Preliminary investigation of flexibility in learning color-reward associations in gibbons (Hylobatidae)

Justin D'Agostino and Clare Cunningham

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24 **ABSTRACT**

25   Previous studies in learning set formation have shown that most animal species can learn

26 to learn with subsequent novel presentations being solved in fewer presentations than when they

27 first encounter a task. Gibbons (*Hylobatidae*) have generally struggled with these tasks and do

28 not show the learning to learn pattern found in other species. This is surprising given their

29 phylogenetic position and level of cortical development. However, there have been conflicting

30 results with some studies demonstrating higher level learning abilities in these small apes. This

31 study attempts to clarify whether gibbons can in fact use knowledge gained during one learning

32 task to facilitate performance on a similar, but novel problem that would be a precursor to

33 development of a learning set. We tested 16 captive gibbons' ability to associate color cues with

34 provisioned food items in two experiments where they experienced a period of learning followed

35 by experimental trials during which they could potentially use knowledge gained in their first

36 learning experience to facilitate solution I subsequent novel tasks. Our results are similar to most

37 previous studies in that there was no evidence of gibbons being able to use previously acquired

38 knowledge to solve a novel task. However, once the learning association was made, the gibbons

39 performed well above chance. We found no differences across color associations, indicating

40 learning was not affected by the particular color / reward association. However, there were

41 variations in learning performance with regard to genera. The hoolock (*Hoolock leuconedys*) and

42 siamang (*Symphalangus syndactylus*) learned the fastest and the lar group (*Hylobates sp.*)

43 learned the slowest. We caution these results could be due to the small sample size and because

44 of the captive environment in which these gibbons were raised. However, it is likely that

45 environmental variability in the native habitats of the subjects tested could facilitate the

46 evolution of flexible learning in some genera. Further comparative study is necessary in order to

47 incorporate realistic cognitive variables into foraging models.

48 **INTRODUCTION**

49   Despite being the most diverse group of extant apes, gibbons continue to be the most

50 understudied of all higher primates, particularly with regard to their cognitive abilities. Gibbons

51 are native to South East Asia and can be found in Vietnam, Cambodia, Thailand, Burma, China,

52 Malaysia, and the islands of Indonesia. They are omnivores and in ideal resource availability

53 conditions, high-energy fruit constitutes the majority of their diet with the remainder consisting

54 of leaves, flowers, seeds, tree bark, insects, small birds, eggs and tender plant shoots [Curran &

55 Leighton, 2000]. These small arboreal apes primarily live in monogamous pairs with their

56 associated offspring and are characterized by limited sexual dimorphism, complex vocal duets

57 between the male and female bonded pair and brachiating mode of locomotion [Cunningham &

58 Mootnick, 2009].

59   Representing an interesting evolutionary divergence between monkeys and great apes, a

60 better understanding of gibbon learning ability and their capacity for complex mental processes

61 would allow us to track both the progression of advanced cognition and the evolutionary

62 pressures that have led to the emergence of abilities characteristic of great apes (including

63 humans). This research therefore aims to investigate whether gibbons are able to learn sequential

64 color-reward associations and if they can extract relevant information from the first stimulus-

65 response association to enable them to make future associations more readily.

66   Research on gibbon vision has shown there are separate M and L photo pigments and

67 other characteristics that are almost identical to those of the common chimpanzee (*Pan*

68 *troglodytes*) – known to have trichromatic color vision, suggesting their searching behavior is

69 heavily guided by vision. As all genera of gibbon enjoy the benefits of full trichromatic color

70 vision [Deegan & Jacobs, 2001; Jacobs, 1993; Jacobs, et al., 1996], they should easily

71 discriminate color information from the cues provided during this series of studies.

72 Experimental tests of associative learning in non-human primates in a controlled setting

73 typically employ object discrimination tasks where the subject is presented with two arbitrary

74 shapes, one that if chosen will lead to a reward and one that will not. For example, selection of

75 the red square would lead to reinforcement whereas selecting the blue triangle presented with it

76 in a two-way choice paradigm would leave the subject unreinforced. Data are collected on the

77 number of trials needed to reach a pre-determined criterion level that is assumed to result from

78 the subject learning the rules of the task; that is, which of the two shapes will lead to

79 reinforcement.

80 Using this basic paradigm, Harlow [1949] postulated that rhesus macaques (*Macaca*

81 *mulatta*) made more than a simple association between stimulus and reinforcement, suggesting

82 'cognitive mediation' occurred as subjects learned subsequent stimulus – reward associations

83 more quickly. This seemed to indicate they were extracting some level of information from their

84 first learning experience that they used to inform their actions in novel configurations. This has

85 since been termed 'learning to learn' or 'learning set formation' [Rumbaugh & McCormack,

86 1967].

87 Since the early observations by Harlow, studies of learning set formation have shown that

88 many species including rhesus macaques (*Macaca mulatta*) and chimpanzees (*Pan troglodytes*),

89 can in fact 'learn to learn' with subsequent problems being solved in fewer presentations

90 [Passingham, 1981; Fobes & King 1982]. However, gibbons have typically struggled with these

91 tests that require the subjects to solve different sets of similar problems over time and do not

92   show the learning to learn pattern found in other species [Rumbaugh & McCormack, 1967;

93   Tomasello & Call, 1997; Abordo, 1976].

94   In the Rumbaugh and McCormack study [1967] five immature gibbons (*H. lar* N=2, *H.*

95   *moloch* N=1; *H. pileatus* N=2) were presented with a simple discrimination task that required

96   subjects to push bins marked by a red square (reinforced) or a red circle (unreinforced) to reveal

97   a reward beneath the reinforced shape. The gibbons had a tendency not to push the bins at all –

98   taking upwards of 100 trials to acquire this basic motor action when compared to other primates

99   tested. However, once they were reliably making a choice, the gibbons did not appear to find

100   learning the discrimination any more difficult than the other apes and monkeys tested (*Pongo,*

101   *Gorilla, Pan Sp., and Macacca*) [Rumbaugh & McCormack, 1967]. Unlike the other monkeys

102   and apes, when novel shape pairs were presented, gibbons seemed to learn each new association

103   as a completely new problem, taking the same number of trials to reach criterion performance as

104   they had for the first stimulus pair. Other species took fewer trials to learn each new association

105   suggesting they were using information gained during their first learning experience to inform

106   their choices on subsequent novel presentations. This seemed to be beyond the capacities of the

107   gibbons tested.

108   Other studies have provided contrasting results; for example, in a learning reversal study

109   (where the rewarded shape in a paired association task is 'reversed' once the subject reaches

110   criterion performance), Gosette [1970] reported gibbons (*H.lar*) did show evidence of learning to

111   learn making fewer errors than squirrel monkeys (*Saimiri* sp.) and owl monkeys (*Aotus* sp.), but

112   being inferior to capuchins (*Cebus* sp.). As some prior studies have found gibbons generally

113   struggle with learning set formations [Rumbaugh & McCormack, 1967] while others have shown

114   conflicting evidence with better performance [Gosette, 1970], we were interested in clarifying

115 whether gibbons can use knowledge gained during one learning task to facilitate performance on

116 a similar but novel problem that would be a precursor to learning set formation.

117   Gibbons are large-brained primates with their relative brain size being comparable to the

118 great apes and large-brained monkeys [Cunningham & Mootnick, 2009]; therefore, their reported

119 poor performance on discrimination tasks and little evidence of learning set formation is

120 surprising. Several gibbon behavioral characteristics could explain their apparent lack of

121 abilities and contradicting results of previous studies. Gibbons have notoriously short attention

122 spans [Fedor et al., 2008] potentially losing interest after only a few trials, impeding learning set

123 formation. Also, gibbons rely heavily on their visual cognitive abilities - it has been found that

124 gibbons are competent in detecting the visual orientation of other species as well as their own

125 and possess some knowledge of how visual gaze direction relates to external stimuli [Horton &

126 Caldwell, 2006]. Therefore, results will be inconsistent if a subject with a short attention span

127 becomes distracted by a visual cue outside of the experiment.

128   The aim of this study was to determine whether gibbons could learn to associate preferred

129 foods with colored signals when the food items were hidden out of direct sight and once learned,

130 whether they could use their acquired learning to facilitate future learning. That is, once they had

131 learned a particular stimulus-reward association, would they learn subsequent novel associations

132 more easily? We also tested whether genera or sex had an impact on this ability based on

133 previous work that indicated differences in cognitive performance of gibbons were related to

134 subject-variables in that hoolock (*Hoolock leuconedys*) and siamang (*Symphalangus syndactylus*)

135 learned faster than the lar group (*Hylobates sp.*) [Cunningham et al., 2011] potentially due to

136 selection for flexibility caused by environmental variability.

137 **METHODS FOR EXPERIMENT 1**

138　*Ethics statement*

139　　　All behavioural studies were non-invasive and subjects were fed their normal daily diet

140　of fruits and vegetables throughout. Participation in all testing described below was voluntary on

141　the part of the gibbons. The research adhered to the legal requirements of the USA (the country

142　in which the research was conducted) and the research adhered to the American Society of

143　Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates. The research

144　methods were also approved by the Institutional Animal Care and Use Committee of California

145　State University, Los Angeles (IACUC protocol number 12-4). The research also had permission

146　from the Gibbon Conservation Center (permit number 2013-1) and adhered to the ASAB

147　Guidelines for the treatment of animals in behavioural research (2006).

148　*Study site and subjects for Experiment 1 and 2*

149　　　The gibbons were housed at the Gibbon Conservation Center (GCC), California. Some

150　subjects had a limited history of cognitive testing previously taking part in two studies of object-

151　mediated problem-solving tasks [Cunningham et al., 2006, 2011]. However, to the authors'

152　knowledge, none had been exposed to any tasks similar to those reported here. The subjects in

153　Experiment 1 consisted of 13 gibbons (age 4-14 years) with representatives from three of the

154　four extant genera [Groves, 2002] (*Hylobates pileatus (N = 2), Hylobates moloch (N = 2),*

155　*Symphalangus syndactylus (N = 2), Hoolock leuconedys (N = 7))* (Table I). Ten gibbons

156　participated in Experiment 2 (age 4-23 years), five that were also subjects in Experiment 1 plus

157　two additional females (*H. moloch (N = 1); H. pileatus (N = 1)*) and one male (*H. pileatus*) that

158　took part in Experiment 2 only (Table II). Unavoidable problems prevented the same gibbons

159　being tested in both experiments; Violet (*H. pileatus*) was in isolation while recovering from an

160　arm injury and a family of *H. leuconedys* moved enclosures during testing.

161   Gibbons were housed in outdoor enclosures (10 X 3 X 4 m) with a connected section (4

162   X 3 X 2.5 m) generally available at all times that could be closed off to separate subjects as

163   required. This did not have a significant impact on the experiments as the gibbons were typically

164   separated a few times per week when the staff cleaned the enclosures and the veterinarian

165   checked the health of the animals. If we did notice any change in the animal's behavior that

166   could affect their performance in testing (due to separation or other distraction), we stopped the

167   current trial and resumed the following day. All enclosures were spaced by a minimum of 5 m

168   and visual barriers and planted vegetation obstructed direct views between adjacent cages [see

169   Mootnick, 1997 for more details of enclosure design]. The gibbons were fed their normal daily

170   diet being fed five times per day with fruits and monkey biscuits in the morning and apples,

171   bananas and greens in the afternoon. The design of the enclosures allowed the gibbons to reach

172   their arms through fencing to access the feeding platforms used in the experiments (Figure 1).

173   *Experiment 1*

174   Experiment 1 consisted of two phases; Phase 1 was to determine the rank order of

175   preferred food items (banana, cucumber and monkey biscuits) for each individual. Phase 2

176   assessed whether they could learn an association between their preferred foods and a color cue.

177   In this discrimination task, the incentive was out-of-sight (concealed under a colored bucket) and

178   we assessed how quickly the gibbons could learn to associate the position of the food reward

179   with the cue. Three color/preferred food associations were presented consecutively, and we

180   evaluated whether subsequent configurations were learned more efficiently suggesting gibbons

181   were able to extract information from the first configuration to facilitate future learning. As prior

182   studies have showed gibbons struggle with learning set formations, possibly due to short

183   attention spans or being easily distracted, we attempted to limit these potential problems by

184 focusing the gibbon's attention on visual cues within the experiment. A video that illustrates the

185 animals' behavior during both phases of Experiment 1 can be viewed by clicking the following

186 link: (AJP Production Team – Please Create Link to Video 1)

Phase 1 apparatus and procedure

188 Before testing began, subjects were desensitized to the new feeding platform that would

189 be used for the experimental trials. The subject's motor skills and grasping abilities were taken

190 into consideration when constructing the feeding platform, 130 cm long and 31 cm wide. If the

191 platform were smaller, the gibbons would be able to easily pick it up, flip it over, and potentially

192 lose interest in the test. If the platform were larger, it would make it difficult to transport to

193 various enclosures. Three plastic buckets, 25 cm tall and 15 cm in diameter were painted red,

194 yellow, and green. Three hinges were drilled into the wooden feeding platform 25 cm apart that

195 attached the buckets open-end down, to the feeding platform. The hinges allowed the buckets to

196 be flipped open by the gibbons to reveal food items hidden beneath (Figure 1).

197 To make the association between food and the feeding platform, the experimenter placed

198 a known favorite snack (as suggested by the staff at the GCC) of pumpkin seeds and blueberries

199 around and underneath the closed buckets on the feeding platform. This was to motivate the

200 gibbons to touch the buckets and feel comfortable with the task of opening them to reveal the

201 hidden food items. The experimenter presented the feeding platform to the subjects by sliding

202 along the floor until it was aligned with the enclosure and the rewards and buckets were within

203 the gibbons' reach when they extended their arm through the wire mesh. The pumpkin seeds

204 were scattered around the buckets and the buckets were closed over the blueberries. This feeding

205 platform set-up was same on every presentation in the desensitization phase. The platform was in

206 this position until all of the food items were consumed or for a maximum of five minutes if only

207 a portion of the food was eaten. If the subject did not approach the platform at all, it was

208 presented again later that same day with a gap of two hours between desensitization trials. The

209 desensitization period continued on consecutive days until the subjects were comfortable using

210 the feeding platform. The gibbons were assumed to associate presence of the platform with a

211 reward when they readily approached, investigated and ate the pumpkin seeds, and finally

212 flipped the colored buckets and ate the blueberries. On average, five presentations of the feeding

213 platform were needed before there was evidence of an associative connection between the

214 feeding platform and the potential for reward.

215 Gibbons at GCC demonstrated preferences for specific food types when a variety of

216 choices were presented. This was recognized when staff at the center brought multiple items to

217 the enclosures and gibbons consistently picked and ate food in the same order. However, the

218 order of preference was not the same for every gibbon, although regardless of order, they were

219 usually individually consistent. As the experimental test relied on the association between

220 preferred food and colored signal being learned and remembered, we first had to assess

221 individual preference for the three items that would be used in the experimental tests.

222 General observations indicated that favorite foods were high in sugar and bright in color

223 (bananas, yams, and bell peppers). The least favorite foods had lower sugar content and were

224 usually plain in appearance (monkey biscuits). For these reasons, we predicted a favorite food

225 item would be banana, a moderate food item would be cucumber and the least favorite food item

226 would be monkey biscuits.

227 Each trial consisted of the experimenter presenting the feeding platform, within reaching

228 distance of each enclosure with the food items in full view. Incentives were placed on the

229 feeding platform out of view of the subjects in one of three locations that corresponded to the

230   placement of the buckets that would be used on the test. Thus, rewards were in a horizontal line

231   relative to the enclosure fence, with the middle location being at the center of the feeding

232   platform and one reward positioned equidistant to the left and right of center. The position of the

233   three items changed in every trial in a randomly determined order. For example, on the first trial,

234   the piece of banana was on the left, cucumber in the middle and monkey biscuit on the right. For

235   the second, the position was switched so that the banana became central, cucumber right and

236   monkey biscuit left. The position of presentation was changed on every trial thereafter within the

237   constraint that the food items never appeared in the same position twice, to make sure the

238   gibbons did not get used to reaching for a particular food item in a specific direction. Notes were

239   taken of the order in which gibbons selected and ate the food items with the assumption that the

240   preferred food would be consumed first and the least preferred item, last.

241   *Phase 2 - Associative learning of color cue and preferred reward*

242   The purpose of Phase 2 was to determine if gibbons could associate colors to their rank

243   order of food items when they are out of direct sight (hidden under buckets). If the subjects were

244   able to make an association between the food items and color that signaled their preference

245   determined in Phase 1, they should select their preferred incentive as their first choice. All

246   buckets were baited with one item of the subjects preferred food (banana for all gibbons) and one

247   item of each of the other foods (cucumber and monkey biscuits) used in Phase 1 placed so that

248   when buckets were closed, the reward was out-of sight.

249   Studies using similar paradigms usually bait one location meaning the animal will only

250   receive a reward if they pick the correct cue. We chose to place a food reward under all buckets

251   and vary the 'value' of the food items to the individual (preferred or non-preferred) for a number

252   of reasons: 1) Sham baiting is normally employed of the non-rewarded locations to ensure the

253   animals do not pick up on inadvertent experimenter-given cues during the baiting procedure

254   [Garber & Dolins, 1996]. Rather than use a sham manoeuver which may still be different in

255   some way to an actual baiting, we baited all buckets ensuring our actions were the same at each

256   location; even though the actual placement of the rewards took place out of the subjects direct

257   sight, they could potentially have monitored the experimenter's movements. 2) By including the

258   two-distractor food items, we potentially increased the cognitive load by requiring subjects to

259   target their preferred food from three possible food/color cue associations presented in each trial.

260   3) As gibbons would be rewarded on all trials, their motivation to participate should not be

261   negatively affected across repeated trials.

262   Once baited, the apparatus were presented in the same way as for the food preference

263   trials with the feeding platform supporting the buckets being slid along at floor level until

264   aligned with the enclosure. The subjects could then extend their arms through the mesh and make

265   their choice of which bucket to flip open. The first trials allowed gibbons to learn the association

266   between the color cue and their preferred food item. The three colored buckets were baited out of

267   direct sight of the gibbons and the apparatus presented with the three food items concealed under

268   each one. On the first few presentations, the choice made would be inevitably random as the

269   gibbons did not know where their favorite food item was hidden. However, with repeated trials,

270   it was possible for the apes to acquire all the necessary knowledge to learn the association

271   between the color cue and the value of the reward beneath it. If they learned this association,

272   they should selectively choose the high value (preferred) food as their first choice on subsequent

273   trials. For example, during the first trial block, if 'green' was designated as the color cue that

274   would yield the highest reward, the preferred food item for the test subject (identified during

275   Phase 1) would be concealed under the green bucket for all trials in that block a block consists of

276   all trials needed to reach criterion before moving to a new color association to a maximum of

277   100). For the first trials, the position of the green bucket was held constant to allow the

278   association between 'green' and the high value reward to be learned. Once the gibbon had

279   selected the green bucket as their first choice, the position of the green cue on all remaining trials

280   in the block was randomized; that is, the high value reward was always under the green bucket,

281   however, the position of the green cue varied on each trial.

282   The subject was considered to have learned the color-reward association when they

283   reached criterion performance set at 10 consecutive choices (out of a maximum100 trials) of the

284   preferred food type. Once criterion had been reached, presentations continued of the same color-

285   reward association until all 100 trials had been given. Trials that occurred after criterion had been

286   reached were referred to as 'post-criterion' trials.

287   Once gibbons had completed the required trials in the first block (learning and post-

288   criterion N = 100) with the first color/reward pairing, they moved to the second block of testing

289   where a new color/reward association had to be learned. Thus, individuals had to suppress the

290   previously learned rule and make a new association between a colored signal and reward. Three

291   blocks were presented (for each of the three color-reward associations to be learned) with each

292   block consisting of 100 presentations (learning and post-criterion trials) in total. The order of

293   presentation of each color-reward pairing was consistent across subjects. The trial was only

294   scored if the subject showed direct interest, measured by approaching the feeding platform

295   within 30 seconds. Trials were considered 'correct' if the gibbon chose the preferred item as their

296   first choice, however, they were allowed to continue lifting buckets until all rewards were

297   obtained (to maximize their motivation to take part). The trial was complete once all food items

298   has been consumed or after one minute elapsed. Any additional activity after one minute was

299   considered "play" and the feeding platform was then taken away from the subject. If no choice

300   was made within the minute of exposure time, the trial was marked as incomplete and would be

301   resumed on the next day of testing. Similarly, if the subject lost interest during the trials, the

302   experiment was stopped and resumed at a later date, continuing where the subject left off until

303   100 presentations were completed. The inter-trial duration was approximately three minutes.

304   This was the time needed to change the location of the buckets into a random order and bait the

305   buckets with the food items. Most subjects needed four sessions to complete 100 successful trial

306   presentations; however Reg and Truman (*Hylobates sp.*) needed five sessions.

307   *Data analysis*

308   Data were not normally distributed and so non-parametric statistics were used to evaluate

309   the effect of color on learning speed. Friedman's tests assessed differences in number of trials

310   needed to reach criterion performance (10 consecutive choices of preferred food first) for each

311   'color-preferred food' association (3 levels – Yellow, Green and Red). An extension of

312   generalized linear models (GZLM), generalized estimating equations (GEE) that accommodates

313   small, correlated within-subjects data sets and allows for comparisons between subjects [Garson

314   2013], determined how subject parameters (sex and genus) influenced learning the color-food

315   association. As data comprised counts of trials, Poisson loglinear regression with a log link

316   function was specified for all models with number of trials to criterion (as the response variable).

317   Genus, sex and food-color association (consecutive choices of preferred food first) were factors

318   in the model, with main effects tested. *Hylobates* was always the referent category for GEE

319   parameter estimates.

320   For the post-criterion performance analyses (trials that occurred after the initial

321   association had been learned), the number of trials varied across individuals due to differences in

322 the acquisition of criterion performance and the maximum of 100 trials per individual summed

323 across learning and post-criterion trials (Post-criterion trial number = Maximum number of trials

324 (100) – number of trials to criterion). Counts were therefore transformed into percentages for the

325 main analyses. Friedman's tests assessed differences in number of trials where preferred food

326 was selected first once learning had taken place for each color/preferred food association (3

327 levels – Yellow, Green and Red). GEE was again used to assess the retention of the color-reward

328 association across trials in the post-criterion stage with the same factors and covariates as

329 previously described; however, as data were no longer counts, a linear model was specified with

330 an identity link function. Again, *Hylobates* was the reference genus for the parameter estimates.

331 An additional Wilcoxon analysis was performed comparing the first ten trials post-criterion to

332 the last ten to evaluate whether performance was consistent throughout trials presented. Alpha

333 was set at 0.05 throughout and all tests were 2-tailed.

RESULTS FOR EXPERIMENT 1

335 *Learning trials to criterion*

336 All subjects tested demonstrated a preference for banana in the initial food choice trials

337 with nine of the 13 subjects choosing this food item first on 100% of presentations. The

338 remaining four subjects selected the banana first on the majority of preference trials in Phase 1

339 (86.67 – 93.33%) with cucumber being the occasional first choice. No subject selected monkey

340 biscuits as first choice in the preference tests. Therefore, banana was selected as the primary

341 color/reward referent for all subjects and responses scored as correct when the first choice made

342 on test trials was to select the location of this food type.

343 The number of trials needed to learn the primary food/reward association varied across

344 individuals (range 16-100); however, all subjects were able to reach criterion performance in all

345   conditions within the 100-trial maximum. The color paired with the preferred food did not

346   influence learning speed across all individuals (Median (Yellow) = 26.00(IQR = 15.5), Median

347   (Green) = 25.00(13.50), Median (Red) = 28.00(18.00), Freidman's test: $\chi^2(2) = 0.840$, p =

348   0.657). However, there were significant differences between the genera on acquisition of the

349   color/reward association.

350   In general, *Hylobates* gibbons needed more presentations to learn the 'color-preferred

351   food' association than either *Hoolock* or *Symphalangus* (Table III). There was a significant effect

352   of genus on learning speed with *Hoolock* and *Symphalangus* needing significantly fewer trials

353   than *Hylobates* to learn the color associations (GEE: *Hoolock* B = -0.677, $\chi^2(1) = 124.87$, p <

354   0.001; Symphalangus B = -0.854, $\chi^2(1) = 33.94$, p < 0.001) (Figure 3a). There were no

355   significant differences between sexes on number of trials to criterion (GEE: B = -0.216, $\chi^2(1) =$

356   2.854, p = 0.091). Color paired with the preferred reward remained insignificant in this analysis

357   (GEE: $\chi^2(2) = 1.965$, p = 0.374).

358   *Post-criterion trials*

359   One subject did reach criterion in the all color-reward associations, however, only on the

360   final presentation of the green-reward configuration. This individual was therefore removed from

361   the post-criterion performance analyses. Selection of preferred food item was generally high

362   across all post-criterion trials (Mean (Yellow) = 91.56(SE = 1.35)%, Mean (Green) =

363   78.71(7.39)%, Mean (Red) = 88.51(1.88)%,), with no significant differences in performance

364   across color cues (GEE: $\chi^2(1) = 1.941$, p = 0.379). Sex was also non-significant as a predictor of

365   post-criterion performance (GEE: $\chi^2(1) = 0.001$, p = 0.970). Genus however, did significantly

366   impact performance with *Symphalangus* performing significantly better than *Hylobates* (B

367   =10.184, $\chi^2(1) = 10.468$, p < 0.01). *Hoolock* also obtained fewer rewards than *Symphalangus*,

368 although performance was not significantly different from that of *Hylobates* subjects (B = 4.961,

369 $\chi^2(1) = 1.838$, p = 0.175) (Figure 3b). No color/preferred food association showed diminished

370 persistence in the first block post-criterion compared to the last block (Wilcoxon matched pairs:

371 Yellow Z = 0.00, p = 1.00; Green Z = -0.905, p = 0.366; Red Z = -0.707, p = 0.480).

DISCUSSION FOR EXPERIMENT 1

373   We were able to determine the rank order of food items and the most preferred for all

374 subjects was banana. We also determined that gibbons could successfully select their preferred

375 food when colored buckets covered it, suggesting they could use the color as a signal to the high

376 value food's location. There were no differences across color-reward associations, indicating

377 learning was not affected by the particular color/reward.

378   There was no evidence the gibbons tested here generalized from their learning in the first

379 round to other rounds as there were no differences between number of trials to reach criterion

380 performance with each successive color-reward association to be learned. Effectively, they

381 seemed to be learning each new association from scratch – as if they had not seen or experienced

382 the task before. This could be the result of multiple food items being used that distracted the

383 gibbons and obscured the intended question of whether gibbons can generalize and use

384 information learned in the first association to inform their learning in subsequent novel

385 associations.

INTRODUCTION FOR EXPERIMENT 2

387   Since we found the gibbons tested showed no evidence of generalizing from their

388 learning, we changed the methods and feeding platform in a second experiment where only one

389 food item would be searched for with three possible locations cued by a colored background that

390 we hoped would provide a more salient cue to the rewards location. We aimed to further

391   investigate the flexibility of learning by assessing whether there was any evidence of gibbons

392   generalizing from the first color/reward association learned to other, novel associations.

393   In Experiment 1, gibbons were required to learn an association between a preferred food

394   and specific color while simultaneously presented with two further possible color choices that

395   would also provide a reward, all be it of lower value. In Experiment 2, we reduced the cognitive

396   load be removing the secondary food items and the competing color cues in an attempt to focus

397   the gibbon's attention on a single preferred food reward (banana). We hypothesized that by

398   simplifying the cues presented, the gibbons tested may be better able to extract information from

399   their initial learning experience that would aid them in subsequent novel associations: that is,

400   they should be able to generalize from their learning in the first presentations and show improved

401   performance in subsequent similar learning situations.

402   **METHODS FOR EXPERIMENT 2**

403   The feeding platform for Experiment 2 required the gibbons to reach through doors to

404   select a hidden food item. Only one door was baited with a piece of banana and the position was

405   determined by the color cue on the front of the platform that measured 1.2 meters long, 0.3

406   meters wide and 0.6m high. It was large enough for the experimenter to hide behind and "reload"

407   the food item between trials without subjects seeing where the food item was placed. The

408   experimenter also wore dark sunglasses during the trials to avoid giving inadvertent gaze cues to

409   the subject.

410   The front of the feeding platform had three doors located at the base – on the left, center

411   and right. The doors were six inches long and six inches wide – large enough for the animals to

412   easily reach through (Figure 2). On the back of the doors was secured a sheet of heavy fabric that

413   prevented the animals seeing through to the reward. Thus, in order to retrieve a reward, the

414   subject had to move aside the fabric and reach through the door. Wooden dividers acted as

415   barriers on the offside of the feeding platform, between the three possible feeding locations, to

416   prevent the animals from reaching in one door and stretching their arms to the location of a food

417   item behind another door. Three laminated color boards were inserted onto the front of the

418   feeding platform behind a Plexiglas screen. The reason for the Plexiglas was because it is easily

419   cleaned between trials and provided a mechanism to hold the interchangeable laminates in place

420   (Figure 2). The laminates provided the color cue and varied dependent on the trial block between

421   red, blue and yellow.

422   A video that illustrates the animals' behavior as well as visually displaying the

423   experimental design of Experiment 2 can be viewed by clicking the following link: (AJP

424   Production Team – Please Create Link to Video 2)

425   *Desensitization and Learning Trials*

426   Similar to Experiment 1, desensitization trials were conducted before experimental trials

427   began. This was to desensitize the subjects to using the new feeding platform. The experimenter

428   placed pumpkin seeds in front of the closed doors and blueberries behind the closed doors. The

429   feeding platform was then presented to the subjects by positioning it outside the enclosure,

430   within direct reach of the gibbons. This feeding platform set-up was exactly the same on every

431   presentation.

432   Identical to Experiment 1, the platform was in this position until all of the food items

433   were consumed or for a maximum of five minutes if only a portion of the food was eaten. The

434   gibbons were assumed to have learned to associate the presence of the platform with a reward

435   when they readily approached, investigated and ate the food items. If the subject did not

436   approach the platform at all, the presenter would try again later that same day with a gap of two

437   hours between desensitization trials. The desensitization period continued on consecutive days

438   until the subjects were comfortable using the feeding platform.

439   The gibbons were recorded as associating the presence of the platform with a reward

440   when they completed two steps: 1) readily approached, investigated and ate the pumpkin seeds

441   and 2) reached through the doors and ate the blueberries. It took slightly longer for the gibbons in

442   Experiment 2 to make this association with as many as seven presentations of the feeding

443   platform required before there was evidence of an associative connection between the feeding

444   platform and the potential for reward in all gibbons. Once all subjects were consistently using the

445   new platform, we began trials to provide an opportunity for the gibbons to learn the task

446   requirements for Experiment 2.

447   During the initial learning trials, a food reward (piece of banana) was concealed behind

448   one of the doors which the gibbon was given the opportunity to retrieve. The location of the food

449   reward was determined by the color background (laminate) that was held constant to allow

450   gibbons to make the association between the rewards position and the color cue. Each subject

451   was initially presented with the red background which signified the reward (banana) was located

452   behind the left door. This configuration was repeatedly presented until the gibbon reliably chose

453   the left door, and retrieved the banana on their first selection for three consecutive trials

454   (criterion for the learning phase). Once criterion was reached for this color/position association,

455   the background color and the position of the reward were changed to a blue background with the

456   banana behind the center door, and finally a yellow background with the banana behind the right

457   door (Table II) with criterion being three consecutive correct choices for each color/reward

458   association.

459　　　　Similar to Experiment 1, a trial was only scored if the subject showed direct interest,

460　　measured by approaching the feeding platform within 30 seconds. The trial was marked as

461　　correct if the subjects' first choice was for the rewarded location and a trial was considered

462　　complete once the food item had been consumed or after one minute elapsed (if no choice was

463　　made). Any additional activity after one minute was considered "play" and the feeding platform

464　　was then taken away from the subject. If the food item was not consumed within the minute of

465　　exposure time, the trial was marked as incomplete and would be resumed on the next day of

466　　testing. Similarly, if the subject lost interest during the trials, the experiment was stopped and

467　　resumed at a later date, continuing where the subject left off until all possible presentations were

468　　completed. The inter-trial duration for all trials (learning and experimental) was approximately

469　　three minutes.

470　　　　Once criterion was reached for all three possible positions in block 1 (all trials where

471　　position of reward was always placed in accordance with the color/reward associations learned in

472　　the training trials), the subject moved on to the experimental trials (see below). On completion of

473　　the first round of testing in block 1 (learning and experimental trials), the learning trials for block

474　　2 commenced following the same protocol as for block 1, where the position of the reward

475　　changed dependent on the color background association (block 2 - Red/Center, Blue/Right,

476　　Yellow/Left). Thus, the subject experienced a series of learning trials followed by the

477　　experimental trials for block 1, and then returned to learning trials for block 2. Once the

478　　experimental trials for block 2 were completed, the learning trials for block 3 commenced (Block

479　　3 – Red/Right, Blue/Left, Yellow/Center).

480　　*Experimental Trials*

481   Once the subject completed the learning trials for each block, they progressed to the

482   experimental phase where 30 trials were presented with all three possible color/position

483   associations for that block were presented an equal number of times across in a randomized

484   pattern. Between each trial, the background color was changed and this determined where the

485   reward would be placed dependent on the block. There was a similar constraint as in Experiment

486   1 that the position could not be the same for two consecutive trials.

487   For example, in block 1, the blue background signaled the food item (banana) was behind

488   the center door, the red background, the food item was behind the left door and the yellow

489   background, the food item behind the right door. Once all 30 experimental trials were completed,

490   the subject went back to the learning trials for block 2 after which the experimental trials for the

491   second block were presented. This procedure was then repeated for block 3. Overall, each

492   individual experienced 90 experimental trials (30 for block 1, 30 for block 2 and 30 for block 3)

493   interspersed with the relevant learning trials as described above. Scoring was the same as the

494   learning trials.

495   *Data analysis*

496   Trials were scored as correct if the gibbon retrieved the food reward with their first

497   choice when presented with the apparatus. For the learning trials, the number of trials needed to

498   reach criterion (three consecutive correct choices) were analyzed using Friedman's repeated

499   measures test to assess whether any background color association was more difficult to learn.

500   GEE models were used to evaluate whether performance on the learning trials differed across

501   genera or by sex. As data were counts, Poisson distribution with a log function was specified,

502   genus and sex being factors in the model.

503   Performance on the experimental trials was evaluated at the group and individual level.

504 To determine the effects of learning on subsequent color/position associations, a GEE was

505 conducted with a binomial distribution and logit link function. Events in trials data were

506 specified with a fixed value of 30 (number of experimental trials per block). Genus and sex were

507 added as factors in the model with *Hylobates* as the referent category for the former.

508   Whether the gibbons were using the color cues to guide their choices was assessed by

509 determining whether they were selectively choosing the correct door significantly above chance.

510 Binomial tests with the test proportion set at 0.33 (as there were three possible choices) were

511 conducted at the group and individual level. During the observations, a location bias seemed

512 possible. Therefore, Chi square goodness of fit tests were used to evaluate whether the gibbons

513 as a group and individually, were selecting any particular door (center, left or right) more that

514 would be expected. Alpha for all tests was set at 0.05.

515 **RESULTS FOR EXPERIMENT 2**

516 *Learning trials*

517   Eight gibbons cooperated enough to engage in experimental trials and generate useable

518 data. Although it was planned to include representatives from all four genera, none of the

519 northern white-cheeked gibbons (*Nomascus leucogenys*) would participate in the experiment.

520 Only one female white-cheeked gibbon would approach the feeding platform and remove the

521 food items in the training trials. However, this gibbon was apprehensive to reach through the

522 doors to remove the hidden food items in the learning or experimental trials. The male white-

523 cheeked gibbons would not approach the feeding platform. This could be due to the daily feeding

524 routine that involves feeding each gibbon separately with some food being handed directly or

525 gently tossed to them to catch. They do not typically approach a feeding platform, hesitated

526 doing so in these experiments, which made them unwilling participants. Therefore, the final

527 sample consists of subjects from three genera (Table I).

528 The number of trials needed to learn each background color/reward association ranged

529 from 3 to 11 with most individuals reaching criterion in 5 or less trials for each color-reward

530 configuration. There were no significant differences between number of trials to criterion for

531 each background color association in the learning trials (Median (Yellow background) =

532 14.50(IQR = 6.0), Median (Blue background) = 13.00(9.0), Median (Red background) =

533 15.00(9.00), Freidman's test: $\chi^2(2) = 2.769$, p = 0.250). There was a main effect of genus on

534 number of trials to criterion with *Hoolock* and *Symphalangus* needing fewer presentations than

535 *Hylobates* (GEE: *Hoolock* B = -0.529, $\chi^2(1) = 99.887$, p < 0.001; *Symphalangus* B = -0.493,

536 $\chi^2(1) = 31.124$, p <0.001) (Figure 4). Sex was not a significant predictor of performance in the

537 learning trials (GEE: $\chi^2(1) = 2.971$, p = 0.085).

Experimental trials

539 Consistent with the learning trials, there was no evidence that the gibbons were

540 generalizing from the learned association in block 1 to the novel associations in block 2 and 3

541 (GEE: $\chi^2(2) = 0.719$, p = 0.698). The effect of genus on performance in the experimental trials

542 was significant with *Symphalangus* gaining significantly more rewards than *Hylobates*

543 (*Symphalangus* Mdn = 57.00, *Hylobates* Mdn = 43, B = 0.658, $\chi^2(1) = 65.161$, p <0.001).

544 *Hoolock* did gain more rewards than *Hylobates*, however this did not reach significance

545 (*Hoolock* Mdn = 46, B = 0.290, $\chi^2(1) = 2.771$, p = 0.096). Sex was again non-significant in this

546 analysis ($\chi^2(1) = 0.791$, p = 0.372.

547   As a group, gibbons were selectively choosing the correct reward location above chance

548   levels gaining 378 out of 720 possible rewards collectively (Binomial: p < 0.001). Individual

549   performance is shown in Table IV, with six gibbons selecting the rewarded door significantly

550   above chance overall. Within this group, three gibbons dropped below chance level on one set of

551   the three with the remaining three performing above chance in all sets. Developing a bias for one

552   location over the others may have influenced performance. Five of the eight gibbons showed a

553   positional bias (Table V) selectively favoring the center door in general. This bias did not

554   however emerge consistently across all blocks.

GENERAL DISCUSSION

556   In Experiment 1, we found no evidence the gibbons tested generalized from their learning

557   and we cautioned this could be the result of multiple food items and competing color cues being

558   used that distracted the gibbons. Therefore, we changed the experimental design to a more

559   specific task in Experiment 2 to focus the gibbon's attention on a single food/color association to

560   see if the gibbons were able to use information from their first learning experience of the task to

561   facilitate future learning of novel color/reward associations. Despite making these changes, the

562   data show they learned each new association from scratch – as if they had not seen or

563   experienced the task before as in Experiment 1. Our findings are similar to other studies

564   [Rumbaugh & McCormack, 1967] that found gibbons struggle with learning set formation and

565   do not show the learning to learn pattern as found in other species. However, once the learning

566   association was made, the gibbons performed well above chance. We found no differences

567   across color associations indicating learning was not affected by the particular color / reward

568   association

569   The results reported here could be due to the small sample size and because of the captive

570   environment in which these gibbons were raised. Karenina and Marlow, siamang gibbons

571   (*Symphalangus syndactylus)* who performed quite well in the tasks reported here, had a lot of

572   human interaction from a young age. Perek, a Javan gibbon (*Hylobates moloch*) who did not

573   perform as well in these experiments, was born at Howlets Wild Animal Park, UK, and did not

574   have as much human interaction.

575   The Gibbon Conservation Center provided a unique opportunity being the only institution

576   in the world to house and breed all four genera of gibbon [Mootnick, 1997]. However, obtaining

577   large sample sizes is very challenging as there are very few gibbons (particularly of the *Hoolock*

578   genus) in captivity. Another possibility for these results is the low criterion level set for

579   Experiment 2. We lowered the number of consecutive correct learning trials to compensate for

580   the gibbons short attention spans but this may not have given them sufficient time to really learn

581   the association. Results from previous experiments where hundreds of trials have been presented

582   in the learning phase [Rumbaugh & McCormack, 1967] suggest performance may have been

583   much better had they been given more opportunity to learn. Despite such a low criterion, many

584   of the gibbons did perform well above chance in the experimental trials although they may not

585   have had the opportunity to learn the rules of the task that could then be generalized to future

586   novel presentations.

587   We found a key difference in the learning and association rates between male and female

588   gibbons with the males learning at a faster rate than females. Reproductively active females may

589   be highly motivated to explore potential resources due to the additional energy requirements of

590   pregnancy and lactation; however, increased investment in developing offspring could make

591   them more guarded in their investigations and so reluctant to engage with unknown objects such

592   as our testing equipment [Cunningham et al., 2011]. Males, without the investment in offspring,

593   may be more devoted to the search of potential resources and more willing to explore novel

594   objects.

595   We have shown that when given provisioned food items, the subjects tested have

596   preferred foods and can associate color signals with these foods. However, there were no

597   differences across color associations and the rate of learning was no different from the colors red,

598   green, yellow, blue, or if the food item was on the left, center or right. This suggests the subjects

599   can associate each of the colors tested to the food items at the same rate and accuracy with no

600   particular preference to a specific color or location.

601   The *Hylobates sp.* had the slowest learning rate before they made the association between

602   their preferred foods and the color cue in Experiment 1 and 2. *Hoolock* learned the association

603   significantly quicker, needing fewer trials in all color/preferred food association learning phases.

604   For all gibbons tested, males learned faster than the females, however age did not impact

605   learning rate although younger gibbons did show more inconsistencies in their performance,

606   selecting other food items as their first choice on some trials in Experiment 1, especially in the

607   post-criterion phase. This however did not have a significant impact on results with all subjects

608   selecting their preferred food item with a high level of accuracy in all post-criterion trials.

609   *Possible Foraging Implications*

610   This ability to associate colors to preferred foods can be an advantage in a changing

611   environment. For instance, *Hoolock* gibbons, which performed well compared to the lar-group in

612   this study, are from an environment that is variable and resources can be scarce. The lar-group

613   gibbons, who performed the poorest, live in an area where the climate is more stable and food is

614   likely to be plentiful year round [Brockman & van Schaik CP, 2005; Curran & Leighton, 2000].

615 This suggests that animals required to search more vigorously for high quality food items due to

616 environmental variability are more flexible in their learning than animals that do not have the

617 same foraging pressures.

618 There have been previous investigations that support the assumption that trichromatic

619 color vision provides an advantage related to foraging [Caine & Mundy, 2000; Nagle & Osorio,

620 1993; Osorio & Vorobyev, 1996; Regan et al., 1998, 2001; Lucas et al., 1998]. However, these

621 investigations did not take into account using colors as visual landmarks or make the direct

622 connection between preferred foods and how animals can associate colors to these foods.

623 To consider possible foraging implications as well as the ecological validity of the

624 experimental design and results reported here, the fact that color is an ephemeral cue in the

625 environment must be taken into account. In general, forests retain a homogenous set of colors

626 with changes in accordance with fruit ripening and leave leaf maturation across time. Mostly,

627 animals focus on more permanent environmental cues while navigating such as the size and

628 shape of trees. However, if an animal can take advantage of the changing colors in the

629 environment and learn to make the association of these new color cues to the location of ripe

630 fruit, they will have a foraging advantage over animals that do not possess this ability.

631 Resource availability is rarely ideal. Research has found yearly fluctuations in the

632 availability of resources which has a significant impact on the demography, foraging ecology,

633 life history patterns, population density, anti-predator strategies, and social behaviour of

634 nonhuman primates [Brockman & van Schaik, 2005]. When preferred foods are scarce, optimal

635 foraging theory predicts primates should attempt to maintain the net energy intake required for

636 physiological maintenance by either increasing their ranges to continue utilizing preferred foods

637 or relying on alternative foods [e.g., MacArthur & Pianka, 1966; Stephens & Krebs, 1986; van

638   Schaik & Brockman, 2005]. Thus, primates may act as "energy maximizers," increasing their

639   day journey length (DJL) or home range size to consume as many scarce preferred resources as

640   possible, or "energy minimizers," decreasing their DJL and home range size while consuming

641   more low-quality resources [e.g., Clutton-Brock, 1977; Boinski, 1987; Barton et al., 1993;

642   Barton, 1998, 1999; Overdorff, 1993; Hemingway & Bynum, 2005; Riley, 2007].

643   Given a gibbon's body size, morphological and physiological adaptations, grouping

644   patterns and social organization, they fit the description of energy maximizers. They spend a

645   great deal of energy searching for and traveling between patches of foods. They use their

646   adaptations, expand their ranges, and continue to search for preferred foods that are usually high-

647   energy fruits that are bright in color. In order understand the foraging advantages conferred by

648   the ability to associate ephemeral color cues to preferred food items in relation to resource

649   distribution, further testing is needed in both captivity and nature.

650   *Conclusions and Future Study*

651   Since we have shown the gibbons tested had difficulty generalizing from their learning in

652   one context and using it to facilitate learning in a similar situation, we must conclude that these

653   apes are capable of making color/reward associations but cannot use their learning flexibly. This

654   makes it unlikely that they would, with further testing, demonstrate learning set formation

655   consistent with results from earlier research [Rumbaugh & McCormack, 1967]. However, the

656   emergence of learning to learn patterns may occur with the use of more structured small steps to

657   facilitate learning of the rules of the task in an incremental way. For example, repeated

658   presentations of one color cue that signifies a reward presented with a neutrally colored

659   unreinforced cue before changing the color cue but not the rule (color would still indicate the

660   position of the reward) after the subject experienced many more trials than used here may allow

661   gibbons to extract the general rule that can be used to solve future novel presentations rather than

662   just a simple stimulus-reward association. With this more intensive training regime, they may be

663   able to apply their learning in a more flexible way.

664   **ACKNOWLEDGEMENTS**

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3   791   **Figure Legends**
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6   793   Figure 1. Betty (Female *H. leuconedys*) engaged in Experiment 1. The gibbons reached through
7   794   the fencing and flipped open the buckets to reveal the food items. The buckets were drilled in
8   795   place with hinges that allowed them to be easily flipped and replaced to the different sets.
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12   798   Figure 2. Feeding platform used for Experiment 2. This platform required the gibbons to reach
13   799   through doors to select the hidden food item. Three laminated color boards were inserted onto
14   800   the front of the feeding platform behind a Plexiglas screen.
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18   803   Figure 3: Adjusted means for number of trials needed to reach criterion performance (10
19   804   consecutive first choices of preferred food type) by genus (a) and percentage of correct responses
20   805   by genus in the post-criterion phase (b). Error bars represent $\pm$1SE. ** denotes significance at $p <$
21   806   0.001
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23   808
24   809   Figure 4: Adjusted means for number of trials to reach criterion performance in the learning
25   810   trials of Experiment 2 by genus. Error bars represent $\pm$1SE. ** denotes significance at the 0.001
26   811   level.
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837   **Tables**:

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839   Table I. Names, species, sex, and age of the subjects in Experiment 1 and Experiment 2.

Subject	Species	Sex	Age in yrs	Experiment
Marlow	*Symphalangus syndactylus*	Female	8	1 & 2
Karenina	*Symphalangus syndactylus*	Female	14	1 & 2
Khin Maung Win	*Hoolock leuconedys*	Male	5	1 & 2
U Myint Swe	*Hoolock leuconedys*	Male	4	1 & 2
Hmawe Ni	*Hoolock leuconedys*	Female	11	1 & 2
Betty	*Hoolock leuconedys*	Female	14	1
Chan Thar	*Hoolock leuconedys*	Female	6	1
U Maung Maung	*Hoolock leuconedys*	Male	12	1
Win Bo	*Hoolock leuconedys*	Male	10	1
Reg	*Hylobates moloch*	Male	13	1
Perak	*Hylobates moloch*	Male	11	1
Truman	*Hylobates plieatus*	Male	10	1
Violet	*Hylobates pileatus*	Female	4	1
Tuk	*Hylobates pileatus*	Female	20	2
Chloe	*Hylobates moloch*	Female	23	2
Domino	*Hylobates pileatus*	Male	18	2

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863   Table II: Experimental sets used in Experiment 1 and 2.
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Sets	Experiment 1[1]	Experiment 2[2]
1	Red left, yellow center, green right	Red left, blue center, yellow right
2	Red left, green center, yellow right	Blue right, yellow left, red center
3	Yellow left, red center, green right	Yellow center, red right, blue left
4	Yellow left, green center, red right	
5	Green left, red center, yellow right	
6	Green left, yellow center, red right	

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867   [1]For Experiment 1, color refers to the bucket covering the food and position (left, right, center)
868   designates the position of the colored bucket on the feeding platform.
869   [2]In Experiment 2, the color refers to the background and the position to the location of the food
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902 Table III: Unadjusted means for number of trials to criterion performance.
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Preferred food color association[1]	*Hoolock* (n = 7) mean(SE)	*Hylobates* (n = 4) mean(SE)	*Symphalangus* (n = 2) mean(SE)
YELLOW	22.29(1.782)	50.25(11.161)	29.50(10.500)
GREEN	28.57(2.277)	48.50(19.294)	23.00(0.000)
RED	27.14(2.064)	48.75(11.116)	21.00(0.000)

904
905 [1]Ten consecutive correct choices for three genera of gibbon for each color-preferred food
906 association in Experiment 1

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Table IV: Number of correct responses in the experimental trials of Experiment 2.

Subject	S1		S2		S3		Total	
	Correct	*p*	*Correct*	*p*	*Correct*	*p*	*Correct*	*p*
Marlow	19	0.001***	19	0.001***	18	0.002**	56	0.001***
Khin Maung Win	15	0.001***	12	0.002	11	0.001	38	0.042
U Myint Swe	16	0.017*	21	0.001***	19	0.002**	56	0.001***
Karenina	23	0.001***	19	0.002**	16	0.017*	58	0.001***
Hmawe Ni	16	0.017**	14	0.017	16	0.017**	46	0.001***
Chloe	14	0.017	15	0.001***	16	0.017**	45	0.001***
Domino	11	0.001	11	0.001	14	0.017	36	0.017
Tuk	15	0.001***	12	0.263	16	0.017**	43	0.003**

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Across each set (maximum correct is 30 trials per set), and in total (maximum score is 90 trials) and binomial test results. Values noted as significant represent performance above chance level. P values that are significant but not annotated represent performance below chance levels.

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949   *significant at the 0.05 level
950   **significant at the 0.01 level
951   ***significant at the 0.001 level

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975 Table V: Chi square tests to evaluate individual positional bias on experimental trials of
976 Experiment 2.
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Subject	S1		S2		S3		Total	
	$\chi^2(2)$	*p*	$\chi^2(2)$	*p*	$\chi^2(2)$	*p*	$\chi^2(2)$	*p*
Marlow	4.200	0.122	6.200	0.045*	4.200	0.122	14.067	0.001***
Khin Maung Win	4.200	0.122	3.800	0.150	1.800	0.407	4.067	0.131
U Myint Swe	9.800	0.007**	7.800	0.020*	9.800	0.007**	26.467	0.001***
Karenina	0.200	0.905	3.800	0.150	15.800	0.001***	13.867	0.001***
Hmawe Ni	3.800	0.150	4.200	0.122	32.00	0.202	9.624	0.008*
Chloe	0.600	0.439	0.133	0.715	13.400	0.001***	13.867	0.001***
Domino	6.200	0.045*	- [a]	- [a]	2.600	0.273	4.467	0.107
Tuk	1.400	0.497	11.400	0.003**	3.800	0.150	10.400	0.006**

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979 Significant values denote a deviance from the expected values of 10 choices at each location. For
980 all gibbons with a bias, it was for the center door.
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982 [a] observed and expected values were the same therefore Chi square was not calculated
983 *significant at the 0.05 level
984 **significant at the 0.01 level
985 ***significant at the 0.001 level

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Figure 1. Betty (Female H. leuconedys) engaged in Experiment 1. The gibbons reached through the fencing and flipped open the buckets to reveal the food items. The buckets were drilled in place with hinges that allowed them to be easily flipped and replaced to the different sets.
152x86mm (220 x 220 DPI)

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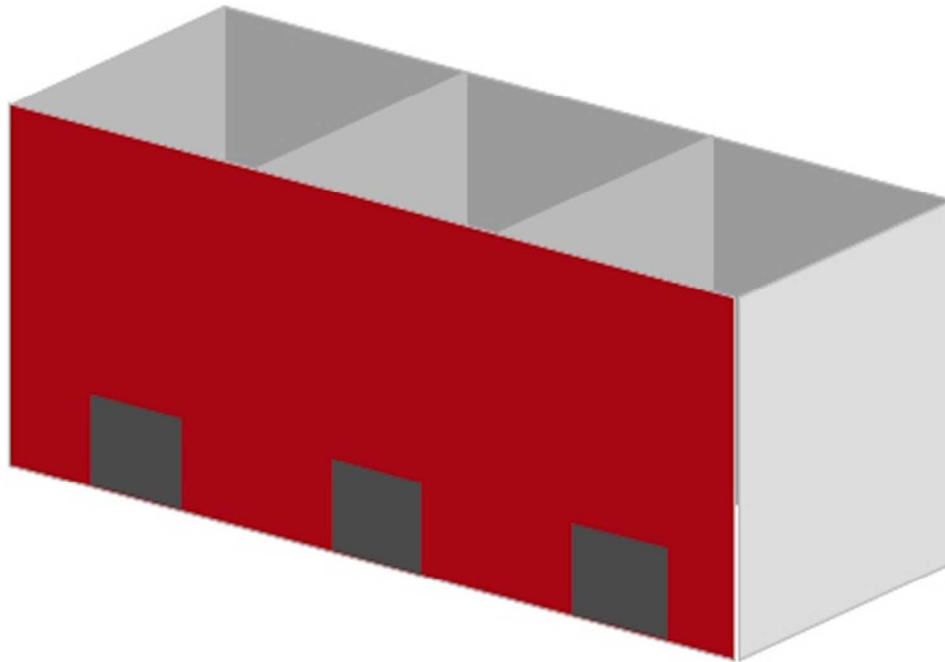21
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Figure 2. Feeding platform used for Experiment 2. This platform required the gibbons to reach through doors to select the hidden food item. Three laminated color boards were inserted onto the front of the feeding platform behind a Plexiglas screen.
246x166mm (72 x 72 DPI)

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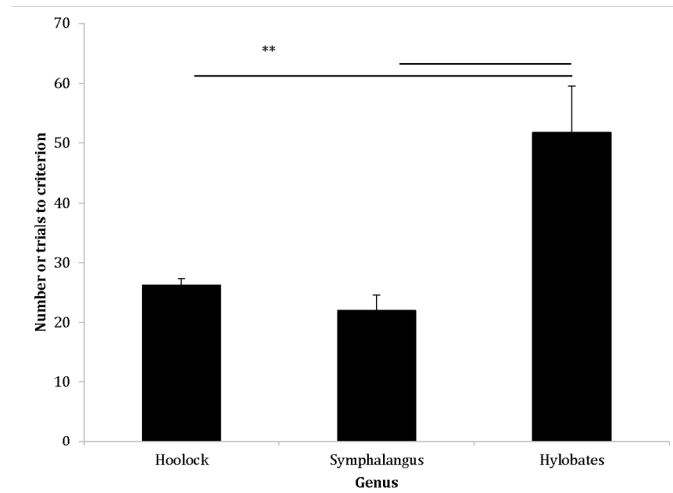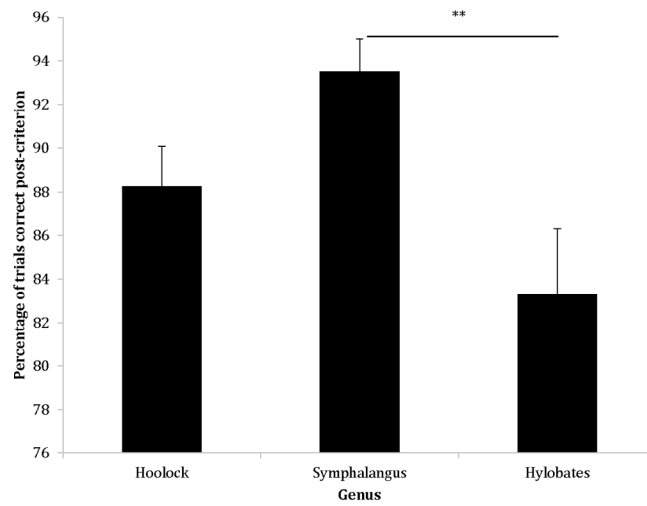51
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Figure 3: Adjusted means for number of trials needed to reach criterion performance (10 consecutive first choices of preferred food type) by genus (a) and percentage of correct responses by genus in the post-criterion phase
215x279mm (200 x 200 DPI)

(b). Error bars represent ±1SE. ** denotes significance at p < 0.001
215x279mm (200 x 200 DPI)

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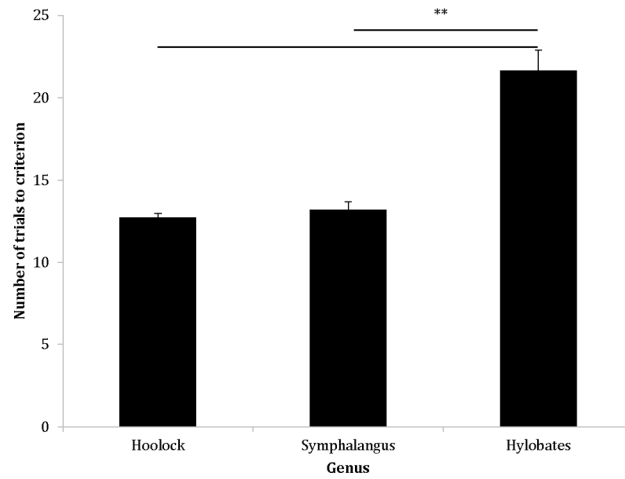41
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Figure 4: Adjusted means for number of trials to reach criterion performance in the learning trials of Experiment 2 by genus. Error bars represent ±1SE. ** denotes significance at the 0.001 level.
215x279mm (200 x 200 DPI)