Catcalls: exotic cats discriminate the voices of familiar caregivers

Taylor Crews [1] , Jennifer M Vonk [Corresp., 2] , Molly McGuire [3]

1 Oakland University, Rochester, Michigan, United States

2 Psychology, Oakland University, Rochester, Michigan, United States

3 Animal Wellbeing, Zoo Miami, Miami, Florida, United States

Corresponding Author: Jennifer M Vonk
Email address: vonk@oakland.edu

Background. The ability to differentiate familiar from unfamiliar humans has been considered a product of domestication or early experience. Few studies have focused on voice recognition in *Felidae* despite the fact that this family presents the rare opportunity to compare domestic species to their wild counterparts and to examine the role of human rearing. **Methods**. We tested whether 25 members of 10 non-domestic *Felidae* species recognized familiar human voices by exposing them to audio playbacks of familiar and unfamiliar humans. In Study One, we presented seven cats of five species with sessions involving three playbacks of voices that varied in familiarity and use of the cats' names. In Study Two, we presented 24 cats with unfamiliar and then familiar voice playbacks using a dishabituation paradigm. We anticipated that human rearing and use of the cats' names would result in greater attention to the voices, as measured by the latency, duration, and intensity of responses regardless of subject sex and subfamily. **Results.** Cats overall responded more quickly to the most familiar voice in both studies. They also responded with greater duration and intensity to the familiar voice compared to the unfamiliar voices in Study Two. However, in this study, only human-reared cats showed significantly faster latencies to respond to familiar voices compared to unfamiliar voices, suggesting that close human contact rather than domestication is associated with the ability to discriminate between human voices. With cats of all species being prevalent in the human world, information regarding how they perceive and discriminate auditory cues could be beneficial for their husbandry and conservation.

11 **Catcalls: Exotic cats discriminate the voices of familiar caregivers**

14 Taylor Crews[1], Jennifer Vonk[1*], & Molly McGuire[2]

16 [1]Department of Psychology, Oakland University, Rochester MI, United States

17 [2] Animal Welfare, Zoo Miami, Miami FL, United States

20 *Corresponding Author:

21 Jennifer Vonk Orcid ID: 0000-0002-4362-5989,

22 654 Pioneer Drive, Rochester MI, 48309, United States

23 Email address: vonk@oakland.edu,

Abstract

Background. The ability to differentiate familiar from unfamiliar humans has been considered a product of domestication or early experience. Few studies have focused on voice recognition in *Felidae* despite the fact that this family presents the rare opportunity to compare domestic species to their wild counterparts and to examine the role of human rearing.

Methods. We tested whether 25 members of 10 non-domestic *Felidae* species recognized familiar human voices by exposing them to audio playbacks of familiar and unfamiliar humans. In Study One, we presented seven cats of five species with sessions involving three playbacks of voices that varied in familiarity and use of the cats' names. In Study Two, we presented 24 cats with unfamiliar and then familiar voice playbacks using a dishabituation paradigm. We anticipated that human rearing and use of the cats' names would result in greater attention to the voices, as measured by the latency, duration, and intensity of responses regardless of subject sex and subfamily.

Results. Cats overall responded more quickly to the most familiar voice in both studies. They also responded with greater duration and intensity to the familiar voice compared to the unfamiliar voices in Study Two. However, in this study, only human-reared cats showed significantly faster latencies to respond to familiar voices compared to unfamiliar voices, suggesting that close human contact rather than domestication is associated with the ability to discriminate between human voices. With cats of all species being prevalent in the human world, information regarding how they perceive and discriminate auditory cues could be beneficial for their husbandry and conservation.

Keywords: Felid, vocal discrimination, familiar human, rearing history

Introduction

49

50   The ability to recognize familiar and unfamiliar individuals plays a pivotal role in the

51   social lives of animals, and this is often accomplished through voice recognition. For example,

52   mother cats (*Felis cactus*) recognize the cries of their kittens (Szenczwe et al., 2016), lions

53   (*Panthera leo)* identify members within and outside of their social groups (Gilfillan et al., 2016),

54   spotted hyenas (*Crocuta crocuta*) respond more strongly to the whoops of cubs to whom they are

55   related (Holekamp et al., 1999), bottlenose dolphins (*Tursiops truncatus*) distinguish individuals

56   from whistle signatures (Janik, Sayigh, &Wells, 2016), and female great tit birds (*Parus major)*

57   discriminate their mate's call from highly similar neighbors' vocalizations (Blumenrath,

58   Dabelsteen & Pedersen, 2007). In addition to recognizing individual and familiar conspecifics, it

59   can be useful to identify familiar heterospecifics as demonstrated by nonhuman primates

60   (Candiotti, Zuberbühler, & Lemasson, 2013) and birds (Dhondt, & Lambrechts, 1992) that

61   identify individuals of neighboring species. In the modern world, animals and humans interact

62   with greater frequency, both in the wild and in the context of animals housed in human care.

63   With humans becoming a more common heterospecific for many animal species, other species

64   may develop the ability to discriminate human voices, and this may depend upon the nature of

65   exposure to humans. The ability has been attributed to the process of domestication, with

66   researchers pointing to the coetaneous nature of this behavior presenting alongside other methods

67   of cross-species communication, such as pointing and gaze-following, which seems to be found

68   primarily in domestic species (Hare et al., 2002; Topál et al., 2005). However, megachiropteran

69   bats (*Pteropus*) were able to follow point signals to locate hidden food items only when

70   socialized with humans from an early age (Hall et al., 2011), suggesting that socialization with

71   humans may be more important than domestication in facilitating an understanding of human

72   communicative behaviors. We tested recognition of familiar voices in non-domestic cats, some

73   of which were human reared, to explore these hypotheses.

74   Although recognition of human vocal cues has been investigated in many species, there is

75   little investigation of vocal recognition in exotic cats despite their prevalence in human care. The

76   majority of the research on this subject has been conducted with domestic species, such as

77   domestic dogs (*Canis lupus familiaris)* (Adachi, Kuwahata, & Fujita, 2007), horses (*Equus*

78   *caballus)* (d'Ingeo et al., 2019), pigs *(Sus scrofa domesticus)* (Bensoussan et al., 2019), and

79   domestic cats *(Felis catus)* (Saito & Shinozuka, 2013). The few studies that have examined non-

80   domestic species focused on animals that are naturally gregarious, such as gorillas *(Gorilla*

81   *gorilla)* (Salmi et al., 2021) and elephants (*Loxodonta africana)* (McComb et al., 2014). A single

82   study has been conducted with wild cats, on a group of eight hand raised (raised by humans)

83   male cheetahs (*Acinonyx jubatus*) (Leroux et al., 2018). In a review paper on the topic of

84   nonhumans discriminating human voices (Kriengwatana, Escudero, & Ten Cate, 2014), the only

85   relatively asocial species tested was the domestic cat (Saito & Shinozuka, 2013). The current

86   study extends this research to 25 individuals of 10 non-domestic felid species housed in human

87   care to provide insight into the necessary precursors of this ability.

88   The cat family, or *Felidae*, are of interest given their relatively asocial natural history

89   coupled with their close association with humans in modern society. They are a highly diverse

90   group consisting of 38 species (IUCN Red List, n.d.) divided into two subfamilies, *Pantherinae*

91   and *Felinae*. The single domestic member of the family *Felidae*, *Felis catus*, has a unique

92   domestication history. Unlike dogs, which may have been domesticated for the purpose of

93   hunting (Horard-Herbin, Tresset, & Vigne., 2014), or livestock animals domesticated for food

94   and labor (Mignon-Grasteau et al., 2005), much of the art and physical evidence of early

95   domestic cats show no signs of a specific function for cats in human care. They seemed instead

96   to have been primarily companions and figures of worship, although some researchers speculate

97   that their initial entrance into the human home was for pest control (Bradshaw, 2013). The most

98   difficult aspect for decoding the domestication timeline for cats has been the fact that it was not a

99   linear process. Breeding and back-crossing with wild populations of *F. silvestis lybica* continued

100   to bring the domestic cat back to its wild origins in Egypt, where it is believed that cat

101   domestication began. Even today, domestic cats can hybridize with members of the *F. silvestrus*

102   subgroup (*F. silvestrus lybica, F. silvestrus silvestris, F. silvestrus ornate,* etc.*)* to produce fertile

103   offspring. Hybridization between the domestic cat and other felid species, such as the African

104   serval (*Leptailurus serval)*, the Asian leopard cat (*Prionailurus bengalensis),* and the Geoffroy's

105   cat *(Leopardus geoffroyi)* are becoming more common in the pet trade. Domestic cats today

106   often behave so similarly to wild cats that studies of their behavior have been used to model

107   behavioral research for wild cat species (Mellen, 1992). This relatively short domestication

108   history, as well as the genetic proximity that domestic cats share with their wild cousins, puts

109   cats in the unique position of having a paw in two worlds, that of the human home and the wilds

110   from which they came.

111   Of the 38 species of cat, 37 are wild species dispersed across every continent, save for

112   Australia and Antarctica. Within the *Felidae* family, there are two subfamilies, Pantherinae and

113   Felinae. Pantherinae consists of what are colloquially known as "big cats" and includes seven

114   species: lions (*Panthera leo*), tigers (*Panthera tigris*), leopards (*Panthera pardus*), jaguars

115   (*Panthera onca*), snow leopards *(Panthera uncia),* and two species of clouded leopard (*Neofelis*

116   *nebulosa* and *Neofelis diardi)*. The remaining 31 species are included in the subfamily Felinae,

117   or "small cats" (Castello, Sliwa, & Kitchener, 2020). This subfamily is responsible for the

118   evolutionary line that produced the modern domestic cat, but members of both Pantherinae and

119   Felinae are commonly found in human care, housed in zoos, sanctuaries, preserves, and personal

120   collections in great numbers.

121   If wild cats share with domestic cats the ability to differentiate human voices, this would

122   suggest that this ability is not dependent on domestication or frequent human interaction. Saito

123   and Shinozuka (2013) demonstrated that domestic cats respond differently to their owner's voice

124   compared to the voices of unfamiliar humans. A single study has examined recognition of

125   familiar human voices in exotic cats. Leroux et al. (2018) found that a group of hand raised male

126   cheetahs discriminated between the voices of familiar and unfamiliar humans, as indicated by

127   greater visual attention and more rapid response to familiar human voices compared to

128   unfamiliar human voices. Anecdotal reports from keepers working with exotic cats at zoos and

129   sanctuaries are consistent with Leroux et al.'s findings that these species have the ability to

130   recognize familiar humans by their voices (personal observation, 2019). If social ecology is

131   critical for the development of this ability, lions (*Panthera leo*) may show stronger

132   discrimination of familiar voices compared to other species, as they are the only wild cat known

133   to live in large social groups (M. Sunquist & F. Sunquist, 2002).

134   In addition to social structure, rearing experiences with conspecifics can be a critical

135   component of social cognition. Hampson and Schwitzer (2016) examined the effects of hand

136   rearing on reproductive success in four big cat species (*panthera tigris*, *uncia uncia, acinonyx*

137   *jubatus* and *neofelis nebulosa)* and found decreases in litter size, higher rates of infant mortality,

138   and fewer instances of generational rearing (an individual's offspring successfully rearing

139   offspring of their own) from hand reared individuals compared to mother individuals for several

140   species. Mellen (1992) investigated the difference in adult sexual and non-sexual social behavior

141   in mother-raised versus human-raised domestic cats and found a significant difference in species-

142   normative behaviors as a function of rearing. Most relevant to the current study, there were also

143   differences in responses to familiar and unfamiliar humans such as heightened aggression, less

144   interest in social interaction, and a higher presentation of fear-related behaviors in the human-

145   reared kittens to unfamiliar (relative to familiar) humans. Mellen's results have informed

146   husbandry and rearing techniques in zoos, encouraging mother-rearing whenever possible

147   (Hampson & Schwitzer, 2016).

148   Whereas the preference for most species and facilities is that offspring are mother-raised

149   (Hampson & Schwitzer, 2016), there are some circumstances that require human intervention. In

150   the case of clouded leopards (*Neofelis nebulosa*), there is a high rate of infanticide with captive

151   mothers, as well as stress in mother reared offspring, which leads many facilities to hand rear

152   their clouded leopards (Clouded Leopard SSP, 2000). In cases of maternal neglect, wild orphans,

153   infanticide, or large litters that are physically taxing on the mother, animal care staff will rear the

154   cats to increase their chances of survival (Hines, n.d.). Although the findings of Saito and

155   Shinozuka (2013) and Leroux et al. (2018) suggest that the ability to discriminate voices is

156   present for domestic cats and cheetahs exposed to human voices at an early age, it is important to

157   extend these findings to other species, and to individuals that vary with regard to early contact

158   with humans. The animals housed in managed care frequently work closely with their human

159   caretakers, as a necessary aspect of their daily husbandry. Animal caretakers commonly use

160   verbal cues when working with the animals, especially during training and when calling the

161   animals by their names. These animals also may interact to some degree with the public

162   regularly, so that they hear many different voices and words, including their own names if those

163   are known by the public. It would be beneficial to know if these animals have the ability to

164   distinguish words and cues given by their keepers from those they may hear from the public.

165   With wild cats being common species to find in managed care, understanding how they perceive

166   and respond to vocal cues, including their names, when spoken by familiar or unfamiliar

167   individuals may have implications for captive felid management, as well as the welfare of wild

168   populations. With one of the gravest threats to wild cat species being negative human interaction

169   (Inskip & Zimmermann, 2009), these findings might provide further rationale to examine

170   human-feline relationships.

171   In managed care, it is common for individual animals to have names that follow them

172   throughout their lives. These names are used not only for record keeping, but also in training and

173   daily interactions with animal care staff. A follow-up to the vocal recognition study by Saito and

174   Shinozuka (2013) found that domestic cats responded more to their names than other words

175   (Saito et al., 2019), but whether exotic cats are more responsive to commands or greetings when

176   their names are spoken is unknown. There is much debate in the captive animal industry as to

177   whether names of animals should be posted publicly for visitors to know. The giving of a name

178   to an animal is a form of anthropomorphism, in which humans might unconsciously assign

179   characteristics and be more sympathetic to a named animal than to an unnamed animal

180   (Chartrand, Fitzsimons, & Fitzsimons, 2008). There is some evidence showing that

181   anthropomorphism has notable effects on a person's perceptions of and willingness to support

182   wildlife conservation (Manfredo et al., 2020). However, the constant repetition of a behavioral

183   cue, such as the calling of a name, without a subsequent reinforcer may desensitize the animal to

184   that cue, which could lead to complications in training and frustration for the animal

185   (Miltenberger, 2015). If the cats are responsive to their names regardless of whether they are

186   spoken to by a familiar or unfamiliar voice, the public might be discouraged from knowing and

187   calling the cats' names. On the other hand, if the cats selectively respond to their names when

188   spoken by familiar individuals, this will have relevance to understanding the cats' bond with

189   their keepers.

190   The purpose of this study was to examine recognition of familiar human voices in

191   captively-managed exotic cats excluding the domestic cat, *F. catus*, as well as any hybrids of the

192   domestic cat, such as savannah (*Felis catus × Leptailurus serval*) and bengal cats (*Felis catus x*

193   *Prionailurus bengalensis)*. We conducted two studies using slightly different playback

194   procedures. In Study One, we presented a small group of captive cats with six 3-trial sessions

195   including playbacks of unfamiliar, less familiar and more familiar caregiver voices either using

196   their name or not. In Study Two, we used the habituation-dishabituation paradigm (Saito &

197   Shinozuka, 2013) with a larger group of cats. These subjects were presented with a series of

198   audio playbacks of three different unfamiliar humans speaking the same phrase, then a playback

199   of a familiar voice and, finally, a fourth unfamiliar voice. This procedure allowed effects of

200   familiarity to be assessed in a single session with no prior training. If the subjects habituate to the

201   sound of strangers' voices, but show a rebound effect in attention and responsiveness during the

202   fourth familiar voice playback, this would suggest recognition and discrimination of the familiar

203   voice from among other voices. We compared the intensity, latency, and duration of responses

204   (gaze direction, locomotion, head movement, ear movement, and vocalizations) to the five vocal

205   cues in sessions in which the subjects' names were or were not spoken, and examined the

206   predictive factors of sex, subfamily (*Pantherinae* versus *Felinae*) and rearing history (hand-

207   reared vs. mother-reared).

208   We hypothesized that familiarity would lead to greater attention and stronger responses,

209   as measured by faster latencies to respond and greater intensity and duration of reactionary

210   behaviors following the familiar voice relative to the other voices. Measures of attentiveness and

211   responsiveness include behaviors such as head, ear, and body orientation, movement towards or

212   away from the sound, and vocalizations. Responses are collapsed across all measured behaviors

213   as was done by Saito and Shinozuka (2013), due to the rarity of any single behavior, making

214   these behaviors challenging to measure individually. We also predicted an interaction between

215   rearing and familiarity in that cats that have been hand-reared will respond with greater attention

216   and responsiveness to voices they are familiar with compared to cats that have been mother-

217   reared. Lastly, we predicted that cats will respond with greater attention and stronger responses

218   when the cues include their names, as opposed to the cues with no name spoken, and that the use

219   of a name will interact with familiarity to predict the intensity of responses, such that the cats

220   would show a stronger response to their name only when spoken by a familiar speaker.

221   **Study One**

222   **Materials and Methods**

223   The experiments reported here were reviewed and approved by Oakland University's

224   IACUC (Protocol # 2021-1155).

225   *Subjects*

226   Subjects included seven individuals of five species (*P. tigris, A. jubatus, L. serval, P.*

227   *concolor, L. canadensis*) housed at Zoo Miami in Florida and the Creature Conservancy in Ann

228   Arbor, MI. Information about each subject's subfamily (Pantherinae or Felinae), sex, and rearing

229   history (hand-reared or mother-reared) was gathered. Rearing history was categorized as hand

230   reared (reared exclusively by humans starting at no later than four months of age - the start of the

231   weaning period for most large exotic cats; Jhala & Sadhu, 2017) or mother reared (raised

232   exclusively by their mother, or co-raised with the mother and humans, from birth to at least four

233   months of age).

234   ***Materials***

235   Audio recordings for each subject were taken using a Zoom h1n Handy recorder and

236   played back for the subjects using an Ultimate Ears BOOM 3 Bluetooth speaker. Observations

237   were recorded using a GoPro Hero 10. Data were coded and analyzed by a naïve coder using

238   freely available BORIS v.8.20. software. All testing occurred at the cat's home facility, in their

239   typical enclosure. The researcher performed all playback sessions, as well as recorded all

240   observations, from outside of the enclosure. Each cat was exposed to three different voices and

241   two different cue types during their playback sessions. The voices were categorized as Most

242   Familiar (MF), Less Familiar (LF), and Unfamiliar (UF). The MF voice came from a human that

243   the cat was very familiar with, ideally the cat's primary keeper or trainer. If the facility did not

244   assign primary trainers or keepers, then we used the voice of the person who had worked with

245   the cat for the longest period of time. The LF voice was a human that the cat had heard before,

246   but had minimal structured interaction with. This person was either a member of staff that did

247   not work with the cat, an intern, or a volunteer. The LF voice could not have actively participated

248   in training or care of the cat, which included but was not limited to feeding, directly providing

249   enrichment, or participating in husbandry tasks such as veterinary care. The UF voices were the

250   voices of four different sex-matched people the cat had never encountered or heard before. These

251   recordings were provided by individuals that had not been to the facility the cat currently resided

252   at or had resided at in the past. The two cue types the subjects were given were Name Absent

253   (NA) and Name Present (NP). The Name Absent cue was a short phrase that the cat was familiar

254   with, "Good morning, how are you doing today?". This phrase was selected from the results of a

255   poll from exotic cat keepers on zookeeping Facebook pages, in which they submitted a phrase

256   they speak regularly to the cats in their care. Some variation of the used phrase was found to be

257   the most common occurrence across facilities. The Name Present cue matched the Name Absent

258   cue, but the cat's name was said in the phrase, i.e., "Good morning, Harper, how are you doing

259   today?". In instances where the cat had multiple names, such as registered names, house names,

260   or public names, the name that was used was the one that the animal care staff used most

261   frequently.

262   Each speaker provided six different recordings, three of them speaking the NA cue, and

263   three of them speaking the NP cue. All recordings were made in a quiet room with no additional

264   voices in the background. The recordings were less than 30 seconds long. The speakers were be

265   controlled for sex, volume, and tone of voice, matching the MF voice. A total of 18 recordings

266   were collected for each cat to ensure the cats never heard the same recording more than once to

267   control for habituation.

268   ***Procedure***

269   Each cat participated in six 3-trial playback sessions, with each session consisting of one

270   playback from each speaker (MF, LF, UF). The type of cue given by each speaker (NA or NP) as

271   well as the order of the speakers was randomized for each session. Each speaker's voice was

272   presented three times in each name condition across the course of the study.

273   A wireless speaker was set up outside of the enclosure in the visitor area, and was no

274   closer than three feet away from the primary containment barrier. The researcher and observation

275   recording equipment were also outside of the enclosure in visitor space (Figure 1). Prior to each

276   trial, the cat must have been on exhibit for at least 15 minutes and must have been awake. The

277   time allotment was to avoid potential distraction or inattention due to examining the space for

278   food or enrichment items. All trials were performed in the absence of visitors, either before or

279   after operating hours, during lulls in visitation, or on days the facility was not open to the public.

280   Each three-trial session lasted for 28 minutes total. Observations occurred for a total of six

281   minutes per trial, with three minutes of baseline prior to the playback, and for three minutes

282   following the end of the playback with a minimum of five minutes between each trial. If more

283   than one session was conducted for the same subject in a day, each session occurred at least one

284   hour following the previous session, and no more than three sessions were conducted in a single

285   day.

286   The behaviors coded were those inferred to indicate interest or attention to the location

287   of the playback, such as change in gaze direction, ear and head movement, locomotion towards

288   or away from the sound, or response vocalizations. Behaviors were recorded for three minutes

289   before the playback, during the playback and for three minutes following the end of the

290   recording. Pre-trial recording allowed the establishment of baseline behaviors for the cat prior to

291   the introduction of the cue. Recording for an extended period after the playback also gave us the

292   ability to code for latency (how long after the recording did the reaction take place), intensity

293   (how strong of a reaction was there), and follow up behaviors. Behaviors were coded from video

294   recordings taken of each trial by two coders.

295   **Results**

296   *Reliability*

297   To control for the reliability of our behavioral coding, each video was coded by two coders.

298   Results were compared between a random selection of 25% of the sessions. A Pearson's

299   Correlation found significant correlations between the two coders for latency *(r= .998 p=*

300   *<.001), duration (r=.997, p= <.001), and intensity (r=.900, p= <.001).*

301

302   ***Response to Playbacks***

303   A repeated-measures ANOVA of latency to respond with name (absent, present) and

304   familiarity (unfamiliar, less familiar, most familiar) along with their interaction as within-

305   subjects factors revealed a significant main effect of familiarity ($F_{2,10} = 4.026$, $p = .052$) that was

306   qualified by its interaction with name ($F_{2,10} = 6.082$, $p = .019$). Within-subjects contrasts

307   revealed that response to the unfamiliar voice differed from response to the most familiar voice

308   ($F_{1,5} = 7.895$, $p = .038$). To explore the interaction, we conducted separate ANOVAs for name

309   present and absent conditions. There was no significant main effect of familiarity when the cats'

310   names were spoken, ($F_{2,10} = 2.816$, $p = .107$) but the effect approached significance when the

311   names were not spoken ($F_{2,10} = 3.310$, $p = .072$). Cats responded most quickly to the most

312   familiar voice in both name conditions. However, the pattern of results differed slightly (see

313   Figure 2). If the name was spoken, the cats responded more quickly to both familiar voices

314   compared to the unfamiliar voice, but if the name was not spoken, cats responded more quickly

315   to the most familiar and unfamiliar voices compared to the less familiar voice.

316   A repeated-measures ANOVA of duration of response with name (absent, present) and

317   familiarity (unfamiliar, less familiar, most familiar) along with their interaction as within-

318   subjects factors revealed no significant effects. However, the main effect of name approached

319   significance, ($F_{1,10} = 4.610$, $p = .085$). The tendency was for the cats to respond for longer when

320   their name was not spoken.

321   A repeated-measures ANOVA of intensity of response with name (absent, present) and

322   familiarity (unfamiliar, less familiar, most familiar) along with their interaction as within-

323   subjects factors revealed no significant effects. However, the effect of familiarity approached

324   significance ($F_{2,10} = 3.503$, $p = .070$) with cats responding more intensely to the most familiar

325   versus the unfamiliar voice ($F_{1,5} = 6.958$, $p = .046$).

326 **Discussion**

327   We had a fairly small sample of cats in Study One so our analyses were under-powered.

328   Nonetheless, the trends pointed to the possibility that cats responded differentially to familiar

329   versus unfamiliar voices. Specifically, they were significantly quicker to respond when the voice

330   was of their most familiar caregiver relative to less familiar and unfamiliar voices. They

331   responded more similarly to the two familiar voices versus the unfamiliar voice when their name

332   was spoken. We needed a larger sample of cats to further explore these potential effects and to

333   examine the effects of human-rearing, so we decided to streamline the procedure and focus on

334   voices most familiar to cats in Study Two.

335 **Study Two**

336   Given the promising results of Study One, we wished to continue testing with a larger

337   sample of cats. To include cats from various facilities, we decided to minimize the number of

338   required sessions by shifting to the dishabituation paradigm used by Saito and Shinozuka (2013)

339   and focusing on the most familiar caregiver's voice. We believed this method would allow us to

340   witness a stronger response to the familiar voice when directly contrasted with unfamiliar voices

341   within the same sessions.

342 **Materials and Method**

343 ***Subjects***

344   Our sample included 24 individuals across 10 species (Table 1). Some cats participated in

345 both studies. We did not differentiate between subspecies in this study, i.e., Malayan tigers (*P.*

346 *tigris tigris)* and Sumatran tigers (*P. tigris sumatrae)* were classified as tigers. Rearing history

347 was categorized as in Study One.

348 ***Materials***

349   Audio recordings for each subject were secured using a Zoom h1n Handy recorder and

350 played back for the subjects using an Ultimate Ears BOOM 3 Bluetooth speaker. Observations

351 were recorded using a GoPro Hero 10. Data were coded and analyzed by two naive coders using

352 freely available BORIS v.8.20. software. All testing occurred at the cats' home facilities, in their

353 typical habitat or back holding area. The researcher performed all playback sessions, as well as

354 recorded all observations, from outside of the enclosure. Each cat was exposed to five different

355 voices and two different cue types during the playback sessions. The voices were categorized as

356 Most Familiar (MF) and Unfamiliar (UF). The MF voice was a human that the cat was very

357 familiar with, ideally the cat's primary keeper or trainer. If the facility did not assign primary

358 trainers or keepers, then we used the voice of the individual currently working with the cat who

359 had worked with the cat for the longest duration. The UF voices were the voices of four different

360 people the cat had never encountered or heard before. These recordings were provided by

361 individuals that had not been to the facility at which the cat currently resided or had resided in

362 the past. The two cue types the animals were given were Name Absent (NA) and Name Present

363 (NP) as in Study One.

364   Each human speaker provided two different recordings, one for the NP condition, and

365   one for the NA condition. All recordings were made in a quiet room with no additional voices in

366   the background and were each less than five seconds. The speakers were matched for sex (within

367   subjects), volume, and tone of voice. All audio files were edited so that the playbacks all played

368   with 1 dB and 2 Hz of the familiar voice using Audacity audio editing software. The order of the

369   UF voices was randomized for each subject to control for preferences for specific voices.

370   ***Procedure***

371   We used the habituation-dishabituation paradigm (Saito & Shinozuka, 2013). The

372   playbacks for each session were in the order of unfamiliar voice 1, unfamiliar voice 2, unfamiliar

373   voice 3, most familiar voice, unfamiliar voice 4. Unfamiliar voices were randomized in order

374   between NA and NP sessions. Each cat participated in two playback sessions (one NA and one

375   NP), with each session consisting of five audio recordings, three UF voices, the MF voice, and a

376   final UF voice with 30 seconds of interstimulus silence between each voice. The order of

377   sessions, either NA or NP, was randomized across subjects. A wireless speaker was positioned

378   outside the habitat or back holding area, in the visitor area if possible, and was no closer than

379   three feet from the primary containment barrier. The researcher and observation recording

380   equipment were outside of the enclosure and in visitor space, with the researcher standing behind

381   the camera (Figure 1). The researcher did not make eye contact with the subject or engage with

382   them prior to or during recording. Prior to each trial, the cat must have been on exhibit for at

383   least 15 minutes and must have been awake for the duration of the trial to avoid potential

384   distraction or inattention due to the subject examining the space for food or enrichment items.

385   Each subject was provided an acclimation period with the researcher and the equipment. If the

386   subject showed marked interest in the researcher or equipment, sessions did not start until the

387   subject had shown no interest or attention to the recording equipment or researcher for at least

388   two minutes. All trials were performed in the absence of visitors, either before opening hours,

389   during lulls in visitation, or on days the facility was not open to the public. Observations

390   occurred for a maximum of 3.5 minutes. If more than one session was conducted for the same

391   subject in a day, the second session occurred at least one hour following the first session.

392   The subjects were actively monitored for the duration of each session for stress

393   behaviors, such as repeated aggressive reactions, pacing, or other signs of distress. The animal

394   care staff was also consulted prior to any observation to discuss specific behaviors to be aware of

395   for each individual. No abnormal behaviors indicating stress due to the playback sessions were

396   recorded in any of the subjects.

397   Two naïve coders coded the same behaviors as in Study One, such as change in gaze

398   direction, ear and head movement, locomotion towards or away from the sound, or response

399   vocalizations, and were coded for latency (how long after the recording did the reaction occur),

400   duration (amount of time behavior lasted from beginning to end), and intensity (strength of a

401   reaction). A lack of response was recorded for a latency of 30 seconds, the amount of time

402   between each playback, and a duration of 0 seconds. Intensity was rated on a scale of 0-5 with 0

403   indicating no response and 5 indicating a full head turn towards the speaker or locomotion

404   towards the speaker. Behaviors were coded from video recordings of each session. Both positive

405   and negative response behaviors were assessed, as per the Standardized Ethogram for Felidae

406   (Stanton, Sullivan, & Fazio, 2015). A negative behavior was defined as an aversive reaction to

407   the sound, and included movement away from the sound, aggressive movement towards the

408   sound (charging or bluff-charging), or aggressive vocalizations (hisses, roars, growls), although

409   the only negative behaviors recorded were species-typical hissing from two serval subjects. To

410 aid the accuracy of vocalization coding, coders were provided with auditory examples of

411 observed vocalizations, as well as their context. The auditory examples were separate from the

412 video recordings coded. Coding was performed by two naïve observers from the undergraduate

413 Psychology program at Oakland University. The coders were trained on a test video to identify

414 possible behaviors that may be observed in each video, as well as to train them on the BORIS

415 software. Both coders were naive to any difference in the voice playbacks, only being informed

416 that there were five playbacks that would occur, and what words the playback would include for

417 accurate identification.

418 *Data Analysis*

419   Data were analyzed using a mixed-model ANOVA for each of the outcomes of latency,

420 duration, and intensity of responses. The within-subject variables of name use (NA, NP) and

421 playback trial (1-5), as well as the between-subject variables of rearing style (mother-reared,

422 hand reared), sex, and subfamily were examined. We could not examine species differences due

423 to the small sample sizes within each species.

424 **Results**

425   All data are available at https://osf.io/9vuk5/.

426 *Reliability*

427   To control for the reliability of our behavioral coding, each video was coded by two naïve

428 coders. Results were compared between a random selection of 30% of the sessions (half name

429 present and half name absent). A Pearson's Correlation found significant correlations between

430 the two coders for latency *(r= .968, p= <.001),* duration *(r=.913, p= <.001),* and intensity

431 *(r=.978, p= <.001).*

432 ***Response to Playbacks***

433   For latency, a main effect was found for subfamily ($F_{1,23}$=*7.386, p= .015*), with subjects

434   from Felinae responding more quickly (M=7.505, SD=1.369) than subjects from Pantherinae

435   (M=13.360, SD=1.767). A statistically significant effect was also found for playback

436   ($F_{1,23}$=3.555, *p*= .011). Simple contrasts indicated that the cats responded significantly more

437   quickly to the fourth playback trial (the familiar voice) compared to each of the other trials.

438   However, playback also significantly interacted with sex ($F_{1,23}$=3.176, *p*=.019, Figure 3) and

439   rearing history ($F_{1,23}$=2.780, *p*=.034, Figure 4). To understand this two-way interaction, a mixed-

440   model ANOVA was conducted, with the data split by sex. A significant effect was found for

441   playback with males ($F_{1,13}$=3.847, *p*=.010*)*, but not for females ($F_{1,9}$=2.683, *p*=.560*)*. A mixed-

442   model ANOVA also was also conducted with the data split by rearing style. A significant effect

443   was found for playback with hand-reared cats ($F_{1,15}$=7.206, *p*=<.001) but not for mother-reared

444   cats ($F_{1,7}$=.536, *p*=.711).

445   For intensity, a statistically significant effect was found for playback ($F_{1,23}$=12.01, *p*=

446   <.001). Simple contrasts indicated that the cats responded with significantly more intensity to the

447   fourth playback trial (the familiar voice) compared to each of the other trials (Figure 5). There

448   were no other significant effects or interactions for intensity.

449   For duration, a statistically significant effect was found for playback ($F_{1,23}$=3.826, *p*=

450   .008). Simple contrasts indicated that the cats responded for significantly longer to the fourth

451   playback trial (the familiar voice) compared to each of the other trials (Figure 6). There were no

452   other significant effects or interactions for duration.

453   **Discussion**

454   The results from Study Two were consistent with those of Study One in that the cats

455   responded more quickly to the familiar compared to the unfamiliar voices, and there was no main

456   effect of name. There was an additional significant effect of intensity, with cats responding with

457   more intensity to the familiar versus the unfamiliar voices. In this study, with the larger sample,

458   we were also able to examine effects of rearing and found that the effect on latency was driven

459   by the hand-reared cats. More surprisingly, the effect was also significant for male, but not

460   female cats. Thus, across two different methods of playback, non-domestic cats showed evidence

461   of differentiating familiar human voices from unfamiliar voices, similar to what has been shown

462   in domestic cats (Saito & Shinozuka, 2013) and cheetahs (Leroux et al., 2018). The findings

463   suggest that this ability to discriminate human voices is not dependent upon the process of

464   domestication but likely depends upon early rearing experiences and daily exposure. It is

465   important to note that all but two of our subjects were reared in captivity (not wild born; the

466   exceptions are two cougars at the Cincinnati Zoo) and that most of the hand-reared cats had

467   transitioned to protected contacted early in life. However, six of the hand-reared cats remain in

468   close human contact – serving as ambassador cats to promote education at the zoos where they

469   are housed. Therefore, it is possible that effects are enhanced by continued close contact with

470   humans.

471   **General Discussion**

472   Across measures of latency, duration, and intensity, exotic cats clearly demonstrated the

473   ability to differentiate familiar and unfamiliar human voices as they reacted more strongly to the

474   voices of familiar humans. Whereas this ability has been observed in domestic cats (Saito &

475   Shinozuka, 2013) and in hand reared, male cheetahs (Leroux et al., 2018), this is the first time

476   such an ability has been demonstrated in nine additional exotic cat species (Table 1), and the first

477   time that early socialization and sex have been examined as possible contributors to

478   responsiveness to human voices in exotic cats. This is also the first time the effects of the use of

479   the cats' name, as spoken by familiar and unfamiliar voices, has been examined.

480   Similar research with domestic species has suggested this ability may be a consequence

481   of long-term domestication, whereas studies with wild, yet highly social species suggest that this

482   ability stems from the selective pressures associated with living in social groups. Exotic cats are

483   neither domesticated nor highly social (other than lions). Of the 25 cats tested, only three

484   belonged to the only truly gregarious cat species - lions. Nearly half were housed individually,

485   and more than a third were raised by their mothers. Results from the only other study of this kind

486   with exotic cats (Leroux et al., 2018) suggest that early socialization may play a role in the cats'

487   abilities to discriminate human voices. The results from Study Two, which are consistent with

488   those of Saito and Shinozuka (2013) using the same habituation-dishabituation paradigm that

489   those authors used with domestic cats, suggest a family-wide ability that is not dependent on

490   domestication or social living. However, early socialization with humans is likely an important

491   factor. This is consistent with findings from fruit bats that followed human point cues only if

492   they had extensive experience with humans (Hall et al., 2011). The fact that rearing significantly

493   impacted latency to respond with only hand-reared cats showing an effect of familiarity bolsters

494   this hypothesis. However, it should be noted that rearing did not impact intensity or duration of

495   response in this sample.

496   Whereas lions may be the only truly social species of cat, all cat species must interact

497   with other animals regularly; whether it be while hunting prey, raising young, finding a mate, or

498   competing for territory. No cat lives a completely asocial life so social behaviors may still be

499   beneficial. A study by Elbroch and colleagues (2017) showed that even relatively asocial pumas

500   (*Puma concolor*) were impacted by changes in the composition of their nearest neighbors. Their

501   social interactions were explained better by reciprocity than by kinship, suggesting an ability to

502   track social behaviors not often attributed to cat species (Vonk, 2018). The present results add to

503   the growing literature suggesting that researchers have misattributed a lack of social cognition to

504   non-group-living species and highlights the need to extend studies of social cognition to less

505   commonly studied species.

506   Although the hypotheses regarding familiarity and rearing were supported, the

507   hypotheses concerning the impact of speaking the cats' names were not. There was not a main

508   effect of name usage (Saito et al. 2019) on any of the outcomes in either study. However, name

509   use did interact with familiarity to predict latency to respond in Study One only. The pattern or

510   results was not straightforward, but there was no effect of name use for latency to respond to the

511   most familiar caregiver. The fact that the use of the cats' name slowed the response to unfamiliar

512   voices in Study One and did not affect the reaction to the familiar voices in Study Two suggests

513   that cats are not unduly distracted by the use of their names by strangers. This information may

514   aid zoological facilities in their decisions about whether to post animal names. With one of the

515   primary concerns being a degradation of the name cue in training if it is repeated frequently by

516   guests without reward, the findings of this study suggest that cats may not be highly responsive

517   to their names, but will be responsive to speakers with whom they are familiar. With studies

518   showing that knowing the name of an animal, a form of anthropomorphism, makes people more

519   sympathetic to the animal (Chartrand, 2008), as well as anthropomorphism affecting people's

520   willingness to engage in conservation efforts (Manfredo et al., 2020), it may be beneficial to the

521   facilities housing exotic cats to post their names for visitors in an effort to engage them further

522   with the conservation mission of the facility.

523 **Limitations and Future Directions**

524   Although this study included representation from many cat species, it was limited by a

525 small sample size within each species due to the relatively small population of captive exotic cats

526 available for testing. Thus, effects of species could not be examined statistically. However,

527 subfamily was included as a predictor despite the lack of clear predictions regarding subfamily

528 differences in outcomes. The only significant effect of subfamily was a main effect of subfamily

529 on latency to respond, with Felinae subjects reacting more than twice as quickly, on average,

530 than Pantherinae subjects. Although we did not have specific hypotheses that would explain this

531 effect, there may be interesting differences regarding reactivity for different species of cat that

532 should be studied further.

533   Another limitation of the current study was an inability to control for individual

534 differences in the cats as well as facility and caretaker differences, such as in training styles.

535 Individual cats may respond differently to humans they encounter based on past and current

536 experience, personal history, and individual personalities. Each facility is unique in not only the

537 amount of time the keepers spend with the cats they care for, but also in the quality and degree of

538 interaction they have. Some facilities may engage in free contact husbandry, where the keeper is

539 in physical contact with the cat without any form of a barrier, or protected contact, where there is

540 a barrier between keeper and cat. The facilities also may participate in different forms and levels

541 of training, with some investing more time and effort into training and behavior management

542 with their cats than others. All of these factors may impact how the cats respond to the sound of

543 different human voices, and the type and degree of response they exhibit. An examination into

544 potential preferences, the positivity or negativity of interactions (such as with veterinary staff),

545 and differing levels of familiarity may reveal even more about how cats relate to and interact

546   with their keepers and care staff, and thereby provide additional insight into how best to care for

547   them. Because six of the hand-reared cats tested here are ambassador cats with free contact with

548   humans, it is also possible that the effects of "rearing" were partially due to some cats having

549   more prolonged continued contact with humans. These differences in daily handling also deserve

550   additional attention in future studies. Future studies might also examine whether time spent with

551   cats, longevity of the human-cat relationship, and quality of the training interactions predict

552   responsiveness to familiar versus unfamiliar caregivers.

553   Importantly, the current results do not allow for the conclusion that cats can discriminate

554   among individual humans. They merely show that cats respond more strongly to the voices of

555   familiar versus unfamiliar humans in general. In addition, future research is necessary to

556   determine whether cats can discriminate between familiar and unfamiliar human scents and

557   visual features. Future studies will need to test the ability to recognize individual humans using

558   methods such as cross-modal matching (Takagi et al., 2019).

559   **Conclusions**

560   This study contributes to the growing literature suggesting that adapting to a social

561   lifestyle and human domestication are not the only important factors in predicting social

562   cognitive abilities – even when considering the ability to read human communicative cues

563   specifically. Early life experiences and current environments may promote the development of

564   abilities that researchers would not be able to observe in the wild – such as the ability of cats to

565   discriminate familiar human voices. This study also adds to the growing body of work showing

566   that even non-domestic cats are capable of forming relationships with familiar humans and may

567 go a long way to dispelling the notion that cats are aloof and inflexible. As any zookeeper or cat

568 owner will tell you, cats know their people, they just show it in their own way.

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575

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List of Subjects

1 **Table 1**

2 Subject Subfamily, Species Common Name, Sex, Rearing History, and Facility

Subject	Subfamily	Species	Sex	Rearing Style	Facility	Study Participation
Diesel	Felinae	Cheetah	M	HR	Zoo Miami	1 and 2
Koda	Felinae	Cheetah	M	HR	Zoo Miami	1 and 2
Nia	Felinae	Cheetah	F	HR	Cincinnati Zoo	2
Tommy	Felinae	Cheetah	M	HR	Cincinnati Zoo	2
Jean	Pantherinae	Clouded Leopard	F	HR	Zoo Miami	2
Harper	Felinae	Cougar	F	HR	Creature Conservancy	1 and 2
Tecumseh	Felinae	Cougar	M	HR	Cincinnati Zoo	2
Joey	Felinae	Cougar	M	HR	Cincinnati Zoo	2
Tallulah	Felinae	Fishing Cat	F	MR	Greensboro Science Center	2
Mako	Felinae	Fishing Cat	M	MR	Greensboro Science Center	2
Gordie	Felinae	Lynx	M	HR	Creature Conservancy	1 and 2
Amirah	Pantherinae	Lion	F	MR	Zoo Miami	2
Imani	Pantherinae	Lion	F	HR	Cincinnati Zoo	2
John	Pantherinae	Lion	M	MR	Cincinnati Zoo	2
Layla	Felinae	Sand Cat	F	MR	Greensboro Science Center	2
Kira	Felinae	Serval	F	HR	Greensboro Science Center	2
Major	Felinae	Serval	M	HR	Zoo Miami	1 and 2
Scout	Felinae	Serval	M	HR	Zoo Miami	1 and 2
Tut	Felinae	Serval	M	HR	Greensboro Science Center	2
Nubo	Pantherinae	Snow Leopard	M	MR	Cincinnati Zoo	2
Renji	Pantherinae	Snow Leopard	F	HR	Cincinnati Zoo	2
Berani	Pantherinae	Tiger	M	MR	Zoo Miami	1
Jin	Pantherinae	Tiger	F	MR	Cincinnati Zoo	2
Rocky	Pantherinae	Tiger	M	MR	Greensboro Science Center	2
Zero	Pantherinae	Tiger	M	HR	Cincinnati Zoo	2

5 *Note*. HR = human-reared, MR = mother-reared

Figure 1

Experimental Set-Up for Playback Trials and Observation
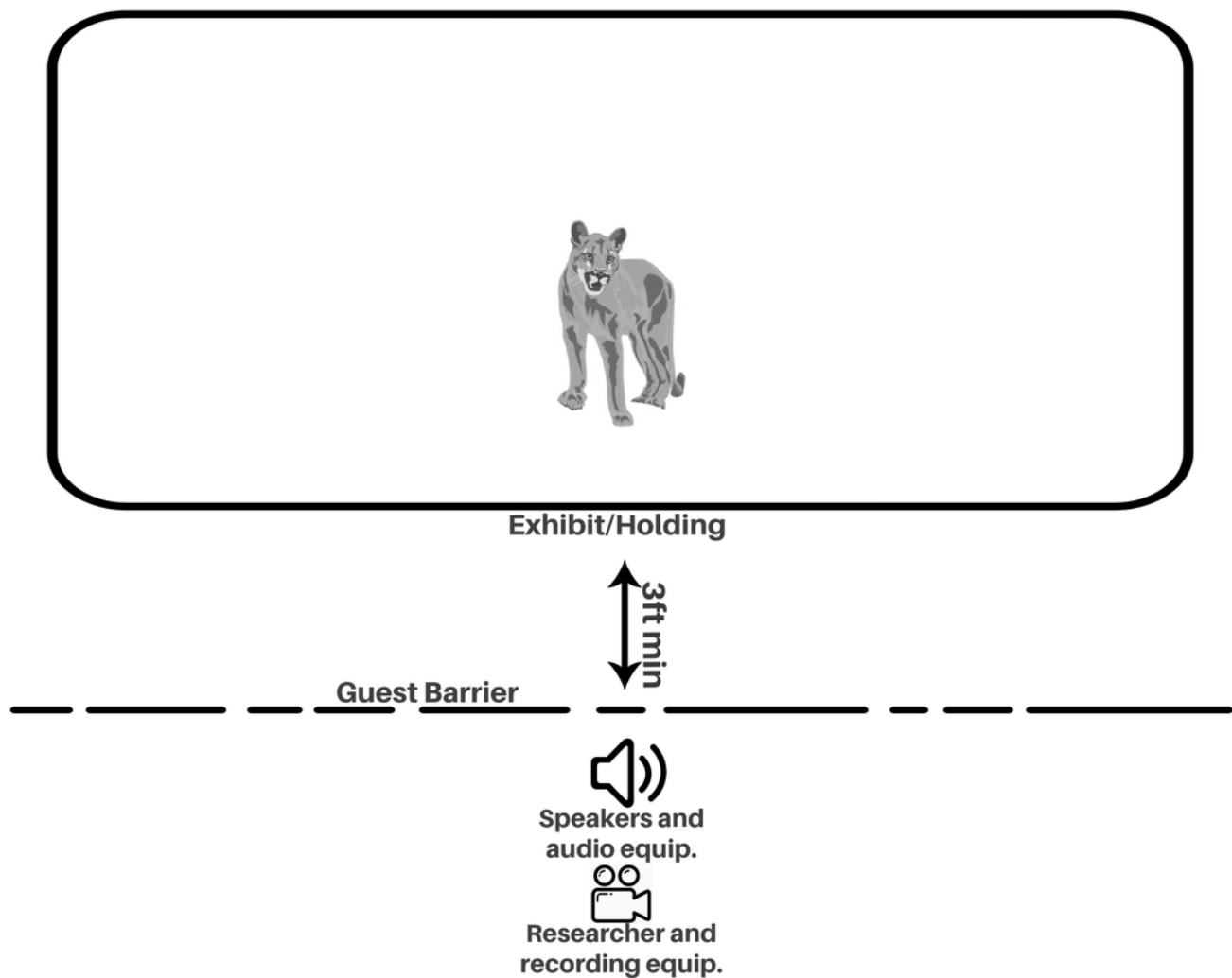
Figure 2

Latency to Respond to Playbacks in Study One

Figure showing a bar chart titled "Latency to Respond" (y-axis, 0–180) versus two conditions "Name Absent" and "Name Present" (x-axis). Legend: Unfamiliar, Less Familiar, Most Familiar.
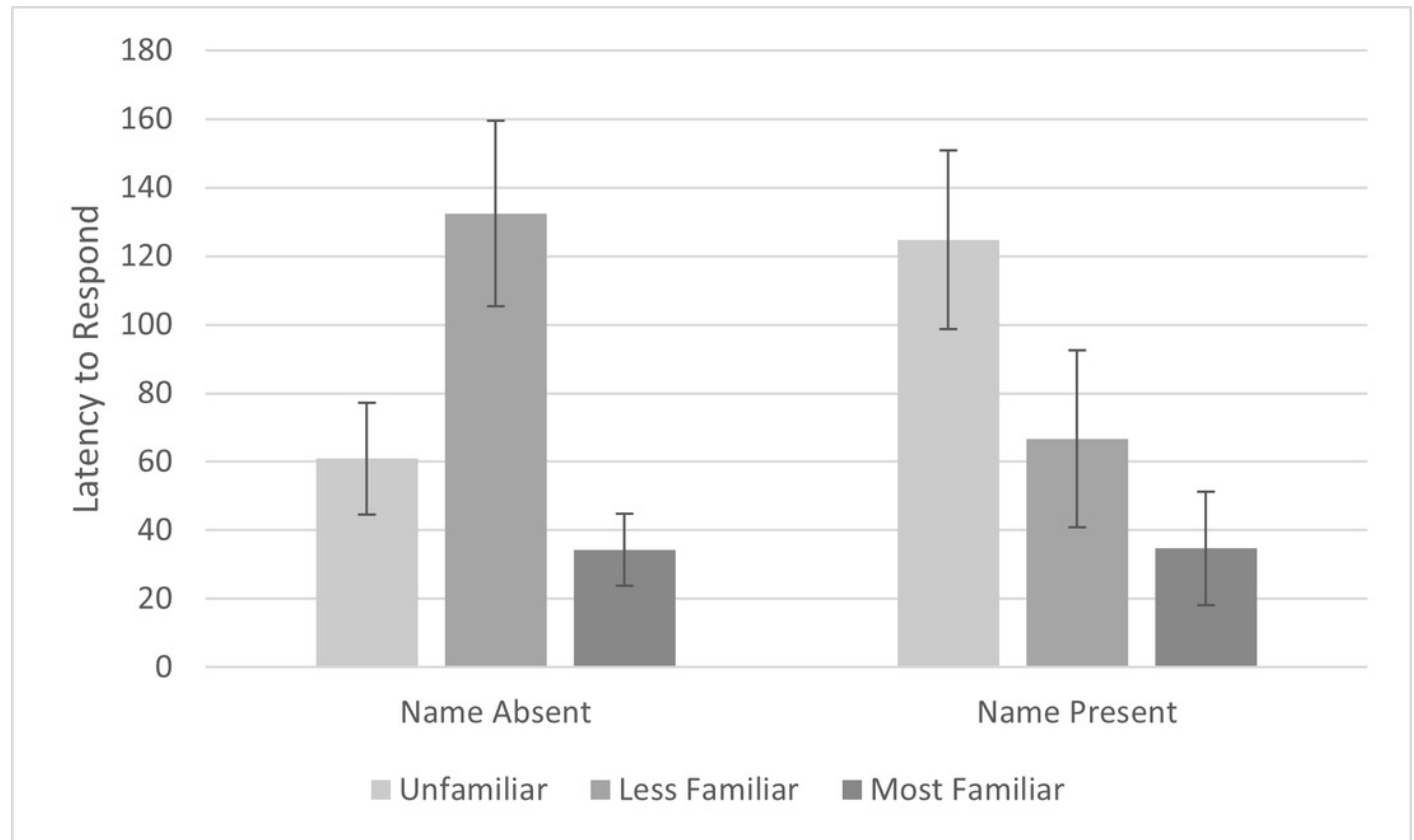
Figure 3

Latency as a Function of Playback Trial and Subject's Sex
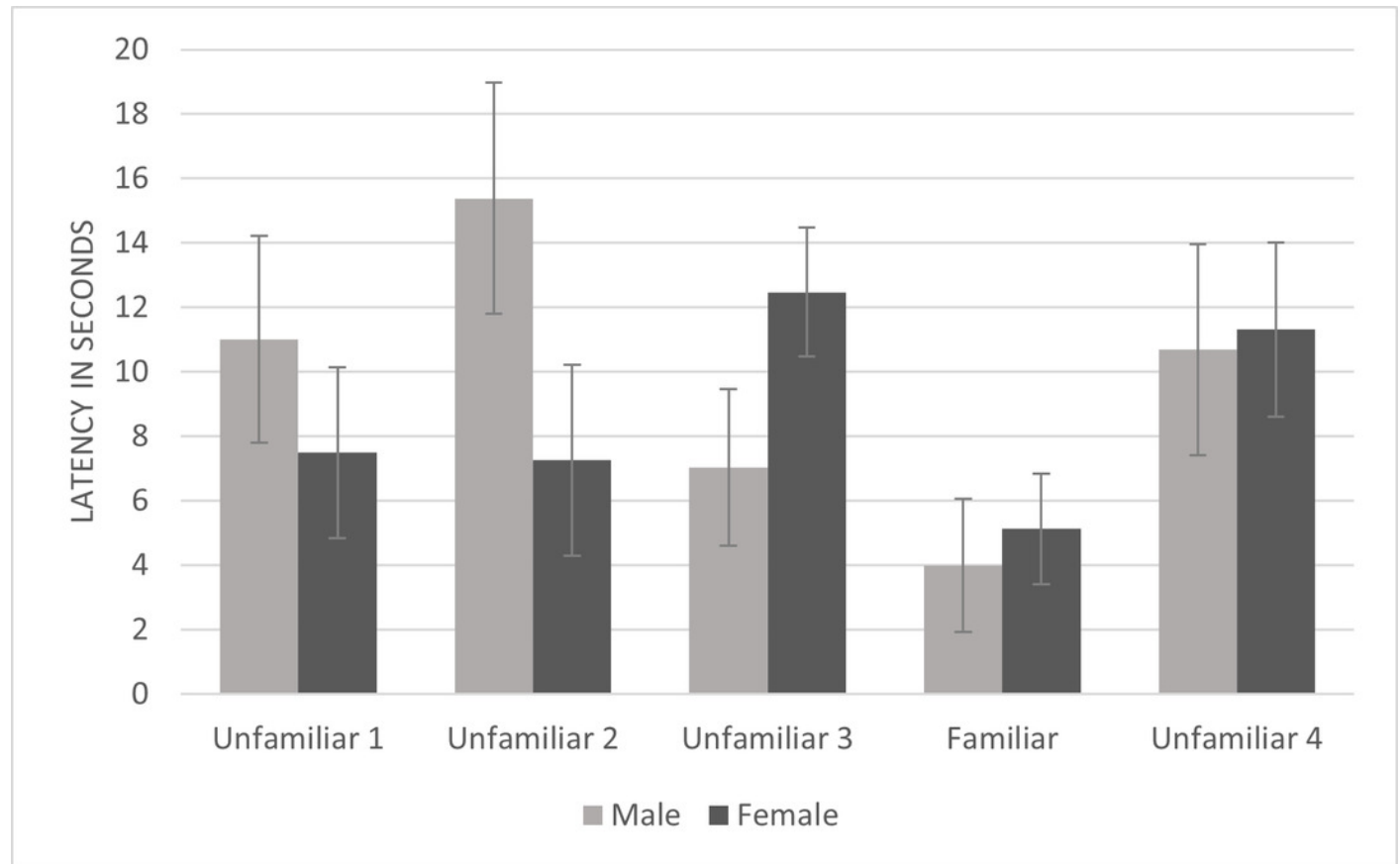
Figure 4

Latency as a Function of Playback Trial and Subject's Rearing Style
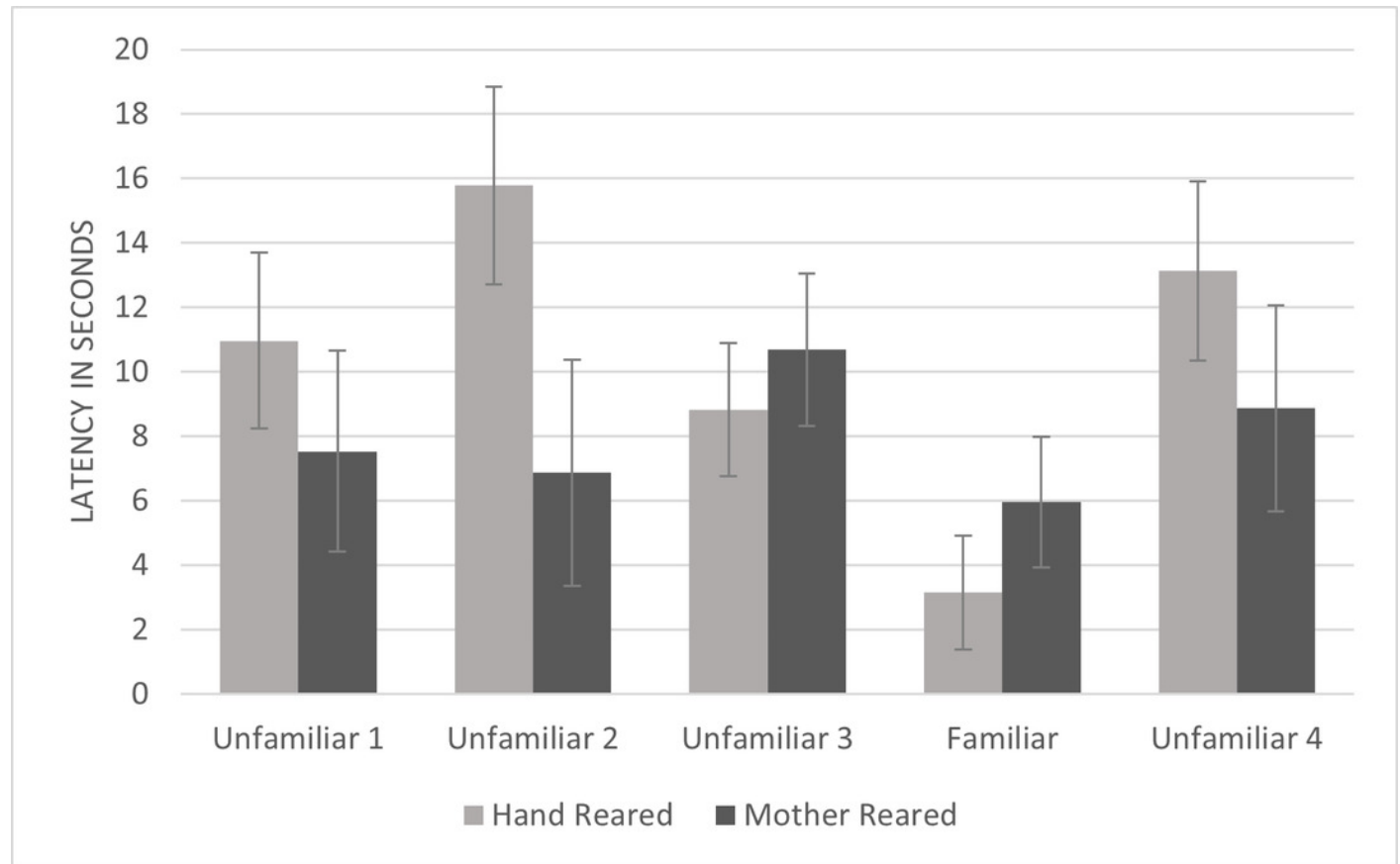
Figure 5

Intensity of Reaction as a Function of Playback Trial.

Note. Intensity was measured from 0 (no response) to 5 (full head turn or locomotion towards speaker) of the first reactionary behavior following each playback.
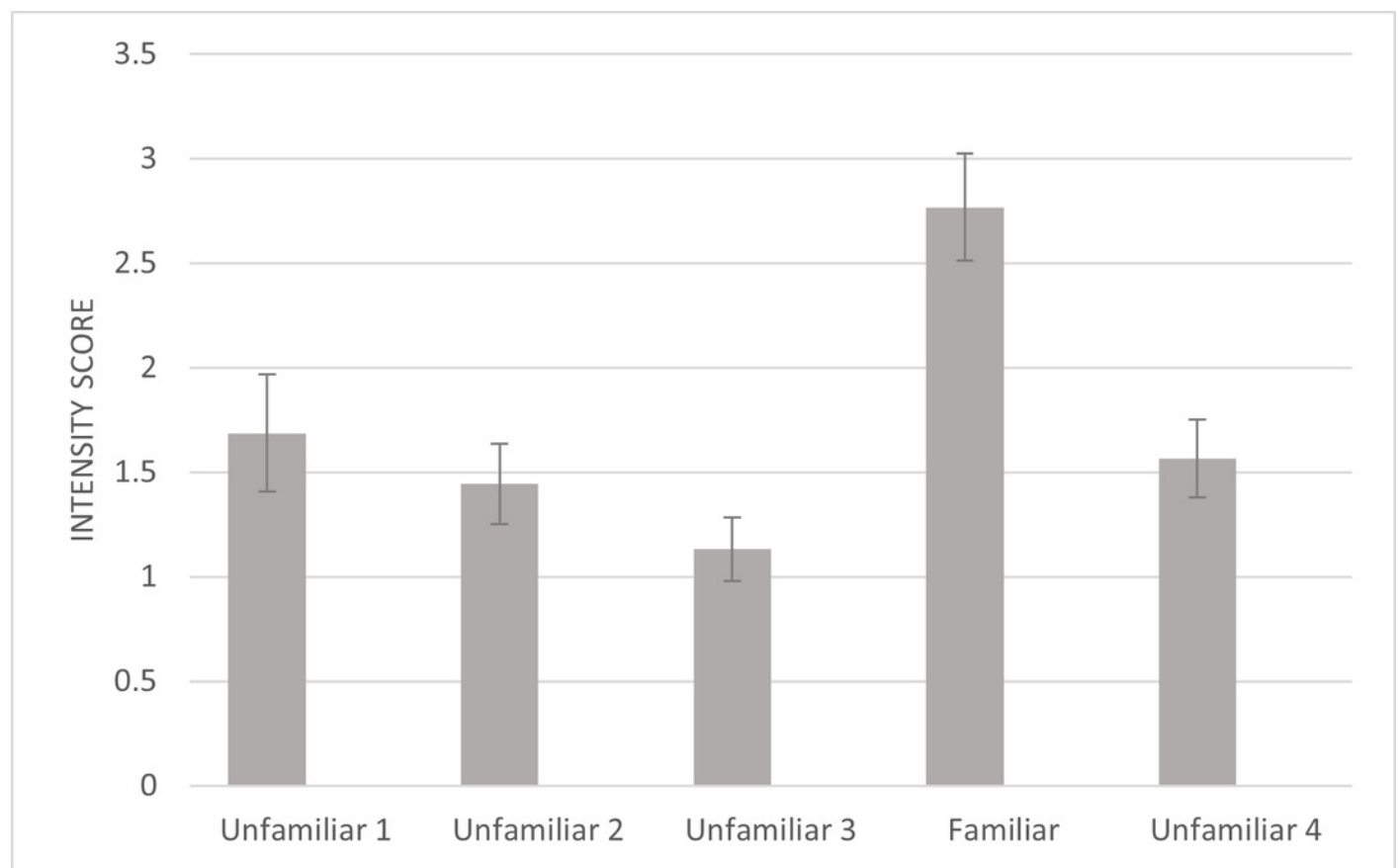
Figure 6

Duration of Behavior as a Function of Playback Trial