

1 Assessing cats' (*Felis catus*) sensitivity to human pointing gestures

2 Margaret Mäses & Claudia A.F. Wascher*

3

4 Behavioural Ecology Research Group, School of Life Sciences, Anglia Ruskin University, United

5 Kingdom

6

7 *Corresponding author: Claudia A.F. Wascher: School of Life Sciences, Anglia Ruskin University, East

8 Road, Cambridge, CB1 1PT United Kingdom; Phone: +44 (0) 1223 698270;

9 e-mail: claudia.wascher@gmail.com

10 **Abstract**

11 A wide range of non-human animal species have been shown to be able to respond to
12 human referential signals, such as pointing gestures. The aim of the present study was to replicate
13 previous findings showing cats to be sensitive to human pointing cues (Miklósi *et al.* 2005). In our
14 study, we presented two types of human pointing gestures - momentary ipsilateral (direct pointing)
15 and momentary cross-body pointing. We tested nine rescue cats in a two-way object choice task.
16 On a group level, the success rate of cats was 74.4 percent. Cats performed significantly above
17 chance level in both the ipsilateral and cross-body pointing condition. Trial number, rewarded side
18 and type of gesture did not significantly affect the cats' performances in the experiment. On an
19 individual level, 5 out of 7 cats who completed 20 trials, performed significantly above chance level.
20 Two cats only completed 10 trials. One of them succeeded in 8, the other in 6 of these. The results
21 of our study replicate previous findings of cats being responsive to human ipsilateral pointing cues
22 and add additional knowledge about their ability to follow cross-body pointing cues. Our results
23 highlight that a domestic species, socialised in a group setting, may possess heterospecific
24 communication skills. Further research is needed to exclude alternative parsimonious explanations,
25 such as local and stimulus enhancement.

26

27

28

29

30 **Key words:** cats, cognition, cross-body pointing, ipsilateral pointing, pointing cues, referential signals

31 Introduction

32 A wide range of non-human animal species has been shown to be able to respond to human
33 referential signals, such as pointing gestures (Krause et al., 2018; Miklósi & Soproni, 2006). Pointing
34 presents a species-specific human communicative signal (Bard et al., 2021). The ability of humans to
35 understand pointing with a hand as an object-directed action develops at the age of 9 to 12 months
36 (Woodward & Guajardo, 2002). The development of pointing comprehension in humans and non-
37 human animals is likely a result of learning, social experience and interactions (Miklósi & Soproni,
38 2006). A variety of non-domesticated mammalian taxa, including dolphins (*Tursiops truncatus*;
39 Herman et al., 1999), elephants (*Loxodonta africana*; Smet & Byrne, 2013), bats (*Pteropus*; Hall et
40 al., 2011) and sea lions (*Zalophus californianus*; Malassis & Delfour, 2015), have demonstrated
41 following some form of human pointing. Several studies have examined the understanding of
42 human pointing cues in chimpanzees (*Pan troglodytes*) and other great apes, specifically in the
43 object choice task. Initial studies suggested subjects were relatively unsuccessful (Kirchhofer et al.,
44 2012; Povinelli et al., 1997). However, recent studies suggest systematic confounds rather than
45 differences between species to cause this effect (Clark et al., 2019; Clark & Leavens, 2019; Hopkins
46 et al., 2013). For example the rearing environment affects the performances of apes in pointing
47 tasks and individuals reared in complex environments outperformed individuals reared under
48 standard conditions (Lyn et al., 2010; Russell et al., 2011).

49

50 When it comes to domestic animals, goats (*Capra hircus*; Kaminski et al., 2005; Nawroth et
51 al., 2020), pigs (*Sus scrofa domestica*; Nawroth et al., 2016), horses (*Equus caballus*; Proops et al.,
52 2010), cats (*Felis catus*; Miklósi, et al., 2005), and most prominently, dogs (*Canis familiaris*;
53 Bhattacharjee et al., 2020; Bräuer et al., 2006; Hare et al., 1998; Soproni et al., 2002; Tauzin et al.,

2015) have been shown to follow pointing signals. In the case of dogs (in particular, the domestication process has been considered to have shaped the evolution of their remarkable socio-cognitive skills that allow them to successfully communicate with humans (Hare et al., 2002). However, this hypothesis is challenged by a range of wild canids such as wolves (*Canis lupus*), coyotes (*Canis latrans*), and foxes (*Vulpes vulpes*) responding to human pointing gestures, as well as socialisation with humans affecting dogs' performance, with pet dogs outperforming dogs housed in kennels and shelters (reviewed in Krause et al., 2018).

Despite domestic cats being one of the most popular pets and very well adapted to human environments, their cognition has been studied notably less than that of dogs (Shreve & Udell, 2015). In a previous study, Miklósi, et al. (2005) demonstrated cats' abilities to follow human pointing were comparable to the abilities of dogs doing so, whereas they performed more poorly compared to dogs in attention-getting behaviour. In another study however, cats responded to the attentional state of a person when presented with an unsolvable task (Zhang et al., 2021). Cats are able to use human gaze as a referential signal (Pongrácz et al., 2019). Performance of cats has recently also been tested in other cognitive tasks. For example they have been shown to differentiate between different quantities (Pisa & Agrillo, 2009), they are able to mentally represent the location of non-visible objects (Takagi et al., 2021) and reproduce a human's familiar action on an object (touch it with hand/paw or face) (Fugazza et al., 2021).

Nevertheless, the body of research on socio-cognitive capacities of cats remains currently considerably small. Interestingly, it has been suggested that the process of cat domestication is different from that of other domestic species, as it was driven by a mutualistic relationship with humans and was subject to significantly less strict artificial selection (Clutton-Brock, 1994; Serpell,

78 2013). Cat domestication can even be claimed to have been self-initiated (Driscoll et al., 2009).
79 Another aspect worth taking into account is that, compared to most other species studied in the
80 context of social cognition, cats have an arguably less social lifestyle, as their ancestors were
81 primarily solitary (Bradshaw, 2016). One might expect that these evolutionary peculiarities have a
82 negative effect on cats' responsiveness to human communicative signals.

83

84 One of the measures by which referential cues can be categorized is their duration, the
85 signal being either momentary or dynamic (Miklósi & Soproni, 2006). For momentary pointing, the
86 signaller keeps the arm in the pointing position for only a second (Miklósi et al., 2005). On the other
87 hand, when giving a dynamic cue, the signal is terminated after the receiver has responded (Miklósi
88 & Soproni, 2006). The momentary cues are arguably more similar to naturally occurring
89 communicative interactions than dynamic cues, as the subject has to remember the signal before
90 making a choice. In the present study, we aimed to test whether cats follow the human momentary
91 ipsilateral (direct) pointing cues in a two-way choice task, choosing the target indicated with the
92 referential signal at above-chance level, thus replicating the findings of Miklósi et al. (2005).
93 Additionally, we tested whether cats follow the human momentary cross-body pointing cues in a
94 two-way choice task. As the cross-body form of the signal was most likely novel to the subjects, we
95 expected the cats to be more successful in following ipsilateral pointing cues. If cats show the ability
96 to respond accurately to different forms of pointing cues this could be indicative of an ability to
97 generalize and potentially referential understanding.

98

99

100

101

102
103
104
105
106
107
108
109
110
111
112
113
114
115
116
117
118
119
120
121
122
123
124
125

Methods

Ethical considerations

The present study received ethical approval from the School Research Ethics Panel of Anglia Ruskin University. The study was approved by and conducted at Pesaleidja cat shelter in the Republic of Estonia. This study complies with the national regulations on ethics and research on animals in Estonia.

Standards for openness and transparency

We report how we determined our sample size, all data exclusions, all manipulations, and all measures in the study.

Study subjects

The experiment was conducted during summer 2020 (29th June - 12th August). Study subjects were housed in a rehoming centre in Tallinn, managed by Pesaleidja NGO. A total of approximately 200 cats were roaming free in different indoor spaces (10 – 51 m²; 0.5 cats per a square metre; Jaroš, 2018), nine of which participated in the study. Cats were individually tested in a separate room.

The cat’s suitability to participate in the experiment was evaluated in three stages (similar to the method of Miklósi et al. (2005), with certain alterations described below). Firstly, the potential subject was approached by the experimenter (M.M.), who sat down next to the individual, and petted it for one minute. If the cat did not leave during this time or express fearful behaviour (e.g.

126 flattened ears (Bennett et al., 2017; Deputte et al., 2021; Gourkow et al., 2014); whiskers held
127 against face; dilated pupils; becoming immobile/freezing; piloerection; arched back; tensely
128 crouched body position; tail tucked tightly between the legs or around the body; hissing or other
129 agonistic vocalizations (Tavernier et al., 2020)); of any kind, the experimenter guided the subject
130 into the testing room (5.5 m²), either by allowing it to follow the experimenter or alternatively
131 carrying it for a maximum of ten seconds. After separation the subject was given time to explore
132 the testing room. Here the subject was isolated from its conspecifics for the duration of the
133 experiment, the doors were closed to prevent the other cats from entering. With those individuals
134 not initially comfortable, i.e. expressing fearful or stressed behaviour (e.g. attempting to hide
135 (Bennett et al., 2017; Gourkow et al., 2014); yowling (Tavernier et al., 2020) and standing fixated to
136 one of the closed doors; pacing back and forth (Gourkow et al., 2014)), with the novel setting, the
137 experimenter sat on the floor and petted them, calmly allowing them to walk around, as well as
138 offering some food. If the cat continued showing signs of stress after five minutes, the
139 experimenter allowed it to exit the room and excluded it from any further testing. As a last stage of
140 habituation, the experimenter put some food into one of the test bowls (green silicone muffin
141 cases) and introduced it to the cat by allowing it to smell the bowl. We used small amounts of wet
142 cat food, as recommended by the shelter staff, as a reward throughout the experiment. Rewards
143 were given to the subjects in addition to their normal diet. The bowl was then placed on the floor,
144 approximately one metre from the subject. The cat was allowed to approach it and eat the food. If
145 the cat was motivated to approach the bowl and showed interest in eating the food, it passed the
146 third stage and was included in the final experiment. This stage additionally familiarised the cats
147 with the bowl containing a food reward. Twenty cats passed the first stage of preliminary testing,
148 but some of them did not habituate to the novelty of testing room environment quickly enough,
149 were not food motivated or showed a persistent side bias (description below). Consequently, ten

150 subjects participated in the final experiment. However, we decided to exclude one of them from
151 data analyses due to side bias. The remaining nine subjects all completed a minimum of ten
152 experimental trials. Seven of them completed 20 trials.

153

154 *Study design*

155 As the cats' everyday diet was provided to them *ad libitum*, timing of the experiment was
156 not dependent on the feeding regime. Before every trial and out of site of the subject,
157 approximately the same amount of food, positioned as similarly as possible, was put into both test
158 bowls (paying attention to prevent visual and odour-induced bias of choice). Next, a bit of food
159 liquid was smeared onto the inner walls of a third silicone bowl, serving as 'bait' distracting the cats
160 while the experimenter got into position. The subject was attracted to a position approximately two
161 metres away the experimenter's final position. The experimenter simultaneously placed the test
162 bowls in front of them, the middle line between the bowls at an approximate distance of 0.5
163 metres. The experimenter then made an attention-drawing sound (common utterance used for
164 calling cats in the local area: 'ks-ks') and presented the pointing cue when the subject was looking
165 in the direction of the experimenter.

166

167 We tested cats' responses to ipsilateral pointing to the left (IL), with the left arm and index
168 finger pointing at the container on the left side of the experimenter, ipsilateral pointing to the right
169 (IR), with the right arm and index finger pointing at the container on the right side of the
170 experimenter, cross-body pointing to the left (CL), with the right arm and index finger pointing at
171 the container on the left side of the experimenter, and cross-body pointing to the right (CR), with
172 the left arm and index finger pointing at the container on the right side of the experimenter. The
173 experimenter maintained a neutral body posture and gaze direction, at all times, while performing

174 the pointing gestures. After pointing, the subject could choose one of the bowls. The cat was
175 considered to make a choice when it looked into the bowl or reached into it with its paw. When the
176 choice corresponded to the direction of the gesture, the cat was allowed to eat the reward from
177 the 'correct' bowl. When the choice was 'unsuccessful', both bowls were picked up before the
178 subject was able to eat the food. In the case of the subject not making a choice (*e.g.*, walked
179 between the test bowls and straight to the experimenter or walked away), the experimenter
180 repositioned themselves and repeated the trial. In one subject, the experimenter could not lead the
181 subject to refocus, and therefore, stopped the session and continued on another day. Order of trials
182 in the four conditions (IL, IR, CL, CR) was pseudo-randomized. Each condition was presented five
183 times in a total of 20 test trials. Each condition was not repeated more than twice in a row and the
184 type or direction a maximum of three times.

185

186 If the subject continuously chose the bowl on the same side for four consecutive trials,
187 regardless of the signal, we considered this as an indication for the subject developing a side bias. In
188 this case, the positioning of the experiment was switched to the opposite side of the room, which
189 seemed to be effective with four subjects. One subject, who had passed the three stages of
190 preliminary testing but reached for the bowl on the right side for ten consecutive trials, was
191 excluded from further participation in the experiment.

192

193 *Data analyses*

194 Data was analysed by M.M., indicating correct, *i.e.* the cat chose the side which was pointed
195 towards, and incorrect, *i.e.* the cat chose the side which was not pointed towards, responses. An
196 inter-observer reliability analysis was conducted on 30 % of randomly chosen trials, which were
197 coded by a second observer (C.A.F.W.). Inter-observer agreement was 100 %. Statistical analyses

198 were performed in R 4.0.3 (The R Foundation for Statistical Computing, Vienna, Austria,
199 <http://www.r-project.org>). A generalised linear mixed model (GLMM) with a binomial distribution
200 and logit link was used to investigate differences in performance between different conditions in
201 the package lme4 (Bates et al., 2015). Trial outcome (successful or unsuccessful) was the response
202 variable, the signal type (ipsilateral or cross-body pointing), location (left or right) and the trial
203 number (1-20) were included as fixed factors, and the subject identity as a random effect. To assess
204 multicollinearity between fixed factors, we calculated variance inflation factors (VIFs) using the vif
205 function in the package car (Fox & Weisberg, 2011). VIFs for all factors were below 2, indicating that
206 there was no issue with multicollinearity (Zuur et al., 2009). To describe the variance explained by
207 our models, we provided marginal and conditional R^2 values that range from 0 to 1 and described
208 the proportion of variance explained by the fixed effects and by the fixed and random effects
209 combined, respectively (Nakagawa & Schielzeth, 2013). We calculated marginal and conditional R^2
210 values using the r.squaredGLMM function in MuMIn (version 1.15.6; Bartoń, 2019). We conducted
211 exact, two-tailed binomial tests to investigate whether cats used pointing gestures significantly
212 above chance. Cohen's h (h) was calculated as a measure of effect size, using the package pwr
213 (Champely, 2020). In individuals who completed the full 20 trials we further conducted binomial
214 tests to see whether individuals were successful above chance level. All datasets and the R script
215 used to conduct the statistical analyses are available as supplementary files.

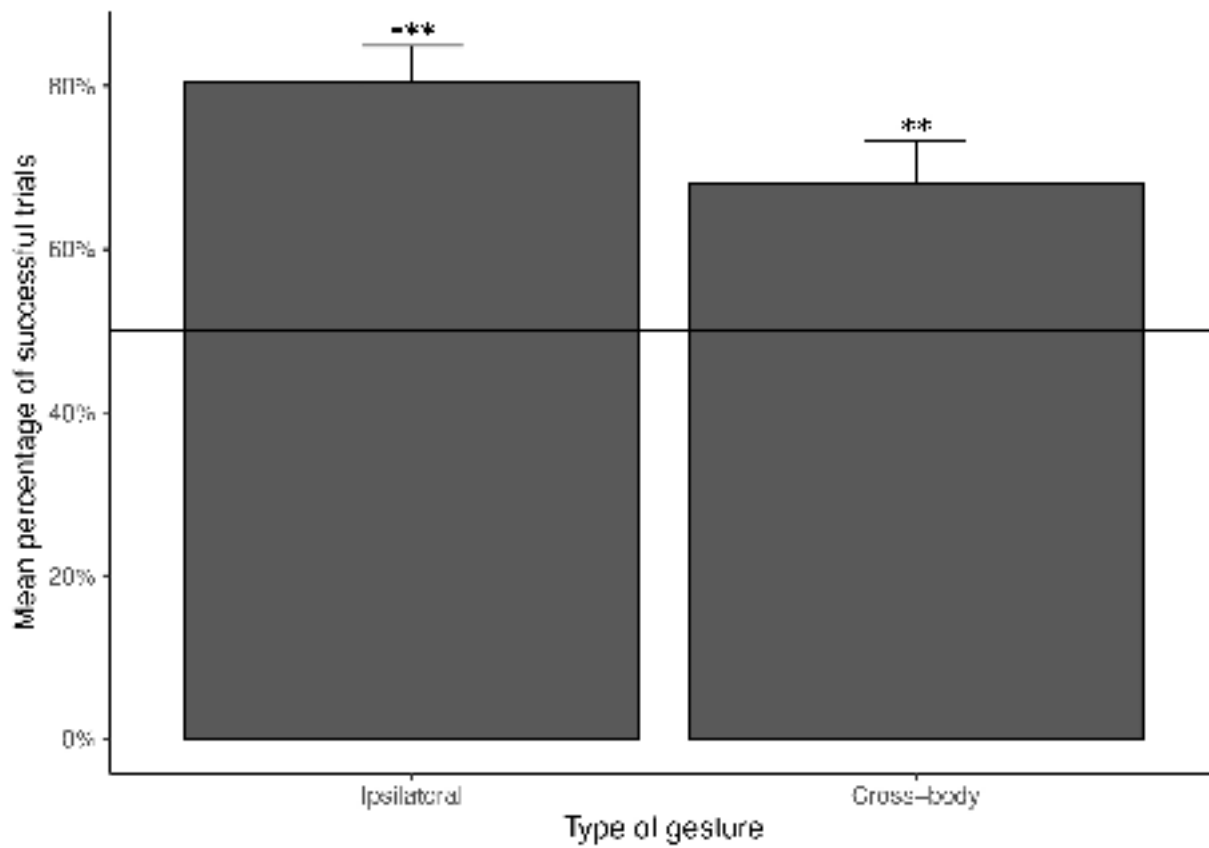
216

217 Results

218 On a group level, the success rate of cats was 74.4 %. Cats performed significantly above
219 chance level in both the ipsilateral pointing (Binomial test: $p < 0.001$, $h = 1.287$, [95% confidence
220 intervals = 0.702 - 0.884]) and cross-body pointing condition (Binomial test: $p = 0.002$, $h = 0.823$,
221 [95% confidence intervals = 0.564 - 0.78]; Figure 1). Trial number (GLMM: estimate \pm standard
222 deviation = -0.009 ± 0.032 , z -value = -0.284 , $p = 0.776$), rewarded side (GLMM: estimate \pm standard
223 deviation = 0.238 ± 0.371 , z -value = 0.372 , $p = 0.709$) and type of gesture (GLMM: estimate \pm
224 standard deviation = 0.667 ± 0.374 , z -value = 1.78 , $p = 0.074$) did not significantly affect the cats'
225 performances in the experiment (intercept: GLMM: estimate \pm standard deviation = 0.797 ± 0.473 ,
226 z -value = 1.685 , $p = 0.091$). Overall, 2 % of the variation in performance was explained by all fixed
227 factors together (R^2 marginal), and an additional 2 % of the variation in performance was explained
228 by the random factor (individual, R^2 conditional). On an individual level, 5 out of 7 cats who
229 completed 20 trials, performed significantly above chance level (individual 2: Binomial test: $p =$
230 0.011 , $h = 1.287$, [95% confidence intervals = 0.563 - 0.942], individual 3: Binomial test: $p < 0.001$, h
231 $= 1.854$, [95% confidence intervals = 0.683 - 0.987], individual 4: Binomial test: $p = 0.503$, $h = 0.402$,
232 [95% confidence intervals = 0.36 - 0.808], individual 5: Binomial test: $p = 0.011$, $h = 1.287$, [95%
233 confidence intervals = 0.563 - 0.942], individual 6: Binomial test: $p = 0.041$, $h = 1.047$, [95%
234 confidence intervals = 0.508 - 0.913], individual 7: Binomial test: $p = 0.823$, $h = 0.2$, [95% confidence
235 intervals = 0.315 - 0.769], individual 8: Binomial test: $p = 0.002$, $h = 1.55$, [95% confidence intervals
236 = 0.621 - 0.967]; Figure 2). Two cats only completed 10 trials. One of them succeeded in 8, the
237 other in 6 of these.

238

239



240

241 Figure 1. Mean percentage of trials plus standard error where the cats followed ipsilateral pointing
242 and cross-body pointing. Full line represents 50 % chance level. **P < 0.01; ***P < 0.001.

243

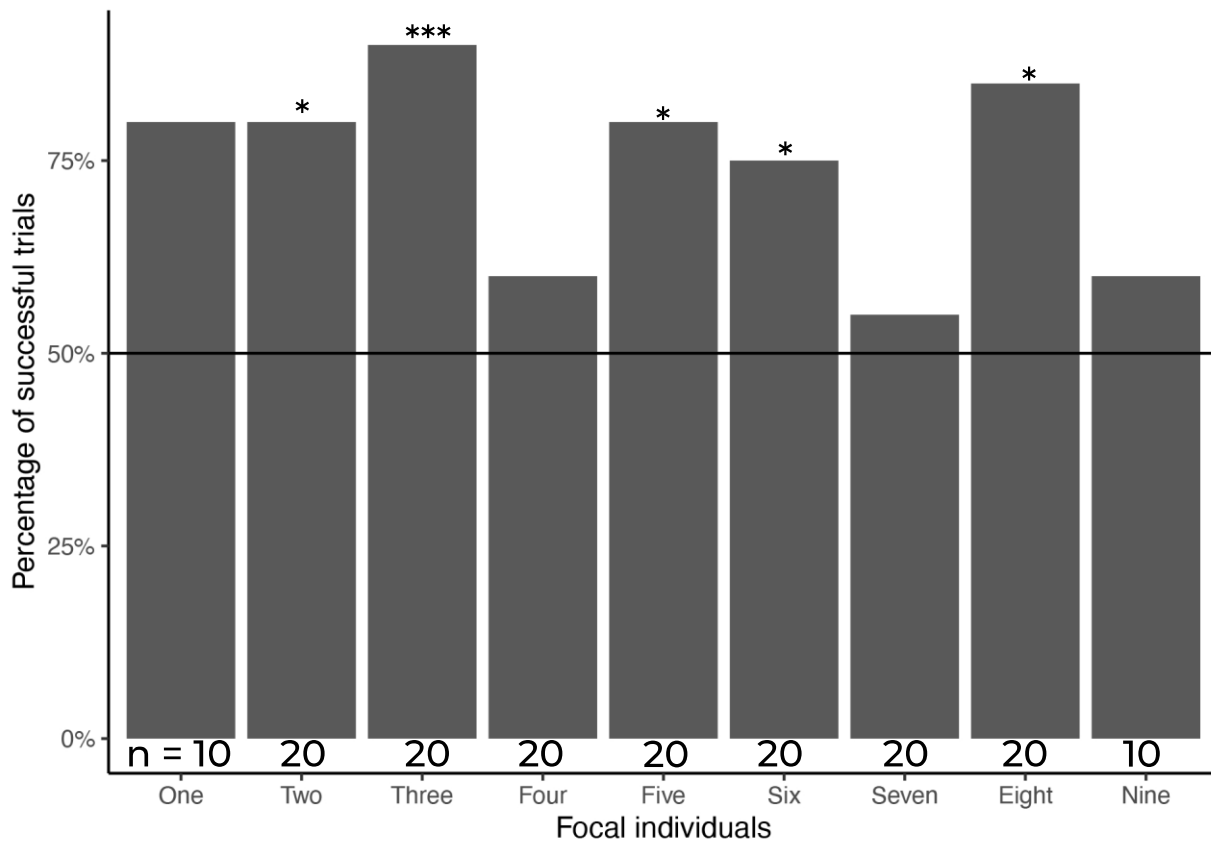


Figure 2: Percentage of successful trials for each focal individual. Sample size (n) indicates the number of trials per individual. Full line represents 50 % chance level. Binomial test: *P < 0.05; ***P < 0.001.

Discussion

The results of the present study show the cat's ability to follow human ipsilateral pointing gestures (Bard et al., 2021), which replicates findings of a previous study (Miklósi *et al.* 2005). Additionally, we show cats are sensitive to cross-body pointing cues. Out of the seven individuals tested in 20 trials, five followed human pointing cues significantly more often than expected by chance. We did not find a significant difference in performance between ipsilateral pointing and cross-body pointing. The ability to follow human cross-body pointing gestures has been previously shown in a wide variety of species (for a review see Pack, 2019).

Our results show that, similarly to dogs and some other species, the more solitary cats use communicative cues from humans. Cognitively, different mechanisms could be involved in the ability of cats to follow human communicative cues, such as stimulus or local enhancement as well as cue learning. If the subjects' choices had been influenced by rapid learning, the performance would be expected to improve over the testing trials (Kaminski et al., 2005; Malassis & Delfour, 2015; Miklósi et al., 2005). The trial number showed no significant influence on trial outcome. Thus, we conclude that subjects are not learning to follow a point during the course of testing.

From an evolutionary perspective, the finding that cats are sensitive to human pointing cues is interesting, as cats and their ancestors do not normally experience conspecifics pointing. It has previously been suggested that the process of domestication has selected for socio-cognitive abilities that enable domesticated species to better communicate with humans compared to wild species (Hare et al., 2002). In a previous study Miklósi et al. (2005) directly compared dogs' and cats' abilities to follow human pointing cues and attention-getting behaviour. While dogs and cats did not differ in their ability to follow human pointing cues, cats lacked some components of

281 attention-getting behaviour compared with dogs, in accord with the domestication hypothesis.
282 However, recent studies directly comparing human-socialized dogs and wolves show the wolves to
283 outperform dogs, in contrast to the domestication hypothesis (Range & Marshall-Pescini, 2022;
284 Udell et al., 2008, 2010). To investigate the effects of domestication on cats' performance, it would
285 be necessary to conduct comparable assessments of the sensitivity to human pointing gestures in
286 socialized individuals of wild cats (*Felis lybica* and/or *Felis silvestris*; Pongrácz, Szapu & Faragó,
287 2019).

288 Importantly, our study adds to a growing body of literature highlighting that less social
289 species are able to master socio-cognitive tasks. For example, non-social reptiles (*Geochelone*
290 *carbonaria*) and fish (*Spinachia spinachia*; *Cottus gobio*; *Barbatula barbatula*; *Platichthys flesus*)
291 have been shown to use social information (Webster & Laland, 2017; Wilkinson et al., 2010). It has
292 been previously suggested that socialisation with humans can enable animals to acquire
293 communicative skills which allow them to respond to cues from heterospecifics (Kaminski et al.,
294 2005; Nawroth et al., 2020; Proops et al., 2010; Range & Marshall-Pescini, 2022). However, we
295 would like to highlight that there are more parsimonious alternative explanations, namely following
296 human pointing via local and stimulus enhancement, which in the present experiment cannot be
297 ruled out.

298

299 Compared to similar studies with cats or dogs, where the experiments have been conducted
300 in the owners' homes (*e.g.*, Miklósi et al., 2005; Pongrácz et al., 2019), the standardisation of the
301 testing environment in the current study could be considered an advantage. In a previous study,
302 family-owned dogs outperformed kennel-housed dogs in their capacity to understand human
303 pointing gestures (D'Aniello et al., 2017; Lazarowski & Dorman, 2015). As mentioned above, cats do
304 not use pointing cues in conspecific communication, hence any previous experience of the cats that

305 participated in this study with pointing must have come from human-cat interactions in the shelter
306 or before cats came to the shelter. The shelter environment also means that cats have been living
307 in a group situation for extended periods of time, which could have allowed them to acquire certain
308 socio-cognitive skills that are less evident in cats without this extensive social experience with
309 conspecifics.

310

311 Similar to all other studies on animal cognition and behaviour, we need to consider potential
312 sample bias of our study population as outlined in the STRANGE framework (Webster & Rutz, 2020).
313 We must consider the social background of focal subjects and as mentioned above, we
314 acknowledge previous experience with conspecifics and heterospecifics (humans) in the group-
315 housed cats. Self-selection could have affected our results, as from the 200 cats in the shelter, we
316 only tested nine individuals who voluntarily participated in the experiment, based on the cat being
317 comfortable when isolated from the group and interacting readily with the human experimenter. It
318 could very well be that this procedure excluded focal subjects who are less responsive to human
319 pointing cues. Future investigations into individual differences in performance and cats' abilities to
320 follow human pointing cues would be desirable. As our focal subjects are shelter cats, we have very
321 little information about their rearing history and past experience, and no information about their
322 genetic make-up. Moreover, our experiment was of a short-term nature, capturing the cats'
323 responses during a short-term period. We did not intend to investigate potential natural changes in
324 responsiveness, *e.g.*, seasonal or ontogenetic changes, and these areas should be considered for
325 future studies.

326

327

328

329 **Acknowledgements**

330 We thank Johanna Miedel, the manager of Pesaleidja, for granting permission to work with
331 the cats. We would also like to thank the rest of the team of staff and volunteers at Pesaleidja
332 shelter for their guidance and cooperation on site. We also thank two anonymous reviewers and
333 the editor, Prof. Dorothy Munkenbeck Fragaszy for their comments, which greatly improved the
334 article.

335

336 **Conflict of interest**

337 The authors declare no conflict in interest

338

339 **Author contributions**

340 Conceptualization: MM and CAFW; Methodology: MM and CAFW; Investigation: MM;
341 Formal analysis: MM and CAFW; Supervision: CAFW; Writing: MM and CAFW.

342

References

- Bard, K. A., Keller, H., Ross, K. M., Hewlett, B., Butler, L., Boysen, S. T., & Matsuzawa, T. (2021). Joint attention in human and chimpanzee infants in varied socio-ecological contexts. *Monographs of the Society for Research in Child Development*, 86(4), 7–217.
- Bartoń, K. (2019). *MuMIn: Multi-Model Inference*. (1.43.6). <https://CRAN.R-project.org/package=MuMIn>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48.
- Bennett, V., Gourkow, N., & Mills, D. S. (2017). Facial correlates of emotional behaviour in the domestic cat (*Felis catus*). *Behavioural Processes*, 141, 342–350. <https://doi.org/10.1016/j.beproc.2017.03.011>
- Bhattacharjee, D., Mandal, S., Shit, P., Varghese, M. G., Vishnoi, A., & Bhadra, A. (2020). Free-ranging dogs are capable of utilizing complex human pointing cues. *Frontiers in Psychology*, 10, 2818. <https://doi.org/10.3389/fpsyg.2019.02818>
- Bradshaw, J. W. S. (2016). Sociality in cats: A comparative review. *Journal of Veterinary Behavior*, 11, 113–124. <https://doi.org/10.1016/j.jveb.2015.09.004>
- Bräuer, J., Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2006). Making inferences about the location of hidden food: Social dog, causal ape. *Journal of Comparative Psychology*, 120(1), 38.
- Champely, S. (2020). *pwr: Basic Functions for Power Analysis*. (R package version 1.3-0). <https://CRAN.R-project.org/package=pwr>
- Clark, H., Elsherif, M. M., & Leavens, D. A. (2019). Ontogeny vs. phylogeny in primate/canid comparisons: A meta-analysis of the object choice task. *Neuroscience & Biobehavioral Reviews*, 105, 178–189. <https://doi.org/10.1016/j.neubiorev.2019.06.001>

367 Clark, H., & Leavens, D. A. (2019). Testing dogs in ape-like conditions: The effect of a barrier on
368 dogs' performance on the object-choice task. *Animal Cognition*, 22, 1063–1072.

369 Clutton-Brock, J. (1994). The unnatural world: Behavioural aspects of humans and animals in the
370 process of domestication. In *Animals and Human Society: Changing Perspectives* (pp. 35–
371 47). Routledge.

372 D'Aniello, B., Alterisio, A., Scandurra, A., Petremolo, E., Iommelli, M. R., & Aria, M. (2017).
373 What's the point? Golden and Labrador retrievers living in kennels do not understand human
374 pointing gestures. *Animal Cognition*, 20(4), 777–787. [https://doi.org/10.1007/s10071-017-](https://doi.org/10.1007/s10071-017-1098-2)
375 1098-2

376 Deputte, B. L., Jumelet, E., Gilbert, C., & Titeux, E. (2021). Heads and tails: An analysis of visual
377 signals in cats, *Felis catus*. *Animals*, 11(9), 2752. <https://doi.org/10.3390/ani11092752>

378 Driscoll, C. A., Macdonald, D. W., & O'Brien, S. J. (2009). From wild animals to domestic pets, an
379 evolutionary view of domestication. *Proceedings of the National Academy of Sciences*,
380 106(Supplement_1), 9971–9978. <https://doi.org/10.1073/pnas.0901586106>

381 Fox, J., & Weisberg, S. (2011). *An {R} Companion to Applied Regression*. (second). Sage
382 Publications.

383 Fugazza, C., Sommesse, A., Pogány, Á., & Miklósi, Á. (2021). Did we find a copycat? Do as I Do in
384 a domestic cat (*Felis catus*). *Animal Cognition*, 24(1), 121–131.
385 <https://doi.org/10.1007/s10071-020-01428-6>

386 Gourkow, N., LaVoy, A., Dean, G. A., & Phillips, C. J. C. (2014). Associations of behaviour with
387 secretory immunoglobulin A and cortisol in domestic cats during their first week in an animal
388 shelter. *Applied Animal Behaviour Science*, 150, 55–64.
389 <https://doi.org/10.1016/j.applanim.2013.11.006>

390 Hall, N. J., Udell, M. A. R., Dorey, N. R., Walsh, A. L., & Wynne, C. D. L. (2011). Megachiropteran
 391 bats (pteropus) utilize human referential stimuli to locate hidden food. *Journal of*
 392 *Comparative Psychology*, 125(3), 341–346. <https://doi.org/10.1037/a0023680>
 393 Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social
 394 cognition in dogs. *Science*, 298(5598), 1634–1636. <https://doi.org/10.1126/science.1072702>
 395 Hare, B., Call, J., & Tomasello, M. (1998). Communication of food location between human and dog
 396 (*Canis familiaris*). *Evolution of Communication*, 2(1), 137–159.
 397 Hare, B., & Tomasello, M. (1999). Domestic dogs (*Canis familiaris*) use human and conspecific
 398 social cues to locate hidden food. *Journal of Comparative Psychology*, 113(2), 173–177.
 399 Herman, L. M., Abichandani, S. L., Elhajj, A. N., Herman, E. Y. K., & Sanchez, J. L. (1999).
 400 Dolphins (*Tursiops truncatus*) comprehend the referential character of the human pointing
 401 gesture. *Journal of Comparative Psychology*, 113(4), 347.
 402 Hopkins, W. D., Russell, J., McIntyre, J., & Leavens, D. A. (2013). Are chimpanzees really so poor
 403 at understanding imperative pointing? Some new data and an alternative view of canine and
 404 ape social cognition. *PLoS ONE*, 8(11), e79338.
 405 <https://doi.org/10.1371/journal.pone.0079338>
 406 Jaroš, F. (2018). Cat cultures and threefold modelling of human-animal interactions: On the example
 407 of Estonian cat shelters. *Biosemiotics*, 11(3), 365–386. [https://doi.org/10.1007/s12304-018-](https://doi.org/10.1007/s12304-018-9332-0)
 408 9332-0
 409 Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2005). Domestic goats, *Capra hircus*, follow gaze
 410 direction and use social cues in an object choice task. *Animal Behaviour*, 69(1), 11–18.
 411 <https://doi.org/10.1016/j.anbehav.2004.05.008>
 412 Kirchhofer, K. C., Zimmermann, F., Kaminski, J., & Tomasello, M. (2012). Dogs (*Canis familiaris*),
 413 but not chimpanzees (*Pan troglodytes*), understand imperative pointing. *PLoS ONE*, 7(2),
 414 e30913. <https://doi.org/10.1371/journal.pone.0030913>

415 Krause, M. A., Udell, M. A. R., Leavens, D. A., & Skopos, L. (2018). Animal pointing: Changing
 416 trends and findings from 30 years of research. *Journal of Comparative Psychology*, 132(3),
 417 326–345. <https://doi.org/10.1037/com0000125>
 418 Lazarowski, L., & Dorman, D. C. (2015). A comparison of pet and purpose-bred research dog (*Canis*
 419 *familiaris*) performance on human-guided object-choice tasks. *Behavioural Processes*, 110,
 420 60–67. <https://doi.org/10.1016/j.beproc.2014.09.021>
 421 Lyn, H., Russell, J. L., & Hopkins, W. D. (2010). The impact of environment on the comprehension
 422 of declarative communication in apes. *Psychological Science*, 21(3), 360–365.
 423 <https://doi.org/10.1177/0956797610362218>
 424 Malassis, R., & Delfour, F. (2015). Sea lions' (*Zalophus californianus*) use of human pointing
 425 gestures as referential cues. *Learning & Behavior*, 43(2), 101–112.
 426 <https://doi.org/10.3758/s13420-014-0165-7>
 427 Miklósi, Á., Pongrácz, P., Lakatos, G., Topál, J., & Csányi, V. (2005). A comparative study of the
 428 use of visual communicative signals in interactions between dogs (*Canis familiaris*) and
 429 humans and cats (*Felis catus*) and humans. *Journal of Comparative Psychology*, 119(2), 179.
 430 Miklósi, Á., & Soproni, K. (2006). A comparative analysis of animals' understanding of the human
 431 pointing gesture. *Animal Cognition*, 9(2), 81–93. <https://doi.org/10.1007/s10071-005-0008-1>
 432 Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R² from
 433 generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133–142.
 434 <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
 435 Nawroth, C., Ebersbach, M., & Borell, E. V. (2016). Are domestic pigs (*Sus scrofa domestica*) able
 436 to use complex human-given cues to find a hidden reward? *Animal Welfare*, 25(2), 185–190.
 437 <https://doi.org/10.7120/09627286.25.2.185>

438 Nawroth, C., Martin, Z. M., & McElligott, A. G. (2020). Goats follow human pointing gestures in an
 439 object choice task. *Frontiers in Psychology*, 11, 915.
 440 <https://doi.org/10.3389/fpsyg.2020.00915>

441 Pack, A. A. (2019). Pointing. In J. Vonk & T. Shackelford (Eds.), *Encyclopedia of Animal Cognition*
 442 *and Behavior* (pp. 1–19). Springer International Publishing. [https://doi.org/10.1007/978-3-](https://doi.org/10.1007/978-3-319-47829-6_753-1)
 443 [319-47829-6_753-1](https://doi.org/10.1007/978-3-319-47829-6_753-1)

444 Pisa, P. E., & Agrillo, C. (2009). Quantity discrimination in felines: A preliminary investigation of
 445 the domestic cat (*Felis silvestris catus*). *Journal of Ethology*, 27(2), 289–293.
 446 <https://doi.org/10.1007/s10164-008-0121-0>

447 Pongrácz, P., Szapu, J. S., & Faragó, T. (2019). Cats (*Felis silvestris catus*) read human gaze for
 448 referential information. *Intelligence*, 74, 43–52. <https://doi.org/10.1016/j.intell.2018.11.001>

449 Povinelli, D. J., Reaux, J. E., Bierschwale, D. T., Allain, A. D., & Simon, B. B. (1997). Exploitation
 450 of pointing as a referential gesture in young children, but not adolescent chimpanzees.
 451 *Cognitive Development*, 12(4), 423–461. [https://doi.org/10.1016/S0885-2014\(97\)90017-4](https://doi.org/10.1016/S0885-2014(97)90017-4)

452 Proops, L., Walton, M., & McComb, K. (2010). The use of human-given cues by domestic horses,
 453 *Equus caballus*, during an object choice task. *Animal Behaviour*, 79(6), 1205–1209.
 454 <https://doi.org/10.1016/j.anbehav.2010.02.015>

455 Range, F., & Marshall-Pescini, S. (2022). Comparing wolves and dogs: Current status and
 456 implications for human ‘self-domestication.’ *Trends in Cognitive Sciences*,
 457 S1364661322000183. <https://doi.org/10.1016/j.tics.2022.01.003>

458 Russell, J. L., Lyn, H., Schaeffer, J. A., & Hopkins, W. D. (2011). The role of socio-communicative
 459 rearing environments in the development of social and physical cognition in apes:
 460 Development of social and physical cognition in apes. *Developmental Science*, 14(6), 1459–
 461 1470. <https://doi.org/10.1111/j.1467-7687.2011.01090.x>

- Serpell, J. A. (2013). Domestication and history of the cat. In D. C. Turner & P. Bateson (Eds.), *The Domestic Cat* (3rd ed., pp. 83–100). Cambridge University Press.
<https://doi.org/10.1017/CBO9781139177177.011>
- Shreve, K. R., & Udell, M. A. R. (2015). What’s inside your cat’s head? A review of cat (*Felis silvestris catus*) cognition research past, present and future. *Animal Cognition*, 18(6), 1195–1206. <https://doi.org/10.1007/s10071-015-0897-6>
- Smet, A. F., & Byrne, R. W. (2013). African elephants can use human pointing cues to find hidden food. *Current Biology*, 23(20), 2033–2037. <https://doi.org/10.1016/j.cub.2013.08.037>
- Soproni, K., Miklósi, Á., Topál, J., & Csányi, V. (2002). Dogs’ (*Canis familiaris*) responsiveness to human pointing gestures. *Journal of Comparative Psychology*, 116(1), 27–34.
<https://doi.org/10.1037/0735-7036.116.1.27>
- Takagi, S., Chijiwa, H., Arahori, M., Saito, A., Fujita, K., & Kuroshima, H. (2021). Socio-spatial cognition in cats: Mentally mapping owner’s location from voice. *PLOS ONE*, 16(11), e0257611. <https://doi.org/10.1371/journal.pone.0257611>
- Tauzin, T., Csík, A., Kis, A., Kovács, K., & Topál, J. (2015). The order of ostensive and referential signals affects dogs’ responsiveness when interacting with a human. *Animal Cognition*, 18(4), 975–979. <https://doi.org/10.1007/s10071-015-0857-1>
- Tavernier, C., Ahmed, S., Houpt, K. A., & Yeon, S. C. (2020). Feline vocal communication. *Journal of Veterinary Science*, 21(1), e18. <https://doi.org/10.4142/jvs.2020.21.e18>
- Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2008). Wolves outperform dogs in following human social cues. *Animal Behaviour*, 76(6), 1767–1773.
<https://doi.org/10.1016/j.anbehav.2008.07.028>
- Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2010). What did domestication do to dogs? A new account of dogs’ sensitivity to human actions. *Biological Reviews*, 85(2), 327–345.
<https://doi.org/10.1111/j.1469-185X.2009.00104.x>

487 Webster, M. M., & Laland, K. N. (2017). Social information use and social learning in non-grouping
 488 fishes. *Behavioral Ecology*, 28(6), 1547–1552. <https://doi.org/10.1093/beheco/arx121>
 489 Webster, M. M., & Rutz, C. (2020). How STRANGE are your study animals? *Nature*, 582(7812),
 490 337–340. <https://doi.org/10.1038/d41586-020-01751-5>
 491 Wilkinson, A., Kuenstner, K., Mueller, J., & Huber, L. (2010). Social learning in a non-social reptile
 492 (*Geochelone carbonaria*). *Biology Letters*, 6(5), 614–616.
 493 <https://doi.org/10.1098/rsbl.2010.0092>
 494 Woodward, A. L., & Guajardo, J. J. (2002). Infants’ understanding of the point gesture as an object-
 495 directed action. *Cognitive Development*, 17(1), 1061–1084. [https://doi.org/10.1016/S0885-](https://doi.org/10.1016/S0885-2014(02)00074-6)
 496 2014(02)00074-6
 497 Zhang, L., Needham, K. B., Juma, S., Si, X., & Martin, F. (2021). Feline communication strategies
 498 when presented with an unsolvable task: The attentional state of the person matters. *Animal*
 499 *Cognition*, 24(5), 1109–1119. <https://doi.org/10.1007/s10071-021-01503-6>
 500 Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed Effects Models*
 501 *and Extension in Ecology With R*. Springer.
 502