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Midiendo diferencias individuales estables en el comportamiento del gato doméstico adulto

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RESUMEN

Introducción

Personalidad animal

En las últimas décadas ha habido un creciente interés entre los biólogos de la conducta sobre la naturaleza y el significado de las diferencias individuales en la conducta, frecuentemente llamadas personalidad animal. Esto se ha reflejado en un número substancial de estudios abarcando una amplia gama de taxa (Gosling, 2001). La personalidad animal se define como las diferencias estables del comportamiento entre individuos, que son consistentes a través del tiempo y/o los contextos (Sih et al., 2004; Stamps y Groothuis, 2010; Wolf y Weissing, 2012).

La personalidad animal también puede ser conocida como temperamento, tipos conductuales, o estilos de afrontamiento ("coping styles"). Este último se refiere más específicamente a los patrones alternos de conducta en respuesta a retos (tales como el afrontamiento proactivo y reactivo; Koolhaas et al., 1999; Coppens et al., 2010). No obstante, la variación conductual entre individuos consistente a través del tiempo y diferentes situaciones es la base detrás de todos los términos mencionados. Otro concepto relacionado es el de síndromes conductuales. Se definen como un conjunto de rasgos de personalidad correlacionados a través de distintos contextos (Sih et al., 2004; Stamps y Groothuis, 2010; Wolf y Weissing, 2012; Carter et al., 2013). Pueden considerarse como una descripción de la distribución de las personalidades (Wolf y Weissing, 2012).

Se han encontrado diferencias individuales estables en el comportamiento de numerosas especies de vertebrados (Gosling, 2001) e invertebrados (Kralj-Fišer y Schuett,

2014). Se ha demostrado que dichas diferencias tienen impacto sobre la adecuación, con influencia en la supervivencia, forrajeo, apareamiento y cuidado parental (Réale et al., 2007). En cuanto a animales domésticos (de compañía, granja, y trabajo), tomar en cuenta sus diferentes personalidades puede tener implicaciones sobre su manejo y bienestar (Gartner y Weiss, 2013).

Métodos comunes y la necesidad de nuevas pruebas

En la literatura encontramos un gran número de pruebas conductuales que varían según el grupo taxonómico, las dimensiones de la personalidad que se desean estudiar, y condiciones de laboratorio vs condiciones naturales (Gosling, 2001). Una de las dificultades de la investigación en esta área es que a menudo no es claro qué se está poniendo a prueba, o si se trata de una variable biológicamente relevante. Relacionado a esto, Carter et al. (2013) mencionan dos problemas centrales al medir rasgos de la personalidad. Primero, que existen muchas pruebas no necesariamente comparables para evaluar un rasgo particular. Y también que aun cuando una prueba mide el rasgo deseado puede ser influenciada por otras conductas, y por lo tanto medir dos o más rasgos de la personalidad al mismo tiempo. Sugieren utilizar un enfoque multi-rasgo, multi-prueba investigando correlaciones entre las mediciones para validar las pruebas. Es por tanto importante buscar y diseñar pruebas relevantes para la especie en cuestión, y tratar de correlacionar resultados entre ellas.

El gato doméstico

El gato doméstico (*Felis silvestris catus*) es un buen candidato para el estudio de la personalidad animal ya que tiene un amplio repertorio conductual, y comúnmente se acepta que demuestra diferencias de personalidad. Es por mucho la especie de felino más estudiada en este aspecto (Gartner y Weiss, 2013). Algunos de los métodos más comunes para estudiar diferencias individuales en el gato doméstico incluyen observaciones conductuales (Lowe y Bradshaw, 2001; Wedl et al., 2011), encuestas (Lee et al., 2007; Bennett et al., 2017), y pruebas, tales como objeto nuevo y acercamiento (reacción) a humanos (McCune, 1995; Siegford et al., 2003). En cuanto a rasgos de personalidad, las vocalizaciones y respuestas locomotoras parecen ser de particular importancia, especialmente en cuanto a la manera que distintas personalidades manejan situaciones potencialmente estresantes (Iki et al., 2011; Hudson et al., 2015; Hudson et al., 2017).

Estudios enfocados en las diferencias individuales del comportamiento entre compañeros de camada han encontrado que hay patrones de conducta consistentes desde una edad muy temprana. Estas diferencias son aparentes en crías de 1-5 semanas de edad aun cuando son juzgadas por observadores no experimentados (Raihani et al., 2014). En otro estudio, experimentos de separación breves con crías durante su primer mes postnatal mostraron diferencias individuales estables en el número de llamados de separación y la actividad locomotora en una prueba de campo abierto (Hudson et al., 2015; Hudson et al., 2017).

Sin embargo, hay mucho por saber sobre personalidad en el gato doméstico. Existe la necesidad de métodos confiables para evaluar gatos adultos, dado que los métodos hasta ahora utilizados podrían no ser la mejor opción para esta especie. La mayoría de los

estudios se han llevado a cabo con animales criados en laboratorio, quienes no tienen un trasfondo heterogéneo. Esto es de especial interés cuando se considera el lado práctico de la personalidad animal, tales como problemas de bienestar y manejo de los animales. Los albergues animales no sólo proveen la oportunidad de evaluar a muchos individuos para futuros estudios, también son lugares con la necesidad de pruebas conductuales confiables. Por ejemplo, para empatar mejor dueños y mascotas o para sugerir un animal que se adapte mejor a una situación específica.

Objetivo general

Desarrollar pruebas de comportamiento que revelen diferencias individuales consistentes a través del tiempo, y que sean relevantes para la vida cotidiana del gato doméstico.

Métodos

Sujetos de estudio y procedimiento

Colectamos datos de 31 gatos adultos (13 machos y 18 hembras) del albergue "Gatos Olvidados" en la Ciudad de México. Todas las pruebas fueron llevadas a cabo en este albergue. Incluimos sólo gatos adultos de edades entre uno y 11 años (promedio= 4.517, DE= 2.548;). Todos los sujetos habían sido esterilizados y estaban bajo la supervisión de veterinarios calificados. Las pruebas se realizaron una vez a la semana. Para cada prueba, todos los gatos fueron evaluados en orden aleatorio el mismo día entre 13:00 y 18:00 hrs una vez a la semana por tres semanas. Todas las pruebas fueron grabadas con una GoPro Hero3+ para su análisis posterior.

Descripción de las pruebas conductuales

Prueba del forcejeo

Algunos autores consideran que forcejear al ser manejado, y que tan rápido lo hace un individuo, pueden interpretarse como una medida de intrepidez o "boldness" (Réale et al., 2007). Es una conducta común y fácil de observar ya que muchos gatos domésticos son manejados constantemente por sus dueños y otras personas. Lowe y Bradshaw (2002) encontraron que la conducta individual de un gato al ser sostenido sobre el regazo de una persona desconocida es un rasgo estable. Rediseñamos esta prueba para evaluar la respuesta de forcejeo cuando son levantados. Uno de los experimentadores (siempre la misma persona) caminaba hacia el gato, lo acariciaba tres veces y lo levantaba sosteniéndolo por debajo de las patas delanteras. La prueba terminaba cuando el gato forcejeaba, definido como levantar una de las patas traseras y tocar o patear el antebrazo del experimentador, o cuando habían pasado 30 segundos. Cuando esto sucedía, el gato era bajado y liberado.

Prueba de la transportadora (separación social)

Las pruebas de separación son utilizadas para evaluar personalidad en muchas especies, particularmente las sociales. Esta prueba representa una situación común en la vida diaria del gato doméstico alrededor de los humanos, ya que los gatos a menudo son llevados en transportadoras cuando salen de casa, por ejemplo, al veterinario. En esta prueba el gato era llevado a un cuarto vacío y colocado dentro de una transportadora comercial (42 x 61 x 38 cm). La transportadora, era colocada en el piso y el experimentador salía del cuarto. Luego de dos minutos en solitario el gato era liberado. Se evaluaron las respuestas locomotoras

(rascar y girar dentro de la transportadora) y el tiempo que pasaron sentados, así como las vocalizaciones y el mirar hacia afuera.

Prueba del ratón (objeto nuevo)

En nuestra experiencia, ni las crías ni los gatos adultos muestran interés prolongado en interactuar con el tipo de objetos inanimados utilizados convencionalmente en este tipo de pruebas. Por tanto, modificamos la prueba de objeto nuevo clásica que se usa para estudiar personalidad en gatos. Elegimos un ratón blanco de laboratorio como el "objeto" para mejor aproximar un estímulo biológicamente relevante para nuestros sujetos de estudio.

Antes de la prueba los gatos tenían dos minutos de habituación dentro del cuarto de prueba. Posteriormente, un experimentador sostenía al gato mientras otro experimentador introducía al ratón dentro de un frasco de vidrio, colocaba el mismo frente a una pared y salía del cuarto. El primer experimentador liberaba al gato y retrocedía a una esquina donde permanecía inmóvil. La tapa del frasco contaba con pequeños orificios, por lo que el gato podía ver y oler al ratón, pero no tenía acceso a él. El experimentador habría intervenido si el ratón hubiese estado en peligro, pero esto nunca fue necesario. El gato podía interactuar con el frasco durante dos minutos, después de los cuales la prueba se daba por terminada. Se midió el tiempo que pasaron cerca del frasco, la latencia a interactuar con el mismo, y los movimientos de la cola.

Prueba de acercamiento a un humano desconocido

Las pruebas de acercamiento a humanos son utilizadas comúnmente para evaluar la conducta de mascotas, incluyendo a los gatos (Collard, 1967; Meier y Turner, 1985;

Mertens y Turner, 1988; Podberscek et al., 1991; McCune, 1995) especialmente en albergues (Slater et al., 2010). Estas pruebas también son usadas frecuentemente para evaluar "docilidad" y "temor" en otras especies domesticadas, como animales de granja, por ejemplo (Hemsworth et al., 1996; Forkman et al., 2007; Gibbons et al., 2009). En nuestra prueba se evaluó la reacción de los gatos a un hombre desconocido. Contamos con un voluntario diferente para cada ensayo de la prueba. La prueba consistía de tres fases. Durante la primera fase, que duraba tres minutos, el humano estaba sentado en el piso con las piernas cruzadas, mirando la pared e ignorando al gato sin importar cuanto se acercara. En la segunda fase, el humano llamaba al gato por su nombre durante un minuto mientras extendía su mano en un esfuerzo por que el gato hiciera contacto. Al comenzar la tercera fase el humano se levantaba con cuidado, se acercaba al gato e intentaba acariciarlo seis veces de cabeza a cola. Las conductas se evaluaron según las fases de la prueba; una escala de acercamiento (1-5) para la primera fase, el contacto nariz-dedo como saludo en la segunda fase, y por último si el humano pudo acariciar al gato con éxito al terminar la prueba.

Análisis de videos y análisis estadístico

Todas las variables conductuales fueron codificadas utilizando el software de análisis de videos Solomon Coder (Péter, 2015). Analizamos la repetibilidad de la conducta de los individuos a través de los tres ensayos mediante correlaciones intra-clase, calculadas como la proporción de variación fenotípica que puede ser atribuida a la variación entre sujetos (Lessells y Boag, 1987). Pusimos a prueba la repetibilidad de las diferencias individuales utilizando cálculos basados en MLGM (modelos lineales generalizados de efectos mixtos)

para datos con distribución Poisson y cálculos basados en MLM (modelos lineales de efectos mixtos) para datos continuos (distribución de Gauss). Los efectos del sexo y edad fueron analizados usando MLM para variables dependientes continuas y MLGM para variables dependientes con distribución Poisson. Los modelos incluyeron sexo (factor con dos niveles), edad (covariante) y la identidad de los gatos como factor aleatorio. Los valores P fueron extraídos con pruebas de chi-cuadrada de Wald (tipo III).

Resultados

El efecto del sexo y la edad no fueron estadísticamente significativos en ninguna de las variables conductuales de las cuatro pruebas.

Prueba del forcejeo

Las diferencias individuales en la latencia para forcejear fueron significativamente repetibles a través de los ensayos. Es decir, los gatos que forcejearon rápido en el primer ensayo lo siguieron haciendo consistentemente semana a semana. El mismo patrón se observó con el número de intentos de forcejeo y la latencia para vocalizar.

Prueba de la transportadora

Encontramos alta repetibilidad en las diferencias individuales respecto a la latencia para vocalizar y el número de veces que los sujetos lo hicieron. En cuanto a la actividad locomotora, tanto la latencia para rascar como la latencia para girar en la transportadora fueron repetibles. La misma consistencia se observó en respuestas tranquilas, como la latencia para sentarse y el tiempo mirando hacia afuera desde la transportadora.

Prueba del ratón

En esta prueba, las variables asociadas con la cercanía al ratón fueron altamente repetibles. Las diferencias individuales en otras conductas asociadas, tales como la latencia para interactuar, el tiempo olfateando el frasco, y caminar alrededor de él también fueron repetibles.

Prueba de acercamiento a un humano desconocido

Todas las variables conductuales analizadas fueron significativamente repetibles. Por lo tanto, las respuestas individuales fueron consistentes en cada fase de la prueba, desde la distancia que mantuvieron del humano al inicio de la prueba, hasta el contacto de la fase dos, y la disposición a ser acariciado en la fase tres.

Discusión

En este estudio, evaluamos la consistencia a través del tiempo de las respuestas individuales del gato doméstico en cuatro pruebas conductuales. En cada prueba, encontramos que casi todas las variables conductuales propuestas mostraron repetibilidad significativa, lo que convierte a las cuatro pruebas en buenas herramientas para el estudio de la personalidad animal en el gato doméstico. Las diferencias individuales estables fueron evidentes a pesar de que los gatos del estudio fueron una población heterogénea; diferían en edad, sexo, y antecedentes.

Proponemos la prueba del forcejeo como un proxy a las pruebas manejo o “handling” descritas para conejos (Rödel et al., 2014), y a otras pruebas como la de suspensión para ratas y la de inmovilidad tónica aplicada a múltiples especies. En general,

los animales que suelen forcejear rápido o se resisten a la inmovilización tienden a ser más intrépidos, más activos y a veces se clasifican como más agresivos. Dentro del contexto de los estilos de afrontamiento, algunos autores considerarían a estos individuos como proactivos.

En cuanto a la prueba de la transportadora, para un gato, ser puesto en una transportadora puede representar un escenario estresante. A pesar de que es una situación común, experiencia con estos animales nos ha enseñado que algunos gatos vocalizan y/ o tratan de salir de la transportadora constantemente, mientras otros se sientan tranquilamente o solo se agitan ocasionalmente. Nuestros resultados son consistentes con esta observación y muestran que el comportamiento de un individuo dentro de la transportadora es repetible semana a semana. Esto nos hace creer que pruebas cortas de separación, como esta, son una herramienta adecuada para estudiar el desarrollo de estos rasgos de la personalidad y su estabilidad a lo largo de distintas etapas de la vida.

Como se mencionó al inicio, las pruebas de objeto nuevo son muy populares en el estudio de la personalidad animal. Pero debemos considerar que en esta prueba la "novedad" no es lo único a lo que reaccionan los animales, el objeto por sí solo es una parte importante de la respuesta. Por eso resaltamos el uso de estímulos biológicamente relevantes a la especie en cuestión. Un ratón tiene relevancia ecológica para todos los gatos. Dados los resultados positivos respecto a la repetibilidad de las conductas relacionadas al ratón, y el hecho de que los gatos consistentemente mostraron conductas predatorias (postura, tocar con la pata, rodear el frasco), proponemos que esta prueba podría ser aplicada con éxito para identificar a individuos con predisposición para ser buenos cazadores.

En la prueba de acercamiento a humanos, encontramos que cada fase que proponemos, y las variables asociadas, son adecuadas para evaluar la disposición de un gato para interactuar con un humano. Las medidas de acercamiento pueden darnos una idea de la socialización temprana del individuo. Y parece ser que las variables más confiables son las respuestas a cuando el humano buscaba hacer contacto, pues tuvieron un valor de R más alto que el acercamiento durante la primera fase (cuando el humano ignora al gato). Tal vez esto es porque la voluntad de un gato con una persona desconocida es influenciada por la voluntad de la persona a interactuar con el gato.

Aplicación

Nuestros resultados apoyan la propuesta de que los gatos adultos muestran diferencias individuales consistentes en diferentes conductas a través del tiempo. Las diferencias fueron evidentes a pesar de que la población era heterogénea. Lo que sugiere que estas diferencias entre individuos son robustas, confirmando lo que ha sido reportado para esta especie. Adicionalmente, el rango de edad en nuestra muestra no sólo aborda la necesidad de pruebas confiables para gatos adultos, sino también la necesidad de pruebas que revelen diferencias individuales consistentes a lo largo de un amplio rango de edades. También es importante mencionar que las cuatro pruebas propuestas en este estudio son simples, rápidas (no más de cinco minutos) y cualquier material requerido es económico y fácil de conseguir. Debido a esto, pueden ser reproducidas prácticamente en cualquier parte del mundo. Todo lo anterior las vuelve una opción adecuada para albergues animales que buscan evaluar personalidad como parte de su programa de adopción.

ABSTRACT

Animal personality is defined as the stable between-individual differences in behavior which are consistent over time and/or contexts. It can have implications, for example, on fitness, coping with stress, and well-being. The domestic cat (*Felis silvestris catus*) provides a good model for the study of animal personality as it has a rich behavioral repertoire and has been found to display differences in personality. The aim of this study was therefore to develop behavioral assays which are relevant to the daily life of the domestic cat and can reveal consistent differences in behavior over time between individuals. We collected data from 31 adult cats (13 males and 18 females; ages one to 11 years), from the shelter "Gatos Olvidados" in Mexico City. Cats were tested individually in four behavioral assays once a week for three weeks: a struggle test, a transport cage (social separation) test, a mouse (novel object) test and a human approach test. In each of these several the behavioral variables recorded were significantly repeatable. Individual's locomotive responses (struggling, circling), vocalizations, and their willingness to interact (both with the human and the mouse) were all found to be consistent across trials. These results support our premise that the simple, inexpensive tests proposed in this study are adequate tools to assess stable inter-individual differences in adult cats. These tests could be applied in animal shelters as a part of adoption programs that seek to better pair cats and owners. However, it still remains to be analyzed if these behavioral traits correlate across tests and form so called behavioral syndromes.

INTRODUCTION

Animal personality

There has been an increasing interest among behavioral biologists in the nature and significance of stable individual differences in behavior. Carere and Maestripieri (2013) describe the study of this subject as "one of the fastest growing areas of research in behavioral biology and behavioral ecology". This has been reflected in a substantial number of studies comprising a wide range of taxa (Gosling, 2001). Inter-individual differences in behavior (or behavioral phenotype) are commonly referred to as animal personality, defined as the stable differences between individuals, which are consistent over time and/or context (Sih et al., 2004; Stamps and Groothuis, 2010; Wolf and Weissing, 2012).

Animal personality is often also known as temperament, behavioral types, or coping styles. Although many authors use these terms as synonyms (Réale et al., 2007; Stamps and Groothuis, 2010), many others have tried to make distinctions between them (Roche et al., 2016). For example, coping styles tend to be used more specifically for alternative response patterns in reaction to challenges (such as proactive and reactive coping; Koolhaas et al., 1999; Coppens et al., 2010). However, consistent behavioral variation between individuals is the basis for all the above-mentioned terms. Another related concept is that of behavioral syndromes, most commonly described as a suite of behaviors correlated across contexts (Sih et al., 2004; Stamps and Groothuis, 2010; Wolf and Weissing, 2012; Carter et al., 2013). Usually, 'behavioral syndromes' are set apart from the above-mentioned terminologies and used only when individuals differ from each other in several correlated behaviors that can be clustered into distinct groups (Briffa and Weiss, 2010). However,

there are researchers who don't appear to differentiate at all between the two terms (Bell, 2007; Coppens et al., 2010). This brings to light the terminological problem of the field, and although there have been attempts to clarify the terminology (Réale et al., 2007; Stamps and Groothuis, 2010; Roche et al., 2016), they have so far been unsuccessful as there is no clear consensus on the matter. In this thesis, we use the term personality to refer to the stable individual differences in behavior consistent across time.

Stable individual differences in behavior have been found to occur in numerous vertebrate (Gosling, 2001) and invertebrate species (Kralj-Fišer and Schuett, 2014). They have been shown to impact fitness, with influence on survival, foraging, mating and parental care (Réale et al., 2007). It has even been suggested that the presence of certain personality types in an initial introduction can drive the success of an invasive species (Chapple et al., 2012). But perhaps the easiest way to visualize individual differences in behavior is through the animals that surround our daily life. Most pet owners will readily acknowledge that their pet(s) exhibit a distinct personality. In addition, the 95 published studies on dog and 24 studies on cat personality estimated by Gartner (2015) agree with them. For domestic animals (companion, farm, and working animals) taking into account their personality differences when adopting them out or selecting them for specific tasks can have implications for coping with stress, management and welfare (Gartner and Weiss, 2013).

Methods and the need for new tests

Just as personality is diverse, so are the methods used to asses it. In the literature we find a great number of tests that vary according to the taxonomic group, the personality

dimensions to be tested, and laboratory vs. natural conditions (Gosling, 2001). Some of the most generally used tests on mammals are the open field test (Fig. 1; Hall and Ballachey, 1932; Walsh and Cummins, 1976), novel object (Ennaceur and Delacour, 1988; Durr and Smith, 1997), forced swim (De Pablo et al., 1989), "Y" and elevated plus maze (Handley and Mithani, 1984; Dellu et al., 1992; Rödel and Meyer, 2011), and reacting to humans (Meier and Turner, 1985; Kilgour, 1998; Søndergaard and Halekoh, 2003).

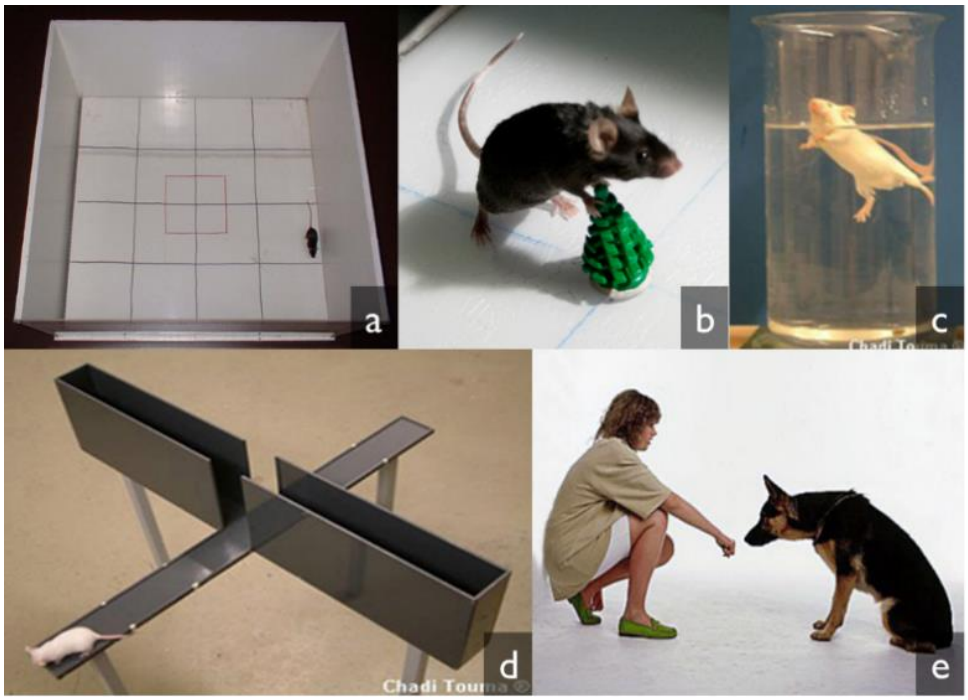

Figure 1. Common behavioral tests: a. open field, b. novel object, c. forced swim, d. elevated plus maze, e. reaction to human.

There is no one single approach to the study of animal personality. Traits can be interpreted as bimodal variables or as continuums with two extremes representing tendencies such as proactive-reactive or shy-bold (Réale et al., 2007). Traits can also be analyzed within a set of broad personality dimensions known as the Five-Factor Model or

Big Five: Extraversion, Agreeableness, Conscientiousness, Neuroticism, and Openness (Digman, 1990). This model is widely used in human psychology, but not all species express dimensions in the same way it's applied to humans (Gosling and John, 1999). One of the difficulties of animal personality research is that it is often not clear what is being tested, or if it is a biologically meaningful behavioral variable. Additionally, two different individuals may display the same behavior for different reasons, or vice versa. For example, if an animal is sitting in the middle of an open field during a test, is it bold or is it "freezing" in fear? If it's moving a lot is it exploring or panicking?

Carter et al. (2013) mention two main problems for measuring personality traits. First, that there are many tests available for a single trait which are not necessarily comparable. Also, even when a test measures a targeted trait it can be influenced by other behaviors and hence measure two or more personality traits simultaneously. They suggest using a multi-trait, multi-test approach investigating correlations among the measurements when validating tests.

Still, in our efforts for standardization, we should consider that a test (or version of a test) useful for one species is not necessarily suitable for another. It is important to take into consideration the model species' ecological and social background, the sensory systems it uses and their constraints, its existing behavioral repertoire, and maybe even the animal's developmental and physiological state. It is therefore important to look for and design tests that are relevant to the species in question, and to try to correlate the results between tests.

The domestic cat

The domestic cat (*Felis silvestris catus*) is a good candidate for the study of animal personality as it has a rich behavioral repertoire and it is commonly agreed to display differences in personality to a greater extent than some other laboratory species. It is by far the most studied feline species in this respect (Gartner and Weiss, 2013). Of 20 feline personality studies reviewed by Gartner and Weiss (2013), 17 were done on the domestic cat. Some of the most common methods used to study individual differences in the cat include behavioral observations (Lowe and Bradshaw, 2001; Wedl et al., 2011), surveys (Lee et al., 2007; Bennett et al., 2017), and tests, such as novel object and human approach (reaction) tests (McCune, 1995; Siegford et al., 2003).

Given cats enormous popularity as pets, there is a tendency to evaluate their behavior in relation to humans. For example, individual differences have been found in cats' "friendliness" when reported by caretakers (Turner et al., 1986) and in the extent to which cats accept the approach or handling by an unfamiliar or familiar person (Podberscek et al., 1991; McCune, 1995; Lowe and Bradshaw, 2002). This has been reported to be influenced by socialization effects, previous handling experiences, and the personality of the tomcat who fathered them (Reisner et al., 1994; McCune, 1995; Lowe and Bradshaw, 2001). Indeed, it should be noted that genes, epigenetics and past experiences are all factors that mold an individual's personality (Stamps and Groothuis, 2010; Trillmich et al., 2015). Durr and Smith (1997) found that the behavioral responses of cats presented with novel stimuli (toy car, unfamiliar animal, and a vacuum cleaner) were consistent despite changes in their environment. This suggests that stability of their environment is not critical to maintain the stability of their personality, at least to some degree (Durr and Smith, 1997;

Vitale Shreve and Udell, 2015). The relation between personality and health has also been investigated, where bolder cats were found to be more vulnerable to feline immunodeficiency virus (Natoli et al., 2005).

In terms of personality traits, vocalizations and locomotor responses seem to be of particular importance, especially in the way different personality types deal with a potentially stressful situation (Iki et al., 2011; Hudson et al., 2015; Hudson et al., 2017). Iki et al. (2011) found a significant negative correlation between the time spent in locomotion and time vocalizing during a stressful situation (a 3-min spray bath in this case). They suggest that cats that respond by moving a lot might represent a proactive coping style; usually characterized by individuals that tend to have reduced impulse control, to be bolder, more exploratory and aggressive (Coppens et al., 2010; Sih and Del Giudice, 2012). Cats that tend to be more vocal, on the other hand, could be expressing a reactive coping style, which has been associated with the high blood cortisol response that was also observed (Koolhaas et al., 2007; Iki et al., 2011). This aspect of personality is possibly defined from a very early life stage.

Studies focused on individual differences in behavior among littermates in cats have found that there are consistent patterns of behavior even at a very early age. These differences in behavior are apparent even in 1-5 week old kittens when judged by inexperienced observers (Raihani et al., 2014). In another study, brief separation experiments with kittens during their first postnatal month showed stable individual differences in the frequency of separation calls and locomotor activity in an open field test (Hudson et al., 2015; Hudson et al., 2017). Both were repeatable across age, but they were not correlated with each other, suggesting that they were measuring different aspects or

dimensions of personality. Vocal responses have been found to be a particularly useful behavioral measure of stress in cats and other mammals (Johnson et al., 1994; Bristow and Holmes, 2007; Stoeger et al., 2012), as the neural control of vocalizations is closely integrated with and reflects the emotional state of an individual (Briefer and Le Comber, 2012). Furthermore, most cats emit distress calls when separated from companions or familiar environments across their whole lifespan (personal observations).

There is, however, still much to be learned about personality in cats. Most of the studies that involve behavioral testing have been conducted with laboratory-born animals, which don't have a heterogeneous background. Therefore, the relevance of their results for the animals' everyday lives could be questioned. There is a need for reliable methods for testing adult cats given that previously used methods may not be the best option for this species. Although almost all domestic cat studies have been done with adults, these have generally been on animals approximately 1-5 years old (Gartner and Weiss, 2013), and so it is necessary to include a wider range of ages. This is of special interest when considering the practical side of individual differences, such as issues regarding the welfare and management of the animals. Animal shelters not only provide an opportunity to test many subjects for future research but are also places with a need for reliable personality tests. For example, to better match owners and pets or suggest a cat that better fits a specific situation, such as working or therapy cats. Many shelters have begun to implement personality testing as part of their adoption program. Two popular test batteries are the Feline Temperament Profile (FTP; Siegford et al., 2003) and the Meet Your Match Feline-Ality assessment (Weiss et al., 2015) used by the American Society for the Prevention of Cruelty to Animals (ASPCA).

AIM

The aim of this study was to develop behavioral assays which reveal consistent differences in behavior over time between individuals, and that are relevant to the daily life of the domestic cat.

Specific objectives

- Develop new tests which are (i) relevant to the daily life of the animal, (ii) inexpensive, (iii) easy to apply anywhere in the world.
- Evaluate the repeatability of individual behavioral responses within each test.

METHODS

Animals

We collected data from 31 adult cats (13 males and 18 females) from the shelter "Gatos Olvidados" in Mexico City. All the tests were performed at this shelter. The cats' ages were not always known with certainty, in which case this was estimated by veterinarians. We used only adult cats with ages between one to 11 years (mean= 4.517, SD= 2.548; Table S1). The shelter was a 4-story house divided into sections; cats were placed in its area according to how they tolerated each other. All sections consisted of at least two rooms (approx. 2.5 x 3.5 m) with access to a fenced balcony (approx. 2 x 4 m). Each cat was free to roam within its section. Every room had several cat beds, boxes of assorted sizes with blankets, scratchers, and toys. All the cats were spayed/ neutered and under the supervision of qualified veterinarians. Water, commercial dried cat food and litter trays were always available.

Procedures

The study took place from February 27th to April 9th of 2016; tests were performed on a weekly basis. For each test, all cats were tested on the same day between 13.00 and 18:00 h once a week for three weeks in a randomized order on the test days. Not every cat was available for all tests, therefore sample sizes differ between the tests (Table 1 and Table S1 for information on which cat participated in each test).

Table 1. Tests and number of animals per test.

Test name	Sample size	Males	Females	Mean age ± SD
Struggle test	30	13	17	4.504 ± 2.640
Transport cage test	28	12	16	4.600 ± 2.718
Mouse test	24	8	16	4.309 ± 2.595
Human approach test	28	11	17	4.562 ± 2.734

Description of proposed behavioral tests

Struggle test

Different versions of tests that measure a struggle response while the animal is handled and restrained in some way have been used on several mammals to find individual differences; such as mice (Steru et al., 1985), rabbits (Mullan and Main, 2007; Trocino et al., 2013; Rödel et al., 2014), North American red squirrels (Boon et al., 2007; Taylor et al., 2012), and pigs (Hessing et al., 1993; Erhard et al., 1999). Some authors consider that struggling, and how quickly the animal does it, could be interpreted as a measure of boldness (Réale et al., 2007). According to these studies animals that are quick to struggle or resist being immobilized, in general, tend to be bolder, more active and in the case of red squirrels and pigs are also classified as more aggressive.

In cats, Lowe and Bradshaw (2002) found that individuals' behavior when held on an unfamiliar person's lap is a stable character trait. Many domestic cats are constantly handled by their owners, other familiar and unfamiliar humans and veterinarians; thus, we redesigned this test to evaluate the struggle response when they are picked up and restrained.

We collected data from 30 adult cats (13 males and 17 females; age 4.504 ± 2.640, min = 1, max = 11). The tests were performed in the room where the cat normally resided. One of the experimenters (always the same person) walked up to the cat and stroked it three times from head to tail, then picked it up by holding the cat up from under its armpits, surrounding the chest with her fingers (Fig. 2a). The test lasted until the cat started to struggle, defined as lifting one of the hind paws and touching or kicking the experimenter's arm (Fig. 2b), or when 30 seconds had passed. When this happened, the cat was immediately put down and set free. A second experimenter recorded the test from at least two meters away (with a GoPro Hero3+). The first experimenter always wore gloves to prevent injuries. The behaviors measured are listed and defined in Table 2.

Figure 2. *a*. Holding position during the struggle test. *b.* Cat struggling: cat lifting one of the hind paws and touching the experimenter's arm.

Table 2. Behavioral variables recorded in the struggle test

Behavior measured	Definition	Variable
Vocalization	Meow-type vocalization	Latency, frequency
Attempt to struggle	Lifting one of the hind paws in an apparent attempt to touch or kick the experimenter's arm, but unsuccessfully	Frequency
Struggle	Lifting one of the hind paws and touching or kicking the experimenter's arm	Latency

Transport cage (social separation) test

Separation tests are used for personality testing in many animals, particularly in social species, for example, horses (Le Scolan et al., 1997), cows (Boissy and Bouissou, 1995; Müller and Schrader, 2005), yellow-bellied marmots (Petelle et al., 2013) and dogs (Konok et al., 2011). In previous studies, separation tests have been successfully used for evaluating individual differences in kittens of domestic cats too. In these brief experiments during their first postnatal month, kittens showed highly repeatable individual differences in the frequency of calls and locomotor activity (Hudson et al., 2015; Hudson et al., 2017). Moreover, this test represents a common situation in a cat's daily life around humans, since cats are often put and separated in a carrier to take to other places outside their home, for example, to a veterinarian.

We collected data from 28 adult cats (12 males and 16 females; age 4.600 ± 2.718, min = 1, max = 11). The tests were performed in a small closed room, which was unfamiliar to the animals. The room was cleared of any objects that could be distracting to the cat. During the test, no other animals were allowed to enter either the testing room or the room connected to it.

The cat was brought into the room by an experimenter and was placed in a commercial transport carrier (42 x 61 x 38 cm), which was a closed plastic box with a wire grill door at one end, and holes along the sides which the cat could look out of. The carrier, with the cat, was placed immediately at a marked position, and the experimenter left the room. All tests were recorded with a video camera (GoPro Hero3+) which were set up in front of the carrier, one meter away. To facilitate observation, a red light was mounted inside the carrier (Fig. 3). The test lasted two minutes. Once this time had elapsed, the cat was returned to its homeroom. The carrier was cleaned between tests with alcohol. The behaviors measured are listed and defined in Table 3.

Figure 3. Camera view of a cat inside the transport cage with the red light in the background.

Table 3. Behavioral variables recorded in the transport cage test.

Behavior measured	Definition	Variable
Vocalization	Meow-type vocalizations	Latency, frequency
Scratching	Pawing or placing one or two paws for at least one second on the door, walls or ceiling of the transport cage	Latency, frequency
Turning	We considered it a turn every time the subject rotated its whole body 180°	Latency, frequency
Sitting or laying	Adopting a resting posture sitting on its hind legs or laying on its stomach	Latency, duration
Looking out	Looking out of the carrier from the door or the sides, determined by following the gaze of the cat	Duration

Mouse (novel object) test

In our experience, neither kittens nor adult cats show sustained interest in interacting with the kinds of inanimate objects conventionally used in these scenarios, thus we slightly modified the classic novel object test that could be used to measure stable individual differences in the domestic cat. We chose a white laboratory mouse as the "object" to more closely approximate a biologically relevant stimulus for the cats (see below for details on how it was presented).

We collected data from 24 adult cats (8 males and 16 females; age 4.309 ± 2.595, min = 1, max = 11). Cats were individually tested in a room which was familiar for some of them but unfamiliar to most, therefore before the test we let them habituate to the room for two minutes. The room was cleared of all cats and any objects that could be distracting to the subject. During habituation, an experimenter (always the same person) remained with the cat, standing motionless and silent in a corner.

Figure 4. Experimenter 1 holding the cat at the start point while experimenter 2 reveals the mouse.

At the end of the habituation period, the experimenter held the cat at the start point, which was basically the middle of the room, while another experimenter brought in a mouse inside a clear, thick glass jar, covered with a cardboard box (Fig. 4). The jar was set down next to a wall (at a marked position approximately 1.5m away from the cat) and was revealed to the cat, who was released once the second experimenter left the room. The first experimenter returned to the corner and stayed there during the test motionless, silent and without making eye or vocal contact. The lid of the jar had small holes, so the cat could see and smell the mouse but could not access it. The jar was also glued to an acrylic board (46 x 31 cm) to prevent the cats from tipping it over. The experimenter would have intervened if the mouse was ever in danger, though this was never necessary. The cat was free to interact with the jar for two minutes, after which the test ended, and the cat was returned to its section of the shelter. All tests were recorded with a camera (a GoPro

Hero3+) fitted 2 m above the jar, so as to record the whole room (Fig. 5). The behaviors measured are listed and defined in Table 4.

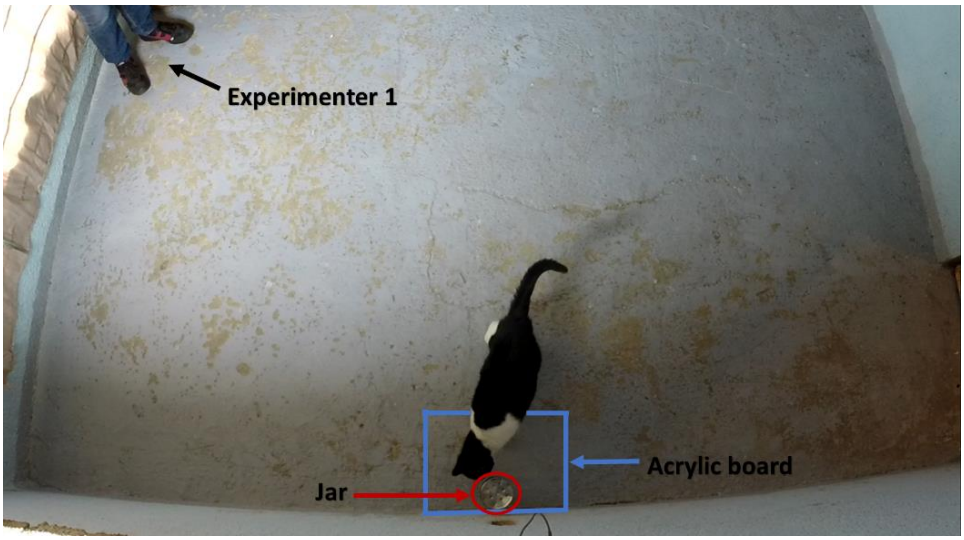

Figure 5. View of the test room during the mouse test. The cat can be seen interacting with the jar.

A total of five mice were used in rotation for this test; three of them were taken to the shelter on test days. The mouse was switched after being in the jar for three trials (approx. 15 min) to minimize any possible stress[1]. While in the shelter, when they were not participating in a test, the mice were kept in a large plastic container with wood shavings, cardboard tubes, pellets, and fruits and vegetables with a high-water content. When they were not at the shelter they were kept in a private home in a standard large laboratory cage (50 x 40 x 19 cm) lined with wood shavings, which was regularly cleaned and contained cardboard tubes and boxes for enrichment. They had *ad libitum* access to food and water.

The behavior of the mouse during the test was observed by the experimenter who remained in the room to see if possible differences in activity level between the mice would

[1]Thermal pictures of the mice were taken before and after being in the jar on several occasions. Analysis with the Fluke Smart View software showed that the maximum eye temperature of the mouse increased 1°C when the cat was in the room, similar to the change in temperature reported during an open field test (Lecorps et al. 2016). Therefore, the stress experienced by the mice in this test is comparable to that experienced in routine tests.

affect the cats' response. Since the mice all behaved in a similar way we did not consider any further analysis necessary.

Table 4. Behavioral variables recorded in the mouse test

Behavior measured	Definition	Variable
On the acrylic board	Having at least its front paws on the acrylic. We used this as a marker of distance from the jar.	Latency, duration
Interaction	First contact with the jar, either sniffing or pawing	Latency
Sniffing	Sniffing the jar	Duration
Pawing	Batting any part of the jar with either or both paws.	Frequency
Tail wagging	Anytime the cat moved its tail from side to side at least twice.	Duration
Walking around the jar	Walking from one side of the jar to the other while being near or on the acrylic board	Duration

Human approach test

Human approach tests are commonly used for evaluating cat behavior (Collard, 1967; Meier and Turner, 1985; Mertens and Turner, 1988; Podberscek et al., 1991; McCune, 1995) especially in shelters (Slater et al., 2010). Interacting with an unfamiliar human is part of both the ASPCA's Feline-Ality assessment (Weiss et al., 2015) and the Feline Temperament Profile, validated by Siegford et al. (2003). This test is also widely used to measure "docility", "tameness" and "fearfulness" in other domesticated species, such as farm animals (Hemsworth et al., 1996; Forkman et al., 2007; Gibbons et al., 2009).

We collected data from 28 adult cats (11 males and 17 females; age 4.562 ± 2.734, min = 1, max = 11). Cats were individually tested in a familiar room. It was cleared of all cats and any objects that could be distracting to the subject (same room used previously for

the mouse test). Before testing, two concentric circles, 1.5 meters and 3 meters in diameter, were drawn on the floor with chalk to use as a measure of the distance from the human. Then a person was asked to sit in the center of the circles. This person was always the same male on a given test day, but there was a different volunteer each week (ages between 21 and 25 years). The test was repeated with each cat three times, a week apart with different males; all of whom were unfamiliar to the cats.

The test consisted of three phases. First, the cat was brought by a familiar experimenter in the room and placed in a shallow (20 cm) open wooden crate next to the entrance of the room. The test started as soon as the experimenter closed the door, leaving the cat alone with the unfamiliar person. During the first phase, which lasted three minutes, the human sat cross-legged on the floor, looking at the wall and ignoring the cat no matter how close it came (Fig. 6a). In the second phase, the human spent one minute calling the cat by its name while extending his arm and index finger pointing in the cat's direction in an effort to get the cat to make contact (Fig. 6b). This was done even if the cat was already in physical contact or on the person. As soon as the minute had passed the third phase began. The human gently got up (first setting the cat on the floor if it was on his lap), walked up to the cat and attempted to pet it three times from head to tail (Fig. 6c). He then took a step back, waited a few seconds, and tried to pet it three more times. After the sixth petting attempt, the test was ended and the cat was taken back to its homeroom by the experimenter. All tests were recorded (with a GoPro Hero3+) with a wide field of view setting, so the whole room was visible during the video analysis. The behaviors measured are listed and defined in Table 5. For the measure of approach during phase 1 we used an approach score from 1 to 5, depending on whether the cat:

1. Was always far, outside the large circle

2. Got near, within the large circle

3. Got very near, within the small circle

4. Got very near and established physical contact with the human (rub, sniff, touch with paw)

5. Was on the human, at least its front paws

Table 5. Behavioral variables recorded in the human approach test

Behavior measured	Definition	Variable
Approach score	How much the cat approached the human during the first phase.	Score from 1 to 5
Vocalization	Meow-type vocalizations emitted during phase one and two.	Frequency
Finger-nose contact	Every time the cat established contact by touching its nose to the human's outstretched finger in phase two.	Latency, binary
Petting success	If the cat allowed itself to be petted from head to tail all six times in phase three it was considered “pettable”.	Binary variable

Other behaviors such as pawing, growling, hissing, clawing, biting and licking which were displayed by only a few cats were also recorded, but since these were very infrequent, statistical analysis was not possible.

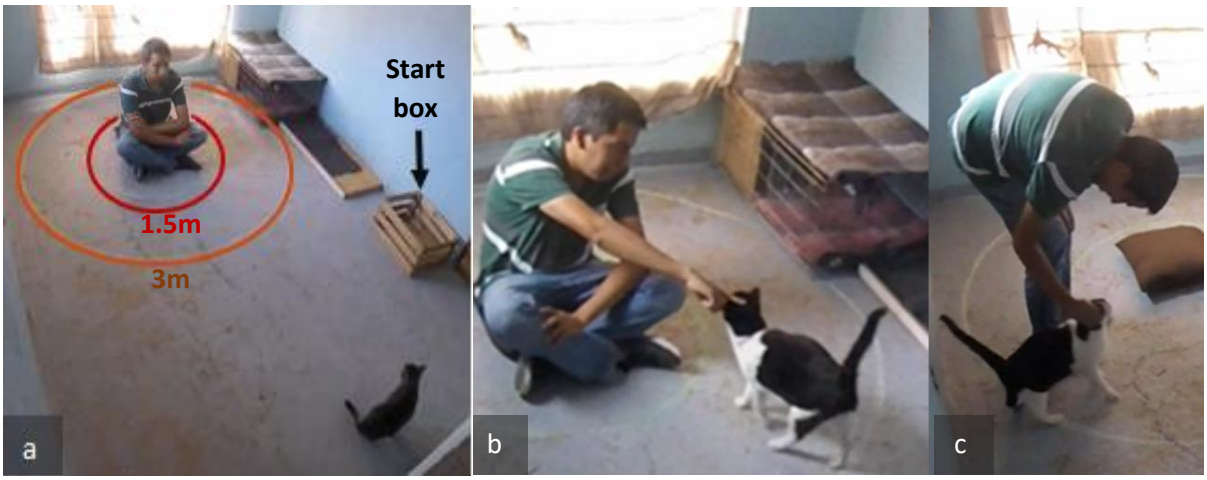

Figure 6. a. First phase, the person ignores the cat. b. Second phase, the human tries to establish contact by calling the cat and presenting his finger as a greeting. c. Third phase, petting attempts.

Video and statistical analysis

All behavioral variables were coded using the Solomon Coder software for video analysis (Péter, 2015). Statistical analyses of the data were carried out using the program R, version 3.4.2 (R Core Team, 2017). We analyzed the across-trial repeatability of the individuals' behavior across the three trials by intra-class correlations calculated as the proportion of phenotypic variation that can be attributed to between-subject variation (Lessells and Boag, 1987). We used GLMM-based calculations for count (Poisson distributed) or binary data (Binomially distributed) and LMM-based calculations (Gaussian distributed) for continuous data for testing the repeatability of individual differences with the aid of the R package rptR (Nakagawa and Schielzeth, 2010). Individual identity was used as a random factor. For all intra-class correlations, we assessed 95% confidence intervals by 1000 bootstrap steps, P-values were calculated by 1,000 permutations. Continuous variables were log-transformed to achieve normality.

Effects of sex and age were analyzed using linear mixed-effects models (LMM) for continuous, and generalized linear mixed-effects models (GLMM) for count (i.e. Poisson

distributed) dependent variables. Models included sex (factor with two levels), age (covariate) and cat's identity as random factor. P-values were extracted by Wald chi-square tests (type III).

Ethics notes

Throughout the study animals were treated according to the guidelines for the treatment of animals of the Instituto de Investigaciones Biomédicas, Universidad Nacional Autónoma de México.

RESULTS

In all four tests, the effect of age or sex was not statistically significant for any of the behavioral variables, as expected (supplementary material Table S2).

Struggle test

All cats (N=30) struggled within the 30-second time frame, with only one cat still being held at 30 seconds on one occasion. Individual differences in the latency to struggle were significantly repeatable across trials. That is, cats that struggled early or later on the first trial did so consistently week to week (Fig. 7). The same was true for the number of struggle attempts and the latency to vocalize (Table 6).

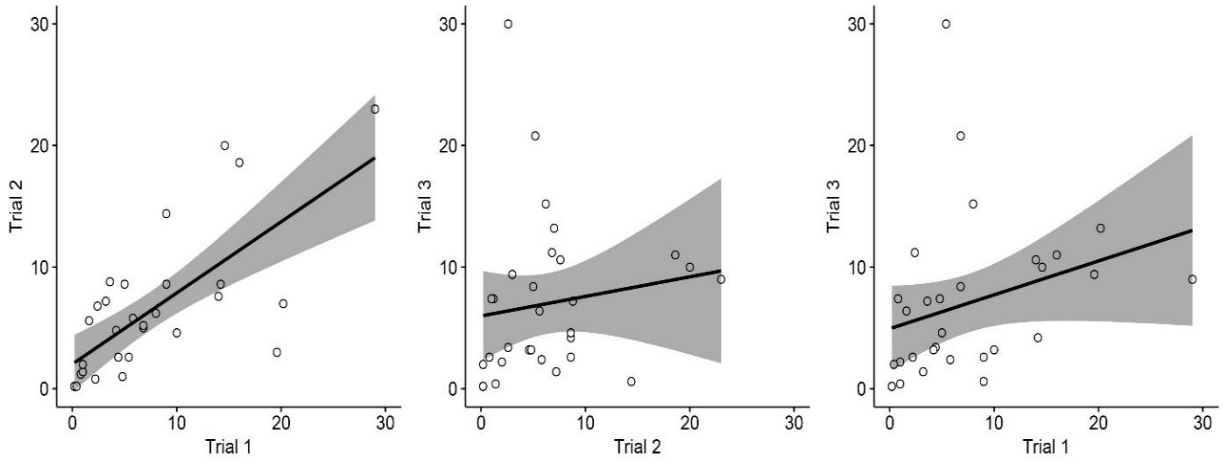

Figure 7. Latency to struggle (s) across the three trials. The shaded area depicts the regression line with 95% confidence intervals; circles represent values of individual cats.

Table 6. Repeatability analysis for the behaviors recorded in the struggle test. Intra-class correlation coefficient (R), 95% confidence intervals (CI-, CI+) based on 1000 bootstrap steps and significance values (P) are given. Significantly repeatable variables are bolded. N= 30

Behavioral variable	R	CI-	CI+	P
Latency to vocalize	**0.389**	**0.155**	**0.583**	**0.005**
Number of vocalizations	0.869	0	0.996	0.722
Latency to struggle	**0.589**	**0.348**	**0.744**	**0.001**
Number of struggle attempts	**0.518**	**0.099**	**0.745**	**0.002**

Transport cage test

Individual differences in the latency to vocalize and the number of times they did so were highly repeatable across trials (Fig. 8). In terms of locomotor activity, both the latency to scratch and to turn in the carrier were repeatable; although the frequency of these behaviors was not. The same week to week consistency was found in "calmer" responses, like the latency to sit /lie, and the time spent looking out of the door or sides of the carrier (Fig. 9; Table 7).

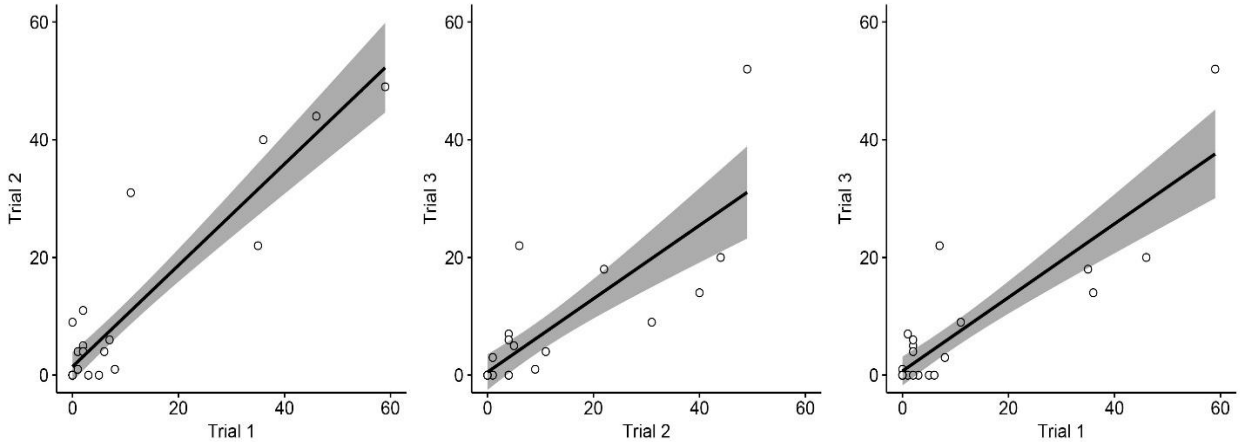

Figure 8. Number of meow-type vocalizations emitted week to week in the carrier. The shaded area depicts the regression line with 95% confidence intervals; circles represent values of individual cats. Circles can overlap and appear to be less than the N for the test.

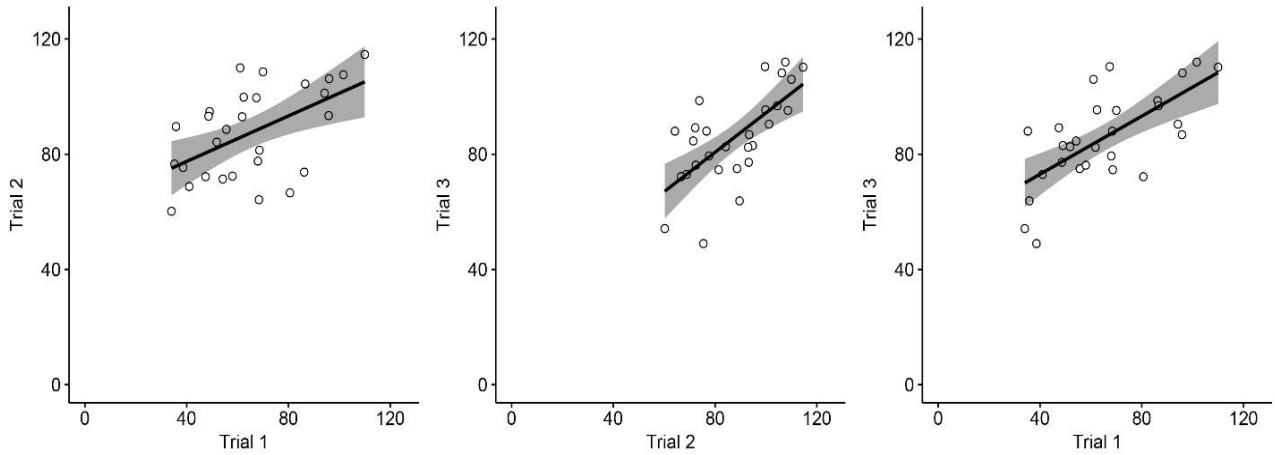

Figure 9. Time individual cats spent (s) looking out of the carrier across the three trials. The shaded area depicts the regression line with 95% confidence intervals; circles represent values of individual cats.

Table 7. Repeatability analysis for the behaviors recorded in the transport cage test. Intra-class correlation coefficient (R), 95% confidence intervals (CI-, CI+) based on 1000 bootstrap steps and significance values (P) are given. Significantly repeatable variables are bolded. [a]These variables have a CI- close to 0, therefore we considered them to be only marginally significant. N= 28

Behavioral variable	R	CI-	CI+	P
Latency to vocalize	**0.771**	**0.6**	**0.859**	**0.001**
Number of vocalizations	**0.929**	**0.8**	**0.977**	**0.003**
Latency to scratch	**0.256**	**0.0132[a]**	**0.473**	**0.024**
Number of times they scratched	0.248	0	0.506	0.158
Latency to turn	**0.24**	**0[a]**	**0.464**	**0.025**
Number of times they turned	0.364	0	0.643	0.295
Latency to sit or lie	**0.238**	**0[a]**	**0.469**	**0.028**
Duration sitting or laying	0.193	0	0.424	0.053
Duration looking out	**0.272**	**0.0048[a]**	**0.496**	**0.015**

Mouse test

In the mouse test (N=24), variables associated with the nearness to the mouse, such as the latency to be on the acrylic board and the time cats spent there were highly repeatable (Fig. 10). Individual differences in associated behaviors, such as the latency to interact, time spent sniffing the jar, and walking around it were also repeatable (Table 8).

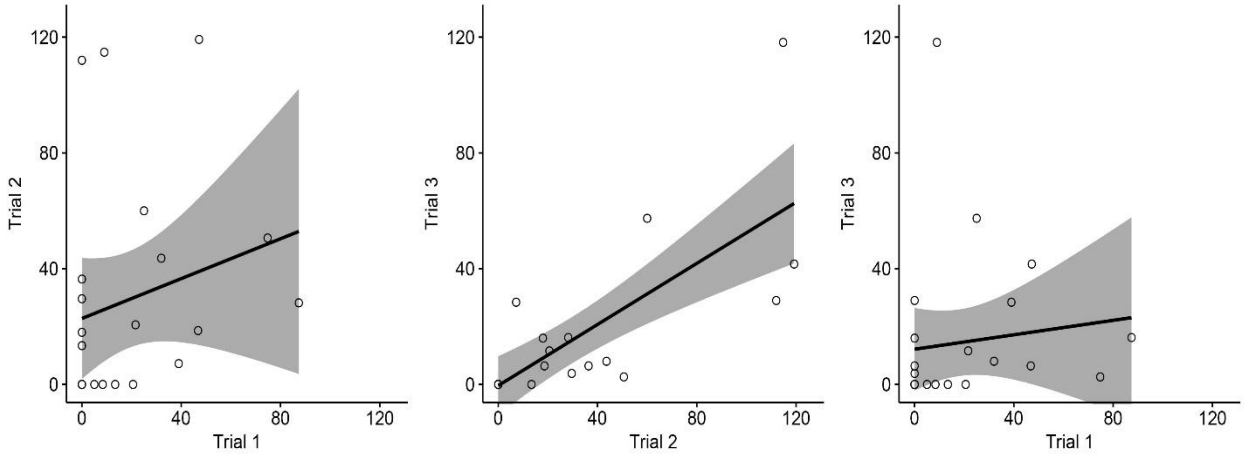

Figure 10. Time spent (s) on the acrylic board across the three trials. The shaded area depicts the regression line with 95% confidence intervals; circles represent values of individual cats. Circles can overlap and appear to be less than the N for the test.

Table 8. Repeatability analysis for the behaviors analyzed in the mouse test. Intra-class correlation coefficient (R), 95% confidence intervals (CI-, CI+) based on 1000 bootstrap steps and significance values (P) are given. Significantly repeatable variables are bolded. N= 24

Behavioral variable	R	CI-	CI+	P
Latency to be on the acrylic board	**0.483**	**0.205**	**0.675**	**0.001**
Duration on the acrylic board	**0.583**	**0.275**	**0.727**	**0.001**
Latency to interact	**0.469**	**0.203**	**0.667**	**0.002**
Duration sniffing	**0.468**	**0.175**	**0.689**	**0.001**
Number of times they pawed	0	0.01	0.037	1
Duration tail wagging	**0.806**	**0.409**	**0.811**	**0.001**
Duration walking around	**0.312**	**0.0254**	**0.551**	**0.016**

Indeed, the only recorded behavior not consistent over time was the pawing frequency. Even the tail wagging, which was coded from any area of the room, showed repeatable individual differences (Fig. 11), a possible sign of interest or arousal of the animal even from afar.

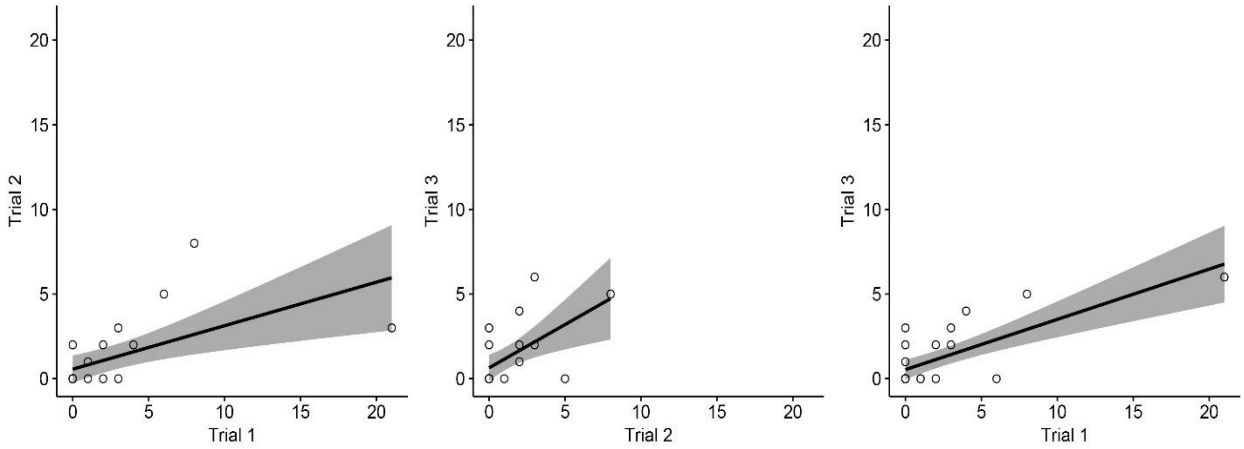

Figure 11. Duration of tail wagging (s) across trials. The shaded area depicts the regression line with 95% confidence intervals; circles represent values of individual cats. Circles can overlap and appear to be less than the N for the test.

Human approach test

All reported behavioral variables were significantly repeatable, meaning that individuals' responses were consistent in each of the three phases across trials (N=28). Individual differences in the approach score given during the first phase were repeatable over time (Fig. 12). Hence, the distance that cats kept from the human, whether a lot or none at all, was consistent. The same was true for the finger-nose contact of phase two, and the cats' willingness to be petted in phase three (Table 9). Notably, the number of vocalizations emitted during the first two phases was highly repeatable (Fig. 13), similar to what was found in the transport cage test.

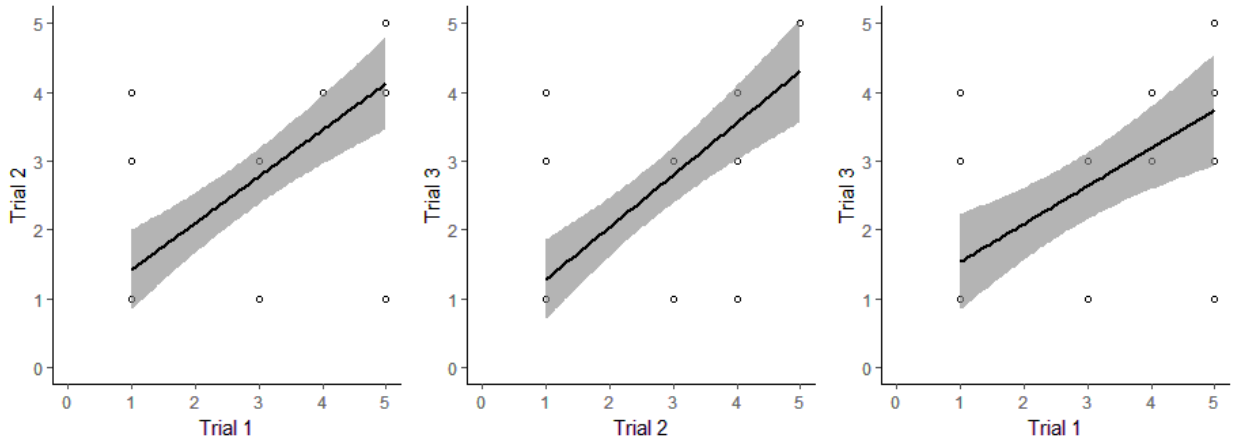

Figure 12. Approach score during phase one of the human approach test from week to week. The shaded area depicts the regression line with 95% confidence intervals; circles represent values of individual cats. Circles can overlap and appear to be less than the N for the test.

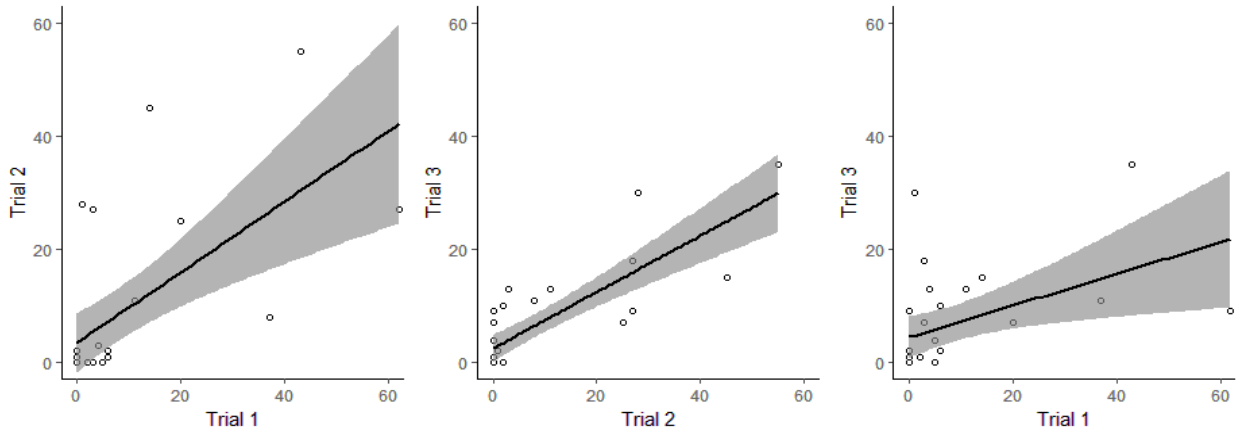

Figure 13. Number of meow type vocalizations emitted across trials in the human approach test. The shaded area depicts the regression line with 95% confidence intervals; circles represent values of individual cats. Circles can overlap and appear to be less than the N for the test.

Table 9. Repeatability analysis for the behaviors analyzed in the human approach test. Intra-class correlation coefficient (R), 95% confidence intervals (CI-, CI+) based on 1000 bootstrap steps and significance values (P) are given. Significantly repeatable variables are bolded. N= 28

Behavioral variable	R	CI-	CI+	P
Approach score	**0.345**	**0.015**	**0.503**	**0.004**
Number of vocalizations	**0.854**	**0.643**	**0.939**	**0.013**
Finger-nose contact (binary)	**0.72**	**0.318**	**0.973**	**0.001**
Pet success (binary)	**0.911**	**0.863**	**0.998**	**0.002**

DISCUSSION

In this study, we evaluated the consistency across time of individual behavioral responses in four tests. In each test, we found that almost all proposed behavioral variables showed significant repeatability, which makes all four tests good tools for the study of personality in the domestic cat. The stable individual differences were evident even though the cats in this study were a very heterogeneous population; they differed in age, sex, and background. It is true that in some behaviors, although significantly repeatable, the degree of differentiation between individuals was rather small. Such small consistent differences may not seem important for the purposes of recommending a specific cat to a possible owner, but once they are studied outside of the shelter context they could be a more prominent aspect of personality.

In the struggle test, we found week to week consistency in the number of attempts and latency to struggle. This is similar to what was previously reported by Lowe and Bradshaw (2002). They found that the behavior of a cat when handled by an unfamiliar person for one minute is a stable trait across age, even when considering the effects of early handling. Therefore, the consistent individual differences of the struggle response might not be solely explained by the socialization (or lack thereof) experiences that the cats might have had. This is important, given that we can often only guess about the background of shelter animals, as was our case. This also means that this test could be a good way to build on Lowe and Bradshaw's work by evaluating how different experiences during development influence this seemingly partially innate response.

We proposed the struggle test as a proxy to the handling test described for European rabbits (Rödel et al., 2014). It can also be compared to the tail suspension test used for mice (Steru et al., 1985), and the tonic immobility tests that have been applied to rabbits (Trocino et al., 2013), pigs (Erhard et al., 1999) and chickens (Wang et al., 2013). What these and similar tests have in common is that, in general, animals that struggle fast or resist being immobilized tend to be bolder, more active and are sometimes classified as more aggressive.

Regarding the transport cage test, for a cat, being put in a carrier can represent a stressful situation. In our test, not only were the cats confined in a small space, but they were also separated from humans and other cats. Although it's a common situation, we have found from everyday experience that some cats will constantly meow and/ or try to get out of the carrier, while others might sit quietly or only stir occasionally. Our results are consistent with this and show that an individual's behavior while in the carrier is repeatable from week to week. Indeed, repeatability of the behavior displayed during a brief separation exists even across the first month of age (Hudson et al., 2015; Hudson et al., 2017). Not only that, but there is repeatability in the same type of behaviors: separation calls and locomotive responses. The latter is coded as whole-body displacement in kittens, and turning, scratching and pawing in the adults. This leads us to believe that short separation tests, such as this one, are an adequate tool for studying the development of these personality traits and their stability across life stages.

As mentioned before, novel object tests are very popular in animal personality research. They have been used to study personality in a wild range of taxa (Jones, 1988; Carlstead et al., 1999; Forkman et al., 2007). However, we must consider that in such tests,

"novelty" is not the only thing the animals are reacting to, the object itself is an important part of their response. One of the problems with the novel object test is that a non-curious/ indifferent animal and a fearful animal will both have a long latency to approach the object, as noted by Forkman et al. (2007). Indeed, this is something to consider whenever we subject an animal to any test, as their underlying motivation may not coincide with our interpretation of their behavior. For example, after analyzing the response of wild baboons in a novel object test, Carter et al. (2012) concluded that they had tested anxiety rather than boldness, contrary to their initial intention. That is why we emphasize the use of biologically relevant stimuli specific to the species. It's hard to find an inanimate object or moving toy that will continuously interest most cats. A mouse, on the other hand, is ecologically relevant to all cats.

Some cats are better suited for companionship than others; frequently animals that are more cautious when approaching humans, or are considered aggressive, land in shelters and are often put down because they are harder to give in adoption. However, even if these cats are not suitable as pets in homes, they can fill an increasing need in other places as "working cats". All over the world more and more farms and warehouses are looking to reduce the use of poisons for rodent control for environmental and health reasons. In these cases, a perhaps not so friendly cat but which is a good hunter is a good option. Many shelters across the United States and the United Kingdom are now successfully implementing special adoption programs for such cats[2]. Given the positive results regarding repeatability of behaviors related to the mouse, and the fact that cats consistently displayed

[2] UK: Dereham Adoption Center; Battersea Dogs & Cats Home
US: Animal Humane Society; Best Friends Animal Society; Baltimore Animal Rescue and Care Shelter; Dumb Friends League

high-interest predatory behaviors (pawing, walking around), we propose the mouse test could be successfully applied to identify individuals with a predisposition to be good hunters.

The repeatability we found for tail wagging is also worth noting for future research. It is not clear why a cat would or would not wag its tail consistently during the test, perhaps it's a measure of interest in the mouse, or of overall arousal. It might have something to do with the hunting situation, as cats rely on their tails for balance and might be readying themselves to lunge. Even so, it is interesting that a predator, such as the cat, would move its tail in such a way when stalking prey, since it might be giving away its position.

In the human approach test, we found repeatability in the behaviors of all three phases; which means that each proposed phase, and the variables associated with it, are adequate to evaluate a cat's willingness to interact with the human. The number of vocalizations emitted during the first two phases were highly repeatable, further supporting vocalizations as a reliable personality trait. Being introduced to an unfamiliar person is potentially stressful for "shy" or "unfriendly" cats. Therefore, like in the carrier, being very vocal could be indicating which are the more reactive cats. Although we should keep in mind that, at least during phase 2, the number of vocalizations could have been influenced by the human calling. In theory, reactive animals also attend more to environmental stimuli and are slow to approach strangers, while proactive individuals act "boldly", confidently and even aggressively towards strangers (Coppens et al., 2010; Turner and Bateson, 2013).

The measures of approach can give us some insight into the cat's early socialization. Handling experiences during development help shape personalities and factor into the individuals' behavior during the test. Kittens socialized during their first three months of

age have an increased willingness to approach and be held by people, they are also overall "friendlier" towards familiar and unfamiliar people at later ages (McCune, 1995; Lowe and Bradshaw, 2001; Casey and Bradshaw, 2008).

Even though they were all repeatable, the R value of both the finger-nose contact in phase two and the petting success in phase three were considerably higher than that of the approach score of phase 1. Hence, it appears that our most reliable measures of approach are those responses to when the human was actively seeking contact. Perhaps this is because a cat's willingness to interact with an unfamiliar person is influenced by the person's willingness to interact with the cat. There is some evidence that cats, like dogs, react to human emotion cues, such as posture and facial expression (Merola et al., 2015; Galvan and Vonk, 2016). Although we instructed the volunteers to sit in a neutral posture, it is possible that subtle differences affected the extent to which the cat approached each person, but still we found consistency across trials.

Application

Returning to the main aim of our study, our results support the proposal that adult cats show consistent individual differences in different behaviors across time. These differences were evident despite how heterogeneous our population was. This suggests that these between-individual differences are robust, confirming what has been repeatedly reported for this species. Additionally, the age range in our sample not only addresses the need for reliable tests for adult cats, but also the need for tests that reveal consistent individual differences over a wide range of ages across adulthood as cats grow older. It is also important to note that all four tests proposed in this study are simple, fast (no more than 5

min.) and any materials used are inexpensive and easily procured. Because of this, they can be reproduced practically anywhere in the world. All of this makes them a suitable option for shelters looking to evaluate personality as part of their adoption program.

While millions of cats enter animal shelters every year, in the United Stated only 11.5% of pet cats come from a shelter (Gartner, 2015; Weiss et al., 2015), and we don't even know the numbers for Mexico. Even if a cat is adopted, there is still a high chance that it will be returned due to not fulfilling the new owner's expectations. For example, a family with small children needs a cat that tolerates handling; a calm person might want a calm cat; someone who is not home most of the day would do better with a cat that isn't stressed by separation. Working cats are another example; they have a better chance of being successfully adopted if the individuals with more interest in hunting are the ones recommended for this task. A good mouser can significantly reduce or even eliminate a rodent problem. For example, the most prolific mouser on record is Towser, a female cat that lived in Glenturret Distillery (UK), where she averaged three mice per day totaling an estimated 28,899 mice by the time she died (Guinness World Records, 2018). Organizations like the ASPCA have managed to decrease the number of returned cats by implementing questionnaires and personality tests, such as the ones we recommend in this study, that help them match cats with the right owner (Weiss et al., 2015).

Behavioral syndromes

Animal personality is defined by two types of consistency: over time, and across context (Sih et al., 2004; Stamps and Groothuis, 2010; Wolf and Weissing, 2012). So far, the repeatability within tests this thesis has focused on has only validated our tests to evaluate

personality across time. According to the multi-trait multi-test approach proposed by Campbell and Fiske (1959), the validation of a test involves exploring the associations between multiple traits and multiple methods or contexts. Across-context validity could be evaluated through behavioral syndromes (Sih et al., 2004; Wolf and Weissing, 2012; Carter et al., 2013; Stamps and Groothuis, 2010).

Although we did not delve into the behavioral syndromes, we can make some predictions about which behaviors might correlate between our tests. It has been previously described that there is no correlation between locomotor activity and emitting vocalizations in kittens less than a month old (Hudson et al., 2015; Hudson et al., 2017), and we would expect this to be true in adults as well. This lack of association would indicate that these behaviors have different underlying regulatory mechanisms, and they might represent different domains of personality. But, contrary to this hypothesis, Iki et al. (2011) found a negative relationship between time spent vocalizing and locomotive behaviors; they suggest that cats that move a lot during a stressful situation are being proactive, while very vocal cats are reactive. If this is the case, given the relation that vocal centers in the brain have with emotionality via the amygdala and the HPA axis we would expect 'reactive' cats to have higher levels of cortisol after the separation or a stressful situation as previously found in other species (Goldstein et al., 1996; Koolhaas et al., 2007; Jürgens, 2009).

We would also expect for behaviors indicative of proactive or easily aroused individuals to correlate with each other. For example, a short latency to struggle with high locomotor activity during the transport cage test. The same would be true for reactive responses; notably vocalizations. Since vocalizations have been found to be reliable

behavioral traits across time, we expect them to be equally stable. For example, between the transport cage and the human approach test.

However, we might find unexpected correlations or an unexpected lack of correlation. If we were to encounter this, it doesn't automatically mean that there are no behavioral syndromes to be found. Coping styles, behavioral types, personalities, or however we choose to call them, are not a fixed feature. Being proactive/ bold/ etc. in one context does not strictly reflect that the animal will behave the same in all situations. For example, two cats considered equally "friendly" by their caretakers might have different responses to an unfamiliar person. As per the definition of animal personality, there should be some level of consistency across context. But, we should keep in mind that the personality of an animal can be plastic and more complex than we sometimes make it out to be.

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SUPPLEMENTARY MATERIAL

Table S1. Animals that participated in the present study (F = female, M = male)

Name	Sex	Estimated age (years)	Tests
Ani	F	4	All tests
Ann	F	5	All tests
Blanca	F	9	All tests
Blue	M	5	All tests
Casandra	F	1	All tests
Chipilina	F	1	All tests
Dora	F	11	All tests
Fekete	F	4	Human approach test
Felix	M	4	All tests
Grisino	M	4.5	All tests
Guiseppe	M	--	All tests
Ina	F	4	All tests
Johanna	F	--	Struggle test Transport cage test Human approach test
Lenin	M	1	All tests
Lilic	F	3	Struggle test Mouse test Human approach test
Lim	M	2	All tests
Lulu	F	6	All tests
Munch	M	6	All tests
Naomi	F	7	All tests
Nenia	F	3	All tests
Obit	M	8	Struggle test Transport cage test Human approach test
Ollin	M	4	Struggle test Transport cage test Human approach test
Orange	M	2	Struggle test Transport cage test Human approach test
Siberia	F	7	All tests
Skit	M	3.5	Struggle test Mouse test
Squixi	F	4	Struggle test Transport cage test Mouse test
Sutmi	F	4	All tests

Tigre	M	9	Struggle test Transport cage test Human approach test
Tiqueri	M	4	Struggle test Transport cage test
Tsuki	F	4	All tests
Yokir	M	1	All tests

Table S2. Age and sex differences for each of the behaviors evaluated in the tests

Struggle test	**mean**	**SD**	**mean$_{males}$**	**SD$_{males}$**	**mean$_{females}$**	**SD$_{females}$**	**P sex**	**P age**
Number of vocalizations	0.411	1.253	0.071	0.342	0.708	1.637	0.140	0.815
Latency to vocalize	26.473	9.155	6.143	24.575	10.858	28.643	0.129	0.893
Number of struggle attempts	1.067	1.668	1.024	1.239	1.104	1.981	0.494	0.643
Latency to struggle	6.949	6.463	5.895	5.960	7.871	6.802	0.525	0.062
Mouse test								
Latency to be on the acrylic	64.056	52.753	71.408	52.614	59.809	52.954	0.300	0.418
Duration on the acrylic	20.394	30.780	12.431	19.465	24.996	35.111	0.243	0.509
Latency to interact	48.620	50.530	49.346	49.626	48.200	51.597	0.896	0.968
Duration sniffing	7.699	8.805	7.538	8.778	7.791	8.917	0.943	0.890
Number of times they pawed	2.521	6.016	1.385	3.545	3.178	7.017	0.242	0.976
Duration tail wagging	5.755	11.193	6.100	10.386	5.556	11.744	0.785	0.218
Duration walking around	1.423	3.460	1.185	2.920	1.560	3.761	0.526	0.196
Transport cage test								
Number of vocalizations	7.405	13.828	10.744	18.010	4.511	7.882	0.822	0.234
Latency to vocalize	72.188	52.253	68.421	56.869	75.453	48.311	0.308	0.497
Number of times they scratched	2.738	3.319	3.128	3.585	2.400	3.070	0.635	0.890
Latency to scratch	66.557	49.495	64.436	50.644	68.396	48.976	0.717	0.713
Number of times they turned	2.048	3.498	2.513	4.109	1.644	2.854	0.780	0.121
Latency to turn	85.048	46.935	87.400	44.706	83.009	49.195	0.555	0.546
Latency to sit or lie	26.914	30.897	18.585	23.892	34.133	34.540	0.126	0.082
Duration sitting or laying	78.581	36.096	83.764	34.442	74.089	37.267	0.499	0.073

Duration looking out	79.519	20.508	82.882	22.214	76.604	18.668	0.282	0.335
Human approach test								
Approach score	2.619	1.567	2.278	1.542	2.875	1.552	0.832	0.099
Number of vocalizations	5.048	10.360	6.222	12.490	4.167	8.456		
Finger-nose contact (binary)	0.560	0.499	0.500	0.507	0.604	0.494	0.816	0.722
Pet success (binary)	0.869	0.339	0.833	0.378	0.896	0.309	0.934	0.580