1   **Megachiropteran Bats Utilize Human Referential Stimuli to Locate Hidden Food**

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Abstract

2   Spontaneous point-following behavior has been considered an indicator of advanced

3   social cognition unique to humans. Recently, it has been suggested that a close

4   evolutionary relationship with humans could result in similar social skills in

5   domesticated species. An alternative view is that the mechanism is not genetic

6   domestication alone but instead a combination of phylogenetic and ontogenetic

7   variables. Here we test the necessity of phylogenetic domestication by investigating the

8   point-following behavior of a captive population of non-domesticated megachiropteran

9   bats (*Pteropus pumilus, Pteropus rodricensis, Pteropus conspicillatus, Pteropus*

10   *vampyrus*). Three of five subjects were highly successful in following an unfamiliar

11   human's point to a target location providing the first empirical evidence of cross-species

12   social referencing in bats. The three successful bats were all born in captivity and

13   socialized to humans early in life whereas unsuccessful bats were wild born individuals.

14   This study provides evidence that referential point following is not restricted to

15   domesticated animals and indicates that early experience may be important.

16   Megachiropteran bats may prove to be a useful model for studying social behaviors.

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18   *Keywords:* megachiropteran bats, social cognition, human gestures, social referencing

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26   Joint attention and point following are considered important markers of socio-

27   cognitive development in human infants and are often used as indicators for theory of

28   mind capabilities in pre-verbal human children (Carpenter, Nagell & Tomasello, 1998;

29   Charman et al., 2000). Recently, comparative research on spontaneous point following

30   behavior in an object-choice task has been used to support the claim that domestic dogs

31   and possibly domesticated species in general, have evolved human-like social skills

32   (Hare & Tomasello, 2005). This domestication hypothesis proposes that selection

33   pressures present during domestication led to the development of heritable human-like

34   social skills that increased genetic fitness (Hare, Brown, Williamson & Tomasello,

35   2002; Miklósi et al., 2003). Thus, dogs, and domesticated species in general, have

36   evolved a specialized capacity to read human social and communicative behavior (Hare

37   & Tomasello, 2005)

38   Support for the domestication hypothesis comes from evidence demonstrating

39   that some domesticated species (goats, *Capra hirucs;* horses, *Equus caballus*; cats, *Felis*

40   *catus)* show proficiency in following a human point to a target without explicit training

41   (for goats see Kaminski, Riedel, Call & Tomasello, 2005; for horses see Maros, Gácsi &

42   Miklósi, 2008; McKinley & Sambrook, 2000; for cats see Miklósi, Pongrácz, Lakatos,

43   Topál & Csányi, 2005). However, to determine if domestication is *necessary* for the

44   development of responsiveness to human social and communicative gestures, adequate

45   comparisons to the social behavior of non-domesticated species must also be made.

46   Most of the available literature comparing domesticated and non-domesticated

47   species' point-following behavior has focused on canids, specifically pet dogs (*Canis*

48   *lupus familiaris*) and wolves (*C. l. lupus*) (Agnetta, Hare & Tomasello, 2000; Gácsi et

49   al., 2009; Hare et al. 2002; Miklósi et al., 2003; Udell, Dorey & Wynne, 2008; Virányi

50   et al. 2008). Some researchers have found that wolves do indeed follow human pointing

51   gestures spontaneously (Gácsi et al., 2009; Udell, Dorey & Wynne, 2008), while others

52   report that untrained wolves perform at chance levels (Hare et al., 2002; Virányi et al.,

53   2008). In a related line of investigation, Hare et al. (2005) reported that silver foxes

54   artificially bred over many generations for tame behavior (Trut, 1999), were

55   spontaneously more sensitive to human pointing gestures than wild-type foxes.

56   However, the wild type foxes in this study nonetheless followed the experimenter's

57   point more often than would be expected by chance, suggesting that domestication may

58   have influenced performance but did not predict absolute success or failure on the task.

59   While there is strong evidence for the interplaying roles of phylogeny and ontogeny in

60   the development of dogs' social skills (Udell & Wynne, 2010), the precise role of

61   domestication is still an ongoing debate within the canid literature.

62   Other non-domesticated species tested for sensitivity to human gestures include

63   dolphins (*Tursiops truncates*) and fur seals (*Arctocephalus pusillus*) (Pack & Herman,

64   2004; Scheumann & Call, 2004; Tschudin, Call, Dunbar, Harris & van der Elst, 2001).

65   While some subjects in these studies utilized human points at above chance levels, their

66   status as animals trained for public display or other experiments has sometimes made

67   direct comparisons with untrained domesticated animals difficult (Miklósi & Soproni,

68   2006). More recently, an experiment conducted with a species known to engage in

69   cooperative social behavior in the wild, Jackdaws (*Corvus monedula*), demonstrated

70   that hand raised individuals would spontaneously follow a point issued by their familiar

71   caretaker (Von Bayern & Emery, 2009). The findings of this study suggest that giving a

72   species that engages in cooperative social behaviors with conspecifics early experiences

73   with humans may be important for spontaneous point following behavior. The degree to

74   which point following behaviors may extend to unfamiliar experimenters is unknown.

75   Both Megachiropteran and Microchiropteran bats are considered generally social

76   (for a review see Kerth, 2008). Various bat species have been recorded engaging in

77   conspecific grooming, transfer of information, reciprocal food sharing, and mutual

78   warming (Kerth, 2008; McCracken & Bradbury, 1981; Safi & Kerth, 2007; Wilkinson,

79   1984; Wilkinson, 1986; Wilkinson, 1992). Of the species in this study, *Pteropus*

80   *rodricensis* have been recorded aiding conspecifics in parturition (Kunz& Allgaier,

81   1994). In addition, *Pteropus vampyrus* are considered a gregarious species (Kunz &

82   Jones, 2000). Unfortunately, detailed information on many bat species' social

83   organization is sparse compared to what is known of other social species (Kerth, 2008).

84   Furthermore, Megachiropterans have vision adequate to participate in traditional object

85   choice tasks (Müller, Goodman & Piechl, 2007).

86   In this study we investigated the performance of five captive bats, belonging to

87   the suborder Megachiroptera, in an object choice task which required them to

88   spontaneously utilize the point of an unfamiliar human to locate a hidden target.

89   **Methods**

90   **Subjects/Setting**

91   Five megachiroptera from four different species currently residing at a bat

92   conservancy were selected for participation in this study. The bats were kept in outdoor,

93   enclosed, octagonal pens (side length of 4.52 m) with other bats of varying species.

94   While a familiar keeper acted as an assistant, calling or returning the subject back to the

95   starting point between trials, the experimenter who issued the pointing gesture during

96   experimental trials was previously unfamiliar to the bat subjects.

97   Three of the five bats were captive-born (*Pteropus pumilus, Pteropus*

98   *rodricensis, Pteropus conspicillatus)*, while two bats were wild-caught (*Pteropus*

99   *pumilus, Pteropus vampyrus)*. The captive-born bats had varying histories (mother

100 reared or hand reared on or off the premises of the conservancy) but are distinct from

101 wild-caught bats in that they were born in captivity, provided regular interactions with

102 humans from birth, and reached adulthood in captivity. Wild-caught bats matured to

103 adulthood before being captured and brought to the conservancy, but had spent about 16

104 years in captivity prior to testing. The captive-born bats were also mature adults at 8, 10

105 and 11 years of age and had spent their entire lives in captivity. Thus, the major

106 difference between the groups was that captive-born bats had early experiences with

107 humans handling or entering their enclosure, while wild-caught bats did not. Once at the

108 conservancy, wild-caught and captive-born bats cohabitated and had similar experiences

109 with humans and feeding.

110 **Materials**

111   The bats were tested individually in vacant triangular outdoor pens (6.2 m x

112 4.52 m x 4.52 cm). Two opaque plastic containers served as the response objects and

113 were fixed 1.6 m apart at an appropriate height for the individual bat to reach (see figure

114 1). Each response object held a 250 ml Mason jar that was out of sight of the bat (see

115 figure 2). Both Mason jars contained 1ml of Kern's Nectar™ (Kern's Beverages, LLC

116 4002 Westminster Ave. Santa Ana, CA 92703). The lids normally used to seal Mason

117 jars were removed, but the rims used to affix the lid to the jars were retained for the

118 purposes of this study.

119   The rims were placed on both Mason jars, however, one jar's rim was fitted with

120 a fiberglass screen (sham rim) while the other jar's rim was not manipulated (free rim)

121   (figure 2A).The screen on the sham rim permitted air flow from both jars, and hence

122   equalized smell from the jars, while preventing the bat access to the nectar in the sham

123   jar. The other rim provided free access to the nectar. As demonstrated previously,

124   hiding equal amounts of nectar in each box was necessary, because some species of

125   megachiroptera can not only determine the location of food by odor alone in a two

126   choice experiment, but can even discriminate whether the fruit is ripe (Luft, Curio &

127   Tacud, 2003). One bat in our study, Easter, was also initially suspected of using

128   additional scent cues that she may have left on the rim of the free lid when allowed to

129   access the free food during her first set of control trials. This potential confound was

130   resolved by cleaning both jars between each trial, both control and experimental, after

131   which her performance on control trials dropped to chance while her performance on

132   experimental trials remained significantly above chance.

133   **Experimental Testing**

134   Prior to participation in the study each bat was required to readily approach and

135   take food from the experimenter and experimental apparatus when it was freely

136   available. This was done on the day of testing by the experimenter holding up a

137   container of nectar next to the bat. If the bat approached the container, the container was

138   placed inside one of the experimental boxes. This procedure was repeated until the bat

139   consumed food from the each experimental box twice. The procedure ensured that the

140   bat subjects were food motivated, and were not fearful or distracted within the testing

141   environment. Four bats never approached the experimenter or the experimental

142   apparatus despite being given hours to habituate to the apparatus. These four bats never

143   began testing.

144   Each experimental trial began with the assistant bringing the bat to the starting

145   location 1m back from the experimental boxes (figure 2B). Once the bat was in position

146   the experimenter raised his ipsilateral arm to chest height and directed his hand towards

147   the bat. The point started this way to allow for a range of motion of the arm and to gain

148   the bat's attention. The experimenter called the bat's name, and then moved his arm

149   laterally in the direction of the correct box. Movement stopped once the arm was

150   pointing to the correct box and the finger was approximately 12 cm from the box (figure

151   2C). The gesture, a dynamic proximal point as defined by Miklósi & Soproni (2006),

152   did not move further until the bat made a choice or the trial timed out after 2 minutes.

153   The point is considered dynamic because the subject is able to see the movement of the

154   point, and the arm remains in the gesturing position throughout the trial. While

155   gesturing, the experimenter looked straight ahead and avoided eye contact.

156   Trials lasted 2 minutes to give the bats sufficient time to move from the start

157   location to the target container by pulling themselves across the enclosure roof (the

158   bats' locomotor method of choice) in a climbing motion. None of the bats flew in the

159   experimental pen during testing. An observer outside the enclosure recorded the bats'

160   choice for each trial as it occurred. The observer recorded a choice when the bat

161   physically touched one of the response objects (figure 2D), which were located 1.6 m

162   apart. In every trial where a bat made a choice, the bat subsequently entered the

163   response object to obtain accessible or inaccessible nectar. Thus, the bats' choice

164   between response objects was unambiguous. If a bat made a correct choice, but had

165   difficulties in consuming the nectar, the experimenter assisted the bat by lifting the jar

166   to increase accessibility. If the bat made an incorrect choice, the assistant called the bat

167   back to the start position without it receiving nectar. If the bat moved towards the

168 testing apparatus but had not made a choice within two minutes, the assistant called the

169 bat back to start the next trial and a 'no choice' was recorded. No choice responses

170 were analyzed as incorrect responses. Only one 'no choice' response occurred during

171 experimental trials (Easter, session 1).

172   After each trial, the experimenter removed both jars from the response objects.

173 If the bat had made a correct choice on the previous trial and subsequently consumed

174 the nectar from the jar in the target container, the experimenter removed both lids from

175 the jars and re-filled the emptied jar with 1ml of nectar. If the bat had made an incorrect

176 choice on the previous trial (and therefore did not consume the nectar), the experimenter

177 removed the jars and the lids, but did not add any more nectar to the jars. Out of the

178 view of the bat, the experimenter simultaneously replaced both lids and placed the lid

179 allowing access to the nectar on the appropriate jar that was then put into the target

180 container. Both jars were then placed in their respective boxes.

181   The target container for each trial was determined pseudorandomly with the

182 stipulation that no side could be used more than twice in a row or for more than 50% of

183 the trials.

184   Each subject received a total of 20 experimental trials, divided into two sessions

185 of ten trials each. If a bat satiated with nectar, experimental trials for that day were

186 suspended. Satiation was determined when the bats failed to take food offered by the

187 assistant (a familiar caretaker). Experimental trials were resumed on another day. Four

188 of the five bats participating in experimental trials completed testing, while one bat,

189 Arthur, refused to participate after the first six trials.

190 **Control trials**

191   Three to seven control trials followed every 10 experimental trials. Control

192   trials were identical to experimental trials, except that no pointing cue was administered.

193   **Statistical analysis**

194   A one-sample t-test was used to determine if the group performance of the bats

195   was better than would be expected by chance within each session. A paired t-test was

196   used to determine if performance differed between session one and session two. Both

197   tests were two-tailed and had an alpha level of .05. Binomial tests were used to assess

198   the individual performance of each bat for each session, with success criterion set at

199   8/10 trials correct or better within an individual session ($p \leq$ .05). Analyses were

200   conducted using Excel and SPSS.

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Results

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202   As a group, the bats were successful in following a human point in each testing

203   session (one sample t-test, session 1: $t_3 = 4.37$, $p = .022$; session 2: $t_3 = 7.35$, $p = .005$).

204   At the individual level, all three captive-born bats, Grace, Kuri, and Easter, were

205   successful in reliably following a human point to the target in each session (session 1

206   and session 2: binomial test, $p < .05$, see figure 3), and pooled across both sessions

207   (Grace: 16 out of 20, $p \leq .01$; Kuri: 18 out of 20, $p < .01$; Easter: 16 out of 20 $p \leq .01$).

208   Neither wild-caught bat performed significantly above chance on the task. Arthur, one

209   of the wild-caught bats, began testing but only completed six experimental trials before

210   refusing to participate, even after multiple breaks and revisits on other days. Out of

211   those six completed trials, he chose correctly only twice (33% correct). Taba, the other

212   wild-caught bat, readily approached a container in search of the accessible food on

213   every trial, however her performance never reached statistical significance (session 1

214   and session 2: binomial test, $p > .05$).

215   We also analyzed first trial performance for each bat, and compared performance in

216   the first session to that in the second session of testing to assess whether performance

217   was more likely a product of a bat's capacity before testing or learning within the course

218   of the experiment. There was no difference in performance between the first and second

219   sessions of testing (paired t-test, $t_3 = 1.00$, $p = .39$). A bat's first response on the first

220   trial was not a good predictor of subsequent performance. The three successful bats

221   (Easter, Grace and Kuri) made a correct choice on the first trial of testing, so did one of

222   the unsuccessful bats, Taba. Arthur was the only bat to make an incorrect response on

223   the first trial.

224   Control trials were conducted during and after testing in which the bat was

225   allowed to choose a container in the absence of a human point. Bats performed at

226   chance levels on control trials, both on average and at the individual level (mean

227   performance on control trials for all subjects, 49% correct, binomial test, $p = .50$),

228   indicating that they were not locating the accessible food based on smell or

229   unintentional cueing by the experimenter. As mentioned above, Easter was initially

230   suspected of using smell cues to locate the target container on control trials. This was

231   resolved by cleaning the lids and jars in between trials. Prior to cleaning the lids she

232   scored 8 correct out of 10 trials; after the introduction of the cleaning lid method,

233   performance on control trials dropped to chance, 6 out of 14 (43% correct, binomial

234   test, $p = .77$). Performance on experimental trials remained above chance despite

235   cleaning between trials (80% correct, binomial test, $p \leq .05$). The control trials of the

236   other bats did not indicate the use of any unintentional cues (Taba session 1 and session

237   2: 50% correct on controls; Grace session 1 and session 2: 25% correct; Kuri session 1

238   and session 2: 55% correct; Arthur did not complete control trials).

239   **Discussion**

240   These results demonstrate that several species of experimentally naïve bats are

241   capable of spontaneously utilizing human points to find the location of concealed food

242   in an object-choice task. This suggests that domestication is not necessary for the

243   responsiveness to the human gesture tested. Instead, the proclivity of bats towards

244   conspecific social interactions may be important in understanding their ability to engage

245   in heterospecific interactions such as following human points. Nonetheless,

246   responsiveness to the actions of heterospecifics does not appear to be automatic.

247   Human socialization and regular interaction with humans from an early age emerged as

248   an important predictor of an individual bat's performance. All three captive-born

249   individuals that participated in the experiment followed the experimenter's point to the

250   target location successfully. Both wild-born bats were unsuccessful on the task despite

251   having spent 16 years of their adulthood in captivity.

252   Early and intensive exposure to humans has been linked to the success of other non-

253   domesticated species on human-guided tasks (Udell et al., 2008; Von Bayern & Emery,

254   2009). Taken together with this study, this may suggest that there is an important

255   sensitive period for socialization that can help predict success on human guided tasks.

256   However, an additionally important factor in this study was that the successful bat

257   subjects were able to follow the point of an unfamiliar experimenter; demonstrating the

258   ability to generalize their response to referential stimuli provided by humans in general.

259   While in previous reports, chimpanzees have been reported to perform at lower

260   levels than both human children and domestic dogs on human guided tasks (Hare et al.,

261   2002; Bräuer, Kaminski, Riedel, Call & Tomasello, 2006), this might have been due, at

262   least in part, to significant differences in the quantity and quality of daily exposure to

263   humans. Differences between enculturated and wild born chimpanzees indicate

264   environmental factors contribute to the ontogeny of primate social cognition (Tomasello

265   & Call, 2004). Tomasello and Call hypothesized that growing up in the presence of

266   humans changed the way individuals attended and reacted to human actions and

267   enculturation acted as a catalyst for further development of an already present socio-

268   cognitive capacity (Tomasello & Call, 2004).

269   The individual socialization experiences of the bats in this study differ only at

270   birth until one to two years of age. Captive-born individuals received at least some close

271   human interaction from birth, where wild-caught bats did not. Experiences as adults in

272   captivity were nearly identical for all subjects. The hypothesized role of early

273   socialization in the development of responsiveness to human gestures is consistent with

274   the differences found between our captive-born and wild-caught bats thus far.

275   The success of species generally considered social may indicate an important

276   phylogenetic component to point following behavior in object choice tasks. Species that

277   regularly interact with conspecifics may be more apt at cooperative interactions with

278   heterospecifics. Thus a two-pronged strategy may be needed to further identify species

279   and individuals likely to display sensitivity to human gestures: 1. recognizing species

280   characteristics that suggest a phylogenetic capacity, including evidence of conspecific

281   social interactions of the species, while 2. also taking into account ontogenic factors.

282   With the current sample size, accurate first trial responding was difficult to

283   interpret conclusively, however larger sample sizes might be more conducive to a first

284   trial analysis and may be able to provide information about spontaneous responding in

285   future studies. In addition, further research is needed to determine whether the bat's

286   performance should be explained as a learned association between human hands and the

287   presentation of food, a form of local enhancement, stimulus enhancement, or as

288   requiring an understanding of reference or intentionality. More point types should also

289   be used in future studies to ascertain whether success with proximal pointing would

290   extend to more distal points. With the current data, we propose that the social proclivity

291   of bats and early exposure to humans during ontogeny *both* likely contributed to the

292   development of increased responsiveness to humans.

293   Bats could serve as an important non-domesticated animal model for investigating

294   the origins of human-like social cognition. More generally, bats are rich but

295   underrepresented subjects in animal cognition research, and ought to be better

296   represented in future studies.

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311   References

312   Agnetta, B., Hare, B., & Tomasello, M. (2000). Cues to food location that dogs (*Canis*

313   *familiaris)* of different ages do and do not use. *Animal Cognition, 3,* 107-112.

314   Bräuer, J., Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2006). Making

315   inferences about the location of hidden food: social dog, causal ape. *Journal of*

316   *Comparative Psychology, 120*, 38-47.

317   Carpenter, M., Nagell, K., & Tomasello, M. (1998). Social cognition, joint attention,

318   and communicative competence from 9 to 15 months of age. *Monographs of the*

319   *Society for Research in Child Development, 6*, 1-174.

320   Charman, T., Baron-Cohen, S., Swettenham, J., Baird, G., Cox, A., & Drew, A.

321   (2000). Testing joint attention, imitation, and play as infancy precursors to

322   language and theory of mind. *Cognitive Development 15*, 481-498.

323   Gácsi, M., Győri, B., Virányi, Z., Kubinyi, E., Range, F., Belényi, B., & Miklósi, Á.

324   (2009). Explaining dog wolf differences in utilizing human pointing gestures:

325   selection for synergistic shifts in the development of some social skills. *Plos*

326   *One, 4*, e6584, doi:10.1371/journal.pone.0006584.

327   Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R., & Trut, L.

328   (2005). Social cognitive evolution in captive foxes is a correlated by-product

329   of experimental domestication. *Current Biology, 15,* 226-230.

330   Hare, B., Brown, M., Williamson, C., & Tomasello. M. (2002). The domestication of

331   social cognition in dogs. *Science, 298*, 1634-1636.

332   Hare, B., & Tomasello, M. (2005). Human like social skills in dogs? *TRENDS in*

333   *Cognitive Science, 9,* 439-444.

334   Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2005). Domestic goats, *Capra*

335   *hircus*, follow gaze direction and use social cues in an object choice task. *Animal*

336   *Behaviour, 69*, 11-18.

337   Kerth, G. (2008). Causes and consequences of sociality in bats. *Bioscience, 58*, 737-

338   746.

339   Kunz, T.H., & Allgaier, A.L. (1994). Allomaternal care: Helper-assisted birth in the

340   rodrigues fruit bat, *Pteropus rodricensis* (chiroptera: Pteropodidae). *Journal of*

341   *Zoology, 232*, 691-700.

342   Kunz, T.H., & Jones, D.P. (2000). Pteropus vampyrus. *Mammalian Species*, *642*, 1-6.

343   Luft, S., Curio, E., & Tacud, B. (2003). The use of olfaction in the foraging behavior

344   of the golden-mantled flying fox, *Pteropus pumilus*, and the greater musky fruit

345   bat, *Ptenochirus jagori* (Megachiroptera: Pteropodidae). *Naturwissenschaften,*

346   *90*, 84-87.

347   Maros, K., Gácsi, M., & Miklósi, Á. (2008). Comprehension of human pointing

348   gestures in horses (*Equus caballus*). *Animal Cognition, 11*, 457-466.

349   McCracken, G.F., & Bradbury, J.W. (1981). Social organization and kinship in the

350   polygynous bat Pyllostomus hastatus. *Behavioral Ecology and Sociobiology, 8*,

351   11-34.

352   McKinley, J., & Sambrook, T. (2000). Use of human-given cues by domestic dogs

353   (*Canis familiaris*) and horses (*Equus caballus*). *Animal Cognition, 3*, 13-22.

354   Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A

355   simple reason for a big difference: wolves do not look back at humans, but dogs

356   do. *Current Biology,13*(9)*,*764-766.

357   Miklósi, Á., Pongrácz, P, Lakatos, G., Topál, J., & Csányi, V. (2005). A comparative

358   study of the use of visual communicative signals in interactions between dogs

359   (*Canis familiaris*) and humans and cats (*Felis catus*) and humans. *Journal of*

360   *Comparative Psychology, 119,* 179-186.

361   Miklósi, Á., & Soproni, K. (2006). A comparative analysis of animals'

362   understanding of the human pointing gesture. *Animal Cognition, 9*, 81-93.

363   Pack, A. A., & Herman, L. M. (2004). Bottlenosed dolphins (*Tursiops truncatus*)

364   comprehend the referent of both static and dynamic human gazing and pointing in

365   an object-choice task. *Journal of Comparative Psychology, 118*, 160-171.

366   Safi, K., & Kerth, G. (2007). Comparative analyses suggest that information transfer

367   promoted sociality in male bats in the temperate zone. *American Naturalist, 170*,

368   465-472.

369   Scheumann, M., & Call, J. (2004). The use of experimenter-given cues by south

370   african fur seals (*Arctocephalus pusillus*). *Animal Cognition, 7*, 224-230.

371   Tomasello, M., & Call, J. (2004). The role of humans in the cognitive development of

372   apes revisited. *Animal Cognition, 7,* 213-215.

373   Trut, L. 1999. Early canid domestication: the farm-fox experiment. *American Scientist,*

374   *87,* 160-169.

375   Tschudin, A., Call, J., Dunbar, R. I. M., Harris, G., & van der Elst, C. (2001).

376   Comprehension of signs by dolphins (*Tursiops truncatus*). *Journal of Comparative*

377   *Psychology, 115*, 100-105.

378   Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2008). Wolves outperform dogs in

379   following human social cues. *Animal Behaviour, 76*, 1767-1773.

380   doi:10.1016/j.anbehav.2008.07.028.

381   Udell, M. A. R., & Wynne, C. D. L. (2010). Ontogeny and phylogeny: both are essential

382   to human-sensitive behavior in the genus Canis. *Animal Behaviour, 9*, e9-e14.

383   doi:10.1016/j.anbehav.2009.11.033.

384   Virányi, Z, Gácsi, M, Kubinyi, E, Topál, J, Belényi, B., Ujfalussy, D., & Miklósi, Á.

385   (2008). Comprehension of human pointing gestures in young human-reared

386   wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Animal Cognition, 11*, 373-

387   387.

388   Von Bayern, A.M.P., & Emery, N.J. (2009). Jackdaws respond to human attentional

389   states and communicative cues in different contexts. *Current Biology 19*, 602-

390   606.

391   Wilkinson, G.S. (1984). Reciprocal food sharing in the vampire bat. *Nature, 308*, 181-

392   184.

393   Wilkinson, G.S. (1986). Social grooming in the common vampire bat desmodus-

394   rotundus. *Animal Behaviour, 34*, 1880-1889.

395   Wilkinson, G.S. (1992). Information transfer at evening bat colonies. *Animal Behaviour,*

396   *44,* 501-518.

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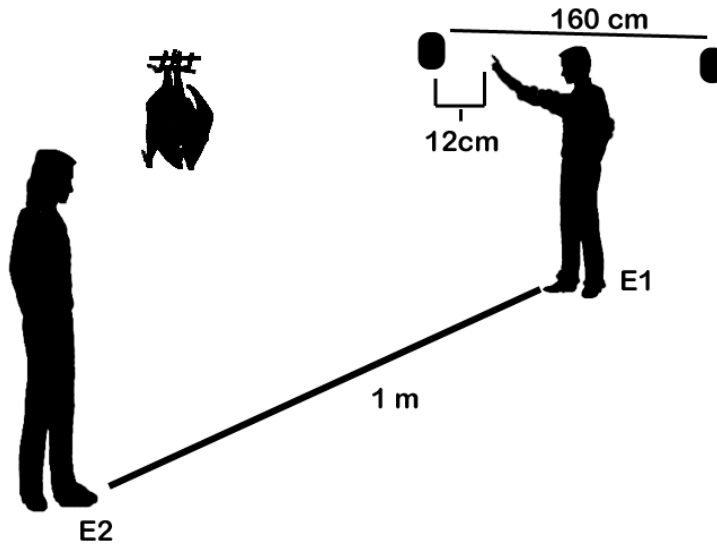
406 *Figure 1.* Testing Layout. Experimenter 1 (E1) pointed to the target object and

407 continued to point until the bat made a choice. A familiar caretaker, Experimenter 2

408 (E2), served as the call back experimenter. E2 retrieved the bat and placed the bat at the

409 correct starting place before every trial begun.

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Figure 2. Experimental Materials and Design. (A) The jar on the left has an open lid making the nectar inside accessible; this jar was placed in the target container. The right jar has a wire mesh lid making the nectar inaccessible, this jar was located in the incorrect testing container. (B) A subject being recalled to the start by the assistant. Bats travelled between the assistant and experimenter by pulling themselves across the roofing. (C) An unfamiliar experimenter is making a dynamic proximal point towards the target container. (D) The subject has made a correct response, entered the target container and is obtaining nectar.
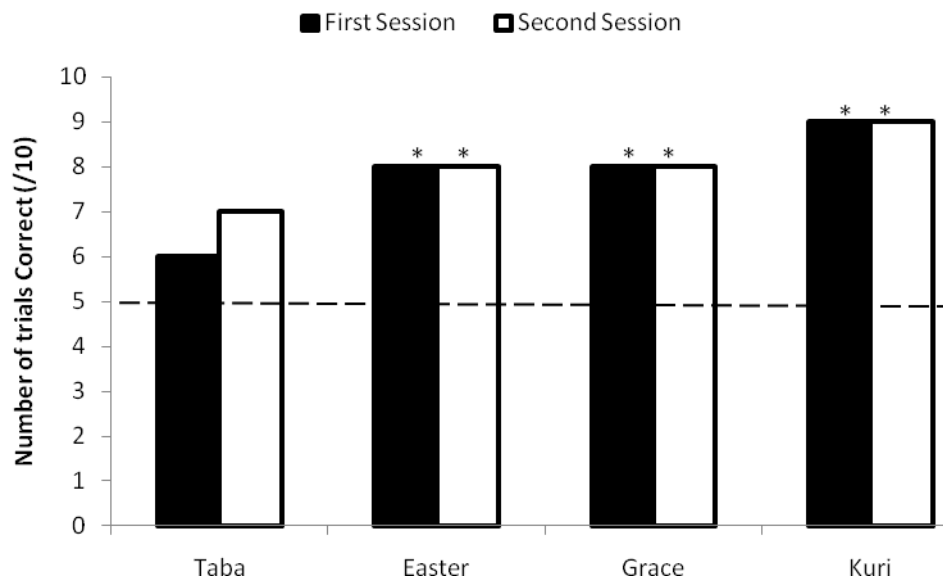
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433   *Figure 3*. Individual performance in each testing session. The number of successful

434   trials, out of 10 for each session, for each bat that completed testing is displayed. Three

435   captive-born bats (Easter, Grace and Kuri) and one wild-caught bat (Taba) are shown.

436   The second wild-caught bat (Arthur) did not complete testing (completed only 6 trials,

437   two of which were correct choices) and is not shown in this figure. * indicates

438   performance significantly above chance in that session (binomial test, p ≤ .05). The

439   dashed line indicates chance responding on the task.