), or rolling and popping (5.6 %; Table 1). Only one coyote was observed growling, showing teeth, or attempting to bite a person. Growling and showing teeth were exhibited by males, while attempting to bite person was exhibited by a female.

Flight-initiation-distance test

There was no relationship between age and FID when controlling for sex ($r^2 = -0.009$, $p = 0.43$), so age was excluded from further analysis. There was no difference in the distance at which males (17.5 ± 4.0 m) and females fled (20.7 ± 5.4 m; $p = 0.64$, $n = 30$).

Novel object test

There was no relationship between age and latency to approach a novel object ($r^2 = 0.017$, $p = 0.22$), so age was excluded from further analyses. All coyotes showed interest in the object by looking at it or circling around it; however, only 74 % ($n = 26$) of the males and 53 % ($n = 16$) of the females moved toward the object within the 15-min test period. Of those, 51 % of the males and 30 % of the females approached within 5 m, and 27 % of males and 10 % of females approached within 1 m. There were no differences between males and females in latency to move toward the object (males: 146.1 ± 42.5 s, females: 148.5 ± 56.5 s; $p = 0.83$) or latency to approach within 5 m of the object (males: 146.1 ± 51.1 s, females: 148.5 ± 75.3 s; $p = 0.83$). Although not statistically significant, females (37.3 ± 18.6 s) took less time to approach within 1 m compared to males (136.7 ± 50.4 s; $p = 0.09$). One male and two females touched the novel

object. A 7-year-old male touched the novel object within 9 s, while the 2-year-old females varied; one female touched the novel object in 4 s and the other in 160 s. Since the trend was similar for latency to approach (at any distance) and latency to approach within 5 m, and our sample size was larger for latency to approach, we used it for analyses of combined data.

Combined data

There was no relationship among the three tests ($r^2 = 0.15$, $p = 0.45$). There were no relationships between FID and agitation index ($r^2 = 0.13$, $p = 0.12$) or time to approach a novel object and agitation index ($r^2 = 0.001$, $p = 0.89$; Fig. 1). However, we found a slightly positive relationship between FID and time to approach a novel object ($r^2 = 0.15$, $p = 0.03$; Fig. 1).

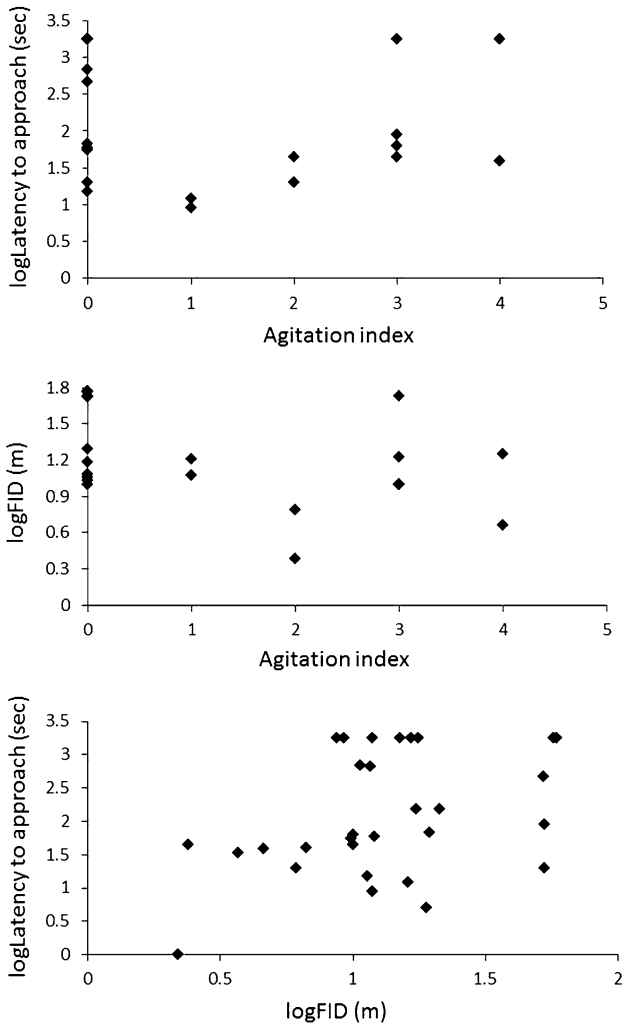

Fig. 1 Relationship for captive coyotes between response to **a** handling (agitation index) and latency to approach a novel object, **b** handling (agitation index) and FID, and **c** FID and latency to approach. There were no significant relationships except between FID and latency to approach a novel object ($r^2 = 0.15$, $p = 0.03$)

Discussion

Identifying behavioral syndromes in wild animals is challenging, especially in cryptic or nocturnal species (Sih et al. 2004b). Wild coyotes are often difficult or impossible to directly observe to assess behaviors. Direct observations of captive coyotes and indirect observations of wild coyotes have enabled researchers to obtain values of exploratory behavior through novel object testing (e.g., Harris and Knowlton 2001). Researchers are also starting to measure coyote behaviors during capture and handling to score agitation (e.g., Gehrt, personal communication). However, this may lead to inaccurate assessments since the experience of being trapped is negative and, in some cases, researchers use tranquilizer trap devices that could alter coyote behavioral responses (Balser 1965). FID tests may provide a measure of boldness and do not require direct observation if coyotes are equipped with VHF or GPS collars. A researcher could identify a coyote at rest and walk directly towards it until it fled, which could be noted by a change in location or the frequency at which a signal is emitted from the collar. Because these tests take considerable effort in the field, it is important to know whether any or all can be used to identify behavioral syndromes.

We tested the hypotheses that there were correlations among responses to the different tests. Results suggest there is no association among all three tests for boldness, exploration, and aggression in coyotes. While there was some evidence that FID and time to approach a novel object are related, we found no other statistically significant relationships. Boldness and exploration may, therefore, be part of a suite of correlated behaviors within a syndrome, while agitation may belong to a different behavioral syndrome or be malleable in coyotes. The absence of consistency between functionally different tests relating boldness and exploration to aggression suggest these three behaviors do not together comprise a behavioral syndrome in coyotes (Bremner-Harrison et al. 2004; Sih et al. 2004a; Bell 2007; Smith and Blumstein 2010; Conrad et al. 2011; Stamps and Groothuis 2010b). Our results are supported by the fact that we did not find correlations despite contextual overlap across our tests (i.e., animals in same testing pens; Sih et al. 2004a). Instead, fitness may not be associated with these consistent behavioral types (Wolf et al. 2008; Wolf and Weissing 2010).

The positive relationship observed between FID and latency to approach a novel object suggests coyotes show behavioral syndromes in dealing with risk. The types of risk were discrete between FID (i.e., predator risk) and novel

object testing (i.e., unknown risk). Responding similarly to all risks could be advantageous if coyotes are unable to distinguish among risk types. This would prevent an individual from erroneously classifying a high risk situation as low risk.

Although overall patterns were not evident across all tests, there were some interesting results within each. We observed eleven types of aggressive behavior during handling procedures. Although not statistically significant, females had higher agitation scores than males, suggesting a higher level of aggression. This is the opposite of what has been observed in other canids, such as domestic dogs (*Canis familiaris*) where aggression was more clearly defined by sex (Beaver 1983; Sherman et al. 1996). No coyote performed all behaviors, and most performed few to none. The majority of coyotes were observed biting at the y-stick. Because coyotes captured in the wild are typically caught in foot-hold traps or snares and restrained via a y-stick, this behavior may provide an easy method to gauge agitation and enhance its utility and comparative value across studies. This would also simplify data collection by reducing the use of multiple canid behaviors when scoring handling agitation, especially since it may be more nuanced than our simple category of agitation describes (e.g., Podberscek and Serpell 1996). For example, coyotes attempting to roll and pop or lunge out of a box may not be showing signs of aggression but were simply attempting to escape capture. Although aggression during handling has been correlated to boldness (e.g., Réale et al. 2000), it is possible that agitation during handling by humans may not relate to conspecific aggression but instead indicate shyness or anxiety (Carter et al. 2012a, b; Verdolin and Harper 2013). In a field setting, where coyote body posture can also be observed, identification of aggressive behaviors versus fear/anxiety behaviors could be elucidated.

The lack of statistical differences between males and females in FID and novel object tests may be because most are housed as male–female pairs and are reacting to one another when both are present or have learned to respond based on previous reactions by their mate when only one is present. Coyotes are social and most are found as mated pairs or in packs. Although some FID tests were conducted on pairs, individual coyotes housed in the same pen showed different FIDs. We did not have sufficient numbers of coyotes tested individually to compare with those tested as pairs to determine whether there are differences, and future studies should attempt to test for differences. Further, coyotes at the facility are housed in pens that can be observed by other coyotes in nearby pens. We controlled for this by only testing coyotes that were found at rest, which typically resulted in pens being widely dispersed during a single testing period. However, we hypothesize that coyotes in more closed habitats with similar levels of human interactions, such as urban coyotes, would have shorter FIDs. Additional data on FID in coyotes located in different habitats are needed. If such differences do occur, it is possible FID will better correlate to other behavioral metrics. Coyotes at the research facility behave in a similar way to wild coyotes (Shivik et al. 2009), so we hypothesize that our findings would also be similar in wild coyotes found in open habitats.

Despite using previous studies to determine the length of testing time with a novel object, several coyotes did not approach the object within 15 min and only three touched the object in that time. It is unclear whether more coyotes would have approached or touched the object if given more time and whether the absence of correlation was a result of the number of coyotes that did not approach the novel object. However, we did include any approach to the novel object instead of exclusively evaluating proximity and used these data in analysis to increase sample size. Further, the trade-off between additional time and novelty of the object may have also changed what was being tested. The object may have lost its novelty if left in the pen longer or coyotes may have simply approached the object during regular captive movement patterns (e.g., Burns 2008).

Although there was no difference between sexes and latency to approach a novel object, the three females that approached within 1 m of the object did so faster than males and two proceeded to touch it. Only one of nine males that approached the object within 1 m touched it. The results were similar for latency to approach at any distance and latency to approach to within 5 m of the novel object. These categories may be unnecessary, and simply determining the latency to approach a novel object may be sufficient in future studies, especially since this metric was correlated with FID. A larger sample size may have determined, as these results suggest, whether males are more exploratory but risk-aversive at proximity, while females are less exploratory in general but those females that are exploratory show high-risk behaviors at proximity.

The three tests we selected are often used across mammalian species to assess risk-taking and create behavioral profiles, typically associated with boldness (Bremner-Harrison et al. 2004; Sih et al. 2004a, b; Bell 2007; Smith and Blumstein 2010; Conrad et al. 2011; Stamps and Groothuis 2010b). Because our study showed only two of these tests are correlated, it suggests the tests measure different behavioral traits and have discriminant validity (Carter et al. 2012a, b) or the three behaviors are not linked in a behavioral syndrome (Sih et al. 2004a). We recommend researchers use caution in inferring behavioral syndromes in coyotes from these three tests. Instead, each test may be used independently to compare coyotes across populations. At most, FID and novel object tests can be combined to create a more complete picture of a behavioral

profile related to risk in coyotes. Our findings are particularly useful to research and management for urban coyotes, where coyote behavior may be used to determine mediation strategies for human–wildlife conflict. Managers and researchers should use caution in interpreting what behavioral traits are being measured within each test and should instead focus on how test results relate to interactions with humans or their pets.

Acknowledgments Stacey Brummer and Stan Gehrt assisted with project design. We thank Stacey Brummer and Delphine Napoletano for field assistance. We are especially thankful to the NWRC staff and many volunteers that assisted with coyote captures. Heath Weaver was helpful in reviewing the manuscript. This project was funded by USDA-Wildlife Services-National Wildlife Research Center. Funding had no role in study design, collection, analysis and interpretation of data, writing, or the decision to submit the article for publication.

References

Adams NJ, Farnworth MJ, Rickett J, Parker KA, Cockrem JF (2011) Behavioural and corticosterone responses to capture and confinement of wild blackbirds (*Turdus merula*). Appl Anim Behav Sci 134:246–255

Andelt WF (1985) Behavioral ecology of coyotes in south Texas. Wildl Monogr 90:3–45

Atwood TC, Weeks HP, Gehring TM (2004) Spatial ecology of coyotes along a suburban-to-rural gradient. J Wildl Manag 68:1000–1009

Balser DS (1965) Tranquilizer tabs for capturing wildlife carnivores. J Wildl Manag 28:438–442

Baudains TP, Lloyd P (2007) Habituation and habitat changes can moderate the impacts of human disturbance on shorebird breeding performance. Anim Conserv 10:400–407

Beaver BV (1983) Clinical classification of canine aggression. Appl Anim Ethol 10:35–43

Bekoff M (1977) *Canis latrans*. Mamm Species 79:1–9

Bell AM (2007) Future directions in behavioural syndromes research. Proc Royal Soc B Biol Sci 274:755–761

Blumstein DT (2003) Flight-initiation distance in birds is dependent on intruder starting distance. J Wildl Manag 67:852–857

Blumstein DT (2006) Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. Anim Behav 71:389–399

Blumstein DT, Fernandez-Juricic E, Zollner PA, Garity SC (2005) Inter-specific variation in avian responses to human disturbance. J Wildl Manag 42:943–953

Both C, Dingemanse NJ, Drent PJ, Tinbergen JM (2005) Pairs of extreme avian personalities have highest reproductive success. J Anim Ecol 74:667–674

Bowen WD (1981) Variation in coyote social organization: the influence of prey size. Can J Zool 59:639–652

Bremner-Harrison S, Prodohl PA, Elwood RW (2004) Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). Anim Conserv 7:313–320

Broom M, Ruxton GD (2005) You can run—or you can hide: optimal strategies for cryptic prey. Behav Ecol 16:534–540

Burns JG (2008) The validity of three tests of temperament in guppies (*Poecilia reticulata*). J Comp Psychol 122:344–356

Carrete M, Tella JL (2010) Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance induced habitat selection. Biol Lett 6:167–170

Carter AJ, Feeney WE, Marshall HH, Cowlishaw G, Heinsohn R (2012a) Animal personality: what are behavioural ecologists measuring? Biol Rev 88:465–475

Carter AJ, Marshall HH, Heinsohn R, Cowlishaw G (2012b) How not to measure boldness: novel object and antipredator responses are not the same in wild baboons. Anim Behav 84:603–609

Cockrem JF (2007) Stress, corticosterone and avian personalities. J Ornithol 148:169–178

Conrad JL, Weinersmith KL, Brodin T, Saltz JB, Sih A (2011) Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. J Fish Biol 78:395–435

Cooper WE, Frederick WG (2007) Optimal flight initiation distance. J Theor Biol 244:59–67

Crooks KE, Soulé ME (1999) Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566

Darrow PA, Shivik JA (2009) Bold, shy, and persistent: variable coyote response to light and sound stimuli. Appl Anim Behav Sci 116:82–87

Diamond JM (1986) Rapid evolution of urban birds. Nature 324:107–108

Evans J, Boudreau K, Hyman J (2010) Behavioural syndromes in urban and rural populations of song sparrows. Ethology 116:588–595

Fernandez-Juricic E, Jimenez MD, Lucas E (2002) Factors affecting intra- and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. Can J Zool 80:1212–1220

Forkman B, Boissy A, Meunier-Salaün MC, Canali E, Jones RB (2007) A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. Physiol Behav 92:340–374

Frid A, Dill L (2002) Human-caused disturbance stimuli as a form of predation risk. Conserv Ecol 6:11

Gese EM, Ruff RL, Crabtree RL (1996) Social and nutritional factors influencing the dispersal of resident coyotes. Anim Behav 52:1025–1043

Godin JGJ, Dugatkin LA (1996) Female mating preference for bold males in the guppy, *Poecilia reticulata*. Proc Natl Acad Sci 93:10262–10267

Hall ER (1981) The mammals of North America, 2nd edn. Wiley, NY

Harris CE, Knowlton FF (2001) Differential responses of coyotes to novel stimuli in familiar and unfamiliar settings. Can J Zool 79:2005–2013

Heffernan DJ, Andelt WF, Shivik JA (2007) Coyote investigative behavior following removal of novel stimuli. J Wildl Manag 71:587–593

Koolhaas JM, Korte SM, De Boer SF, Van Der Vegt BJ, Van Reenen CG, Hopster H, De Jong IC, Ruis MAW, Blokhuis HJ (1999) Coping styles in animals: current status in behaviour and stress physiology. Neurosci Behav Physiol 23:925–935

Metcalf BM, Davies SJ, Ladd PG (2002) Adaptation behaviour by two bird species as a result of habituation to humans. Aust Birdwatcher 18:306–312

Mettler AE, Shivik JA (2007) Dominance and neophobia in coyote (*Canis latrans*) breeding pairs. Appl Anim Behav Sci 102:85–94

Mills LS, Knowlton FF (1991) Coyote space use in relation to prey abundance. Can J Zool 69:1516–1521

Möeller AP, Garamszegi LZ (2012) Between individual variation in risk-taking behavior and its life history consequences. Behav Ecol 23:843–853

Möeller AP, Nielson JT (2010) Fear screams and adaptations to avoid imminent death: effects of genetic variation and predation. Ethol Ecol Evol 22:1–20

Nowak RM (1978) Evolution and taxonomy of coyotes and related *Canis*. In: Bekoff M (ed) Coyotes: biology, behavior and management. Academic Press, San Diego

Nyqvist MJ, Gozlan RE, Cucherousset J, Britton JR (2013) Absence of a context-general behavioural syndrome in a solitary predator. Ethology 119:1–11

Patterson BR, Messier F (2001) Social organization and space use of coyotes in eastern Canada relative to prey distribution and abundance. J Mamm 82:463–477

Podberscek AL, Serpell JA (1996) The English cocker spaniel: preliminary findings on aggressive behaviour. Appl Anim Behav Sci 47:75–89

Réale D, Gallant BY, Leblanc M, Festa-Bianchet M (2000) Consistency of temperament in bighorn ewes and correlates with behaviour and life history. Anim Behav 60:589–597

Réale D, Dingemanse NJ, Kazem AJN, Wright J (2010) Evolutionary and ecological approaches to the study of personality. Philos Trans R Soc Lond Ser B Biol Sci 365:3937–3946

Rose MD, Polis GA (1998) The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. Ecology 79:998–1007

Ruis MAW, Te Brake JHA, Van De Burgwal JA, De Jong IC, Blokhuis HJ, Koolhaas JM (2000) Personalities in female domesticated pigs: behavioural and physiological indications. Appl Anim Behav Sci 66:31–47

Sherman CK, Reisner IR, Taliaferro LA, Houpt KA (1996) Characteristics, treatment, and outcome of 99 cases of aggression between dogs. Appl Anim Behav Sci 47:91–108

Shivik JA, Palmer GL, Gese EM, Osthaus B (2009) Captive coyotes compared to their counterparts in the wild: does environmental enrichment help? J Appl Anim Welf Sci 12:223–235

Sih A, Bell AM, Johnson JC (2004a) Behavioural syndromes: an ecological and evolutionary overview. Trends Ecol Evol 19:372–378

Sih A, Bell AM, Johnson JC, Ziemba RE (2004b) Behavioural syndromes: an integrative overview. Q Rev Biol 79:241–277

Smith BR, Blumstein DT (2010) Behavioral types as predictors of survival in Trinidadian guppies (*Poecilia reticulata*). Behav Ecol 21:919–926

Stankowich T (2008) Ungulate flight responses to human disturbance: a review and meta-analysis. Biol Conserv 141:2159–2173

Stamps JA, Groothuis TGG (2010a) Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. Philos Trans R Soc Lond Ser B Biol Sci 365:4029–4041

Stamps J, Groothuis TGG (2010b) The development of animal personality: relevance, concepts and perspectives. Biol Rev 85:301–325

Stankowich T, Blumstein D (2005) Fear in animals: a meta-analysis and review of risk assessment. Proc R Soc B 272:2627–2634

Verdolin JL, Harper J (2013) Are shy individuals less behaviorally variable? Insights from a captive population of mouse lemurs. Primates 54:309–314

Wolf M, Weissing FJ (2010) An explanatory framework for adaptive personality differences. Phil Trans Royal Soc B Biol Sci 365:3959–3968

Wolf M, Van Doorn GS, Weissing FJ (2008) Evolutionary emergence of responsive and unresponsive personalities. Proc Nat Acad Sci 105:15825–15830

Ydenberg RC, Dill LM (1986) The economics of fleeing from predators. Adv Stud Behav 16:229–249

Young SP, Jackson HHT (1951) The clever coyote. Stockpole, Harrisburg and Wildlife Management Institute, Washington, DC