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A review of the development and functions of cat play, with future research considerations

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ABSTRACT

Although attention to domestic cat (*Felis silvestris catus*) behavior and cognition has increased in recent years, numerous questions remain regarding their play. Few studies have included play as a variable of interest, and to the best of our knowledge no behavioral studies focusing on cat play have been published in the last 15 years, and there is no recent review of our current understanding of its development, behavioral components, function, or outstanding research questions. This is despite the accessibility of the cat as a convenient model for more difficult to study members of the Carnivora, as recognized by pioneering studies of cat play in the 1970s and 1980s. We address this gap by reviewing and synthesizing the existing literature on play development, identifying and discussing eliciting factors and possible functions of play in cats. Additionally, we conducted an extensive review of the literature to identify how play has been operationalized in peer-reviewed publications (N = 46). We identified 138 behaviors measured in these studies, with 84 of them unique behavioral labels. Our findings demonstrate the diversity—and sometimes commonalities—of descriptions of play behavior across these studies, while highlighting the challenge of inconsistent operationalization of cat play in the literature. We conclude by proposing and exploring several open questions and offering suggestions for future research, particularly related to pet cats.

> "It would be quite absurd to assume that a cat, who in its daily existence had already killed and eaten thousands of prey animals, could not recognize the difference between a mouse and a ball of paper; it knows that a ball of paper is not a mouse just as precisely as it immediately recognizes the difference between a familiar and a new prey animal, or between a harmless and a potentially dangerous one." – Paul Leyhausen, Cat Behavior, 1979

1. Introduction

Perhaps one of the most pervasive stereotypes about the predatory behavior of domestic cats (*Felis silvestris catus*) is that they play with prey. This suggests that we believe we can recognize functional differences discriminating some interactions between cats and prey from others—some behaviors appear strictly predatory, others not. This stereotype highlights the potential difficulty both in defining play and in drawing a line between play and predation in a naturally predatory species, particularly given that cats display several forms of play outside the context of hunting, such as toward inanimate objects and other cats.

Despite an increase in general empirical inquiry related to cats, and recent reviews of cat behavior and cognition (e.g., Vitale Shreve and Udell, 2015, 2017), numerous scientific questions remain regarding cat play. Although a few studies have included play as a variable of interest (e.g., Vitale Shreve et al., 2017; Ellis et al., 2017), to the best of our knowledge there have been no peer-reviewed behavioral studies focusing on cat play in the last 15 years, and no recent review of our current understanding of the development, behavioral components, and functions of cat play, framed within the context of their relationship to other wild felids and Carnivora. This is despite the accessibility of the domestic cat as a convenient model for more difficult-to-study members of Carnivora, as recognized by Bateson and Caro in their pioneering studies (e.g., Barrett and Bateson, 1978; Bateson, 1981; Caro, 1979, 1980a; Caro, 1980b,c). This paper addresses that gap by reviewing the presently available research, by proposing several open questions and challenges related to cat play—including the problem of inconsistent operationalization of play in the literature, and by suggesting future research directions with a focus on pet cats.

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Table 1
Operationalization of play behavior in 46 studies where play was an explicitly measured variable, exactly as defined in the referenced studies.

Behavior	Definition	How measured	Categorization	References
Allogrooming	Licking the dog's face or body.	Duration and frequency	Play behavior patterns (toward dogs)	Feuerstein and Terkel (2008)
Approach	Movement of any sort (excluding canter) towards another cat.	Frequency	Social play	Caro (1981b)
Arch	Each occurrence of a marked upward curving of the spine while standing still, leaping upwards, or moving sideways. The orientation is usually side-on in relation to another cat or object. This combined West's (1974) 'Horizontal leap' and 'Side-step.'	Frequency	Playful activity	Barrett and Bateson (1978); Bateson and Young (1981)
Arch	A marked upward bending of the spine while standing still, leaping upwards or moving sideways.	Frequency	Social play	Caro (1979), 1980a
Arch	A marked upward bending of the spine while standing still, leaping upwards or moving sideways, with or without piloerection.	Frequency	Social play	Caro (1981b)
Attack	Jump onto a cat and grasp it with forepaws or forelegs.	Frequency	Social play	Caro (1981b)
Bat	Cat touches object with a front paw, claws retracted.	Frequency	Object play	Hall and Bradshaw (1998)
Bat	Striking the mouse from above with the palm of the paw parallel to the ground. The mouse was moved or compressed by the strike, but the paw was quickly withdrawn.	Frequency	Predatory behavior	Pellis et al. (1988)
Belly up	To move the back legs in a treading motion and to make reaching or pawing movements with the front legs. The mouth is held open and the teeth are exposed. In a social encounter, one kitten assumes the belly-up position and another kitten stands over it. Thus, the treading and pawing movements bring the kitten into contact with parts of the body of the standing kitten. Usually, these areas are the head, neck and ventral area.	Frequency	Social play	West (1974)
Bite	Bringing jaws into contact with a cat and closing them.	Frequency	Social play	Caro (1981b)
Bite	Bites are less forceful than killbites.	Frequency	Object play	Hall and Bradshaw (1998)
Bite	The mouth was closed around the mouse. This could be subdivided into light bites, in which the skin was only grasped and the mouse uninjured, and heavy bites, in which the skin was broken and a firm grip on structures beneath the skin was achieved.	Frequency	Predatory behavior	Pellis et al. (1988)
Canter	Jerky running gait during which all paws repeatedly and simultaneously leave the ground; head and tail often held high.	Frequency	Social play	Caro (1981b)
Cat contact	Each pat with a paw making contact with another cat and each bite of another cat. Bites could be given in the course of 'Wrestling' (see below) but were scored separately. Frequencies of patting and biting were not scored by West (1974).	Frequency	Playful activity	Barrett and Bateson (1978); Bateson and Young (1981)
Cat contact	Each pat with a forepaw making contact with another cat (including the mother) and each bite of another cat.	Frequency	Social play	Bateson et al. (1981)
Cat contact	Each pat with a forepaw, and each bite, making contact with another cat (mother or sibling). Scored separately for each kitten.	Frequency	Social play	Bateson et al. (1985a)
Cat contact	The kitten paws, pats or bites a conspecific.	Frequency	Social play	Bateson et al. (1990)
Chase	Running after a moving kitten.	Frequency	Social play	Caro (1979, 1980a)
Chase	Running after a moving cat.	Frequency	Social play	Caro (1981b)
Chase	Each bout of running after another individual/mobile object with the chased individual running away from the chaser for at least a distance of 1 m.	Frequency	Social or object play	Mendl (1988)
Chasing	Cat runs rapidly in pursuit of (modifier).	N/A	Solitary or social play	Stanton et al. (2015)[a]
Chase	A chase involves a kitten running after or from another kitten. It could, perhaps, be differentiated into pursuit and flight.	Frequency	Social play	West (1974)
Chew	Cat holds object in the mouth and chews it with rapidly repeated, small bites.	Frequency	Object play	Hall and Bradshaw (1998)
Chirping	Making a sound similar to a high-pitched phone ring, tone often rises near the end.	Duration and frequency	Play behavior patterns (toward dogs)	Feuerstein and Terkel (2008)
Clutch	Cat holds the toy close to the body with one or both front paws.	Frequency	Play	Hall et al. (2002)
Clutch	Object is held close to the body with one or both front paws.	Duration	Object play	Hall and Bradshaw (1998)
Crouch	Belly on the ground with all limbs by the side of the body, oriented and attentive to a conspecific; back legs often treading.	Frequency	Social play	Caro (1981b)
Exploration	Visual regard, licking, sniffing and/or touching without manipulation of an object with the paws or mouth while moving slowly toward or around an object.	Duration	Object play	West (1977)
Exploratory and play responses	Responses included looking at the string, approaching it, pawing or batting it, mouthing it, and pursuing and pouncing on it.	Frequency	Object play	Collard (1967)
Face off		Frequency	Social play	Caro (1981b)

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Table 1 (*continued*)

Behavior	Definition	How measured	Categorization	References
	Sitting next to another cat, often with tail lashing and head twisting; recipient in a rolled position or similar face off stance (see West (1974)).			
Face off	A kitten sits near another kitten and hunches its body forward, moving its tail back and forth, and lifts a front paw and moves it in the direction of the other kitten. The kitten's head and eyes are also oriented toward the other kitten. Two kittens may face-off simultaneously and direct their front paw movements at one another's face.	Frequency	Social play	West (1974)
Flee	Running while being followed by a moving cat.	Frequency	Social play	Caro (1981b)
Foot contact	Contacting another cat with one or two back paws or back legs, e.g. stepping on, kicking once or repeatedly kicking with back legs in unison.	Frequency	Social play	Caro (1981b)
Four paw contact	All four paws in contact with another cat while subject is in a rolled position.	Frequency	Social play	Caro (1981b)
Grasp	Cat uses both front paws to take hold of object, claws either extended or retracted.	Frequency	Object play	Hall and Bradshaw (1998)
Hit	Cat touches object with paw with a front paw, claws extended, with more force than above. Object may be thrown aside.	Frequency	Object play	Hall and Bradshaw (1998)
Hold	Bringing forepaws or forearms simultaneously into contact with a cat.	Frequency	Social play	Caro (1981b)
Hold cat	Each occurrence of grasping another cat between the lower part of the forelimbs.	Frequency	Playful activity	Bateson and Young (1981)
Hold object	Each occurrence of grasping an object between the lower part of the forelimbs.	Frequency	Playful activity	Bateson and Young (1981)
Hold/Bite object	Each bout of an individual holding an immobile object in the forepaws, with hindquarters slightly raised, and biting/chewing at it.	Frequency	Object play	Mendl (1988)
Holdmouth	Object is held firmly and retained in the mouth, for a greater duration than is necessary for a single bite.	Duration	Object play	Hall and Bradshaw (1998)
Horizontal leap	The kitten assumes a lateral position, with respect to another kitten, arches back slightly and curves its tail upwards and towards its body then leaps off the ground. The sixth position is somewhat similar.	Frequency	Social play	West (1974)
Independent play	Manipulates an object with its paws in an apparently playful manner, without active engagement of another. Cat may also chase or paw at its own tail.	Duration	Play	Potter and Mills (2015)
Interruptive behavior	Non-obligatory patterns occurring during catching, killing or eating a prey. Occur when kittens have difficulty killing prey, are often denoted as play. Examples: growling, hissing, mewing (and other vocalizations), walking (without prey), grooming, carrying, touching, tossing, head rubbing, rolling. touching the prey with the paws and tossing it with the mouth are frequent. In particular these activities, combined with walking and running, are the main components of what generally is called play in cats.	Frequency	Predatory play	Baerends-van Roon and Baerends (1979)
Kick	Cat rakes and kicks object with hind legs, while lying on one side, clutching or holding object in the mouth.	Frequency	Object play	Hall and Bradshaw (1998)
Killbite	Cat delivers a forceful bite to the toy.	Frequency	Play	Hall et al. (2002)
Killbite	Cat delivers a strong bite to object.	Frequency	Object play	Hall and Bradshaw (1998)
Kneading	Kneading motion using the fore-legs, with sheathed claws.	Duration and frequency	Play behavior patterns (toward dogs)	Feuerstein and Terkel (2008)
Lick	Cat licks object.	Frequency	Object play	Hall and Bradshaw (1998)
Locomotor play	Playful activity that carries the individual about its environment, but is neither specifically directed at other individuals, nor involves manipulating inanimate objects.	Frequency	Locomotor play	Martin and Bateson (1985b)
Mouth open	Gaping at another cat while in a rolled position.	Frequency	Social play	Caro (1981b)
Mouthing	The lips of the mouth were brought into contact with the mouse, which could involve gentle touching all along the mouse's body.	Frequency	Predatory behavior	Pellis et al. (1988)
Moving the tip of the tail	A slow movement of part of the tail only.	Duration and frequency	Play behavior patterns (toward dogs)	Feuerstein and Terkel (2008)
Neck flex	Each occurrence of a marked downward flexion of the neck. The head is also turned to face another cat if the body is side-on. It can occur simultaneously with the Arch and can be given while standing still or moving sideways. It was not scored by West (1974).	Frequency	Playful activity	Barrett and Bateson (1978); Bateson and Young (1981)
Non-manipulatory contact	Any activity occurring on or under an object not involving manipulation of it such as lying or sitting on, in, or under an object.	Duration	Object play	West (1977)
Nonsocial play	Directed either toward inanimate objects and described as "manipulation of an object by tossing, grasping, scooping, poking, batting, and/or mouthing often preceded by pouncing or leaping on the object and often followed by the same 2-	Frequency	Nonsocial play	Mendoza and Ramirez (1987)

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Table 1 (*continued*)

Behavior	Definition	How measured	Categorization	References
	behaviors" (West, 1977), or toward itself in apparently spontaneous movements that carry the individual about its environment (Martin and Caro, 1985).			
Nose contact	The cat's nose was brought into close proximity or actual contact with the mouse and the nostrils flared. This probably included both tactile and olfactory input from the prey.	Frequency	Predatory behavior	Pellis et al. (1988)
Object contact	Each pat with a paw making contact with an object (particularly the toy dog and the ball) and each bite of these objects. This category is the same as Egan's (1972, 1976) 'Object Play.' It was not scored by West (1974).	Frequency	Playful activity	Barrett and Bateson (1978); Bateson and Young (1981)
Object contact	Each pat with a forepaw making contact with an object, or each bite of an object.	Frequency	Object play	Bateson and Young (1979)
Object contact	Each pat with a forepaw making contact with an object and each bite of these objects.	Frequency	Object play	Bateson et al. (1981)
Object contact	Each pat with a forepaw, and each bite, making contact with any inanimate object. Scored separately for each kitten.	Frequency	Object play	Martin and Bateson (1985a)
Object contact	The kitten paws, pats or bites an inanimate object.	Frequency	Object Play	Bateson et al. (1990)
Object play	Kittens in the study were divided into two groups, one given exposure to play objects and the other who was not.	Frequency	Object play	Caro (1980a)
Object play	Striking, chasing, pouncing on, and vigorous manipulation.	Frequency	Object play	Guyot et al. (1980)
Object play	No definition.	Duration	Object play	Mertens (1991)
Object play	Cat manipulates an object with its paws in an apparently playful manner. The cat may pat, throw, pounce or wrestle with the object.	Frequency and duration	Object play	Stella et al. (2014)
Pat/Paw/Bite	Each occurrence of a pawing/patting/biting movement directed at another individual/mobile object which lasts no longer than 1 s and also involves no grasping or holding of the individual/mobile object. This excludes any occurrences which are defined in the Hit/Bite category (incorporates Cat contact and Object contact, Barrett and Bateson, 1978).	Frequency	Social or object play	Mendl (1988)
Paw	Bringing the forepaw into contact with a cat.	Frequency	Social play	Caro (1981b)
Paw	Cat pats (modifier) with its forepaw(s). Claws are usually retracted.	N/A	Solitary or social play	Stanton et al. (2015)[a]
Paws up	Front paws, and sometimes back paws as well, held up to but not touching another cat, while subject is in a rolled position.	Frequency	Social play	Caro (1981b)
Pin	The initial strike was the same as the bat, but then the paw was held down, pinning the mouse to the ground.	Frequency	Predatory behavior	Pellis et al. (1988)
Play	Play was also indicated when bites and pats delivered to another kitten did not elicit flight, agonistic behavior, or vocalization - in other words, when they did not seem to hurt or annoy the recipient.	N/A	Play	Barrett and Bateson (1978)
Play	Behavior that is active, where the cat's attention is focused on the prey, or where the prey is touched, manipulated or approached, but not injured.	Frequency	Predatory behavior	Biben (1979)
Play	Through cracks in cage with neighbor or with object.	Duration	Play	Carlstead et al. (1993)
Play	Approaching, sniffing, pawing, holding, biting, and having rolled contact with siblings.	Frequency	Social play	Caro (1981a)
Play	Hunt-like postures which could be directed to people or toys.	Frequency	Play	Edwards et al. (2007)
Play	Either chases, pounces, bites or wrestles with another cat or an object, in a playful manner.	Frequency and duration	Playful	Feaver et al. (1986)
Play	No definition.	Duration and frequency.	Friendly interactions	Gouveia et al. (2011)
Play	Play with a laser light; play with a 5 cm diameter ball.	Intensity	Play	Kennedy et al., 2018
Play	Any playful behavior that was observed regardless of whether this play involved other kittens, the cat itself, or some aspect of the environment.	Frequency of intervals behavior is present in	Play	Koepke and Pribram (1971)
Play	This play behavior is very active and may last for several minutes. The cat performs rapid jumps and several playing bites.	Duration	Predatory play	Langfeldt (1974)
Play	Cat is engaged in activity for sake of amusement, either alone or with other individual.	Frequency	Play	McGlone et al. (2018)
Play	Pounces, chases, horizontal leaps, belly-up patterns, and stand-up patterns.	Frequency	Play	Mendoza and Ramirez (1987)
Play	Cat is performing a behavior in a "non-serious" or playful manner (Recommended for use when distinguishing between affiliative and aggressive or agonistic social interactions). Observer must have certainty that the cat has no intention to harm.	N/A	Modifier / Dispositional - Descriptions of modifiers to be used in conjunction with base behaviors.	Stanton et al. (2015)[a]

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Table 1 (*continued*)

Behavior	Definition	How measured	Categorization	References
	May look for facial expressions indicating play, such as mouth slightly open without showing teeth, ears and eyes appear relaxed or fairly alert (based on Estes, 1991).			
Play	Cat interacts with something in a "non-serious" manner (i.e. where there is no intention to harm).	N/A	Categorized as both 'Active' and 'Affiliative'	Stanton et al. (2015)[a]
Play	Chasing, pawing, pouncing, wrestling with and throwing an (object) into the air, or pawing at its own tail.	N/A	Solitary play	Stanton et al. (2015)[a]
Play	Chasing, wrestling, biting, pouncing and pawing.	N/A	Social play	Stanton et al. (2015)[a]
Play	Manipulation of an object by tossing, grasping, scooping, poking, batting, and/or mouthing often preceded by pouncing or leaping on the object and often followed by the same 2-behaviors.	Duration	Object play	West (1977)
Play (social or object),	No definition.	Frequency/relative occurrence	Play	Ottway and Hawkins (2003)
Play (whether social or not)	No definition.	Duration	Play	Mertens and Turner (1988)
Play behavior	Cat shows self play, object play, or social play.	Occurrence or nonoccurrence	Play	Arhant et al. (2015)
Play behavior	Pawing or sniffing at objects or in corners, chasing the tail, or batting at pieces of food, feces, etc.	Frequency	Play	Jacobs et al. (1977)
Play Initiation	The tester moves away from the cat and moves a piece of string (or ball) along the floor slowly to initiate play.	Occurrence or nonoccurrence	Playfulness as part of Feline Temperament Profile (FTP)	Iki et al. (2011)
Play involving another	Any manipulating, patting, throwing, pouncing, chasing, wrestling of toys involving the active interaction with the owner or stranger. Acceptable responses: Comes back for more stroking, Watches the string intently, Chases the string. Questionable responses: Attends something else in the room and avoids eye contact, Ignores the string.	Duration	Social play	Potter and Mills (2015)
Play roll on back	Cat rolls onto its back, with its belly exposed and all paws in the air, within a playful context. All agonistic behaviors are absent (i.e. hissing, ears back).	N/A	Affiliative behavior	Stanton et al. (2015)[a]
Play with object	Cat manipulates an object with its paws in an apparently playful manner. It may pat at the object with claws retracted, throw the object into the air, pounce upon it or wrestle with it (This is a very broad category and can be considerably subdivided - see Barrett and Bateson, 1978; West, 1979).	N/A	Solitary behavior pattern	UK Cat Behaviour Working Group (1995)[a]
Play-exploration	Exploration of an object always preceded by running or leaping over, around, or into an object and often followed by the same locomotor responses.	Duration	Object play	West (1977)
Playfulness	Engages in play with cats and/or objects.	Rating on a visual scale of observed intensity	Playful	Feaver et al. (1986)
Playing	No definition, but describes rationale for including—"as playing is of interest here as a measure of motor activity only, no distinction will be made between various aspects of play."	Frequency	Play/motor activity	Albonetti (1988)
Playing	Chasing, wrestling, inhibited paw strikes, without vocalization, for 3 or more s.	Duration	Social play	Bennett and Mellen (1983)
Playing	Proportion of time spent engaging in physical interaction with each stimuli.	Duration	Object Play	Vitale Shreve et al. (2017)
Playing with toys	Watches toy intently; chases toy.	Occurrence or nonoccurrence	Play	Moore and Bain (2013)
Pounce	Cat leaps onto (modifier).	N/A	Solitary or social play	Stanton et al. (2015)[a]
Pounce	The kitten crouches with its head held low or touching the ground and its back legs moves its hindquarters back and forth and tucked in and its tail straight back. The tail moves forward, the thrust coming from the may be moved back and forth. The kitten extension of its back legs.	Frequency	Social play	West (1974)
Predatory play	Directed toward living or dead prey.	Frequency	Predatory play	Mendoza and Ramirez (1987)
Purring	Low, often quiet noise, made both during inhalation and exhalation.	Frequency	Play behavior patterns (toward dogs)	Feuerstein and Terkel (2008)
Rake	Each bout of kicking movements at another cat or at an object with one or both hind legs. A component of Barrett and Bateson's (1978) 'Wrestling'.	Frequency	Playful activity	Bateson and Young (1981)
Rear	Each occurrence of sitting, standing or vertical leaping on the hindlegs with forelegs raised and splayed. It was performed beside another cat or object. Similar to West's 'Vertical stance.'	Frequency	Playful activity	Barrett and Bateson (1978); Bateson and Young (1981)
Rear	Standing or vertical leaping on hindlegs, with forelegs raised and splayed.	Frequency	Social play	Caro (1981a); Caro 1981b)
Rear	Cat stands on hind legs to reach object.	Frequency	Object play	Hall and Bradshaw (1998)
Roll	Each occurrence of rolling on the side or back (see Caro, 1980a,b,c). Overlaps with Barrett and Bateson's (1978) 'Wrestling.'	Frequency	Playful activity	Bateson and Young (1981)

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Table 1 (*continued*)

Behavior	Definition	How measured	Categorization	References
Rolled contact	Lying on dorsal or lateral surface and employing any contact pattern; (a similar pattern to Barrett and Bateson's 'wrestle').	Frequency	Social play	Caro (1981b)
Rolling on the ground	Exposing the belly, with sheathed claws.	Duration and frequency	Play behavior patterns (toward dogs)	Feuerstein and Terkel (2008)
Self play	Each bout in which the individual chases its own tail.	Frequency	Solitary play	Mendl (1988)
Self play	Cat plays with its own body, usually the tail.	Frequency and duration	Self play	Stella et al. (2014)
Self play	A cat chases or paws at its own tail (see Mendl, 1988).	N/A	Solitary behavior pattern	UK Cat Behaviour Working Group (1995)[a]
Side-step	The kitten arches its back, curls its tail upwards and walks sideways toward or around another kitten or object.	Frequency	Social play	West (1974)
Sniff	Cat sniffs object.	Frequency	Object play	Hall and Bradshaw (1998)
Social play	Two cats play with the same toy simultaneously or within 3 s between.	Frequency	Social play	Loberg and Lundmark (2016)
Social play	Directed at conspecifics and described as a "stereotyped form of physical interaction between individuals" (Ewer, 1968).	Frequency	Social play	Mendoza and Ramirez (1987)
Social play	No definition.	Frequency	Social play	Mertens and Turner (1988)
Social play	Cat directs play at another cat or the observer.	Frequency and duration	Social play	Stella et al. (2014)
Social play	Combination of friendly chasing, biting and wrestling; postures are assumed which do not indicate any agonistic interactions.	Frequency	Social play	van den Bos and de Vries (1996)
Social playing	Play and discontinuing play (cats only, whether initiated by human or cat).	Duration	Social play	Mertens (1991)
Solitary play	One cat plays with a toy, without any other cat playing with the same toy within 3 s.	Frequency	Object play	Loberg and Lundmark (2016)
Solitary play or social play	No definition.	Duration	Play	Uetake et al. (2013)
Stalk	Each bout of low crouching with hindlegs treading, or creeping (or running briefly) with belly close to the ground and head low towards another cat or object. Similar to West's 'Pounce.'	Frequency	Playful activity	Barrett and Bateson (1978); Bateson and Young (1981)
Stalk	Each bout of low crouching with hindlegs treading, or creeping (or running briefly) with belly close to the ground and head low towards another individual/mobile object.	Frequency	Social or object play	Mendl (1988)
Stand off	Standing next to another cat, often with head twisting; recipient usually in a rolled position.	Frequency	Social play	Caro (1981b)
Stand up	The kitten stands near or over another kitten with its head oriented toward the head and neck region of the other kitten. The stand-up kitten's mouth is open and it may direct "bites" toward the other kitten. The kitten may also raise one of its front paws and paw at the other kitten.	Frequency	Social play	West (1974)
Swipe	Striking the mouse laterally from the side with the palm of the paw perpendicular to the ground. The mouse was moved along the ground by the strike.	Frequency	Predatory behavior	Pellis et al. (1988)
Tap	Same as the bat but gentle, so that the mouse was not moved or compressed by the strike.	Frequency	Predatory behavior	Pellis et al. (1988)
Touch	Same as the swipe but gentle, so that the mouse was not moved by the strike.	Frequency	Predatory behavior	Pellis et al. (1988)
Vertical stance	A kitten assumes a sitting position and then rocks back on its hindquarters, lifts its front paws off the ground and stretches them out perpendicular to its body. The kitten also extends its back legs so that it is in a stationary bipedal position.	Frequency	Social play	West (1974)
Wrestle	Each bout of lying while clasping with the forelegs and kicking with the hind legs another cat or object. This pattern formed part of West's 'Belly-up.'	Frequency	Playful activity	Barrett and Bateson (1978); Bateson and Young (1981)
Wrestle	Time spent by an individual holding/grabbing another individual/mobile object, sometimes kicking at it with the back legs (incorporates Hold cat, Hold object and Rake, Bateson and Young, 1981).	Duration	Social or object play	Mendl (1988)
Wrestle	Cat engages in physical contact with (modifier), whereby the cat struggles with (modifier). Can include pulling (modifier) toward itself with its forelegs and perform raking movements with the hind legs.	N/A	Solitary or social play	Stanton et al. (2015)[a]
Wrestle	One cat struggles with another cat, raking with its hind legs and pulling the "opponent" towards its body with its forelegs. It is mainly a play behavior, and is distinct from FIGHT (being much less intense and lacking the additional elements of FIGHT).	N/A	Social behavior patterns	UK Cat Behaviour Working Group (1995)[a]

[a] Ethogram-based publication.

2. Framing the domestic cat

Domestic cats come from a lineage of solitary, shy hunters (the genus *Felis*) who emerged approximately 8–10 million years ago within the biological family Felidae (Slattery and O'Brien, 1998). Members of the Felidae family, which include the subfamilies of big (*Panthera*) and small (*Felinae*) cats, have bodies that are well adapted for hunting. All cats are considered hypercarnivores, and they primarily use stalk-and-rush methods to hunt their prey (Kleiman and Eisenberg, 1973; Morris, 2002). Other extant members of the *Felis* genus include jungle cats, sand cats, and domestic cats' closest relatives and progenitor, the wildcats (*Felis silvestris*; Driscoll et al., 2007).

Current findings estimate that cat domestication began around 10,000 years ago in the Middle East as humans were first establishing settlements (Driscoll et al., 2007). Cat domestication began as a commensal relationship with humans, where cats benefited from humans' storage of grain that attracted small rodents. Cats who hunted and killed these rodents were more likely to have surviving offspring and thus pass on genotypes favoring hunting as well as a greater tolerance for humans and conspecifics (Bradshaw, 2016).

Despite domestication, considerable similarities in behavioral repertoires and personality structure have been identified across felids (Cameron-Beaumont et al., 2002; Gartner et al., 2014; Stanton et al., 2015). Humans have no doubt influenced domestic cat genetics, as some cats are selectively bred (pedigree), and those who are spayed and neutered are likely the most social or easiest to capture which may limit the ability of certain genes to propagate in the population while promoting others (Bradshaw et al., 1999). Even so, humans have likely placed few strong selective pressures on cats during domestication, given that most cats mate freely and only a minority of cats are under human-controlled breeding (Driscoll et al., 2009a, b). As cats remain obligate carnivores, the hunting instinct has probably not been selected against in the modern-day domestic cat, except perhaps in the past four decades (Bradshaw, 2013).

At the same time, domestication has led to some expected changes to the genome, physiology, and behavior of domestic cats, some of which may influence play and predation. These changes include selection for genes related to memory, reward-learning, and fear-conditioning (Montague et al., 2014), as well as physical changes such as smaller brains compared to their closest relatives, although brain size does not appear to predict levels of play-related behaviors (Iwaniuk et al., 2001). Selection for social tolerance and juvenile features and behaviors may have increased cats' tendencies toward social or object play (Cameron-Beaumont et al., 2002; Driscoll et al., 2009a; Pontier et al., 1995). This feline blueprint lays the foundation to explore the potential biological and relational factors that influence play and its development.

3. Development of play in *Felis silvestris catus*

Play in domestic cats is commonly categorized as social, locomotor, predatory, or object play. Each play type appears to have a different developmental trajectory with both unique and overlapping features, and studies of feral colonies, pet cats, and cats in laboratories have contributed to this understanding.

3.1. Emergence of play behavior

Play behavior generally emerges in kittens between 2 and 3 weeks of age when they start engaging socially with littermates or, in the absence of littermates, with their mother (Caro, 1981a; Mendoza and Ramirez, 1987; Villablanca and Olmstead, 1979). By four weeks, interest in littermate movements is high (Baerends-van Roon and Baerends, 1979) and social play peaks between nine and fourteen weeks (Mendoza and Ramirez, 1987). At this age, social play has several stereotyped sequences, including motor activities like leaping, pouncing, side stepping, and chasing, as well as postures such as presenting the belly and facing off with the littermate (West, 1974; Table 1). As kittens age and their motor skills improve, these play behaviors also include wrestling, holding the other cat with the forelimbs, rolling, stalking, and raking the playmate with the back legs (Barrett and Bateson, 1978; West, 1974). A half-opened mouth display, "play-face," has been described in social play which may further distinguish the encounter from agonism (Bradshaw et al., 2012; West, 1974). These displays are likely in part affected by learning, as separation from littermates renders kittens less responsive to the play signals of other unrelated kittens (Guyot et al., 1980). Attention shifts from playmates to prey at around six weeks of age when predatory behaviors increase rapidly, while social play decreases significantly between 12 and 16 weeks of age (Caro, 1981a, b).

Play-related motor patterns that emerge early in life can be directed toward conspecifics, prey, or objects, or can lack a specific target. Locomotor play is an example of the latter. It begins earlier than or in conjunction with social play, and it describes general activities not directed at other individuals or inanimate objects (Martin and Bateson, 1985b). Kittens engage in locomotor play, such as climbing a multi-level frame without any additional reward by five weeks of age, and they climbed higher and spent more time climbing as they aged (Martin and Bateson, 1985b). This is similar to the locomotor play observed in young lions when they begin climbing trees (Schaller, 2009). Locomotor activities like "bounding gait" and "rushing around" have been observed in other young carnivores, like cheetah cubs (Caro, 1995); similar behavior patterns are also observed in kittens. While the mechanisms of locomotor play focus on motor patterns, its function is likely that it encourages exploration of the environment and contributes to information gathering, which could affect other play and predatory behaviors.

Although kittens become highly interested in moving objects by four weeks of age (Baerends-van Roon and Baerends, 1979), object play emerges and peaks later than social play, when kittens are between 18 and 21 weeks. Kittens gradually switch interest from siblings to object and predatory play (Mendoza and Ramirez, 1987), and kittens who are raised without littermates show higher levels of object play (Guyot et al., 1980). Social behaviors also become less cohesive (less approaching, nose touching, and other physical contact) and more aggressive (more biting and back arching) around this time (Mendoza and Ramirez, 1987). Object-focused play incorporates behavioral sequences like those observed in prey handling, prey capture, and post-hunting prey manipulation such as poke/bat, scoop, leap, pounce, grasp, and bite or mouth (Barrett and Bateson, 1978; Egan, 1976; West, 1977; see Table 1).

3.2. Relationship factors and play development

Relationships with the mother and littermates affect the development of play in cats. The absence of the mother increases social play with littermates (Bateson and Young, 1981), and kittens separated from littermates direct more interactions toward their mother, such as approaching and attempting to wrestle (Mendl, 1988). Increased attempts to interact with available conspecifics in the absence of the mother or littermates highlights the potential importance of social interactions for kitten behavioral development (Crowell-Davis et al., 2004). Similarly, several studies of kittens have demonstrated the impact of social interactions on learning (Chesler, 1969; Herbert and Harsh, 1944; John et al., 1968). Mothers of singleton kittens, however, tend to avoid their offspring, perhaps because they are disturbed by the play behavior directed toward them (Mendl, 1988), so mothers are clearly not always a substitute for play with littermates.

Mothers make prey available and accessible to kittens around 4 weeks of age, which is also the same time that weaning begins and object play appears (Bateson, 1981; Caro, 1980b; Martin, 1986). The mother's behavior around prey in the presence of kittens influences

their predatory behavior; kittens with mothers have a shorter latency to bite and carry their prey and kill more mice compared to kittens without mothers (Caro, 1980b, c). Object play also increases, with the reorganization of play behavior potentially aiding the future handling of prey (Bateson, 1981). Play behaviors that are frequently displayed at 4–7 weeks of age are not highly correlated with play behaviors occurring at 7–8 weeks of age. The play sequence may start to become more refined and predictable, and more like predatory behaviors (Bateson, 1981; Burghardt, 2005). Accordingly, early weaning or food rationing was found to be associated with increased object play in kittens (Bateson et al., 1981, 1990; Bateson and Young, 1981). Weaning of kittens may initiate developmental changes that enhance predation as kittens must become self-sufficient if the normal weaning process is interrupted (Martin, 1986).

Although play with objects is often performed in solitude, social factors, such as litter size, could also affect object play. Notably, members of the *Felis* lineage, as well as lions and cheetahs, tend to have larger litter sizes compared to other, less social cat species (Packer and Pusey, 1995; Sunquist and Sunquist, 2017). Although in experimentally controlled litters of either one or two kittens, there were no differences in object play (Mendl, 1988), the presence of siblings may prompt object-directed play, particularly the quick seizing of an object for solitary play. Such behaviors could be useful when directed toward live prey who otherwise could flee, turn aggressive, or be taken by a competitor if not seized quickly. Cats' tendency to vocalize and draw attention to themselves when in possession of prey with which they are playing, and their tendency to play and predate in the presence of other kittens, suggests a social element to play, either drawing intra- or interspecific attention to the prey item (Egan, 1976). Stimulus enhancement has also been observed in lion cubs, who draw other cubs' attention to an object or to themselves, via chasing, when playing (Schaller, 2009). Comparative data on the playfulness of other felid species is lacking, and data has not yet accounted for possible effects of larger litter sizes on the play behavior of domestic cats. Thus, the relationship between litter size, sociality, and the development of play across felid species is, to date, underexplored and speculative.

Play-related sex differences and sex-based litter effects are observed in kittens, with "developing behaviour affected by an individual's own sex as well as by the litter sex ratio" (Albonetti, 1988, p. 60). For male kittens, interaction with objects appears to be more a function of sex than litter effects, whereas early female object play can be influenced by male presence in the litter (Barrett and Bateson, 1978; Bateson and Young, 1979). Kittens from all-male groups played at higher rates than kittens from all-female groups, and female kittens with male littermates behaved more like males in regard to play than did females with no male companions (Caro, 1981b). Very early in life, males engage in more object play than females (Barrett and Bateson, 1978; Bateson and Young, 1979), but object play increases in both sexes simply as an effect of aging (Bateson and Young, 1979).

3.3. Effects of aging

At 21 weeks of age, activity directed toward small, inanimate objects (or "toys") plateaus and then gradually decreases (Mendoza and Ramirez, 1987). This effect may continue during adulthood. According to a survey of pet owners, there was an effect of age on predation, such that older domestic cats were less likely to bring home prey than younger cats (Churcher and Lawton, 1987). A survey assessing owner-report of cat behavior (Fe-BARQ) identified age-related declines in activity and playfulness as well as predatory behavior (Duffy et al., 2017), which complements developmental observations by veterinary professionals that the nature and amount of activity, including play behavior, can change as cats age (Overall et al., 2005; Overall, 2013). There are no known behavioral or developmental studies of the effects of aging or senescence on the play behavior of cats past the age of six months, which makes it difficult to assess changes in activity throughout the lifespan.

3.4. Adult cat play

Like other members of Carnivora, cats play into adulthood (Fagen, 1981), although it is often characterized as an immature activity of young animals (Martin and Caro, 1985; Smith, 1982). Accordingly, adult cat play has received considerably less attention than that of kittens, but a few behavioral studies have directly explored object play in adult cats, such as those focusing on pet cats between five and eight years (Hall, 1998; Hall and Bradshaw, 1998; Hall et al., 2002) and one and sixteen years (Vitale Shreve et al., 2017). Another study measured play in caged laboratory adult cats (De Monte and Le Pape, 1997). While adult cats do play, we have little understanding of how this play is organized, aside from observational and anecdotal evidence, and whether an ethogram of adult play—object or other—would vary substantially from the play of kittens and juvenile cats. We also have little sense of how often and how exuberantly older adult cats play, and how development and aging influence the form of play. Furthermore, no behavioral analyses exist that explore social play in adult cats living together. Play has been described as part of the relationship between cats who share a colony, but the form of this play has not been detailed (Crowell-Davis et al., 2004).

3.5. Genetic effects

Although most cats are not selectively bred (Driscoll et al., 2009a; Lipinski et al., 2008), breed may have an impact on cats' predatory behavior and tendencies toward playfulness (Duffy et al., 2017; Hart and Hart, 2013). Owners and veterinarians report that some breeds (e.g., Abyssinians, Siamese, and domestic shorthairs) and hybrid cats (Bengals) have higher levels of playfulness and activity when compared to other breeds, such as Persians (Duffy et al., 2017; Hart and Hart, 2013; Mendl and Harcourt, 1988). Although Marchei et al. (2009) did not explicitly measure play behaviors, an open field test of kittens found that Siamese, Abyssinian, and oriental breeds were initially more active than Norwegian Forest cats—exploring more and spending more time walking—but all breeds had similar levels of activity by seven weeks of age. A more recent owner report identified Birmans and Persians as low on playfulness, and Tonkinese and Devon Rexes as playful (Wilhelmy et al., 2016). A relationship between phenotypic coat color and behavior has been suggested in other animals exposed to artificial selection, like dogs (Kim et al., 2010), horses (Brunberg et al., 2013), and foxes (Trut et al., 2004). Although suggested in cats (Delgado et al., 2012; Mendl and Harcourt, 1988; Stelow et al., 2016), appearance-behavior associations may sometimes be explained by breed or, in a few instances, by other aspects of physical appearance (Wilhelmy et al., 2016).

4. Factors and stimuli affecting cat play

4.1. Toy features

Toy size, similarity to prey, and novelty are all predictors of a cat's play response to toys. When cats were presented with toys (both small and large) covered in fake fur (of differing colors) that were moved back and forth in a 45-degree vertical arc for two minutes, cats tended to prefer smaller toys similar in size to a mouse (Hall and Bradshaw, 1998; Hall et al., 2002). Although not explicitly tested, objects moved like prey (whether ground or aerial) could also elicit play (Bradshaw and Ellis, 2016; Egan, 1976; Hall, 1998; Hall and Bradshaw, 1998; Hall et al., 2002; Leyhausen, 1979). In one study, cats preferred toys that moved (feathers attached to a rod or wire) over inanimate toys (a mouse and a stationary feather toy; Vitale Shreve et al., 2017). Movement away from the cat appears to be a particularly strong elicitor of chasing behavior, as observed in domestic cats and European wildcats with prey items, and domestic cats and ocelots with objects (Leyhausen, 1979).

Another important characteristic of the similarity between toys and prey may be how the toy changes while a cat interacts with it. Toys that disintegrate or otherwise change during play should be more engaging because physical damage to the toy (or prey) is a likely eliciting stimulus of pseudo-predatory behavior for cats (Bradshaw et al., 2012; Bradshaw, 2013; Hall et al., 2002).

4.2. Hunger

Hungry cats are generally less inhibited when hunting, showing greater willingness to attack larger prey when food deprived (Adamec et al., 1980a,b,c; Biben, 1979), although one study found no effect of hunger on kittens' tendencies to kill rats (Kuo, 1930). Hunger has a similar effect on play behavior; in general, cats are quicker to interact with a small, mouse-like toy, but when hungry, are more willing to interact with a larger, rat-like toy (Hall, 1998; Hall and Bradshaw, 1998). Cats differ from numerous other species where hunger, malnutrition, and food deprivation can depress play (e.g., in rats, Almeida and De Araújo, 2001; in lions, Schaller, 2009; but see Kuba et al., 2006), whereas for cats, hunger increases hunting behavior as observed in several other predatory species (e.g., Mueller, 1973). This lends further support for a shared function between predation and play in domestic cats (Bradshaw et al., 2012; Hall and Bradshaw, 1998).

4.3. The effect of habituation

Habituation appears to be a large factor in a cat's lack of engagement with toys. When cats were exposed to the same toy—a small fake-fur object attached to a 1-m string, three times in succession—they began to show decreased play intensity. When a toy that was novel in color and odor was presented, the intensity of the play increased, and in some cases, even increased beyond the initial play response (Hall et al., 2002).

Cats will display habituation toward inanimate objects intended as toys (Hall et al., 2002), although not much is known about cats' responses over time to "interactive" fishing pole toys. The latter theoretically should serve as stronger eliciting stimuli for a predator because the toys are mobilized by a human who can move them to mimic prey. We have personally observed that many cats show initial enthusiasm for these toys, but as expected based on Hall et al.'s study (2002), cats appear to habituate over time. Many sources of advice on how to play with cats recommend the rotation and replacement of toys to reduce the possibility of habituation (Alho et al., 2016; Ellis, 2009; Hetts, 1999).

5. Defining play behavior

The exploration of play benefits from operationalization. Most categories of animal behavior, such as foraging and mating, are marked by distinct behavioral features and clear outcomes. Play, too, can be defined by accounting for its structure, functions, and consequences—namely its variable and diverse motor patterns (structure), the potential for motor, social, or cognitive benefits (functions), and its incomplete or unclear outcomes (consequences; Bekoff and Byers, 1981; Fagen, 1981; Martin and Caro, 1985).

Behaviors and interactions occurring outside the typical species-specific contexts, performed in a modified manner, and not producing typical consequences can fall in the category of play (Fagen, 1981; Martin and Caro, 1985). Structural differences in form or timing, such as exaggeration and repetition of movements, and incomplete or non-sequential motor patterns, help to identify play (Burghardt, 2005; Fagen, 1974; Loizos, 1967). Play signals—discrete actions that may indicate its start, continuation, or non-serious nature—could appear in play, e.g., play bows in dogs and the kitten "play face" during social play (Bekoff, 1995; Byosiere et al., 2016; West, 1974). Play is also apparent by its consequences, such as prey approach or manipulation without injury (Biben, 1979). To aid in its identification, Burghardt (2005) proposed five criteria necessary for and indicative of the occurrence of play, including that the behaviors (1) lack complete function; (2) be spontaneous with indications of pleasure or self-reward; (3) differ in form or timing from the more serious—or adaptive—version; (4) contain repetitions without indicating stereotypy; and (5) present outside conditions of acute or chronic stress.

5.1. Functions of play

While numerous biological functions of play have been proposed (Fagen, 1981; Martin and Caro, 1985; Smith, 1982), they can broadly be stated as providing motor training, socialization, and cognitive training (Bekoff, 1995). Functional hypotheses often discuss the adaptive significance of play, whether it be immediate or short-term, or accrued in adulthood to affect outcomes such as reproduction, survival, or social competency (Martin and Caro, 1985; Smith, 1982). Play has also been suggested as a potential indicator of positive emotions and good welfare (Boissy et al., 2007; Held and Špinka, 2011), although given its diverse behavioral composition, it is unknown whether play indicates absolute positive affect or rather a reduction in negative affect (Ahloy-Dallaire et al., 2017). With its heterogenous form and maintenance across developmental periods, play is not assumed to have one underlying function, and this idea has been supported by both experimental and correlational studies (Caro, 1988; Martin and Caro, 1985).

5.2. Testing the functions of play

Although it has been suggested that both social play and object play could affect later predation, experimental studies do not find play necessary or sufficient for future predation (Caro, 1979, 1980a, 1981a). Assessing the functions of play in cats is complicated by the fact that critical adult behaviors—like predation—likely develop via multiple experiential routes, not only through play (Bateson, 2014a; Martin and Caro, 1985). For example, object play was not found to quantifiably affect future predatory behavior (Caro, 1980a). However, the study may have been challenged by a few factors such as: (1) potentially insensitive variables (prey-catching): during test trials few prey animals were killed by either the control group or the experimental group, (2) unaccounted for life experiences: social, locomotor, and opportunistic play (such as playing with litter pellets available in the cage) were not controlled, and (3) insufficient measures of future impact: the repeated observations occurred while cats were still in the juvenile period (at 6 months of age; Caro, 1980a; Martin and Caro, 1985). Additionally, "Kaspar-Hauser" kittens living in a barren environment without visual stimulation or opportunities to play showed similar prey-catching behaviors to kittens reared normally, suggesting play experience is not necessary for the development of predation (Thomas and Schaller, 1954). Bateson (2014b, p. 20)Bateson, 2014bBateson (2014b, p. 20) points to "equifinality"—that the value of developing predatory-type behaviors is of such import to cats that, "the same skill might be achieved because of quite different developmental histories." Thus, it appears a foregone conclusion that most cats will develop into competent hunters. Although play clearly has a role in the development of predation, the function of play for cats is likely multifarious. An expansion on the aforementioned studies would help reveal relationships between different forms of cat play (e.g., social) and their possible functions.

6. Review and analysis of play behavior in the literature

6.1. Methods

To determine how cat play and play behaviors have been defined to date, we surveyed peer-reviewed behavioral studies where some aspect of play in cats was defined, measured, or assessed. We searched Google Scholar and Web of Science using search terms including "domestic

cat," "cat," "*Felis silvestris catus*," "*F. catus*," "play behavior," "play," and "predation." We excluded all publications that were book chapters, conference proceedings or abstracts, survey-based studies, publications that did not include a measure of play as an outcome variable, and that were not about domestic cats. Both authors reached consensus on all included publications, and our search resulted in 46 publications between 1973 and 2018 that met the following inclusion criteria: in English, in a peer-reviewed publication, where cat play or cat play behaviors were measured or defined. We included two publications that were extensive ethograms of feline behavior, including play (Stanton et al., 2015; UK Cat Behaviour Working Group, 1995).

6.2. Results and discussion

Table 1 contains all behaviors from publications in which some aspect of play was measured as a variable, as well as how play was defined (if at all). We included how play was measured, as well as the categorization of play behavior (such as social, object, or other). A total of 138 behaviors were measured, with 84 unique behavioral identifiers used to measure play, although some of the terms were very similar either in label or definition (e.g., "hold object" and "hold/bite object" or "play," "playing," and "playfulness"). The most commonly used term was "play" or some derivation thereof (23 manuscripts); chase, object contact, rear, and social play were each referenced in seven manuscripts; arch, bite, cat contact, object play, playing, self-play, and wrestle were each referenced in five manuscripts; and bat, clutch, face off, killbite, play roll on back, and stalk were referenced in two manuscripts each.

Ninety-three behaviors were measured by frequency, 17 by duration, and 10 by both duration and frequency. Three behaviors were assessed by occurrence or non-occurrence, and two by observed intensity. Social play (41 behaviors) and object play (28) were the most frequently used categories. Play (without further categorization; 16 behaviors), playful activities (11), predatory behavior (10), play behavior patterns toward dogs (6), and social or object play (4 behaviors) were other commonly used categorizations. Some manuscripts included several behaviors in their measures of play (e.g., Caro, 1981b with 18 unique behaviors, Hall and Bradshaw, 1998 with 12), while the majority, 24 manuscripts, defined play using a single variable.

The table is the only exhaustive review to date of how play has been operationalized in empirical studies and peer-reviewed publications of cat behavior. The table demonstrates the diversity of descriptions of play and play behavior, as well as some commonalities across studies. For example, the cat play research in the late 1970s and early 1980s frequently referenced behaviors across studies, for example the shared definition "Arch" that was used by West (1977), Barrett and Bateson (1978), and Bateson and Young (1981). By contrast, the definition of "Social Play" differs greatly between publications, with some referring to interactions with toys, a small minority (two) referring to interactions with people, and some to behavior directed toward conspecifics (e.g., Loberg and Lundmark, 2016; Mendoza and Ramirez, 1987; Potter and Mills, 2015; Stella et al., 2014; van den Bos and de Vries, 1996).

The table also suggests the need for more consistent and comprehensive definitions of play to allow for better understanding of play behavior. In some cases, the definition of play is circular, where play is defined by terms such as "engages in play" or "cat shows self-play, object play, or social play." In this vein, some publications did not operationalize play (as discussed in Martin, 1984b) and instead defined play as "play." Loberg and Lundmark (2016) describe "Solitary Play" as a positive activity defined by, "One cat plays with a toy, without any other cat playing with the same toy within 3 s(econds)." It is not clear if any contact with the toy was considered play or if particular behaviors signaled play, and no inter-rater reliability for what constituted play was reported.

Where detailed descriptions of play behaviors are provided, some are based on a highly detailed ethogram (e.g., Barrett and Bateson, 1978) while others focus on a limited subset of behaviors. In some instances, there was a rationale for restricting the behaviors measured. For example, Hall et al. (2002) only measured the frequencies of two specific behaviors, clutch and killbite. This followed Hall and Bradshaw's 1998 paper which measured the duration of several behaviors during object play, including sniffing and touching the toy, grasping and kicking the toy, as well as frequencies of the killbite and sniffing the toy. Clutch and killbite were most influenced by the cats' hunger levels and were taken as indicative of intermediate and high play motivation (Hall et al., 2002), thus the rationale for extending the subset of behaviors to the subsequent study.

Current definitions of play may omit important behavioral elements. Most studies define object play by direct contact with a toy. Because cats are stalk-and-rush hunters, a large proportion of the hunting process is spent watching the prey from a distance, often for "minutes on end" (Leyhausen, 1979). Prey watching incorporates several behaviors, including creeping, crouching, lying in wait, and rapid alternation or treading the back feet until final preparation for springing. The high average play bout time (22 min) recorded for lions (Schaller, 2009) may be due to the inclusion of stalking and rushing in the measure of play. Only measuring time in direct contact with a toy may offer a misleading underrepresentation of play which should be rectified in future studies and play ethograms. An updated, more thorough and standardized ethogram of cat play behavior should incorporate previous descriptors, as well as all aspects of stalk-and-rush hunting including distal behaviors like staring or watching a toy and pre-ambush behaviors. Given that stalking is a significant part of the hunting process, other similar forms of engagement with prey, objects, or conspecifics should be included as potential descriptors of play.

Play's heterogenous nature indicates it may not have a singular underlying motivation, yet studies differ in how they catalogue play, for example as social, object, predatory, or nonsocial play (Mendoza and Ramirez, 1987), with others adding locomotor play as a separate subcategory (Martin and Bateson, 1985b). To this point, while object play is typically clearly delineated, play that does not target an object often lacks categorical consistency. The term "self-play" has been used to describe behaviors directed towards the self (Table 1), but it is also found as a catch-all label incorporating what could be categorized separately as locomotor or solitary play (e.g., International Cat Care, 2019a). Categorization and sub-categorization of play would benefit from additional delineation and clarification, as well as consideration of how these subcategories may relate to underlying motivations.

7. General discussion and future areas of research

Cat play behavior was the subject of numerous studies in the 1970s and 1980s, but several aspects, including some that may be crucial for cats' welfare as pets, such as how much and what type of play they need, remain poorly understood. Notably, cats' popularity as a pet continues to grow (American Pet Products Association, 2018; GfK, 2016; Murray et al., 2010), and pet cats—particularly in the United States—are increasingly kept predominantly or exclusively indoors (American Veterinary Medical Association, 2011; Humane Society of the United States, 2016), which may reduce their activity if opportunities to hunt and play are limited. The current understanding of cat play contains numerous unaddressed gaps.

7.1. How to define and measure play in cats?

Studies of play rely on either direct observation of cat behavior, or on owner report of "playful" behavior (e.g., Duffy et al., 2017; Mendoza and Ramirez, 1987). Play is usually measured by recording frequencies or durations of specific motor patterns, and may be delineated by function (such as similarity to predatory behavioral sequences; Caro, 1981a), or by consequences (whether a prey animal was killed; Martin, 1984a). Sequences of behavior have also been documented and

analyzed (West, 1974), and play behaviors may also be catalogued based on where the behaviors are directed, such as social play (conspecific), nonsocial play (inanimate object), or predatory play (living or dead prey; Mendoza and Ramirez, 1987). Other studies may categorize play as locomotor (not directed at individuals or inanimate objects) or object (inanimate focused; Martin and Bateson, 1985b).

The operationalized variable "play"—and behaviors falling within—may differ substantially between studies that all purport to measure aspects of cat play behavior. Barrett and Bateson (1978) identified play using a strong reliance on contextual cues and "a subjective sense of certainty." Rather than relying on inference and subjectivity, more explicit descriptions of behavioral measures could improve reliability across studies.

There are several ways researchers could work to improve how cat play is defined across studies; for example, the second author of this manuscript is currently using the Delphi method to identify where cat behavior experts agree on recommendations regarding cat-human play, similar to what has been done to identify behavioral signs of pain in cats (Merola and Mills, 2016). Conference symposia and workshops could further allow for the development of agreement among researchers as to how play should be measured, as well as identify and prioritize areas which could affect cat welfare, as has been done for dog welfare issues (Buckland et al., 2014).

Furthermore, individual studies could work to improve the detail and precision of measures of cat play, at least until it is determined that such detailed measures are not necessary. The overwhelming majority of studies of cat play rely on measuring frequency of behaviors via scan sampling, but we have little understanding of what information is lost by using this method. Remote measurements, such as motion-activated cameras and accelerometers could advance our understanding of play behavior. Readily available video coding programs allow for more reliable, detailed, and precise measures of play behavioral sequences, including frequency and duration, that might be difficult to capture during live observations (Ongena and Dijkstra, 2006).

7.2. Understanding play patterns

Play and predation both involve several behaviors, including seeking or solicitation behaviors, engagement and stalking of the prey or toy, direct contact with the prey or toy, and ultimately consumption, satiation, or a cessation of engagement. While both play and predation have similar behavioral components, according to common definitions of play, the sequences of behavior may differ as the motor patterns of play tend to be less structured (e.g., Fagen, 1974). Quantifying patterns during play is of value in and of itself, but it is equally important to compare patterns of behavior during play to those that occur during predation to better understand behavioral similarities or differences.

Markov models measure sequences of events by assessing the dependence of current behaviors in a sequence on previous behaviors. Such models have previously been applied to such varied behaviors as cat feeding patterns (Bradshaw and Cook, 1996), birdsong (Alger et al., 2016), and social interactions between lemon sharks (Wilson et al., 2015). T-pattern analysis is another method that explores the underlying structures and temporal themes of behavioral sequences (Casarrubea et al., 2015), and has been applied to foraging behavior (Hemerik et al., 2006), courtship (Arthur and Magnusson, 2005), and anxiety-related behaviors (Casarrubea et al., 2010). Wedl et al. (2011) used T-pattern analysis to assess the complexity and frequency of interactions between cats and their owners.

These methods are computationally intensive, but free tools (e.g., Theme, R, Winbugs) exist for conducting such analyses. These models also allow for exploration of the influence of various factors—such as age, sex, and breed—on cat play patterns. To date these statistical methods have been underutilized in studying the patterns of play behavior.

7.3. Sensitivity, thresholds, learning, and experience

Cats likely differ in their sensitivity to prey-like eliciting stimuli present in toys. Some cats will readily respond to minimal signals because over the course of evolution, if it moved like prey, and it looked like prey, it was likely beneficial for cats to presume it was prey and respond accordingly. Toys may even become supernormal stimuli, eliciting a greater response than actual prey items (Leyhausen, 1979). This sensitivity may be further enhanced—or directed—by an individual cat's predatory preferences and specialization (Dickman and Newsome, 2015).

Cats with lower thresholds could receive enough positive feedback from the toy to maintain their interest and reduce habituation. This threshold could also be influenced by previous experience with predation. A cat without experience with live prey, or with less successful experience with prey, should be less dissatisfied with toys. This could be akin to Bayesian learning where cats start with a probability distribution about the likelihood of an object being prey, which is updated as the environment (object) is sampled (Valone, 2006). Cats who received several positive experiences during and following play, such as the release of dopamine, norepinephrine, and serotonin (Siviy, 2008) and anxiolytic responses resulting from exercise (Guszkowska, 2004; Haug, 2008), would find those interactions reinforcing and maintain a greater level of interest in play in the future.

Other individuals may have a higher threshold for eliciting signals and only continue to play with toys if their features have multiple similarities to prey. Cats could learn through repeated presentations or interactions that certain toys are not prey and lose interest, associate them with an incomplete hunting sequence, and possibly experience frustration or boredom (Burn, 2017). If a toy does not give signals that would be part of the normal predation sequence—such as struggle or the physical breaking down of the prey's body like blood or changes in body warmth—these cats could stop engaging with the toy. The lack of effective or prey-like feedback from a toy could explain the "as if" qualities that many owners report they observe in their cats' play behavior, as well as the declining interest in particular toys over time. Regardless of threshold, differences within, not only between, cats would also be expected when factors such as hunger, toy feature, and interaction time are considered.

7.4. Is play displaced predation?

Most theories about the function of play focus on its similarity to predation. Because of the considerable overlap between motor patterns and eliciting stimuli, it is easy to see why. At the same time, predatory-based behaviors performed in play can maintain an "as if" quality, while at other times, a cat in play can perform each component of the predatory sequence—stalk to the bite—in a manner indistinguishable from the "real" version.

What, then, distinguishes play from predation? For example, playful appearing behaviors are commonly observed during hunting, and several felid species—including European wildcats—have been observed playing with dead prey, or catching, tossing, and throwing live prey animals (Leyhausen, 1979; Lindemann, 1955). Whether these behaviors are strictly predatory, practice for predatory behaviors, or whether these behaviors are just a part of the predatory sequence is unknown.

Do domestic cats "know" they are playing? Although IACUC and animal welfare ethics would rightly impede empirical comparison between interactive play and real predation, exploration of the similarity between toy and natural prey movements and their respective ability to stimulate predatory behaviors may provide some answers. Naturalistic observations of free-ranging or feral cats whose predatory behaviors have been well-studied (Loyd et al., 2013; McGregor et al., 2015) could provide a basis for these comparisons.

Although cats will become satiated and tire of hunting within a session (Beaver, 2003; Leyhausen, 1979), it can be assumed that

subsequent exposure to prey animals does not have the same effect, and instead will instigate predatory behavior repeatedly throughout a cat's lifespan (otherwise, said predator would risk starvation). Differences in habituation patterns under these two different conditions could help distinguish play from predation in future studies.

Cats also display defensive behaviors during hunting and will avoid face-to-face interactions with some prey animals, such as rats (Pellis et al., 1988). Anxiolytic medications reduce latency to approach and kill prey, and their effect on cat behavior suggests that fear of prey may increase defensiveness in predatory carnivores (Pellis et al., 1988). Future studies could compare a cat's defensive responses when interacting with toys with what is known about their responses when hunting or with dead prey (Biben, 1979; Leyhausen, 1979; Pellis et al., 1988). Detailed behavioral analyses could determine if interactive toys (approximating prey) elicit behavior more akin to the predatory behavioral sequence than inanimate objects that also resemble prey.

Social referencing toward humans would be another possible test of whether cats' responses to toys differ from responses to prey items. Social referencing occurs when one individual looks to another for information about the safety of or appropriate response to a situation, often when the situation is novel or ambiguous (Feinman et al., 1992; Merola et al., 2015). Previous research found that when attempting to access inaccessible food, cats rarely looked to humans compared to dogs, who looked to humans faster and more frequently (Miklósi et al., 2005). We hypothesize that cats would interact more frequently with humans when interacting with prey-like toys in comparison to what is observed when cats come across prey items in their daily lives, such as a bug in the home or a bird in the backyard. Owners anecdotally report that their pet cats appear to understand a causal relationship between their presence and the movement of a toy, by behaving as if they understand the human is moving the toy or by soliciting play from the human via vocal or visual cues. This does not prove that the motivation for certain types of play is different from predation, but suggests the possibility.

7.5. Intraspecific adult play

Owners report that their adult cats play together (Duffy et al., 2017), but cat owners may have difficulty discerning play from fighting between adult cats living together (e.g., International Cat Care, 2019b). As play may incorporate features of both affiliative and agonistic behaviors (Bateson and Turner, 2000), how do the two cats "know" they are playing?

Adult felids play together in social contexts. In lions and pumas, social play between (captive) adults appears to be a redirection of behavior that would be aimed at prey (Leyhausen, 1979). In this case, play shares the forms of predatory behavior, such as pouncing on the other individual and biting the nape of their neck. A study of 20 species of small captive felids found that interactions between individuals were infrequent, but several individuals showed some behaviors that were potentially playful, such as chasing and "face off" (Mellen, 1993). The exceptions were jungle cats, caracals, African golden cats, and Pampas cats. In sand cats, social interactions were overall infrequent, but play was the most common form (Bennett and Mellen, 1983).

More questions than answers remain in this domain: do adult cats present play signals to one another, and if so, what form do these signals take? Is there a relationship between early conspecific play and later conspecific play, either between different members of the species or early playmates? The effect of cat-cat social play on later intraspecific interactions, whether affiliative or agonistic—is unclear, although a relationship between intraspecific play and affiliative interactions could form the basis of several hypotheses. Do individuals who engage in more solitary types of play—locomotor or object—also engage in more intraspecific play? In other words, is there overlap between the different play systems (as suggested by their morphology) or do they act independently?

7.6. Interspecific play

7.6.1. With humans

Cats and humans play together, but we are still uncovering the composition and effects of these dyadic exchanges. When 295 cat owners who contacted the Iams Consumer Care Center were surveyed about what they thought their cats did for "fun," over 83% of owners reported that their cats played with toys, and respondents also highlighted that cats played with humans (approximately 43%), other cats (approximately 15%), and dogs (approximately 4%; Shyan-Norwalt, 2005). A separate survey of 277 cat owners who were clients at a veterinary clinic revealed that 90% of respondents reported playing with their cat at least once per day (Strickler and Shull, 2014). This high percentage of owners claiming daily play is somewhat surprising given that owners also reported aggressive behaviors in their cats, and a relationship between increased play opportunities and decreased aggression is often implied (Ellis et al., 2013). Exercise decreases aggression in rats, increases endorphin release, and may have anxiety-reducing effects (Guszkowska, 2004; Hebb et al., 2005; Hoffmann et al., 1987), and inadequate play and an under-stimulating environment could be a factor in some forms of reported aggression in cats as in dogs (Haug, 2008; Overall et al., 2005). Unfortunately, in many survey-based studies, play is poorly defined for the participants answering the questions. For example, one survey asked participants, "Does anyone play, groom, or pet the cat daily?" (Alho et al., 2016), suggesting that reports of play may be inflated since they are combined with other types of interactions or are not explicitly defined.

Recommendations for how to play with cats tend to emphasize the use of interactive toys for preventing aggression toward humans (Beaver, 2003; Overall, 2013; Overall et al., 2005), rather than highlighting the benefits that exercise or outlets for normal predatory behavior may provide for all cats (Ellis et al., 2013; Stella et al., 2013). Interactive toys are described as "fishing pole" or wand toys, typically designed to mimic prey (Ellis et al., 2013). Although some of these toys have been automated, they typically require a human to manipulate the toy in a prey-like manner to elicit pseudo-predatory behavior in a cat. Interactive play with humans may represent a separate category of play that incorporates aspects of other currently recognized forms of play (e.g., object, social, locomotor, and predatory play; Bradshaw, 2018). It remains to be seen how and whether human-cat play is unique, and what aspects may overlap with other forms of play. For example, Vitale Shreve et al. (2017) identified that cats preferred interacting with a feather on a wand moved by a human whom they could see compared to other forms of human social interactions like being petted or talked to, and similarly cats preferred a feather moved by a person—who in this case was not visible—over immobile toys. Taken together, it is possible that human-facilitated object play is less about the interspecific social nature of the interaction—like petting—and more about the cat's focus on the toy stimulus, driving the interaction more toward human facilitation of object play or inanimate enrichment (International Cat Care, 2017). Toys have been described as 'inanimate' enrichment strategies and cat-human interspecific interactions as 'animate' enrichment strategy (Ellis, 2009), but human-facilitated object play muddles this divide.

Human-cat interactive play must be initiated by either the human or the cat: do cats learn cues from humans that indicate a human is interested in interactive play? Do cats give play solicitation signals to humans as they do with other cats, such as "play face," and if so, how are these signals similar and different? A recent survey of cat owners (Pongrácz and Szapu, 2018) introduced the question of whether there is a relationship between the initiator of play and other signals, either performed within or outside of play. How does the behavior and movements of the human during play influence the cat's response to an interactive toy? An important addition to our understanding of interspecific play would be the creation of an ethogram of human behaviors that occur during play such as movements of the toy, behaviors of the

cat like eye contact and vocal responses, as well as unique play routines, with or without objects.

7.6.2. With other animals

On a similar note, interspecific play between cats and other non-human animals has received almost no attention. At least 17% of all United States households, and 32% of pet-owning households include both cats and dogs (American Pet Products Association, 2018; Gallup, 2006), yet we have little understanding of how these two species interact or play together. A recent survey of mixed-species homes suggests that owners perceive that their cats and dogs live together amicably, with the possibility that cat factors, such as their comfort with the dog, are predictors of the nature of the interspecific relationship (Thomson et al., 2018). Only one behavioral study has explored whether dogs and cats living together will engage in play (Feuerstein and Terkel, 2008), finding that approximately 65% of dyads experienced amicable relationships. To measure play between cats and dogs, owners instigated two types of interactions: one in which they rolled a tennis ball between the two animals, and another where the owner "attempted to stimulate interaction between the dog and the cat." During 20-minute observations in 25 households, cats and dogs spent a large proportion of time playing (40 and 33%, respectively), although the definitions of play in cats did not resemble social or object play as measured in other studies (see Table 1). Cats may also engage in social forms of play with other common pets (e.g., rabbits, ferrets) or even wildlife (ravens, squirrels; Heinrich and Smolker, 1998).

7.7. Effects of technology

Advances in technology have also changed the types of toys available for cats, with a variety of digital, remote, and automated toys currently available. Digital toys typically take the form of moving imagery (animation or video) depicted on a computer, tablet, or phone screen. The imagery is designed to stimulate a cat's attention, and prey-like movements may be presented. Remote toys may be animated by the owner via smartphone or remote control. Automated toys are objects—typically battery-operated—that move, either via predetermined patterns or in response to a cat's activity or contact with the toy. Some remote and automated toys display a laser light for a cat to chase.

Although some of these toys are exclusively visual and provide no tactile feedback (e.g., laser pointers, video games for cats), they may elicit some aspects of play behavior, such as staring and batting, even though the virtual object cannot be physically touched. A previous study of shelter cats suggested that they responded positively to such types of 2-D enrichment (Ellis and Wells, 2008). However, some have suggested that virtual toys may frustrate cats, as they do not allow completion of the sequence of events involved in predation, i.e. capture and consumption (Ellis, 2009). In general, inaccessibility of reinforcement is associated with frustration, which could be a negatively-valenced state (Delgado and Jacobs, 2016; Finch, 1942). Light-chasing is considered a compulsive disorder in dogs, one that often requires treatment with anti-epileptics or selective serotonin reuptake inhibitors (Luescher, 2004), and there could be concerns about whether there are similar effects in cats. It is unclear if the light-chasing tendencies in dogs are caused by or rather precede any interaction with a laser pointer toy. Since only approximately half of cats' hunting attempts are successful (Rochlitz, 2005), it is not clear that these toys would be intrinsically frustrating to cats. Owner perceptions of cat response to animal-computer interactions, particularly interspecies gaming, has been positive (Noz and An, 2011), yet empirical study of cats' responses to the wide range of virtual toys available is in its infancy (Westerlaken and Stefano, 2014).

Because virtual and other tech toys vary in their sensory modalities, it is now possible to tease apart which toy elements are important for stimulating playful behavior in cats. For example, by comparing digital/2-D toys, stationary object toys, human-controlled interactive toys, and robotic/battery-powered toys, the influence of strictly visual movement or auditory stimuli could be compared to that of multi-sensory objects.

7.8. Play and the catnip response

Cats, both domestic and large, display a suite of behaviors in response to catnip (*Nepeta cataria*)—specifically the compound nepetalactone—including sniffing, licking, chewing, head shaking, chin and cheek rubbing, body rubbing and rolling, as well as pawing, scratching, salivating, and grooming (Hill et al., 1976; McElvain et al., 1942; Palen and Goddard, 1966; Todd, 1962; Tucker and Tucker, 1988). Not all cats display the catnip response and an autosomal dominant inheritance has been suggested (Todd, 1962). The catnip response has increasingly been absorbed into the realm of play, play-like, or predatory-like behaviors. Bradshaw describes catnip-related behavior as "a bizarre mixture of play, feeding, and female sexual behavior, whether the cat is male or female," (2013, p. 115) while Hart and Leedy (1985) highlight that aspects of the response, such as batting and kicking, overlap with play and predatory behavior. A study of olfactory stimulation presented catnip under the guise of a "known stimulant," and highlighted that it "encouraged play-like behavior" (Ellis and Wells, 2010).

The catnip response includes behaviors that explicitly differ from those typically identified within play (Table 1), yet, as with play, it is a mixture of behaviors appearing outside normal or typical contexts and not stereotypic in nature. Additionally, the catnip-response has been described as a "pleasure behavior" (Hatch, 1972) and could be tied to the opioidergic system (Aydin et al., 1998) or even mediated by the same system that makes predation pleasurable to cats (Bradshaw, 2018). Although catnip is marketed to cat owners in the context of cat toys and play (WebMD, 2019), it remains unclear whether the catnip response is truly playful, or some other behavioral response to an olfactory stimulant (Ellis and Wells, 2010). Future studies could examine the scope of its use and effects, not only in terms of cats effected (such as age and breed), but also in terms of both short- and long-term behavioral effects.

7.9. Play preferences

Cats show preferences within play contexts. A recent study suggested that cats in a home environment preferred an interactive toy over static objects, whereas cats in a shelter preferred a hiding enrichment over a toy (Ellis et al., 2017; Vitale Shreve et al., 2017), indicating that the cat's environment can have powerful effects on play motivation. In both studies, individual differences were an important factor.

Because choices can be related to the amount of effort required to obtain access to a resource, preferences can alternatively be assessed using demand curves, which assess the relationship between the demand for a resource and its cost. Studies that measure the number of operant responses (such as lever presses) required to access a resource can reveal the importance of the resource (Dawkins, 1983; Houston, 1997; Matthews and Ladewig, 1994). For example, mink showed greater motivation to work for food and baths than for tunnels and toys (Mason et al., 2001). Cats in a stressful context (an animal shelter) who had to offer an operant response (walking through a cat door) showed preferences for hiding opportunities over play (Ellis et al., 2017), and similar tests could be conducted with domestic cats to assess their preference in the home environment.

What cats want is no doubt highly shaped by their genetics, experience, and motivational state at any given moment. Selective breeding for less predatory cats—to diminish their impact on wildlife—might result in a cat with less need for play, given the overlap between predation and object play (Bradshaw, 2013). However, given the potential welfare and physical benefits of play, suppression of playful behavior may be less beneficial to cats' welfare than

determining how each prefers to play. Cats tend to have specific prey preferences (Dickman and Newsome, 2015), and so it is likely they also have preferences for specific toys and the prey they mimic. Perhaps the most important consideration is that cats should frequently be offered choices, as preferences may be neither static nor exclusive.

8. The whys and wherefores of play in cats, revisited

In 1984, Paul Martin outlined several outstanding research questions and ideas regarding cat play behavior in his essay, "The (four) whys and wherefores of play in cats: A review of functional, evolutionary, developmental and causal issues" (1984b). Thirty-five years later, we are still left with many unanswered questions. Martin wisely noted that to fully understand the nature of play, we must take multiple empirical approaches, incorporate better statistical controls, and observe cat behaviors in more "natural conditions." This was in reference to studying the behavior of wild or feral cats, but we would add that researchers should conduct more observations of cats in one of their most common environments, the human home, especially now that many pet cats do not go outdoors or interact with live prey.

We have also demonstrated that phylogeny and ontogeny are critical to how play behavior develops in cats; there are continuities across the Felidae and important genetic and environmental influences. Play improves hunting, motor, and social skills, and perhaps even the overall welfare of domestic cats. However, assumptions that play must have great survival value simply because play is costly have been challenged. For domestic cats, the costs are small and play is overall relatively infrequent (Martin, 1984a). It is not clear that play is necessary for a cat to develop into a functioning, self-sufficient individual, and numerous questions remain about how play changes across the cat lifespan. To this end, we have presented several potential avenues for inquiry that we believe will greatly improve our understanding of play behavior in domestic cats.

By reviewing the existing literature on cat play, we have also presented a major concern; inconsistent operationalization of play and related behaviors. This lack of consistency and clarity could hinder progress in understanding the importance and functions of play in cats, and we have offered several suggestions to address this problem. In 1979, Leyhausen reflected on the absurdity of thinking that a cat may not be able to distinguish between a toy and a prey animal. Likewise, it may seem absurd to think that scientists cannot distinguish between play and predation, or cannot rely on a "subjective sense of certainty" (Barrett and Bateson, 1978) when measuring play; yet, even the smartest cat appears fooled by a ball of paper from time to time.

Conflict of interest

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