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1 **Individual Differences in Zoo-housed Squirrel Monkeys' (*Saimiri sciureus*) Reactions**
2 **to Visitors, Research Participation, and Personality Ratings**

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14 Short title: SQUIRREL MONKEY INDIVIDUAL DIFFERENCES

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25 **ABSTRACT**

26 Understanding individual differences in captive squirrel monkeys is a topic of importance
27 both for improving welfare by catering to individual needs, and for better understanding the
28 results and implications of behavioral research. In this study, 23 squirrel monkeys (*Saimiri*
29 *sciureus*), housed in an environment that is both a zoo enclosure and research facility, were
30 assessed for (i) the time they spent by an observation window under three visitor
31 conditions: no visitors, small groups, and large groups, and (ii) their likelihood of
32 participating in voluntary research, and (iii) zookeepers ratings of personality. A
33 Friedman's ANOVA and Wilcoxon post-hoc tests comparing mean times found that the
34 monkeys spent more time by the window when there were large groups present than when
35 there were small groups or no visitors. Thus, visitors do not seem to have a negative effect
36 and may be enriching for certain individuals. Through GLMM and correlational analyses, it
37 was found that high scores on the personality trait of playfulness and low scores on
38 cautiousness, depression, and solitude were significant predictors of increased window
39 approach behavior when visitors were present. The GLMM and correlational analyses
40 assessing the links between personality traits and research participation found that low
41 scores of cautiousness and high scores of playfulness, gentleness, affection, and
42 friendliness, were significant predictors. The implications of these results are discussed in
43 relation to selection bias and its potential confounding effect on cognitive studies with
44 voluntary participation.

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46 Key words: squirrel monkeys; zoo visitors; personality; selection bias; animal welfare

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RESEARCH HIGHLIGHTS

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- Squirrel monkey personality ratings correlated with response to visitors and

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research participation.

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- Monkeys approached a viewing window more when visitors were present.

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- Personality differences in research participation may cause selection bias.

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INTRODUCTION

54

Zoos strive to design the best possible environments for their animals, which also allow the animals to be viewed by humans [Hosey, 2005; Fernandez et al., 2009]. As the maintenance of the animals cannot be supported without visitor revenue, and thus high visitor numbers are encouraged, it is important to assess what influence the presence of those visitors has on zoo animal welfare. The “visitor effect,” which argues that animals behave differently when in the presence of human observers than when alone, has been measured across a variety of species in zoos all around the world (for a review, see [Hosey, 2000]). While assessments of non-primate species have generally found that visitors have little impact on animal behavior [Margulis et al., 2003; Quadros et al., 2014], studies on primates have concluded that visitors have a negative influence, finding that human presence generally causes increases in stress-related behaviors, such as attempting to hide, clinging to each other, and aggression [Chamove et al., 1988; Mitchell et al., 1992b; Birke, 2002; Keane & Marples, 2003; Davis et al., 2005].

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However, there are a number of factors that can reduce the visitor effect. Providing zoo animals with enrichment, such as feedings designed to promote foraging (i.e. scattering

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69 food in hay or hiding it in trees), has been shown to reduce the amount of visitor-induced
70 anxiety and other abnormal behaviors that are expressed [Carder & Semple, 2008; Izzo et
71 al., 2011]. Enclosure design is also of vital importance in determining how animals respond
72 to the presence of visitors. Animals that have greater control over their exposure to humans,
73 by having off-show areas or retreat spaces for example, display fewer stress-related
74 behaviors than those animals that do not have control [Anderson et al., 2002; Hosey, 2008;
75 Smith & Kuhar, 2010].

76 A clear example of this can be seen in two studies of orangutan (*Pongo pygmaeus*)
77 welfare that came to starkly contrasting conclusions. One study at Singapore Zoo found that
78 the presence of visitors generally had little effect on the orangutans, but that visitors who
79 were especially active seemed to increase the frequency of play and feeding, behaviors that
80 the authors interpreted as positive [Choo et al., 2011]. Meanwhile, another study at Chester
81 Zoo found that high visitor numbers correlated with stress related behaviors like covering
82 their heads with paper sacks and clinging more closely to each other [Birke, 2002]. Choo et
83 al. suggest that this discrepancy may have been due to Singapore Zoo's unusual free-
84 ranging exhibit design. That enclosure, in addition to allowing the animals more freedom
85 and enrichment, also allowed them a greater sense of security as they were in trees high
86 above visitors rather than being at eye-level with or beneath humans as in other enclosures
87 [Choo et al., 2011]. Having control over their interactions with visitors may be part of the
88 reason why these orangutans did not display the stress behaviors found at other zoos.

89 There may also be individual differences in the reactions of primates to visitors,
90 although few studies have examined this. Determining how individual animals respond to
91 visitors allows for better individual management. For example, if keepers determine that

92 visitors cause one individual to display fear-related behaviors while they cause another
93 individual to engage in play behaviors, the keepers can modify the enclosures and visitor
94 interactions to either decrease or increase the amount of exposure to people, for example by
95 either adding or removing visual barriers in the viewing area. Personality scoring of non-
96 human primates by familiar observers has been established as a useful tool for predicting
97 consistent individual differences in behavior [Weiss et al., 2009; Watters & Powell, 2012;
98 Morton et al., 2013b; Pritchard et al., 2014]. In a study on gorillas (*Gorilla gorilla*) for
99 example, factor scores derived from keeper-rated personality assessments were found to
100 correlate with behaviors relating to visitor crowd size [Stoinski et al., 2012]. In some
101 studies on captive primates, age and sex have also been found to influence how the animals
102 respond to visitors, indicating that those factors should be taken into account as well
103 [Mitchell et al., 1991b, 1992a].

104 Individual differences are not only relevant in the zoo setting but also in research
105 participation. Taking individual differences into account is a vital point of investigation in
106 facilities where primates are given the opportunity to voluntarily participate in studies. In
107 these situations, data only comes from individuals who choose to take part. While this is
108 important from a welfare perspective, it leads to selection bias. [Morton et al., 2013a].
109 Gaining greater knowledge of individual differences allows for a better understanding of
110 not only the animals themselves but also of how they impact research. We hypothesize that
111 animals with more social and playful characteristics are more likely to voluntarily
112 participate in interactive research studies than less social and more fearful animals. This
113 could possibly skew the results of many studies as, on account of their different
114 personalities, the animals could have different problem-solving and behavioral tendencies.

115 In the present study, there was a unique opportunity to assess the connections
116 between these three topics – zoo visitor effects, research participation, and individual
117 differences – by studying squirrel monkeys in an area that is both a zoo exhibit as well as a
118 research facility. The ‘Living Links to Human Evolution’ Research Centre within the Royal
119 Zoological Society of Scotland, Edinburgh Zoo (hereafter Living Links) houses two mixed-
120 species groups of capuchin and squirrel monkeys (see: [Macdonald & Whiten, 2011]). The
121 monkeys are given regular (normally daily) environmental enrichment and also have the
122 opportunity to partake in research that requires problem solving or social learning, which
123 provides them with enrichment in the form of mental stimulation. These sessions also allow
124 for greater numbers of positive interactions with a variety of familiar and less familiar
125 humans than most zoo-housed primates receive. This can lead to the monkeys being
126 enriched by human presence, or at the very least having a non-aversive relationship with
127 them [Hosey, 2008]. Research concerning individual differences in the squirrel monkeys
128 has been ongoing [Wilson et al., in prep; Wilson, 2011], but thus far has not been
129 investigated with regards to either reactions to visitors or participation in research.

130 The goals of this study were threefold: (1) to assess group level reactions to
131 different visitor groups, (2) to assess individual differences in personality and reactions to
132 visitors, (3) to investigate the relationship between personality and research participation.
133 We predicted that (1) due to their high levels of enrichment, their opportunities to regulate
134 their exposure to visitors, and their frequent interactions with keepers and researchers, the
135 monkeys in this study would not react aversively to visitors, as measured by a lack of
136 avoidance of the observation window as visitor numbers increased, (2) the monkeys would
137 show individual differences as measured by consistent ratings of personality traits by the

138 keepers and differences in responses to visitors, (3) monkeys who were scored by their
139 keepers as being highly friendly, playful, and curious would be more likely to come to the
140 observation window when visitors were present than those individuals who the keepers
141 scored as more timid or anxious, and a similar trend with regards to which animals would
142 be most likely to voluntarily participate in studies involving the research cubicles.

143

144

METHODS

145 **Subjects and Enclosure**

146 The subjects of this study were 23 of the 26 squirrel monkeys (*Saimiri sciureus*)
147 housed within the ‘Living Links to Human Evolution’ Research Centre within the Royal
148 Zoological Society of Scotland, Edinburgh Zoo. The monkeys were housed in two separate
149 but identical mirror-image enclosures (‘West’, N = 9 and ‘East’, N = 17, Figure 1). All of
150 the monkeys were female, except for one alpha male in each group, identified by their
151 larger sizes. The remaining monkeys, except for one juvenile in the West group (who was
152 identified by her smaller size), were identified through different colored beads on their
153 necklaces. Three of the monkeys in the East group who had lost their necklaces and could
154 not be differentiated were excluded from the study. The monkeys ranged in age from one to
155 16 years with a mean±SE age of 7±1 years. All of the monkeys had been born in captivity
156 and none had been hand-reared.

157 Each enclosure consisted of five areas: (1) an outdoor area, (2) an indoor area
158 accessible by both the squirrel monkeys and a population of brown capuchin monkeys
159 (*Sapajus apella*; 18 in West and 17 in East), (3) an indoor area that was exclusive to the
160 squirrel monkeys, (4) a research room with testing cubicles located between the two indoor

161 enclosures of each side, and (5) an off-show area with holding cages. The squirrel monkeys
162 were free to move between all these areas at all times, except for the research rooms, which
163 were only available during research and training sessions. All the indoor areas had two full-
164 wall windows: one facing the outdoor area and one observation window on the front wall
165 allowing visitors to look into the enclosure. All windows had slanting ledges that monkeys
166 could perch on. For a full description of the enclosure design, including light cycles,
167 temperatures, and construction materials, see Leonardi et al. [2010]. The focus of this study
168 was the two observation windows on the front walls looking into the two indoor enclosures
169 that were exclusive to the squirrel monkeys.

170 Research/training sessions were a maximum of eight periods of ninety minutes per
171 week. During these sessions, the monkeys were free to enter. The monkeys could be
172 voluntarily isolated for up to 15 minutes once during each session. During training and
173 research sessions monkeys were rewarded for entering the cubicles, isolating, and
174 participating in research. These rewards included sunflower seeds, raisins, peanuts and
175 mealworms.

177 **Data collection**

178 *Window approaching behavior*

179 In order to determine how the monkeys responded to visitor groups of different
180 sizes, the monkeys' use of the observation windows was examined to see how frequently
181 each monkey approached the window under the different conditions. There were three
182 mutually exclusive visitor group size conditions, as determined by previous studies on

183 visitor demographics [Ridgway et al., 2006]: (1) no visitors, (2) small groups (one to three
184 people), and (3) large groups (four or more people).

185 During each observation session, the viewing window of one of the squirrel monkey
186 indoor enclosures (East or West) was observed continuously for 30 minutes by the same
187 observer (ZP). There were 80 data collection sessions (40 per enclosure) over six weeks
188 between the months of April and May 2015. Data was collected every other day always
189 between the hours of 13:00 and 17:00, but never during feeding, cleaning, or training.
190 There was no cubicle research during this time. There were four sessions (two per
191 enclosure) each data collection day, where the sessions alternated between East and West
192 observations. In order to minimize observer effect, prior to each session there was a 10-
193 minute period where the observer was present at the window but did not record data. This
194 time frame was determined based on the experiences of the zookeepers, as well as on
195 previous research that showed that primates habituate to the presence of non-visitor
196 observers within that time frame [Mitchell et al., 1991a].

197 The data was collected using the Time-stamped Field Data event recording
198 application (Neukadye, LLC. Version 1.3) on an iPad (Apple Inc.), which recorded the
199 duration of time that the various groups of visitors spent at the observation window, as well
200 as the duration of time that each monkey spent at the window during that time period. The
201 average proportion of time each monkey spent at the window for each visitor category was
202 then calculated from the total amount of time that visitor category was at the window across
203 the 40 sessions.

204 *Cubicle research participation*

205 Throughout the months of June and July 2015, a separate study was conducted
206 requiring the voluntary isolation of the monkeys in the research cubicles. This study
207 involved training sessions where the monkeys received food rewards for entering and
208 remaining in the cubicles, as well as research sessions where the monkeys were given a
209 novel object to interact with and food rewards for participation. The monkeys chose
210 whether to enter the cubicles during the session and were given the option to return to the
211 group if they showed signs of discomfort (for a more detailed description of the cubicle
212 setup, see: [Macdonald & Whiten, 2011]). Throughout these sessions, the order in which
213 the monkeys chose to enter (or not) the cubicles was recorded for both groups as a measure
214 of likeliness to participate. In these sorts of settings, individuals are often excluded from
215 studies if they do not meet regular participation criteria, therefore the likelihood of
216 participation is a relevant measure to assess [Morton et al., 2013a]. Each monkey was given
217 a score based on their order of entry for each session. This was calculated by taking the
218 total number of monkeys in each group (nine for West, 14 for East) and giving a reverse
219 order score based on that number. For example, the first monkey to enter the cubicles in the
220 West group would receive nine points, the second eight points and so forth, while the first
221 monkey in the East group would receive 14 points, and the second 13. Monkeys who did
222 not enter the cubicles received zero points. In order to make the scores of the two groups
223 comparable, the scores for each monkey were divided by the total number of monkeys in its
224 group. The final score for each monkey was the average of these ratios across all of the
225 cubicle sessions (21 for the West Group, 18 for the East Group).

226 *Keeper-ratings of personality*

227 Three keepers who had worked with the monkeys for at least three years were asked
228 to fill out a shortened version of the Hominoid Personality Questionnaire [Weiss et al.,
229 2009] for each of the monkeys. This shortened version consisted of 12 personality traits for
230 which each monkey was rated on a seven point Likert scale based on one to two descriptive
231 sentences (Table 1). The directions on the questionnaire explained that a score of 1
232 indicated that the monkey displayed a “total absence or negligible amount” of that trait and
233 a score of 7 indicated that the individual displayed “extremely large amounts” of that trait.
234 The original questionnaire was reduced to 12 traits in order to accommodate the
235 zookeepers’ time restraints and to attempt to create a more practical and efficient version of
236 the questionnaire. The personality traits were chosen based on high loadings found in a
237 previous personality assessment of squirrel monkeys using the full 54-item Hominoid
238 Personality Questionnaire. In that study, four components (‘Assertiveness,’
239 ‘Impulsiveness,’ ‘Neuroticism,’ and ‘Agreeableness’) were derived from 46 reliable items
240 and were validated across 57 animals from eight international zoos [Wilson et al., in prep;
241 Wilson, 2011]. Three high-loading traits were chosen from each of the four components.
242 An attempt was made to choose traits that were distinct from each other and that had
243 minimal overlap in their descriptive sentences.

244

245 **Statistical analysis**

246 To compare the proportion of time that the monkeys spent at the observation
247 window for each of the three visitor categories, a Friedman’s ANOVA and post-hoc
248 Wilcoxon tests were used, as the distribution of the residuals proved to be non-normal. A

249 Holm-Bonferroni sequential correction was applied to the results and the adjusted p-values
250 are reported [Holm, 1979].

251 To identify the factors that influence the window approach behavior and
252 participation in cubicle research, two generalized linear mixed models (GLMM) were run
253 using IBM SPSS (Version 22). For the window approach behavior, a binomial distribution
254 with a logit link function was used. For the cubicle participation data, a normal distribution
255 with an identity link function was used. In both models, the random effects included
256 Monkey ID nested within Enclosure. The fixed effects were determined by running the
257 explanatory variables (each of the reliable personality traits and age) through the program's
258 Automatic Linear Modeling function using a forward stepwise model selection method
259 with an Akaike Information Criterion Corrected (AICc) information criterion. Each of the
260 12 personality traits was tested for inter-rater reliability between the three keepers using a
261 two-way interclass mixed-model correlation ($ICC_{(3,k)}$) [Shrout & Fleiss, 1979].
262 Correlational tests and graphical summaries were used to determine the relationships
263 between the predictive and behavioral variables.

264 265 **Ethical consideration**

266 This study was approved by the Scientific Review Team of the University of
267 Edinburgh. As the study was observational and there was no direct manipulation of, or
268 interference with the animals, the team felt it was not necessary to receive approval from
269 the Veterinary Ethical Review Committee (VERC). The study was also approved by the
270 research review board at the 'Living Links to Human Evolution' Research Centre and the
271 Royal Zoological Society of Scotland, Edinburgh Zoo. The research adhered to the

272 American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-
273 Human Primates.

274

275

RESULTS

276 **Group level reaction to visitors**

277 There were significant differences between the mean proportions of time that the
278 monkeys spent at the window during the three visitor group categories (Friedman's
279 ANOVA: $X^2_{(2)}=31.92$, $P<0.001$, see Figure 2). The monkeys spent significantly larger
280 proportions of time at the observation window when there were large groups of visitors
281 present compared to when there were no visitors or small groups present (Wilcoxon: $Z=-$
282 4.009 , $P=0.002$; $Z=-3.09$, $P=0.002$). The monkeys also spent a greater proportion of time at
283 the observation window when there were small groups of visitors there compared to when
284 there were no visitors (Wilcoxon: $Z=-3.444$, $P=0.001$).

285

286 **Individual differences in reactions to visitors**

287 There were considerable individual differences between the monkeys with regards
288 to their proportions of time spent at the window for each visitor category (Figure 3). The
289 individual percentages of time spent at the window for the 'No Visitor' category ranged
290 from 0% to 76% (mean \pm SE: 18 \pm 3%). The individual percentages of time that monkeys
291 spent at the window for the 'Small Group' category ranged from 0% to 37% (mean \pm SE:
292 18 \pm 2%), while the percentage of time for the 'Large Group' category ranged from 0% to
293 88% (mean \pm SE: 59 \pm 5%). The total amount of time each monkey spent at the window

294 across all sessions ranged from zero minutes (one individual never came to the window) to
295 143 minutes (mean±SE: 27±6.5 minutes).

296

297 **Relationship between personality, reaction to visitors, and research participation**

298 For the personality questionnaire scores, the inter-rater reliability of the mean
299 ratings between the three keepers, $ICC_{(3,k)}$, had a mean of 0.38, and ranged from 0.138 for
300 *depressed* to 0.729 for *playful*. One trait (*predictable*) that had an ICC value that was less
301 than zero was considered unreliable (as per the criteria used by other studies of primate
302 personality – see: [Weiss et al., 2011; Wilson, 2011]) and was removed from further
303 analysis. All raters completed the questionnaires fully and there were no missing values.

304 For the data on the proportion of time spent at the viewing window, the Automatic
305 Linear Modeling function showed that the personality traits *playful*, *cautious*, *solitary*,
306 *dominant*, and *depressed* had the highest associations (adjusted $R^2=0.30$). All of these
307 traits, except for *dominant*, had significant effects (Table 2). In order to determine the
308 direction of the effects, Spearman's correlations were run between the significant traits and
309 the difference between the proportion of time spent at the window during the 'Large Group'
310 condition and the 'No Visitor' condition. *Playfulness* was found to have a positive
311 relationship ($R=0.162$) while *cautious* ($R=-0.042$), *solitary* ($R=-0.419$), and *depressed* ($R=-$
312 0.327) had negative relationships (Figure 4).

313 For the cubicle research participation data, the Automatic Linear Modelling
314 function determined that *playful*, *cautious*, *affectionate*, *friendly*, and *gentle* were the traits
315 of greatest importance (adjusted $R^2=0.668$). When these were assessed for their significance
316 in predicting research participation, it was found that all had significant effects (Table 2).

317 Pearson's correlations showed that *playful* ($R=0.729$), *affectionate* ($R=0.405$), *friendly*
318 ($R=0.447$), and *gentle* ($R=0.487$) had positive relationships with cubicle participation
319 scores, while *cautious* ($R=-0.341$) had a negative relationship (Figure 5).

320

321

DISCUSSION

322 The goals of this study were threefold: (1) to assess group level reactions to
323 different visitor groups, (2) to assess individual differences in personality and reactions to
324 visitors, (3) to investigate the relationship between personality and research participation.

325 Our first prediction that the monkeys would not react aversively to visitors was
326 broadly supported. On average, the more people there were at the observation window, the
327 more frequently the monkeys chose to come up to that window. This implies that the
328 monkeys are actively choosing to be around the visitors when they are at the viewing
329 window, as they could easily choose to be in other areas without visitors if they found them
330 aversive. Thus, the visitors do not seem to have a negative impact on their welfare and may
331 even be enriching for some of the individuals. However, previous studies [Mitchell et al.,
332 1992c; Hosey, 2000] investigating relationships between animal behaviors and visitor
333 presence rightfully note the importance of not assuming causality, arguing that zoo visitors
334 may be attracted to animals performing certain behaviors.

335 This is unlikely to be the case for this study for a number of reasons. Firstly, the
336 setup of the enclosures (Figure 1) is such that visitors are not able to see the animals in the
337 indoor enclosure until they are already directly at the window, making it unlikely that the
338 sight of unusual animal behaviors are attracting the larger numbers of visitors to the
339 window from other areas. Additionally, the visitors are not able to see how many other

340 people are at the window until they are there themselves. This makes it unlikely that the
341 presence of crowds looking at interesting behaviors, such as monkeys that are up on the
342 ledge, were attracting more people to the window. Furthermore, the results showed that,
343 when there is no one around, the monkeys do not choose to spend much time up on the
344 ledge, suggesting once again that when they do come up to the window, it is to be closer to
345 the visitors.

346 All of these factors provide support for the conclusion that, for the squirrel monkeys
347 at this facility, the presence of zoo visitors does not appear to negatively influence their
348 welfare and that some individuals may even actively seek it out. This conclusion stands in
349 contrast to the results of the majority of previous primate studies (though not all – see:
350 [Cook & Hosey, 1995; Todd et al., 2007]) suggesting that the presence of humans is
351 primarily a source of stress for the animals [Chamove et al., 1988; Birke, 2002; Keane &
352 Marples, 2003; Wells & Blaney, 2003; Davis et al., 2005; Mallapur et al., 2005]. A number
353 of possibilities could explain this discrepancy. First, the squirrel monkeys in this study are
354 provided with a variety of enrichment opportunities, which has been suggested to reduce
355 stress in some species [Carder & Semple, 2008; Izzo et al., 2011]. Second, they have
356 frequent positive interactions with humans through other research studies, potentially
357 fostering in them a positive human-animal relationship, thus reducing the ‘visitor effect’
358 [Hosey, 2008]. Lastly, the animals had the option to choose from five different enclosure
359 areas with different levels of exposure to zoo visitors. This allowed some monkeys to come
360 into very close proximity to humans, for example by jumping up to the ledge by the
361 viewing window, while allowing other monkeys to avoid them completely.

362 Our second prediction that the monkeys would show individual differences was
363 largely supported. Apart from the trait of *predictable*, all other traits had positive ICC
364 ratings. The trait of *playful* had a particularly strong ICC rating. Similarly, there was a huge
365 variance in the amount of time that individuals chose to be at the window. These individual
366 differences were also found to have significant influences on how the monkeys behaved. As
367 such, our third and fourth hypotheses that personality ratings would be associated with
368 visitor reactions and research participation were also supported. For both approaching the
369 window and participating in research, higher scores of playfulness and lower scores of
370 cautiousness were important factors. This makes sense intuitively, as it is logical that
371 cautious animals would be less inclined to engage in activities that put them in close
372 proximity to relatively unpredictable humans, and that playful animals might see engaging
373 in those same activities as rewarding.

374 Interestingly, the remaining relevant personality traits for the two behaviors fell on
375 opposite spectrums. While for the window approaching behaviors the significant predictive
376 personality scores (correlated with less time spent at the window) were for solitude and
377 depression, both of which are highly loading on the ‘Neuroticism’ factor [Wilson et al., in
378 prep.], for predicting the monkeys’ participation in research, it was the traits that were
379 highly loading on the ‘Agreeableness’ factor (gentle, affectionate, and friendly) that proved
380 to be significant. The suggestion that more neurotic animals do not come to the observation
381 window more frequently when there are visitors present could have welfare implications. It
382 is possible that those animals are simply not interested in the visitors and thus have no
383 motivation to interact with them, or they may find the visitors aversive and are actively
384 avoiding them. More studies are needed to make this distinction.

385 The relationship between personality scores and research participation also has
386 important practical implications, particularly in relation to the existence of selection bias in
387 behavioral research studies. The behavior of the more agreeable animals during the
388 research sessions may be different from the behavior of the non-participating and evidently
389 less agreeable individuals. Indeed, studies have found that individuals with more assertive
390 or aggressive personalities have different problem-solving strategies compared to less
391 assertive individuals. This was demonstrated by a study done with the very capuchins
392 housed with these squirrel monkeys, which found that accuracy was negatively correlated
393 with scores of assertiveness in a number of cubicle-based tasks [Morton et al., 2013a].

394 Studies on chimpanzees (*Pan troglodytes*) have also found that a variety of
395 personality dimensions can have strong correlations with behavioral measures on cognitive
396 tests [Weiss et al., 2012; Reamer et al., 2014; Brosnan et al., 2015]. Agreeableness, for
397 example, was found to be correlated with responses to inequity, where chimpanzees with
398 lower ratings of Agreeableness were more likely to respond to inequity by refusing to
399 exchange rewards than those with higher ratings in that dimension [Brosnan et al., 2015].
400 The existence of personality differences between the monkeys, and the knowledge that
401 these differences may influence not only which monkeys participate in research but also
402 their performance within the tests themselves, suggests that these differences need to be
403 taken into account much more frequently in order to avoid the confounding effects of
404 selection bias.

405 While the results of this study may provide valuable insights for future research and
406 welfare management, it is important to acknowledge its limitation. For example, the
407 amount of choice in enclosure location was a potential confound for the current study.

408 Because the monkeys had many other areas that they could choose to be in, measuring their
409 response to visitors at only one of these spaces may not have been representative of their
410 true overall response. It is possible that, on occasion, some monkeys could have chosen to
411 interact with people in other areas, such as the observation window in the capuchin
412 enclosures, and this would not have been recorded through the methodology of this study.
413 Such an omission may be hiding potential relationships between monkey reactions to
414 visitors and personality ratings.

415 There could also be some confounds in the personality ratings, as the keepers who
416 filled them out have inherently different types of interactions with the monkeys than the
417 visitors. Primates can differentiate between keepers or observers and unfamiliar visitors
418 [Mitchell et al., 1991a]. Because the keepers only see the monkeys when the monkeys are
419 around people they are familiar with (themselves), their assessments of personality may be
420 biased towards those types of situations and may be less able to predict the monkeys'
421 personalities around unfamiliar visitors. This may also explain why personality ratings were
422 found to account for a greater portion of the variance in research participation data, where
423 the monkeys were in situations with familiar keepers and researchers, than for the data from
424 the window approach behavior, which measured interactions with strangers.

425 Of course, the relatively small sample size of the study should be taken into account
426 before generalizing to other populations of squirrel monkeys. In particular, the inequality
427 between the number of male and female monkeys should be noted, as the present study had
428 only two male individuals. Future research should assess squirrel monkey populations
429 across multiple zoos and institutions and should have larger representation of males in

430 order to examine the potential effects of sex on individual differences in behavior and
431 personality.

432

433

CONCLUSIONS

434 This study demonstrates that individual differences exist between squirrel monkeys
435 both in how they respond to varying sizes of zoo visitor groups, and in their likeliness to
436 participate in voluntary behavioral research. While, on average, visitors do not seem to
437 have a negative impact on the welfare of the animals, certain individuals choose to engage
438 with humans more than others, and management practices should take these individual
439 welfare needs into account. Potential ways of doing this would be to design enclosures in
440 such a way that animals could choose to have close-up interactions with visitors via
441 viewing windows, while still maintaining enclosure elements that allow for visitor
442 avoidance. Offering voluntary participation in training sessions or research studies could
443 also prove to be beneficial for some individuals. Keeper ratings based off of personality
444 questionnaires could also be used to predict animal behaviors. With regards to future
445 primate studies, the relationship between personality ratings and research participation
446 suggests that there is a strong possibility for selection bias to occur; therefore, care should
447 be taken in accounting for this issue. Lastly, further study with larger sample sizes and
448 more in-depth personality assessments would shed more light onto what factors influence
449 visitor-effect and research participation.

450

451

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Final Draft

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569 **TABLE I. Personality traits and descriptive sentences that were presented to the**
 570 **keepers in the Squirrel Monkey Personality Questionnaire.**

Trait	Description
Dominant	Subject is able to displace, threaten, or take food from other monkeys. Or subject may express high status by decisively intervening in social interactions.
Curious	Subject has a desire to see or know about objects, devices, or other monkeys. This includes a desire to know about the affairs of other monkeys that do not directly concern the subject.
Cautious	Subject often seems attentive to possible harm or danger from its actions. Subject avoids risky behaviors.
Playful	Subject is eager to engage in lively, vigorous, sportive, or acrobatic behaviors with or without other monkeys.
Solitary	Subject prefers to spend considerable time alone not seeking or avoiding contact with other monkeys.
Gentle	Subject responds to others in an easy-going, kind, and considerate manner. Subject is not rough or threatening.
Timid	Subject lacks self-confidence, is easily alarmed and is hesitant to venture into new social or non-social situations.
Affectionate	Subject seems to have a warm attachment or closeness with other monkeys. This may entail frequent grooming, touching, embracing, lying near others.
Predictable	Subject's behavior is consistent and steady over extended periods of time. Subject does little that is unexpected or deviates from its usual routine.
Depressed	Subject does not seek out social interactions with others and often fails to respond to social interactions of other monkeys. Subject often appears isolated, withdrawn, sullen, brooding, and has reduced activity.
Friendly	Subject often seeks out contact with other monkeys for amiable, genial activities. Subject infrequently initiates hostile behaviors towards other monkeys.
Anxious	Subject often seems distressed, troubled, or is in a state of uncertainty.

572 **TABLE II. GLMM results showing significance of explanatory variables influencing**
 573 **the proportion of time spent at the viewing window and participation in research.**

Trait	Time at Viewing Window		Research Participation	
	F	Sig	F	Sig
Playful	26.273	<0.001	59.335	<0.001
Cautious	10.908	0.002	11.325	0.001
Solitary	8.677	0.005	-	-
Dominant	2.954	0.091	-	-
Depressed	5.646	0.021	-	-
Affectionate	-	-	7.844	0.007
Friendly	-	-	7.803	0.007
Gentle	-	-	7.289	0.009

574 df1 = 1 and df2 = 63 for all values.

575

576 **FIGURE LEGENDS**

577 Fig 1. Enclosure Setup. The East and West sides are identical but separate enclosures. The
 578 squirrel monkeys had access to all areas except the research rooms, which were only
 579 available to them during specific sessions. The observation windows that were used in this
 580 study are marked with red. Key: WS = west squirrel monkeys; WC = west capuchin
 581 monkeys (with squirrel monkey access); EC = east capuchin monkeys (with squirrel
 582 monkey access); ES = east squirrel monkeys. [Living Links to Human Evolution Research
 583 Centre, 2014].

584 Fig 2. The average proportions of time monkeys spent at the observation window for the
 585 three visitor group size categories. Letters (a, b, c) indicate significant differences between
 586 those group categories that have matching letters. Error bars represent standard errors of the
 587 mean.

588

589 Fig 3. The percentage of the total time each monkey spent at the window for each of the
590 three visitor categories. One monkey (Hugo) never came to the window.

591

592 Fig 4. Plots of each significant personality trait against the percentage difference between
593 the proportion of time spent at the window during the 'Large Group' condition and the 'No
594 Visitor' condition.

595

596 Fig 5. Plots of each significant personality trait against research participation scores. Higher
597 participation scores represent greater willingness to enter cubicles during
598 training/experimental sessions.

599