Applied Animal Behaviour Science 241 (2021) 105373

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim

Inexperienced but still interested – Indoor-only cats are more inclined for predatory play than cats with outdoor access

Muhzina Shajid Pyari, Stefania Uccheddu, Rita Lenkei, Péter Pongrácz *

Department of Ethology, ELTE Eötvös Loránd University, Budapest, Hungary

ARTICLE INFO

Keywords:
Predatory play
Object play
Domestic cat
Predatory behaviour
Experience
Keeping condition
Maternal effect

ABSTRACT

Many companion cats (*Felis catus*) in industrialised countries are raised under human supervision and often kept completely indoors. Even if we assume that cats were not selected intentionally against hunting behaviour, we can still hypothesize that because of the differences in their epigeny and prey-related experiences, adult cats would show different willingness to engage in hunting-type behaviours. Play is considered as a useful proxy for testing predatory behaviour in cats under non-invasive conditions. We investigated the influence of raising and keeping conditions on predatory play behaviour in companion cats. We recorded the subjects' (N = 31) reactions to artificial prey-like stimuli such as balls of different sizes (latency of approach and latency of contact), catching wand (frequency of failed attempts of catching, duration of holding) and playback sound of birds, paper crumpling, plastic bags, and mice (latency and duration of search for sound source).

Indoor-only cats approached, touched or played with balls sooner than indoor-outdoor cats. Indoor-only cats started searching sooner than indoor-outdoor cats for the playback sounds. Cats raised with their mother for a longer duration, had less failed attempts in catching the chaser, than subjects that were raised with their mother for a shorter duration, irrespective of the keeping condition.

Indoor-only cats were more interested in the artificial stimuli that show more or less resemblance with the prey, even though these cats have been completely deprived of experience with live prey. There are various theories that can explain these findings, including higher play drive because of the lack of stimulation; less refined prey recognition; or reduced fear due to lack of experience in the indoor-only cats.

1. Introduction

Predatory behaviour, mainly directed towards rodents that imposed and often still represent a threat to the food caches of humans, was the main driving force behind the domestication of cats (Crowley et al., 2020). Even today many cat owners consider 'pest control' as the main task and appeal of having a cat at home (Pongrácz and Szapu, 2018; also see Cecchetti et al., 2020). However, the predatory activity of cats also represents a threat for the local ecosystems (Woods et al., 2003), with an especially heavy impact in such areas where cats were recently introduced by humans (Moseby et al., 2015). From this aspect alone, a better understanding of cats' predatory behaviour is in high demand. The situation is complex as there is no clear feeding ecology based distinction between populations of cats that do (i.e. 'feral' cats), and those that do not, express hunting activity (i.e. 'companion' cats). Several studies have shown that cats with established companion status and provisioned feeding still regularly hunt and kill prey animals (Baker et al., 2008).

Domestic cats show minimal or no functional deviations from their wild ancestor (Driscoll et al., 2007) in their natural nutritional needs or feeding behaviour (Biró et al., 2005; Cecchetti et al., 2020). Domestic cats are the descendants of a hyper-carnivorous predator, which is instantly apparent from their dentition (Serpell, 2000). The African wild cat, *Felis lybica,* is considered to be the closest relative of domestic cats (Driscoll et al., 2007). Domestic cats are more fundamentally constrained within their choice of diet because of the absence of certain key metabolic enzymes that are absent within the common ancestor of all the extant species in the Felidae family (Bradshaw et al., 1996). The end result is a diet which largely consists of vertebrate meat. One of the selection pressures that has caused companion cats to retain their hunting behaviour could be the unsatisfying nutritional content in commercial pet food products (Zoran, 2002; Cecchetti et al., 2020, 2021).

Several factors were found that may influence the frequency, success rate and target of the hunting efforts of cats. Beyond the individual

* Corresponding author at: Department of Ethology, Eötvös Loránd University, Pázmány Péter sétány 1/c, Budapest, 1117, Hungary.
E-mail address: peter.pongracz@ttk.elte.hu (P. Pongrácz).

https://doi.org/10.1016/j.applanim.2021.105373
Received 8 January 2021; Received in revised form 31 May 2021; Accepted 7 June 2021
Available online 10 June 2021

preferences and experience, other cat-related factors that increase the probability of hunting are the age (younger cats hunt more, van Heezik et al., 2010) and body condition (leaner cats hunt more, Woods et al., 2003). It was also found that the location (nearby farmlands) and time budget of the cat (more time spent outside) can boost the hunting activity (McDonald et al., 2015).

The investigation of predatory behaviour in cats is often based on surveys (i.e. kills that cats take home, e.g. McDonald et al., 2015), with less common attempts of direct observations (e.g. Loyd et al., 2013) and experimental approaches (Hall and Bradshaw, 1998). Meanwhile predatory behaviour seems inseparable from being a rural or outdoor cat (Dickman and Newsome, 2015), the presence and manifestation of hunting behaviour in the ever-growing indoor-only companion cat population (Rochlitz, 2005), is much less investigated. Predatory play offers a promising proxy phenotype for a more universal approach to the study of hunting behaviour, because indoor-only cats would be otherwise hard to test without the possibility of exposure to live prey animals.

Predatory play in cats comprises two characteristic subtypes: prey-play, when instead of (or before) killing the captured prey, the cat performs non-lethal elements of hunting behaviour on it; and object play, when the cat performs the behavioural repertoire of hunting/killing on inanimate objects. Earlier studies established a neurophysiological continuum between avoidance behaviour and actual prey-killing, assuming that changes of activity in the neural regulatory system influence the severity of cats' kill-specific behaviours, with prey-play phenotypes in between the two extremities (Pellis et al., 1988). Therefore, authors considered prey-play as a misleading term, by suggesting that the delayed (or omitted) killing phase may signify rather, a hesitant/avoidant behaviour from the cat.

Cats show considerable amount of play behaviour even in their adulthood. Apart from the well-known phenomenon of playing with the still alive prey animals, they show both object and social play behaviour. Multiple factors determine how effective predatory behaviour arises. Two of these factors are developmental determinants occurring while the cat is young. They are the role of the mother in encouraging kittens to catch prey by bringing alive prey to the kittens (Ewer, 1969), and object play in kittens. Apart from these, in adult cats, the experience with prey further enhances their hunting activity (Caro, 1980a, 1980b).

The resemblance and overlap between predatory behaviour and object play in domestic cats was also investigated, with a current view that the two activities may share a considerable motivational background. In this framework, Biben (1979) documented that food deprivation or hunger increases the probability of killing the prey, while satiation decreases killing behaviour in the cat. Also, as the prey size increases, incidence of killing decreases. Hall and Bradshaw (1998) found that hunger enhances not only the interest towards playing with smaller objects in cats, but also the frequency of kill-specific behaviours and observing/stalking the larger toys. Therefore, they concluded that object (predatory) play and actual predatory behaviour may share the same motivational basis.

In the kittens, play-related motor patterns that emerge early in life will be directed towards conspecifics, prey animals, objects ('toys') or they may lack any specific target. Object play emerges and peaks later than social play (around 18–21 weeks of age). During this transitional period, kittens slowly switch interest from playing with their siblings to object and predatory play (Mendoza and Ramirez, 1987). Early weaning or food rationing (i.e. temporarily elevated hunger level) was also found to be associated with increased object play in kittens (Bateson and Martin, 1981; Bateson et al., 1990; Bateson and Young, 1981).

Currently in industrialized countries, most companion cats are raised under human supervision, often indoors (Patronek et al., 1997; Rochlitz, 2005). Some of them are raised in the presence of their mother, but some kittens are adopted shortly after birth, and are fostered by the owner (Delgado and Hecht, 2019). When we investigate keeping conditions, some companion cats are allowed to go out of the house, while some are completely restricted indoors. Even if we assume that cats have not been selected against hunting behaviour (on the contrary, retaining the willingness/ability to hunt proved to be a highly adaptive trait for the larger proportion of domesticated cats, Bradshaw, (2006), we can still hypothesize that there could be differences between the willingness to show hunting-like behaviour in adult cats. As environmental effects could be at least partly responsible for this, in this study we investigated the factors that may affect predatory play in indoor-only cats and cats that have the opportunity to hunt outside. Our main hypotheses were that both the conditions of raising (i.e. kittens had a prolonged time spent with their mother or not) and keeping (indoor-only/indoor-outdoor cats) would affect the presence and intensity of companion cats' willingness to interact with simulated prey-related stimuli. Regarding the raising conditions, we predicted that cats that were raised by their mother for a longer period will show more interest in predatory-type games than cats that had a shorter period together with their mother. Regarding the keeping conditions, no specific prediction was formulated, because both outcomes were equally possible. One could predict that indoor-only cats interact more likely with prey-like stimuli as they miss this type of activity (Cecchetti et al., 2020, 2021); but it is also possible that indoor-outdoor cats show stronger interest towards object play because they are more experienced with prey-like stimuli and predatory play.

2. Methods

2.1. Ethical note

All procedures performed in studies involving animals were in accordance with the ethical standards of the Animal Welfare Committee of the Eötvös Loránd University Ref. no.: PE/EA/1005-5/2018). Companion cats were tested at their homes, with the participation of their owners. We tested the cats with various play-eliciting stimuli, however, we informed the owners that they could interrupt or stop the experiments at any time they felt that their cats experienced high levels of stress. (This never happened).

2.2. Subjects

Participants were recruited through advertisements on the website of our Department and via social media. Criteria for inclusion were simple, any companion cat could participate in our tests if the cat was 6 months old, with the only exclusion being physically challenged companion cats (for example: impaired vision and/or hearing, permanently injured, etc.; all based on the owners' report about the health status of their cats). After exclusions, the effective sample size was 31 subjects (3 intact cats and 28 neutered/spayed cats) these were all included for analysis (mean $\pm$ SD age of subjects = 64.1 $\pm$ 55.77 months). We considered a subject an indoor-outdoor cat (N = 13), when it had *ad libitum* access to the outdoors, but at the same time it was also allowed to be in the house without restrictions (including the room where the actual testing happened). Indoor-only cats (N = 18) were kept strictly indoors, without any access to the outdoors. Twelve cats stayed with their mother till at least 8 weeks of age. 19 cats were adopted by the owner before they were 8 weeks old. Most of our subjects were European short-haired mongrels (28), with the exception of one long-haired Persian and two Siamese cats. Table 1 shows basic details of all the subjects.

2.3. Exclusions

Originally, we tested 54 companion cats. From these, we excluded 8 indoor-only cats and 4 indoor-outdoor cats from the final analysis because of excessively loud background noise (example: construction noise from neighbouring houses, noise from other pets at home) at the testing location. An additional 5 indoor-only and 6 indoor-outdoor cats were excluded from the final analysis because they hid during the test.

Table 1
Demographic details of the subjects.

Subject	Sex	Age (months)	Breed	Keeping condition	Duration raised by mother (months)	Age of adoption (months)	Source of adoption	Does your cat like to play with toys?	Types of toys cat likes to play
IO-1	M	84	Mongrel	Indoor-outdoor	0–2	4–5	Friend	Yes	paper ball, paper bags, boxes, laser pointer, scraper, stick-mounted pen / toy
IO-2	F	204	Mongrel	Indoor-outdoor	More than 2 months	3–4	Friend	Yes	Laser pointer, plastic bags, boxes
IO-3	M	168	Mongrel	Indoor-outdoor	0–2	1–2	Friend	Yes	Paper bags, catnip
IO-4	M	36	Mongrel	Indoor-outdoor	More than 2 months	1–2	Friend	No	Not applicable
IO-5	M	24	Mongrel	Indoor-outdoor	0–2	4–5	Shelter	Yes	ball, paper ball, paper bag, boxes, stick toy, scraper, catnip, any animal / bird toy
IO-6	F	60	Mongrel	Indoor-outdoor	0–2	>6	Friend	Yes	Ball, plastic bags, catching wand
IO-7	F	36	Mongrel	Indoor-outdoor	More than 2 months	3–4	Friend	Yes	Ball, Crumpled paper, bags, boxes, tunnel, Scratch post, Catnip
IO-8	F	210	Mongrel	Indoor-outdoor	More than 2 months	birth	At home	Yes	paper dumplings, laser pointer, wand toy, wand pen / toy, other:
IO-9	M	48	Persian	Indoor-outdoor	0–2	1–2	Friend	Yes	Ball, chaser wand, boxes
IO-10	M	96	Mongrel	Indoor-outdoor	0–2	At home	birth	Yes	Catching wand, plastic bags
IO-11	F	12	Mongrel	Indoor-outdoor	0–2	3–4	Friend	Yes	Ball, Crumpled paper, bags, boxes, tunnel, Catching wand
IO-12	F	84	Mongrel	Indoor-outdoor	More than 2 months	3–4	Friend	Yes	Catching wand, Feather tickler stick
IO-13	M	48	Mongrel	Indoor-outdoor	0–2	1–2	Friend	Yes	Balls, tunnel, boxes
I-1	M	36	Mongrel	Indoor-only	0–2	1–2	Shelter	Yes	Tunnels, plastic bags
I-2	M	24	Mongrel	Indoor-only	More than 2 months	3–4	3–4 Friend	Yes	Catching wand, leather strings
I-3	F	16	Mongrel	Indoor-only	0–2	3–4	Street	Yes	Ball, bags, boxes, tunnel, Catching wand
I-4	M	30	Mongrel	Indoor-only	0–2	1–2	Friend	Yes	paper bags, boxes, string toys, any animal / bird toy
I-5	M	48	Mongrel	Indoor-only	0–2	1–2	Friend	Yes	Balls. Bags, tunnels, catching wand
I-6	F	144	Mongrel	Indoor-only	More than 2 months	3–4	Friend	Yes	paper balls, paper bags, boxes, laser pointer, wand toy, scraper, wand end pen / toy, catnip, any animal / bird toy
I-7	M	24	Mongrel	Indoor-only	More than 2 months	3–4	Shelter	Yes	ball, paper ball, paper bag, boxes, laser pointer, wand toy, scraper, wand end pen / toy, catnip, any animal / bird toy
I-8	F	30	Siamese	Indoor-only	More than 2 months	1–2	Friend	Yes	bags, boxes, tunnel, Laser pointer, Catching wand
I-9	F	16	Mongrel	Indoor-only	0–2	3–4	Street	Yes	Ball, bags, boxes, tunnel, Catching wand
I-10	M	72	Mongrel	Indoor-only	0–2	1–2	Friend	Yes	pen / toy attached to the end of a wand, other:
I-11	F	72	Mongrel	Indoor-only	More than 2 months	3–4	Shelter	Yes	a toy attached to a wand with a cord, a pen / toy attached to the end of a wand
I-12	F	24	Mongrel	Indoor-only	More than 2 months	3–4	Breeder	Yes	bags, boxes, tunnel, Catching wand, strings, toy mouse
I-13	F	6	Siamese	Indoor-only	More than 2 months	3–4	Shelter	Yes	Ball, Crumpled paper, bags, boxes, tunnel, Laser pointer, Catching wand, Scratch post, Feather tickler stick, Catnip, Any animal/bird toys
I-14	F	144	Mongrel	Indoor-only	0–2	>6	Friend	Yes	paper balls, paper bags, boxes, laser pointer, scraper, other:
I-15	M	36	Mongrel	Indoor-only	0–2	Birth	At home	Yes	paper balls, paper bags, boxes, laser pointer, other:
I-16	M	96	Mongrel	Indoor-only	0–2	>6	Friend	Yes	laser pointer
I-17	M	36	Mongrel	Indoor-only	0–2	4–5	Street	Yes	Ball, bags, boxes, tunnel, Catching wand, Catnip
I-18	M	24	Mongrel	Indoor-only	0–2	1–2	Street	Yes	Crumpled paper, bags, boxes, tunnel, Catching wand

This table also shows the answers from the cat owners regarding their cats' playful interactions with the owners, including the type of toys they usually play with.
Explanations: 'Subject' column: IO = indoor-outdoor; I = indoor-only.
'Sex' column: M = male; F = female.
'Age of adoption' column: birth = the cat was born at the owners' house.

2.4. Procedure

Each subject was tested in the home of their owners, typically during daytime, within the range of 10–18 o'clock (depending on the owners' convenience to receive the visit of the experimenter). Each test was recorded with a [Panasonic, HDC-SD10 and moto-g mobile phone camera (had to be replaced in the later stage of data collection as it was damaged)] camcorder for later analysis. The experiment consisted of three tests, always performed indoors, conducted in the same order for all the participants. The three tests followed each other with short intervals between, on the same day. For controlling the hunger level of the cats, we requested that the owners not feed the subjects for 5 h prior to

the test.

2.4.1. Test 1: play with ball

Here we tested whether the cats would interact with a ball that was rolled towards them by the experimenter. Participants were tested with balls of variable sizes; large (10 cm), medium (6 cm) and small (3 cm) in diameter.

Each subject had a free and a restrained trial with each ball size. In the free trial, the owner was asked to gently restrain the subject only until the experimenter rolled the ball towards the subject. When the experimenter rolled the ball (with an approximate speed of 1 m/s), the owner pulled back his/her hands and the subject was allowed to approach/play with the ball for 1 min. In the restrained trial, cats were restrained by their owners during the time the ball was rolling. The restrained trial served to assess the cats' interest in the rolling ball by observing whether they followed it visually. The order of ball size along the three trials was randomly varied across the subjects. Free and controlled trials were conducted in fixed within-subject order. Half of the subjects were tested with free trials first, the other half received the restrained trials first with each ball size.

2.4.2. Test 2: play with chaser wand

Here we tested the interaction of the subjects with a so-called chaser wand toy (a bird shaped soft toy attached with a string (80 cm long) to a stick handle (30 cm long). At the beginning, the cat was gently restrained by its owner on the floor. When the experimenter started to move the chaser wand, the owner released the subject. The experimenter moved the chaser wand as a pendulum in a moderate speed, back and forth keeping it at twice the height of the subject (depends on whether the subject is in standing posture or in a rearing posture (standing on its hind legs). Chaser wand was retracted from the subject each time the subject managed to catch it, and we resumed the movement for a total trial length of maximum 2 min.

2.4.3. Test 3: sound playback

Each subject was presented with pre-recorded vocalizations of a chirping bird, a squeaking mouse, and noise made by crumpling a sheet of paper and rustling a plastic bag, respectively. Sound samples can be accessed in the electronic supplementary material. We formed playsets from the four types of sound samples, arranging them in a random order, with 2-min silent inter-stimulus intervals, and 1-min silence before the first and after the last playback sound. Total duration of each playset was 12 min. Sound intensity was set to 50 percent of the maximum volume. We used a laptop (Lenovo) with a Bluetooth speaker (Sony SRS-XB2) for the playback. The experimenter handled the laptop, and the speaker was placed on the floor, visible to the subject.

2.5. Data collection

To collect basic demographic details of the cats we tested, the owners were asked to complete an online questionnaire. The behaviour of the subjects was coded from the video segments with the help of Solomon Coder (beta 17.03.22 copyright by András Péter). Table 2 shows the list of coded behaviours and their description. Recorded videos of 25 percent of total subjects included in the final analysis were coded by a second observer and interrater reliability scores were calculated in SPSS for all parameters included in the results. Kappa coefficient was estimated in a range between 0.7 and 0.8 for all parameters included in the results.

Table 2
Coded behaviours.

Behaviour	Description
Contact with ball	Hold the ball/ bat/touch with the paw/sniff the ball
Approach the ball	Start moving towards the ball
Hold the chaser	Grab any part of the chaser using fore limbs or hind limbs or in the mouth
Failed attempt	Tries to grab the chaser by jumping or leaning forward/ raising fore limbs, but does not get to hold the chaser
Search for sound	Actively moving around

2.6. Statistical analysis

Latency of approach and latency of contact (balls), latency of search (sound playback) were analysed with Mixed Effects Cox Regression (coxme function) in R environment. We checked the main effects and two-way interactions of keeping condition, raising condition and the size of the ball on the latency of contact with the balls. As we performed a model selection, we report the results of the most parsimonious (final) models. For the pairwise comparisons, we ran Tukey-post hoc tests (emmeans package). Duration of search behaviour during the playback session was analysed in SPSS.25, using GLM repeated measures, where sound playback was the repeated factor, type of playback was the predictor. Here, and in other cases where we run GLM, for complying with the model assumptions, we checked the normal probability plot of the residuals. Frequency of failed attempts to catch the chaser was analysed with separate Mann-Whitney U tests, with keeping condition and raising condition as predictors. Duration of holding the chaser was analysed using 2-way GLM in SPSS to check the effect of different keeping conditions and raising conditions as predictors. As threshold level for significant results, $\alpha = 0.05$ was used in each case.

3. Results

3.1. Test 1: play with ball

During the play with the ball test, cats could show the following behaviors: they approached the ball, sniffed the ball, bat the ball, hold the ball with hind limbs and fore limbs or just approached but did not touch the ball.

For Mixed Effects Cox Regression analysis, we report the results of the final models.

Regarding the contact with the ball we found a significant effect of keeping condition ($\chi^2_1 = 5.0449$, $P = 0.0247$) (see Fig. 1). Indoor only cats touched or played with balls sooner than the indoor-outdoor companion cats ($\exp(\beta) = 2.78[1.449, 4.1104]$, $Z = 2.14$, $P = 0.032$). Size of the ball and raising condition had no effect on latency of contact with the ball. We found a weak significant effect in case of keeping condition

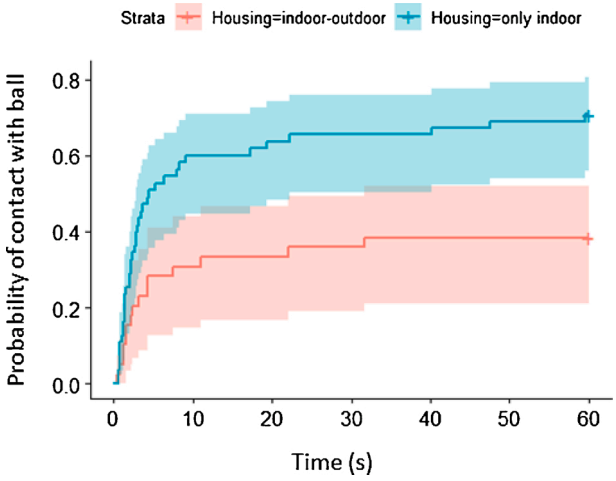

Fig. 1. The cumulative occurrences of contact with balls of indoor only cats and indoor-outdoor cats. Shaded areas represent 95 % CI.

($\chi^2_1 = 4.5336$, $P = 0.03324$) on the latency of approaching the balls. Indoor only cats approached sooner the balls than indoor-outdoor cats (exp(β) = 2.79 [1.3448,3.906], $Z = 1.98$, $P = 0.048$) (see Fig. 2). Size of the ball and raising condition had no significant effect on how fast or slow the cats approached the ball.

3.2. Test 2: play with chaser wand

In case of play with the chaser, cats either grabbed the chaser, sniffed it, bite it; or just ignored the chaser; or tried to grab it but did not succeed. Only in the case of 'play with the chaser wand' test, 4 subjects were not included (3 indoor-outdoor cats and 1 indoor only cat) to the analysis as they did not play at all with the chaser during the trial, and for the analysis, we needed 'frequency of failed attempts to catch the chaser' and 'duration of holding the chaser' data.

From the predictors, raising condition had a significant effect on frequency of failed attempts in catching the chaser ($U = 34.5$, $P = 0.009$) (see Fig. 3). According to this, cats that were raised with the mother only for a shorter period showed more failed attempts to catch the chaser than cats that were raised with their mother for more than 8 weeks. Housing conditions did not show significant effect ($U = 68.0$, $P = 0.414$) on the frequency of failed attempts to catch the chaser.

3.3. Test 3: sound playback

In case of playback session, cats showed active locomotion around, looking around by moving the head without any locomotion; or just remained in the same position without any head movement or locomotion. The repeated factor (sound playback) did not have a significant effect ($F_{11,319} = 0.398$, $P = 0.956$) on the duration of search behaviour. From the predictors, type of sound did not have a significant effect on duration of search behaviour ($F_{3,81} = 1.024$, $P = 0.386$); while the predictor keeping condition had a significant effect on duration of search ($F_{1,29} = 8.989$, $P = 0.006$) (see Fig. 4). Indoor-only cats spent more time searching around than indoor-outdoor cats during the entire session of sound playback.

In case of the latency of the searching ($\chi^2_3 = 8.5519$, $P = 0.03588$), we found a significant effect of keeping condition (Exp(β) = 2.80[1.814, 3.794], $Z = 2.92$, $P = 0.0035$). Indoor-only cats started searching sooner than indoor-outdoor cats, independently of the type of sound (see Fig. 5). We also found significant association between raising condition and type of sound (Exp(β) = 0.1905[0.0677,0.3133], $Z = -2.569$, $P = 0.0102$). Based on the post-hoc test, cats raised with the mother for '0−2 months' reacted faster in searching for the sound of the bird (see Fig. 6).

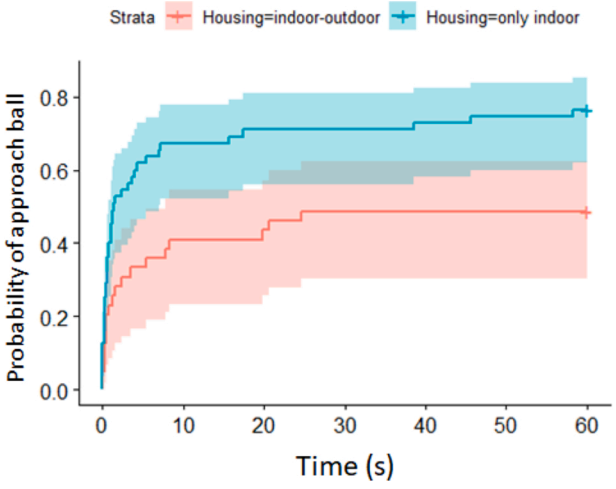

Fig. 2. The cumulative occurrences of approaching the ball of indoor only cats and indoor-outdoor cats. Shaded areas represent 95 % CI.

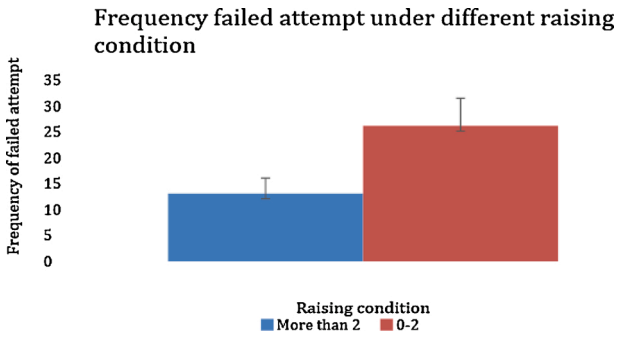

Fig. 3. Frequency of failed attempts to catch chaser under '0–2 months with mother' and 'more than 2 months with mother' raising conditions. Error bars: SE.

4. Discussion

In a series of experiments, we tested companion cats with such stimuli that we expected would elicit predatory play or prey-related interest from the subjects. We found that both keeping and early upbringing conditions had significant associations with cats' reactions to these stimuli. Most importantly, indoor only cats showed stronger interest towards most stimuli (faster approach and contact with the balls, shorter search latencies in case of sound playbacks). Cats raised with their mother for more than 2 months had less failed attempts in catching the chaser than cats raised with their mother for 0−2 months irrespective of the keeping condition.

Cats and dogs are considered as the two main companion animal species worldwide, both have considerably long domestication history, but with markedly different functions and feeding ecology as well. Domestic dogs (owned and ownerless alike) became an omnivorous species (Axelsson et al., 2013), with a wide array of work and leisure functions in the case of working, sports and companion dogs. The domestic cat remarkably retained its 'original' feeding habits as well as function, thus remaining an effective meso-predator (Bradshaw, 2006). Acknowledging the current tendency of keeping more and more cats strictly indoors (which stems both from reasons of urban lifestyle (Foreman-Worsley and Farnworth, 2019) and ecological conscientiousness (Linklater et al., 2019)), we investigated whether being an indoor-only cat would have an effect on companion cats' reactions to stimuli that are intended to elicit predatory play. Our experiments showed that the lack of experience with various prey animals by the indoor-only cats did not coincide with a weaker willingness and intensity of cats' interactions with prey-mimicking toys and stimuli. Our results therefore are in parallel with the recent study of Cecchetti et al. (2020, 2021) who found that a short session of daily object play with the cat can lessen the amount of prey these companion cats killed. Both the results of our and Cecchetti et al.'s experiments thus indicate that actual hunting activity and object-elated play may show a negative association with each other in domestic cats.

From our results it is understood that indoor-only cats are more interested than the indoor-outdoor cats in the toys and sounds that show more or less resemblance with prey. It is important to see that this difference most probably was not the result of simply being more inclined to play with toys or interacting with humans and toys in case of the indoor-only cats, because in the other group the cats were also living with their owners in the house. In other words, both cat groups consisted of indoor-cats with a close and intense relationship with their owners, but one group had an additional access to the outdoors (indoor-outdoor cats). Predatory play can be used as a proxy for actual predatory behaviour (Biben, 1979), therefore we can assume that in the case of our subjects, the differences between the indoor-only and indoor-outdoor cats' reactions to the experimental stimuli may be partly connected to their different experiences with actual prey animals. Caro (1980a,

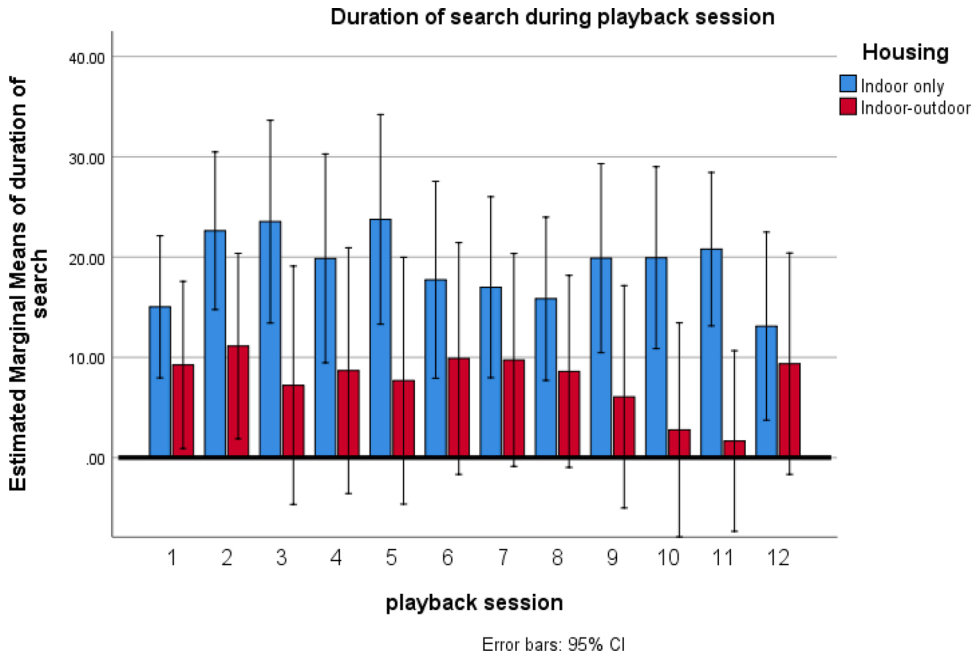

Fig. 4. Duration of search during the entire sound playback session of indoor only cats and indoor-outdoor cats. Error bars: 95 % CI.

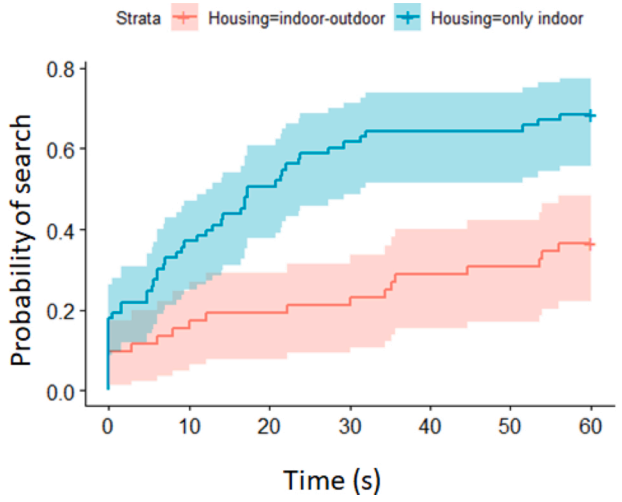

Fig. 5. Latency of search for any type of sound of indoor only cats and indoor-outdoor cats. Shaded areas represent 95 % CI.

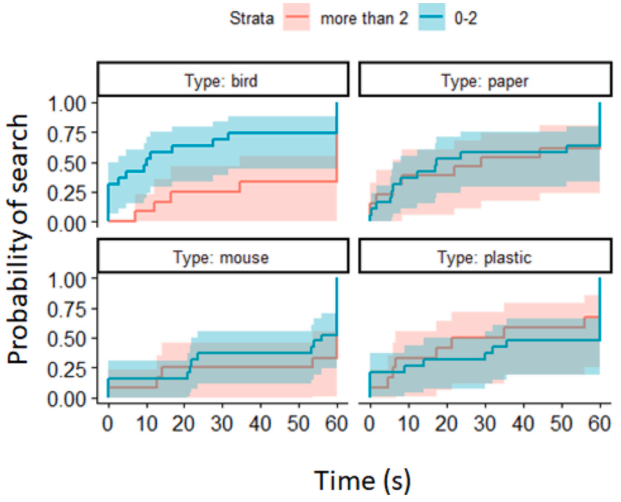

Fig. 6. Latency of search for each type of sounds of under '0–2 months with mother' and 'more than 2 months with mother' raising conditions. Shaded areas represent 95 % CI.

1980b) found that in adult cats, exposure to prey enhanced predatory behaviour. This is seemingly in contradiction with our results, because one could then expect that indoor-outdoor cats would be keener to engage with predatory play. Among the possible explanations, we may consider that (1) outdoor cats are more experienced with real prey therefore they are less interested in improper stimuli (or in general, in predatory play); and/or (2) the indoor only cats are deprived of real prey, therefore they show more intense reaction even towards improper 'replacement stimuli'. For this latter option, support comes from the study of Holloway and Suter (2004), who found that peri-adolescent cats that were temporarily deprived of social play with conspecifics (mainly wrestling type games), showed a significant increase in these activities once their isolation was lifted and they regained access to their companions. Additionally, we can exclude different levels of hunger (Biben, 1979) as an explanation, as in our sample each cat was kept as a companion and they were regularly provisioned by their owners independent of their access to the outdoors. Additionally, we did not find an association between ball size and elicited reaction from the cats neither within, nor between the groups, which could indicate a difference in the hunger-related motivation levels (Biben, 1979).

While indoor-outdoor companion cats have experience in encountering and handling prey in their day to day life (Loyd et al., 2013), indoor only cats have hardly any experience in handling live prey (except for occasional encounters with insects inside the home). Even though indoor only cats are mostly lacking the experience with live prey, in our study they showed faster response to stimuli that mimic some features of prey (sound, movement, perhaps appearance). Pellis et al. (1988) found a continuum in cats between avoidance of prey, 'playing' with prey, and killing the prey, where they suggested that the severity (or lethality) of the cat's interaction with a prey animal depends on the balance between the motivational levels of defence and attack. The more the neural regulatory system moves from defence towards attack, the cat will show less and less defensive (avoidance) behaviour, and goes more

directly for the kill. This theory offers an interesting explanation to our results. As indoor-only cats have no real experience with prey animals, they may show a more curious and less defensive or cautious reaction towards prey-like stimuli. Indoor-outdoor cats with ample experience of potentially dangerous, self-defending prey, may show a more defensive or cautious approach, resulting in longer contact latencies and lower contact frequencies.

Cats may regard the chaser as a bird-like object and holding it can be regarded as a kill-attempt. In a study where indoor-outdoor cats were fitted with small cameras, it was found that small songbirds represent one of the most difficult prey types to catch for even these otherwise successful predators (Loyd et al., 2013). Therefore, killing the prey faster or crippling a bird is important for an experienced hunter for securing it against escape. If we consider that companion cats that have outside access (indoor-outdoor cats) were less interested in the sounds in general, this shows that cats who probably have experience in catching (and killing) birds, would be those that hold the chaser longer ("I surely get it"), but at the same time they are not so interested in the bird sound from playback ("I know that it is impossible here in the room").

It has been shown that the willingness to interact with prey and the efficiency of hunting behaviour in kittens, is associated with the presence of the mother, more precisely, it depends on the parallel exposure to the prey and the mother (Caro, 1980a, 1980b). Moreover, this effect is time-sensitive as kittens become more willing to interact with the prey on their own only if they had the chance to experience their mother's prey-related behaviour till at least 8 weeks of age. The effect of the mother in this case is hard to substitute, as neither object-play, nor other cats (siblings) had the same improving effect on young cats' predatory behaviour than that of the mother (Caro, 1980a, 1980b). In our study, we found that the length of time cats spent with their mother had an association especially with behaviours that can be considered as predatory play connected to bird-like stimuli (sound playback of birds, interacting with the chaser wand). Independent of their keeping conditions, subjects that were raised by their mother for a limited time only, showed more intense interest in bird sound playback, and had more failed attempts of catching the wand. We assume that the longer a cat was raised by its mother, the more its hunting skills were honed as a consequence of the maternal effect (Caro, 1980a, 1980b). In turn, these more effective hunter cats may show weaker interest in sound playback of birds, because either they find these stimuli weaker than the ones originating from real prey animals, or because they can fulfil their need for hunting on a more regular basis (hence they are less deprived of such stimuli). The failed attempts' frequency in the case of catching the chaser would strengthen this explanation, if we consider this behavioural parameter as an indicator of either the inefficiency of the cat as a hunter, or its more playful than serious hunting intent. As the subjects that were provided only a limited period of maternal care showed more failed attempts to catch the chaser, one could assume that this was the result of their less developed hunting skills, or their more playful than predatory approach to this game.

Among the limitations of our study, we should note that we did not have any control or influence over the level of general stimulation our subjects received from their environment, including both the social and asocial factors. Therefore it could happen that apart of prey-related stimuli, indoor-outdoor cats received a more stimulus-rich experience due to their access to the world outside of their owner's house. Theoretically, a more stimulus-rich environment could also contribute in their diminished interest (compared to the indoor-only cats) in the prey-like stimuli we provided them during the tests. Another limiting factor is that the tests were conducted not exactly the same time during the day with the various subjects (due to the fact that we had to adjust our visits to the owners' homes according to their daily schedule). Although the 5 h long food withdrawal before the test should be enough to equalize the hunger level in companion cats, we acknowledge that the wide range of testing times during the day could somewhat influence the activity level of some of our subjects.

5. Conclusions

Keeping conditions play a crucial role in developing predatory play in companion cats. The experience with live prey or lack of experience with prey could affect the willingness and intensity of cats' interaction with prey or prey mimicking toys or stimuli. Also, the role of the mother seems to be influential for companion cats to become efficient hunters. The length of time spent with the mother cat has an association with predatory play as well. However to understand the mechanism for developing skills to become efficient hunters, we need more controlled experiments, especially with information about keeping conditions of mother cats, and the playful interaction of the kittens with the mother cat and siblings.

Acknowledgements

Muhzina Shajid was supported by the Stipendium Hungaricum Scholarship program of the Ministry of Foreign Affairs and Trade of Hungary (SHE-00023-004/2019). Rita Lenkei was supported by the ÚNKP-20-3New National Excellence Program of the Ministry for Innovation and Technology from the source of the National Research, Development and Innovation Fund. Celeste R. Pongrácz provided proofreading of the manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.applanim.2021.105373.

References

Axelsson, E., Ratnakumar, A., Arendt, M.L., Maqbool, K., Webster, M.T., Perloski, M., Liberg, O., Arnemo, J.M., Hedhammar, Å., Lindblad-Toh, K., 2013. The genomic signature of dog domestication reveals adaptation to a starch-rich diet. Nature 495 (7441), 360–364. https://doi.org/10.1038/nature11837.

Baker, P.J., Molony, S.E., Stone, E., Cuthill, I.C., Harris, S., 2008. Cats about town: Is predation by free-ranging pet cats Felis catus likely to affect urban bird populations? Ibis 150 (Suppl.1), 86–99. https://doi.org/10.1111/j.1474-919X.2008.00836.x.

Bateson, F.A., Martin, P., 1981. Effects of interrupting cat mothers' lactation with bromocriptine on the subsequent play of their kittens. Physiol. Behav. 27, 841–845.

Bateson, P., Young, M., 1981. Separation from the mother and the development of play in cats. Anim. Behav. 29 (1), 173–180. https://doi.org/10.1016/S0003-3472(81)80163-7.

Bateson, P., Mendl, M., Feaver, J., 1990. Play in the domestic cat is enhanced by rationing of the mother during lactation. Anim. Behav. 40 (3), 514–525. https://doi.org/10.1016/S0003-3472(05)80532-9.

Biben, M., 1979. Predation and predatory play behaviour of domestic cats. Anim. Behav. 27, 81–94. https://doi.org/10.1016/0003-3472(79)90129-5.

Biró, Z., Lanszki, J., Szemethy, L., Heltai, M., Randi, E., 2005. Feeding habits of feral domestic cats (*Felis catus*), wild cats (*Felis silvestris*) and their hybrids: trophic niche overlap among cat groups in Hungary. J. Zool. 266 (2), 187–196.

Bradshaw, J.W., 2006. The evolutionary basis for the feeding behavior of domestic dogs (*Canis familiaris*) and cats (*Felis catus*). J. Nutr. 136 (7), 1927S–1931S.

Bradshaw, J.W., Goodwin, D., Legrand-Defretin, V., Nott, H.M., 1996. Food selection by the domestic cat, an obligate carnivore. Comp. Biochem. Physiol. A Physiol. 114 (3), 205–209. https://doi.org/10.1016/0300-9629(95)02133-7.

Caro, T.M., 1980a. Effects of the mother, object play, and adult experience on predation in cats. Behav. Neural Biol. 29 (1), 29–51. https://doi.org/10.1016/S0163-1047(80)92456-5.

Caro, T.M., 1980b. The effects of experience on the predatory patterns of cats. Behav. Neural Biol. 29 (1), 1–28. https://doi.org/10.1016/S0163-1047(80)92442-5.

Cecchetti, M., Crowley, S.L., McDonald, R.A., 2020. Drivers and facilitators of hunting behaviour in domestic cats and options for management. Mam. Rev.

Cecchetti, M., Crowley, S.L., Goodwin, C.E., McDonald, R.A., 2021. Provision of high meat content food and object play reduce predation of wild animals by domestic cats *Felis catus*. Curr. Biol. 31 (5), 1107–1111.

Crowley, S.L., Cecchetti, M., McDonald, R.A., 2020. Our wild companions: domestic cats in the anthropocene. Trends Ecol. Evol. 35 (6), 477–483. https://doi.org/10.1016/j.tree.2020.01.008.

Delgado, M., Hecht, J., 2019. A review of the development and functions of cat play, with future research considerations. Appl. Anim. Behav. Sci. 214, 1–17. https://doi.org/10.1016/j.applanim.2019.03.004.

Dickman, C.R., Newsome, T.M., 2015. Individual hunting behaviour and prey specialisation in the house cat *Felis catus*: implications for conservation and

management. Appl. Anim. Behav. Sci. 173, 76–87. https://doi.org/10.1016/j.applanim.2014.09.021.
Driscoll, C.A., Menotti-Raymond, M., Roca, A.L., Hupe, K., Johnson, W.E., Geffen, E., Harley, E.H., Delibes, M., Pontier, D., Kitchener, A.C., Yamaguchi, N., O'Brien, S.J., Macdonald, D.W., 2007. The near eastern origin of cat domestication. Science 317 (5837), 519–523. https://doi.org/10.1126/science.1139518.
Ewer, R.F., 1969. The "instinct to teach". Nature 222, 698. https://doi.org/10.1038/222698a0.
Foreman-Worsley, R., Farnworth, M.J., 2019. A systematic review of social and environmental factors and their implications for indoor cat welfare. Appl. Anim. Behav. Sci. 220, 104841.
Hall, S.L., Bradshaw, J.W.S., 1998. The influence of hunger on object play by adult domestic cats. Appl. Anim. Behav. Sci. 58 (1–2), 143–150.
Holloway, K.S., Suter, R.B., 2004. Play deprivation without social isolation: housing controls. Dev. Psychobiol. 44 (1), 58–67. https://doi.org/10.1002/dev.10151.
Linklater, W.L., Farnworth, M.J., van Heezik, Y., Stafford, K.J., MacDonald, E.A., 2019. Prioritizing cat-owner behaviors for a campaign to reduce wildlife depredation. Conserv. Sci. Pract. 1 (5), e29. https://doi.org/10.1111/csp2.29.
Loyd, K.A.T., Hernandez, S.M., Carroll, J.P., Abernathy, K.J., Marshall, G.J., 2013. Quantifying free-roaming domestic cat predation using animal-borne video cameras. Biol. Conserv. 160, 183–189. https://doi.org/10.1016/j.biocon.2013.01.008.
McDonald, J.L., Maclean, M., Evans, M.R., Hodgson, D.J., 2015. Reconciling actual and perceived rates of predation by domestic cats. Ecol. Evol. 5 (14), 2745–2753. https://doi.org/10.1002/ece3.1553.
Mendoza, D.L., Ramirez, J.M., 1987. Play in kittens (Felis domesticus) and its association with cohesion and aggression. Bull. Psychon. Soc. 25 (1), 27–30. https://doi.org/10.3758/BF03330067.
Moseby, K.E., Peacock, D.E., Read, J.L., 2015. Catastrophic cat predation: a call for predator profiling in wildlife protection programs. Biol. Conserv. 191, 331–340. https://doi.org/10.1016/j.biocon.2015.07.026.
Patronek, G.J., Beck, A.M., Glickman, L.T., 1997. Dynamics of dog and cat populations in a community. J. Am. Vet. Med. Assoc. 210 (5), 637.
Pellis, S.M., O'Brien, D.P., Pellis, V.C., Teitelbaum, P., Wolgin, D.L., Kennedy, S., 1988. Escalation of feline predation along a gradient from avoidance through" play" to killing. Behav. Neurosci. 102 (5), 760. https://doi.org/10.1037/0735-7044.102.5.760.
Pongrácz, P., Szapu, J.S., 2018. The socio-cognitive relationship between cats and humans–Companion cats (*Felis catus*) as their owners see them. Appl. Anim. Behav. Sci. 207, 57–66. https://doi.org/10.1016/j.applanim.2018.07.004.
Rochlitz, I., 2005. A review of the housing requirements of domestic cats (*Felis silvestris catus*) kept in the home. Appl. Anim. Behav. Sci. 93 (1–2), 97–109. https://doi.org/10.1016/j.applanim.2005.01.002.
Serpell, J.A., 2000. Domestication and history of the cat. In: Turner, D.C., Bateson, P. (Eds.), The Domestic Cat: The Biology of Its Behaviour. Cambridge University Press, pp. 83–100.
van Heezik, Y., Smyth, A., Adams, A., Gordon, J., 2010. Do domestic cats impose an unsustainable harvest on urban bird populations? Biol. Conserv. 143 (1), 121–130. https://doi.org/10.1016/j.biocon.2009.09.013.
Woods, M., McDonald, R.A., Harris, S., 2003. Predation of wildlife by domestic cats Felis catus in Great Britain. Mamm. Rev. 33 (2), 174–188. https://doi.org/10.1046/j.1365-2907.2003.00017.x.
Zoran, D.L., 2002. The carnivore connection to nutrition in cats. J. Am. Vet. Med. Assoc. 221 (11), 1559–1567. https://doi.org/10.2460/javma.2002.221.1559.