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

3

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13

14 Short title: SQUIRREL MONKEY INDIVIDUAL DIFFERENCES

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## INTRODUCTION

47

48 Zoos strive to design the best possible environments for their animals, which also  
49 allow the animals to be viewed by humans [Hosey, 2005; Fernandez et al., 2009]. As the  
50 maintenance of the animals cannot be supported without visitor revenue, it is important to  
51 assess what influence visitors have on animal welfare. The “visitor effect,” which argues  
52 that animals behave differently when in the presence of human observers than when alone,  
53 has been measured across a variety of species in zoos all around the world (for a review,  
54 see [Hosey, 2000]). While assessments of non-primate species have generally found that  
55 visitors have little impact on animal behavior [Margulis et al., 2003; Quadros et al., 2014],  
56 studies on primates have concluded that visitors have a negative influence, finding that  
57 human presence generally causes increases in stress-related behaviors, such as attempting  
58 to hide, clinging to each other, and aggression [Chamove et al., 1988; Mitchell et al.,  
59 1992b; Birke, 2002; Keane & Marples, 2003; Davis et al., 2005].

60 However, there are a number of factors that can reduce the visitor effect. Providing  
61 zoo animals with enrichment has been shown to reduce the amount of visitor-induced  
62 anxiety and other abnormal behaviors that are expressed [Carder & Semple, 2008; Izzo et  
63 al., 2011]. Enclosure design is also of vital importance in determining how animals respond  
64 to the presence of visitors. Animals that have greater control over their exposure to humans,  
65 by having off-show areas or retreat spaces for example, display fewer stress-related  
66 behaviors than those animals that do not have control [Anderson et al., 2002; Hosey, 2008;  
67 Smith & Kuhar, 2010].

68 A clear example of this can be seen in two studies of orangutan (*Pongo pygmaeus*)  
69 welfare that came to starkly contrasting conclusions. One study found that the presence of

70 visitors generally had little effect on the orangutans, but that visitors who were especially  
71 active seemed to increase the frequency of play and feeding, behaviors that the authors  
72 interpreted as positive [Choo et al., 2011]. Meanwhile, another study at a different zoo  
73 found that high visitor numbers correlated with stress related behaviors like covering their  
74 heads with paper sacks and clinging more closely to each other [Birke, 2002]. The authors  
75 suggest that this discrepancy may have been due to the first zoo's unusual free-ranging  
76 exhibit design. That enclosure, in addition to allowing the animals more freedom and  
77 enrichment, also allowed them a greater sense of security as they were in trees high above  
78 visitors rather than being at eye-level with or beneath humans as in other enclosures [Choo  
79 et al., 2011].

80         There may also be individual differences in the reactions of primates to visitors,  
81 although few studies have examined this. Determining how individual animals respond to  
82 visitors allows for better individual management. For example, if keepers determine that  
83 visitors cause one individual to display fear-related behaviors while they cause another  
84 individual to engage in play behaviors, the keepers can modify the enclosures and visitor  
85 interactions to either decrease or increase the amount of exposure to people. In some  
86 studies on captive primates, age and sex have been found to influence how the animals  
87 respond to visitors, indicating that those factors should be taken into account [Mitchell et  
88 al., 1991b, 1992a]. Another way to predict these responses is through personality  
89 assessments. In a study on gorillas (*Gorilla gorilla*) for example, factor scores derived from  
90 keeper-rated personality assessments were found to correlate with behaviors relating to  
91 visitor crowd size [Stoinski et al., 2012]. Personality scoring of non-human primates by  
92 familiar observers has been established as a useful tool for predicting consistent individual

93 differences in behavior [Weiss et al., 2009; Watters & Powell, 2012; Morton et al., 2013b;  
94 Pritchard et al., 2014].

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

105 In the present study, there was a unique opportunity to assess the connections  
106 between these three topics –zoo visitor effects, research participation, and individual  
107 differences – by studying squirrel monkeys in an area that is both a zoo exhibit as well as a  
108 research facility. The ‘Living Links to Human Evolution’ Research Centre within the Royal  
109 Zoological Society of Scotland, Edinburgh Zoo (hereafter Living Links) houses two mixed-  
110 species groups of capuchin and squirrel monkeys (see: [Macdonald & Whiten, 2011]). The  
111 monkeys are given regular (normally daily) environmental enrichment and also have the  
112 opportunity to partake in research that requires problem solving or social learning, which  
113 provides them with enrichment in the form of mental stimulation. These sessions also allow  
114 for greater numbers of positive interactions with a variety of familiar and less familiar  
115 humans than most zoo-housed primates receive. This can lead to the monkeys being

116 enriched by human presence, or at the very least having a non-aversive relationship with  
117 them [Hosey, 2008]. Research concerning individual differences in the squirrel monkeys  
118 has been ongoing [Wilson et al., in prep; Wilson, 2011], but thus far has not been  
119 investigated with regards to either reactions to visitors or participation in research.

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

123         We predicted that (1) due to their high levels of enrichment, their opportunities to  
124 regulate their exposure to visitors, and their frequent interactions with keepers and  
125 researchers, the monkeys in this study would not react aversively to visitors, as measured  
126 by a lack of avoidance of the observation window as visitor numbers increased, (2) the  
127 monkeys would show individual differences as measured by consistent ratings of  
128 personality traits by the keepers and differences in responses to visitors, (3) monkeys who  
129 were scored by their keepers as being highly friendly, playful, and curious would be more  
130 likely to come to the observation window when visitors were present than those individuals  
131 who the keepers scored as more timid or anxious, and a similar trend with regards to which  
132 animals would be most likely to voluntarily participate in studies involving the research  
133 cubicles.

134

135

## METHODS

### 136 **Subjects and Enclosure**

137         The subjects of this study were 23 of the 26 squirrel monkeys (*Saimiri sciureus*)  
138 housed within the ‘Living Links to Human Evolution’ Research Centre within the Royal

139 Zoological Society of Scotland, Edinburgh Zoo. The monkeys were housed in two separate  
140 but identical mirror-image enclosures ('West', N = 9 and 'East', N = 17, Figure 1). All of  
141 the monkeys were female, except for one alpha male in each group, identified by their  
142 larger sizes. The remaining monkeys, except for one juvenile in the West group (who was  
143 identified by her smaller size), were identified through different colored beads on their  
144 necklaces. Three of the monkeys in the East group who had lost their necklaces and could  
145 not be differentiated were excluded from the study. The monkeys ranged in age from one to  
146 16 years with a mean $\pm$ SE age of  $7\pm 1$  years. All of the monkeys had been born in captivity  
147 and none had been hand-reared.

148       Each enclosure consisted of five areas: (1) an outdoor area, (2) an indoor area  
149 accessible by both the squirrel monkeys and a population of brown capuchin monkeys  
150 (*Sapajus apella*; 18 in West and 17 in East), (3) an indoor area that was exclusive to the  
151 squirrel monkeys, (4) a research room with testing cubicles located between the two indoor  
152 enclosures of each side, and (5) an off-show area with holding cages. The squirrel monkeys  
153 were free to move between all these areas at all times, except for the research rooms which  
154 were only available during research and training sessions. All the indoor areas had two full-  
155 wall windows: one facing the outdoor area and one observation window on the front wall  
156 allowing visitors to look into the enclosure. All windows had slanting ledges that monkeys  
157 could perch on. For a full description of the enclosure design, including light cycles,  
158 temperatures, and construction materials, see Leonardi et al. [2010]. The focus of this study  
159 was the two observation windows on the front walls looking into the two indoor enclosures  
160 that were exclusive to the squirrel monkeys.



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

167

### 168 **Data collection**

#### 169 *Window approaching behavior*

170           In order to determine how the monkeys responded to visitor groups of different  
171 sizes, the monkeys' use of the observation windows was examined to see how frequently  
172 each monkey approached the window under the different conditions. There were three  
173 mutually exclusive visitor group size conditions, as determined by previous studies on  
174 visitor demographics [Ridgway et al., 2006]: (1) no visitors, (2) small groups (one to three  
175 people), and (3) large groups (four or more people).

176           During each observation session, the viewing window of one of the squirrel monkey  
177 indoor enclosures (East or West) was observed continuously for 30 minutes by the same  
178 observer (ZP). There were 80 data collection sessions (40 per enclosure) over six weeks  
179 between the months of April and May 2015. Data was collected every other day always  
180 between the hours of 13:00 and 17:00, but never during feeding, cleaning, or training.  
181 There was no cubicle research during this time. There were four sessions (two per  
182 enclosure) each data collection day, where the sessions alternated between East and West  
183 observations. In order to minimize observer effect, prior to each session there was a 10-

184 minute period where the observer was present at the window but did not record data. This  
185 time frame was determined based on the experiences of the zookeepers, as well as on  
186 previous research that showed that primates habituate to the presence of non-visitor  
187 observers within that time frame [Mitchell et al., 1991a].

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

#### 195 *Cubicle research participation*

196         Throughout the months of June and July 2015, a separate study was conducted  
197 requiring the voluntary isolation of the monkeys in the research cubicles. This study  
198 involved training sessions where the monkeys received food rewards for entering and  
199 remaining in the cubicles, as well as research sessions where the monkeys were given a  
200 novel object to interact with and food rewards for participation. The monkeys chose  
201 whether to enter the cubicles during the session and were given the option to return to the  
202 group if they showed signs of discomfort (for a more detailed description of the cubicle  
203 setup, see: [Macdonald & Whiten, 2011]). Throughout these sessions, the order in which  
204 the monkeys chose to enter (or not) the cubicles was recorded for both groups as a measure  
205 of likeliness to participate. In these sorts of settings, individuals are often excluded from  
206 studies if they do not meet regular participation criteria, therefore the likelihood of

207 participation is a relevant measure to assess [Morton et al., 2013a]. Each monkey was given  
208 a score based on their order of entry for each session. This was calculated by taking the  
209 total number of monkeys in each group (nine for West, 14 for East) and giving a reverse  
210 order score based on that number. For example, the first monkey to enter the cubicles in the  
211 West group would receive nine points, the second eight points and so forth, while the first  
212 monkey in the East group would receive 14 points, and the second 13. Monkeys who did  
213 not enter the cubicles received zero points. In order to make the scores of the two groups  
214 comparable, the scores for each monkey were divided by the total number of monkeys in its  
215 group. The final score for each monkey was the average of these ratios across all of the  
216 cubicle sessions (21 for the West Group, 18 for the East Group).

#### 217 *Keeper-ratings of personality*

218 Three keepers who had worked with the monkeys for at least three years were asked  
219 to fill out a shortened version of the Hominoid Personality Questionnaire [Weiss et al.,  
220 2009] for each of the monkeys. This shortened version consisted of 12 personality traits for  
221 which each monkey was rated on a seven point Likert scale based on one to two descriptive  
222 sentences (Table 1). The directions on the questionnaire explained that a score of 1  
223 indicated that the monkey displayed a “total absence or negligible amount” of that trait and  
224 a score of 7 indicated that the individual displayed “extremely large amounts” of that trait.  
225 The original questionnaire was reduced to 12 traits in order to accommodate the  
226 zookeepers’ time restraints and to attempt to create a more practical and efficient version of  
227 the questionnaire. The personality traits were chosen based on high loadings found in a  
228 previous personality assessment of squirrel monkeys using the full 54-item Hominoid  
229 Personality Questionnaire. In that study, four components (‘Assertiveness,’

230 ‘Impulsiveness,’ ‘Neuroticism,’ and ‘Agreeableness’) were derived from 46 reliable items  
231 and were validated across 57 animals from eight international zoos [Wilson et al., in prep;  
232 Wilson, 2011]. Three high-loading traits were chosen from each of the four components.  
233 An attempt was made to choose traits that were distinct from each other and that had  
234 minimal overlap in their descriptive sentences.

235

### 236 **Statistical analysis**

237 To compare the proportion of time that the monkeys spent at the observation  
238 window for each of the three visitor categories, a Friedman’s ANOVA and post-hoc  
239 Wilcoxon tests were used, as the distribution of the residuals proved to be non-normal. A  
240 Hon-Bonferroni sequential correction was applied to the results and the adjusted p-values  
241 are reported [Holm, 1979].

242 To identify the factors that influence the window approach behavior and  
243 participation in cubicle research, two generalized linear mixed models (GLMM) were run  
244 using IBM SPSS (Version 22). For the window approach behavior, a binomial distribution  
245 with a logit link function was used. For the cubicle participation data, a normal distribution  
246 with an identity link function was used. In both models, the random effects included  
247 Monkey ID nested within Enclosure. The fixed effects were determined by running the  
248 explanatory variables (each of the reliable personality traits and age) through the program’s  
249 Automatic Linear Modeling function using a forward stepwise model selection method  
250 with an Akaike Information Criterion Corrected (AICc) information criterion. Each of the  
251 12 personality traits was tested for inter-rater reliability between the three keepers using a  
252 two-way interclass mixed-model correlation ( $ICC_{(3,k)}$ ) [Shrout & Fleiss, 1979].

253 Correlational tests and graphical summaries were used to determine the relationships  
254 between the predictive and behavioral variables.

255

### 256 **Ethical consideration**

257 This study was approved by the Scientific Review Team of the University of  
258 Edinburgh. As the study was observational and there was no direct manipulation of, or  
259 interference with the animals, the team felt it was not necessary to receive approval from  
260 the Veterinary Ethical Review Committee (VERC). The study was also approved by the  
261 research review board at the 'Living Links to Human Evolution' Research Centre and the  
262 Royal Zoological Society of Scotland, Edinburgh Zoo. The research adhered to the  
263 American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-  
264 Human Primates.

265

266

## **RESULTS**

### 267 **Group level reaction to visitors**

268 There were significant differences between the mean proportions of time that the  
269 monkeys spent at the window during the three visitor group categories (Friedman's  
270 ANOVA:  $X^2_{(2)}=31.92$ ,  $P<0.001$ , see Figure 2). The monkeys spent significantly larger  
271 proportions of time at the observation window when there were large groups of visitors  
272 present compared to when there were no visitors or small groups present (Wilcoxon:  $Z=-$   
273  $4.009$ ,  $P=0.002$ ;  $Z=-3.09$ ,  $P=0.002$ ). The monkeys also spent a greater proportion of time at  
274 the observation window when there were small groups of visitors there compared to when  
275 there were no visitors (Wilcoxon:  $Z=-3.444$ ,  $P=0.001$ ).

276

277 **Individual differences in reactions to visitors**

278           There were considerable individual differences between the monkeys with regards  
279 to their proportions of time spent at the window for each visitor category (Figure 3). The  
280 individual percentages of time spent at the window for the ‘No Visitor’ category ranged  
281 from 0% to 76% (mean±SE: 18±3%). The individual percentages of time that monkeys  
282 spent at the window for the ‘Small Group’ category ranged from 0% to 37% (mean±SE:  
283 18±2%), while the percentage of time for the ‘Large Group’ category ranged from 0% to  
284 88% (mean±SE: 59±5%). The total amount of time each monkey spent at the window  
285 across all sessions ranged from zero minutes (one individual never came to the window) to  
286 143 minutes (mean±SE: 27±6.5 minutes).

287

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

289           For the personality questionnaire scores, the inter-rater reliability of the mean  
290 ratings between the three keepers,  $ICC_{(3,k)}$ , had a mean of 0.38, and ranged from 0.138 for  
291 *depressed* to 0.729 for *playful*. One trait (*predictable*) that had an ICC value that was less  
292 than zero was considered unreliable (as per the criteria used by other studies of primate  
293 personality – see: [Weiss et al., 2011; Wilson, 2011]) and was removed from further  
294 analysis.

295           For the data on the proportion of time spent at the viewing window, the Automatic  
296 Linear Modeling function showed that the personality traits *playful*, *cautious*, *solitary*,  
297 *dominant*, and *depressed* had the highest associations (adjusted  $R^2=0.30$ ). All of these  
298 traits, except for *dominant*, had significant effects (Table 2). In order to determine the

299 direction of the effects, Spearman's correlations were run between the significant traits and  
300 the difference between the proportion of time spent at the window during the 'Large Group'  
301 condition and the 'No Visitor' condition. *Playfulness* was found to have a positive  
302 relationship ( $R=0.162$ ) while *cautious* ( $R=-0.042$ ), *solitary* ( $R=-0.419$ ), and *depressed* ( $R=-$   
303  $0.327$ ) had negative relationships (Figure 4).

304 For the cubicle research participation data, the Automatic Linear Modelling  
305 function determined that *playful*, *cautious*, *affectionate*, *friendly*, and *gentle* were the traits  
306 of greatest importance (adjusted  $R^2=0.668$ ). When these were assessed for their significance  
307 in predicting research participation, it was found that all had significant effects (Table 2).  
308 Pearson's correlations showed that *playful* ( $R=0.729$ ), *affectionate* ( $R=0.405$ ), *friendly*  
309 ( $R=0.447$ ), and *gentle* ( $R=0.487$ ) had positive relationships with cubicle participation  
310 scores, while *cautious* ( $R=-0.341$ ) had a negative relationship (Figure 5).

311

312

## DISCUSSION

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

316

### 317 **Group level reaction to visitors**

318 Our first prediction that the monkeys would not react aversively to visitors was  
319 broadly supported. On average, the more people there were at the observation window, the  
320 more frequently the monkeys chose to come up to that window. This implies that the  
321 monkeys are actively choosing to be around the visitors when they are at the viewing

322 window, as they could easily choose to be in other areas without visitors if they found them  
323 aversive. Thus, the visitors do not seem to have a negative impact on their welfare and may  
324 even be enriching for some of the individuals. However, previous studies [Mitchell et al.,  
325 1992c; Hosey, 2000] investigating relationships between animal behaviors and visitor  
326 presence rightfully note the importance of not assuming causality, arguing that zoo visitors  
327 may be attracted to animals performing certain behaviors.

328         This is unlikely to be the case for this study for a number of reasons. Firstly, the  
329 setup of the enclosures (Figure 1) is such that visitors are not able to see the animals in the  
330 indoor enclosure until they are already directly at the window, making it unlikely that the  
331 sight of unusual animal behaviors are attracting the larger numbers of visitors to the  
332 window from other areas. Additionally, the visitors are not able to see how many other  
333 people are at the window until they are there themselves. This makes it unlikely that the  
334 presence of crowds looking at interesting behaviors, such as monkeys that are up on the  
335 ledge, were attracting more people to the window. Furthermore, the results showed that,  
336 when there is no one around, the monkeys do not choose to spend much time up on the  
337 ledge, suggesting once again that when they do come up to the window, it is to be closer to  
338 the visitors.

339         All of these factors provide support for the conclusion that, for the squirrel monkeys  
340 at this facility, the presence of zoo visitors does not appear to negatively influence their  
341 welfare and that some individuals may even actively seek it out. This conclusion stands in  
342 contrast to the results of the majority of previous primate studies (though not all – see:  
343 [Cook & Hosey, 1995; Todd et al., 2007]) suggesting that the presence of humans is  
344 primarily a source of stress for the animals [Chamove et al., 1988; Birke, 2002; Keane &



345 Marples, 2003; Wells & Blaney, 2003; Davis et al., 2005; Mallapur et al., 2005]. A number  
346 of possibilities could explain this discrepancy. First, the squirrel monkeys in this study are  
347 provided with a variety of enrichment opportunities, which has been suggested to reduce  
348 stress in some species [Carder & Semple, 2008; Izzo et al., 2011]. Second, they have  
349 frequent positive interactions with humans through other research studies, potentially  
350 fostering in them a positive human-animal relationship, thus reducing the ‘visitor effect’  
351 [Hosey, 2008]. Lastly, the animals had the option to choose from five different enclosure  
352 areas with different levels of exposure to zoo visitors. This allowed some monkeys to come  
353 into very close proximity to humans, for example by jumping up to the ledge by the  
354 viewing window, while allowing other monkeys to avoid them completely.

355

### 356 **Individual differences**

357 Our second prediction that the monkeys would show individual differences was  
358 largely supported. Apart from the trait of *predictable*, all other traits had positive ICC  
359 ratings. The trait of *playful* had a particularly strong ICC rating. Similarly, there was a huge  
360 variance in the amount of time that individuals chose to be at the window. This is discussed  
361 in the following section.

362

### 363 **Relationship between personality, reaction to visitors, and research participation**

364 Our third and fourth hypotheses that personality ratings would be associated with  
365 visitor reactions and research participation were also supported. Certain personality traits  
366 did seem to be predictive of these behaviors. For both approaching the window and  
367 participating in research, higher scores of playfulness and lower scores of cautiousness

368 were important factors. This makes sense intuitively, as it is logical that cautious animals  
369 would be less inclined to engage in activities that put them in close proximity to relatively  
370 unpredictable humans, and that playful animals might see engaging in those same activities  
371 as rewarding.

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

383         The relationship between personality scores and research participation has  
384 implications for the existence of selection bias in behavioral research studies. The behavior  
385 of the more agreeable animals during the research sessions may be different from the  
386 behavior of the non-participating and evidently less agreeable individuals. Indeed, studies  
387 have found that individuals with more assertive or aggressive personalities have different  
388 problem-solving strategies compared to less assertive individuals. This was demonstrated  
389 by a study done with the very capuchins housed with these squirrel monkeys, which found

390 that accuracy was negatively correlated with scores of assertiveness in a number of cubicle-  
391 based tasks [Morton et al., 2013a].

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

403

#### 404 **Limitations**

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

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

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

430

431

## CONCLUSIONS

432           This study demonstrates that individual differences exist between squirrel monkeys  
433 both in how they respond to varying sizes of zoo visitor groups, and in their likeliness to  
434 participate in voluntary behavioral research. While, on average, visitors do not seem to  
435 have a negative impact on the welfare of the animals, certain individuals choose to engage

436 with humans more than others, and management practices should take these individual  
437 welfare needs into account. Potential ways of doing this would be to design enclosures in  
438 such a way that animals could choose to have close-up interactions with visitors via  
439 viewing windows, while still maintaining enclosure elements that allow for visitor  
440 avoidance. Offering voluntary participation in training sessions or research studies could  
441 also prove to be beneficial for some individuals. Keeper ratings based off of personality  
442 questionnaires could also be used to predict animal behaviors. With regards to future  
443 primate studies, the relationship between personality ratings and research participation  
444 suggests that there is a strong possibility for selection bias to occur; therefore, care should  
445 be taken in accounting for this issue. Lastly, further study with larger sample sizes and  
446 more in-depth personality assessments would shed more light onto what factors influence  
447 visitor-effect and research participation.

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449

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565 *boliviensis*.
- 566

567 **TABLE I. Personality traits and descriptive sentences that were presented to the**  
 568 **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.

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

Trait	Time at Viewing Window				Research Participation			
	F	df1	df2	Sig	F	df1	df2	Sig
Playful	26.273	1	63	<0.001	59.335	1	63	<0.001
Cautious	10.908	1	63	0.002	11.325	1	63	0.001
Solitary	8.677	1	63	0.005	-	-	-	-
Dominant	2.954	1	63	0.091	-	-	-	-
Depressed	5.646	1	63	0.021	-	-	-	-
Affectionate	-	-	-	-	7.844	1	63	0.007
Friendly	-	-	-	-	7.803	1	63	0.007
Gentle	-	-	-	-	7.289	1	63	0.009

572

573

574 **FIGURE LEGENDS**

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

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

586

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

589

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

593

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

597