

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

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

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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

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3 46 evolution of flexible learning in some genera. Further comparative study is necessary in order to  
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6 47 incorporate realistic cognitive variables into foraging models.  
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## 8 48 **INTRODUCTION**

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10 49 Despite being the most diverse group of extant apes, gibbons continue to be the most  
11  
12 50 understudied of all higher primates, particularly with regard to their cognitive abilities. Gibbons  
13  
14 51 are native to South East Asia and can be found in Vietnam, Cambodia, Thailand, Burma, China,  
15  
16 52 Malaysia, and the islands of Indonesia. They are omnivores and in ideal resource availability  
17  
18 53 conditions, high-energy fruit constitutes the majority of their diet with the remainder consisting  
19  
20 54 of leaves, flowers, seeds, tree bark, insects, small birds, eggs and tender plant shoots [Curran &  
21  
22 55 Leighton, 2000]. These small arboreal apes primarily live in monogamous pairs with their  
23  
24 56 associated offspring and are characterized by limited sexual dimorphism, complex vocal duets  
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26 57 between the male and female bonded pair and brachiating mode of locomotion [Cunningham &  
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28 58 Mootnick, 2009].  
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34 59 Representing an interesting evolutionary divergence between monkeys and great apes, a  
35  
36 60 better understanding of gibbon learning ability and their capacity for complex mental processes  
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38 61 would allow us to track both the progression of advanced cognition and the evolutionary  
39  
40 62 pressures that have led to the emergence of abilities characteristic of great apes (including  
41  
42 63 humans). This research therefore aims to investigate whether gibbons are able to learn sequential  
43  
44 64 color-reward associations and if they can extract relevant information from the first stimulus-  
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46 65 response association to enable them to make future associations more readily.  
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50 66 Research on gibbon vision has shown there are separate M and L photo pigments and  
51  
52 67 other characteristics that are almost identical to those of the common chimpanzee (*Pan*  
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54 68 *trogodytes*) – known to have trichromatic color vision, suggesting their searching behavior is  
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3 69 heavily guided by vision. As all genera of gibbon enjoy the benefits of full trichromatic color  
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6 70 vision [Deegan & Jacobs, 2001; Jacobs, 1993; Jacobs, et al., 1996], they should easily  
7  
8 71 discriminate color information from the cues provided during this series of studies.  
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10  
11 72 Experimental tests of associative learning in non-human primates in a controlled setting  
12  
13 73 typically employ object discrimination tasks where the subject is presented with two arbitrary  
14  
15 74 shapes, one that if chosen will lead to a reward and one that will not. For example, selection of  
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17 75 the red square would lead to reinforcement whereas selecting the blue triangle presented with it  
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19 76 in a two-way choice paradigm would leave the subject unreinforced. Data are collected on the  
20  
21 77 number of trials needed to reach a pre-determined criterion level that is assumed to result from  
22  
23 78 the subject learning the rules of the task; that is, which of the two shapes will lead to  
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25 79 reinforcement.  
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28  
29 80 Using this basic paradigm, Harlow [1949] postulated that rhesus macaques (*Macaca*  
30  
31 81 *mulatta*) made more than a simple association between stimulus and reinforcement, suggesting  
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33 82 'cognitive mediation' occurred as subjects learned subsequent stimulus – reward associations  
34  
35 83 more quickly. This seemed to indicate they were extracting some level of information from their  
36  
37 84 first learning experience that they used to inform their actions in novel configurations. This has  
38  
39 85 since been termed 'learning to learn' or 'learning set formation' [Rumbaugh & McCormack,  
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41 86 1967].  
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46 87 Since the early observations by Harlow, studies of learning set formation have shown that  
47  
48 88 many species including rhesus macaques (*Macaca mulatta*) and chimpanzees (*Pan troglodytes*),  
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50 89 can in fact 'learn to learn' with subsequent problems being solved in fewer presentations  
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52 90 [Passingham, 1981; Fobes & King 1982]. However, gibbons have typically struggled with these  
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54 91 tests that require the subjects to solve different sets of similar problems over time and do not  
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3 92 show the learning to learn pattern found in other species [Rumbaugh & McCormack, 1967;  
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6 93 Tomasello & Call, 1997; Abordo, 1976].  
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8 94 In the Rumbaugh and McCormack study [1967] five immature gibbons (*H. lar* N=2, *H.*  
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10 95 *moloch* N=1; *H. pileatus* N=2) were presented with a simple discrimination task that required  
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12 96 subjects to push bins marked by a red square (reinforced) or a red circle (unreinforced) to reveal  
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15 97 a reward beneath the reinforced shape. The gibbons had a tendency not to push the bins at all –  
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17 98 taking upwards of 100 trials to acquire this basic motor action when compared to other primates  
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20 99 tested. However, once they were reliably making a choice, the gibbons did not appear to find  
21  
22 100 learning the discrimination any more difficult than the other apes and monkeys tested (*Pongo*,  
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24 101 *Gorilla*, *Pan Sp.*, and *Macacca*) [Rumbaugh & McCormack, 1967]. Unlike the other monkeys  
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26  
27 102 and apes, when novel shape pairs were presented, gibbons seemed to learn each new association  
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29 103 as a completely new problem, taking the same number of trials to reach criterion performance as  
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32 104 they had for the first stimulus pair. Other species took fewer trials to learn each new association  
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34 105 suggesting they were using information gained during their first learning experience to inform  
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36 106 their choices on subsequent novel presentations. This seemed to be beyond the capacities of the  
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39 107 gibbons tested.  
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41 108 Other studies have provided contrasting results; for example, in a learning reversal study  
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43 109 (where the rewarded shape in a paired association task is 'reversed' once the subject reaches  
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46 110 criterion performance), Gosette [1970] reported gibbons (*H.lar*) did show evidence of learning to  
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48 111 learn making fewer errors than squirrel monkeys (*Saimiri* sp.) and owl monkeys (*Aotus* sp.), but  
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50 112 being inferior to capuchins (*Cebus* sp.). As some prior studies have found gibbons generally  
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53 113 struggle with learning set formations [Rumbaugh & McCormack, 1967] while others have shown  
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55 114 conflicting evidence with better performance [Gosette, 1970], we were interested in clarifying  
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3 115 whether gibbons can use knowledge gained during one learning task to facilitate performance on  
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6 116 a similar but novel problem that would be a precursor to learning set formation.  
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8 117         Gibbons are large-brained primates with their relative brain size being comparable to the  
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10 118 great apes and large-brained monkeys [Cunningham & Mootnick, 2009]; therefore, their reported  
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12 119 poor performance on discrimination tasks and little evidence of learning set formation is  
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14 120 surprising. Several gibbon behavioral characteristics could explain their apparent lack of  
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16 121 abilities and contradicting results of previous studies. Gibbons have notoriously short attention  
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18 122 spans [Fedor et al., 2008] potentially losing interest after only a few trials, impeding learning set  
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20 123 formation. Also, gibbons rely heavily on their visual cognitive abilities - it has been found that  
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22 124 gibbons are competent in detecting the visual orientation of other species as well as their own  
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24 125 and possess some knowledge of how visual gaze direction relates to external stimuli [Horton &  
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26 126 Caldwell, 2006]. Therefore, results will be inconsistent if a subject with a short attention span  
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28 127 becomes distracted by a visual cue outside of the experiment.  
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34 128         The aim of this study was to determine whether gibbons could learn to associate preferred  
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36 129 foods with colored signals when the food items were hidden out of direct sight and once learned,  
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38 130 whether they could use their acquired learning to facilitate future learning. That is, once they had  
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40 131 learned a particular stimulus-reward association, would they learn subsequent novel associations  
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42 132 more easily? We also tested whether genera or sex had an impact on this ability based on  
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44 133 previous work that indicated differences in cognitive performance of gibbons were related to  
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46 134 subject-variables in that hoolock (*Hoolock leuconedys*) and siamang (*Symphalangus syndactylus*)  
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48 135 learned faster than the lar group (*Hylobates sp.*) [Cunningham et al., 2011] potentially due to  
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50 136 selection for flexibility caused by environmental variability.  
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## 55 137 **METHODS FOR EXPERIMENT 1**

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3 138 *Ethics statement*  
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5 139 All behavioural studies were non-invasive and subjects were fed their normal daily diet  
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8 140 of fruits and vegetables throughout. Participation in all testing described below was voluntary on  
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10 141 the part of the gibbons. The research adhered to the legal requirements of the USA (the country  
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12 142 in which the research was conducted) and the research adhered to the American Society of  
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14 143 Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates. The research  
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16 144 methods were also approved by the Institutional Animal Care and Use Committee of California  
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18 145 State University, Los Angeles (IACUC protocol number 12-4). The research also had permission  
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20 146 from the Gibbon Conservation Center (permit number 2013-1) and adhered to the ASAB  
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22 147 Guidelines for the treatment of animals in behavioural research (2006).  
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27 148 *Study site and subjects for Experiment 1 and 2*  
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29 149 The gibbons were housed at the Gibbon Conservation Center (GCC), California. Some  
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31 150 subjects had a limited history of cognitive testing previously taking part in two studies of object-  
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33 151 mediated problem-solving tasks [Cunningham et al., 2006, 2011]. However, to the authors'  
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35 152 knowledge, none had been exposed to any tasks similar to those reported here. The subjects in  
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37 153 Experiment 1 consisted of 13 gibbons (age 4-14 years) with representatives from three of the  
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39 154 four extant genera [Groves, 2002] (*Hylobates pileatus* ( $N = 2$ ), *Hylobates moloch* ( $N = 2$ ),  
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41 155 *Symphalangus syndactylus* ( $N = 2$ ), *Hoolock leuconedys* ( $N = 7$ )) (Table I). Ten gibbons  
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43 156 participated in Experiment 2 (age 4-23 years), five that were also subjects in Experiment 1 plus  
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45 157 two additional females (*H. moloch* ( $N = 1$ ); *H. pileatus* ( $N = 1$ )) and one male (*H. pileatus*) that  
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47 158 took part in Experiment 2 only (Table II). Unavoidable problems prevented the same gibbons  
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49 159 being tested in both experiments; Violet (*H. pileatus*) was in isolation while recovering from an  
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51 160 arm injury and a family of *H. leuconedys* moved enclosures during testing.  
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3 161 Gibbons were housed in outdoor enclosures (10 X 3 X 4 m) with a connected section (4  
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6 162 X 3 X 2.5 m) generally available at all times that could be closed off to separate subjects as  
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8 163 required. This did not have a significant impact on the experiments as the gibbons were typically  
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10 164 separated a few times per week when the staff cleaned the enclosures and the veterinarian  
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12 165 checked the health of the animals. If we did notice any change in the animal's behavior that  
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14 166 could affect their performance in testing (due to separation or other distraction), we stopped the  
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16 167 current trial and resumed the following day. All enclosures were spaced by a minimum of 5 m  
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18 168 and visual barriers and planted vegetation obstructed direct views between adjacent cages [see  
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20 169 Mootnick, 1997 for more details of enclosure design]. The gibbons were fed their normal daily  
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22 170 diet being fed five times per day with fruits and monkey biscuits in the morning and apples,  
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24 171 bananas and greens in the afternoon. The design of the enclosures allowed the gibbons to reach  
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26 172 their arms through fencing to access the feeding platforms used in the experiments (Figure 1).  
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32 173 *Experiment 1*  
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34 174 Experiment 1 consisted of two phases; Phase 1 was to determine the rank order of  
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36 175 preferred food items (banana, cucumber and monkey biscuits) for each individual. Phase 2  
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38 176 assessed whether they could learn an association between their preferred foods and a color cue.  
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40 177 In this discrimination task, the incentive was out-of-sight (concealed under a colored bucket) and  
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42 178 we assessed how quickly the gibbons could learn to associate the position of the food reward  
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44 179 with the cue. Three color/preferred food associations were presented consecutively, and we  
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46 180 evaluated whether subsequent configurations were learned more efficiently suggesting gibbons  
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48 181 were able to extract information from the first configuration to facilitate future learning. As prior  
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50 182 studies have showed gibbons struggle with learning set formations, possibly due to short  
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52 183 attention spans or being easily distracted, we attempted to limit these potential problems by  
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3 184 focusing the gibbon's attention on visual cues within the experiment. A video that illustrates the  
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6 185 animals' behavior during both phases of Experiment 1 can be viewed by clicking the following  
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8 186 link: (AJP Production Team – Please Create Link to Video 1)  
9

10 187 *Phase 1 apparatus and procedure*  
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12  
13 188 Before testing began, subjects were desensitized to the new feeding platform that would  
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15 189 be used for the experimental trials. The subject's motor skills and grasping abilities were taken  
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17 190 into consideration when constructing the feeding platform, 130 cm long and 31 cm wide. If the  
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20 191 platform were smaller, the gibbons would be able to easily pick it up, flip it over, and potentially  
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22 192 lose interest in the test. If the platform were larger, it would make it difficult to transport to  
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24 193 various enclosures. Three plastic buckets, 25 cm tall and 15 cm in diameter were painted red,  
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27 194 yellow, and green. Three hinges were drilled into the wooden feeding platform 25 cm apart that  
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29 195 attached the buckets open-end down, to the feeding platform. The hinges allowed the buckets to  
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31 196 be flipped open by the gibbons to reveal food items hidden beneath (Figure 1).  
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34 197 To make the association between food and the feeding platform, the experimenter placed  
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36 198 a known favorite snack (as suggested by the staff at the GCC) of pumpkin seeds and blueberries  
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38 199 around and underneath the closed buckets on the feeding platform. This was to motivate the  
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41 200 gibbons to touch the buckets and feel comfortable with the task of opening them to reveal the  
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43 201 hidden food items. The experimenter presented the feeding platform to the subjects by sliding  
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46 202 along the floor until it was aligned with the enclosure and the rewards and buckets were within  
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48 203 the gibbons' reach when they extended their arm through the wire mesh. The pumpkin seeds  
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50 204 were scattered around the buckets and the buckets were closed over the blueberries. This feeding  
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53 205 platform set-up was same on every presentation in the desensitization phase. The platform was in  
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55 206 this position until all of the food items were consumed or for a maximum of five minutes if only  
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3 207 a portion of the food was eaten. If the subject did not approach the platform at all, it was  
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6 208 presented again later that same day with a gap of two hours between desensitization trials. The  
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8 209 desensitization period continued on consecutive days until the subjects were comfortable using  
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10 210 the feeding platform. The gibbons were assumed to associate presence of the platform with a  
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12 211 reward when they readily approached, investigated and ate the pumpkin seeds, and finally  
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14 212 flipped the colored buckets and ate the blueberries. On average, five presentations of the feeding  
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16 213 platform were needed before there was evidence of an associative connection between the  
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18 214 feeding platform and the potential for reward.  
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22 215 Gibbons at GCC demonstrated preferences for specific food types when a variety of  
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24 216 choices were presented. This was recognized when staff at the center brought multiple items to  
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26 217 the enclosures and gibbons consistently picked and ate food in the same order. However, the  
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28 218 order of preference was not the same for every gibbon, although regardless of order, they were  
29  
30 219 usually individually consistent. As the experimental test relied on the association between  
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32 220 preferred food and colored signal being learned and remembered, we first had to assess  
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34 221 individual preference for the three items that would be used in the experimental tests.  
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38 222 General observations indicated that favorite foods were high in sugar and bright in color  
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40 223 (bananas, yams, and bell peppers). The least favorite foods had lower sugar content and were  
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42 224 usually plain in appearance (monkey biscuits). For these reasons, we predicted a favorite food  
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44 225 item would be banana, a moderate food item would be cucumber and the least favorite food item  
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46 226 would be monkey biscuits.  
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49  
50 227 Each trial consisted of the experimenter presenting the feeding platform, within reaching  
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52 228 distance of each enclosure with the food items in full view. Incentives were placed on the  
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54 229 feeding platform out of view of the subjects in one of three locations that corresponded to the  
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3 230 placement of the buckets that would be used on the test. Thus, rewards were in a horizontal line  
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6 231 relative to the enclosure fence, with the middle location being at the center of the feeding  
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8 232 platform and one reward positioned equidistant to the left and right of center. The position of the  
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10 233 three items changed in every trial in a randomly determined order. For example, on the first trial,  
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12 234 the piece of banana was on the left, cucumber in the middle and monkey biscuit on the right. For  
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15 235 the second, the position was switched so that the banana became central, cucumber right and  
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17 236 monkey biscuit left. The position of presentation was changed on every trial thereafter within the  
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20 237 constraint that the food items never appeared in the same position twice, to make sure the  
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22 238 gibbons did not get used to reaching for a particular food item in a specific direction. Notes were  
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25 239 taken of the order in which gibbons selected and ate the food items with the assumption that the  
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27 240 preferred food would be consumed first and the least preferred item, last.

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29 241 *Phase 2 - Associative learning of color cue and preferred reward*

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32 242 The purpose of Phase 2 was to determine if gibbons could associate colors to their rank  
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34 243 order of food items when they are out of direct sight (hidden under buckets). If the subjects were  
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36 244 able to make an association between the food items and color that signaled their preference  
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38 245 determined in Phase 1, they should select their preferred incentive as their first choice. All  
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41 246 buckets were baited with one item of the subjects preferred food (banana for all gibbons) and one  
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43 247 item of each of the other foods (cucumber and monkey biscuits) used in Phase 1 placed so that  
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46 248 when buckets were closed, the reward was out-of sight.

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48 249 Studies using similar paradigms usually bait one location meaning the animal will only  
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50 250 receive a reward if they pick the correct cue. We chose to place a food reward under all buckets  
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53 251 and vary the 'value' of the food items to the individual (preferred or non-preferred) for a number  
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55 252 of reasons: 1) Sham baiting is normally employed of the non-rewarded locations to ensure the  
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3 253 animals do not pick up on inadvertent experimenter-given cues during the baiting procedure  
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6 254 [Garber & Dolins, 1996]. Rather than use a sham manoeuver which may still be different in  
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8 255 some way to an actual baiting, we baited all buckets ensuring our actions were the same at each  
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10 256 location; even though the actual placement of the rewards took place out of the subjects direct  
11  
12 257 sight, they could potentially have monitored the experimenter's movements. 2) By including the  
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14 258 two-distractor food items, we potentially increased the cognitive load by requiring subjects to  
15  
16 259 target their preferred food from three possible food/color cue associations presented in each trial.  
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18 260 3) As gibbons would be rewarded on all trials, their motivation to participate should not be  
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20 261 negatively affected across repeated trials.  
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24 262         Once baited, the apparatus were presented in the same way as for the food preference  
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26 263 trials with the feeding platform supporting the buckets being slid along at floor level until  
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28 264 aligned with the enclosure. The subjects could then extend their arms through the mesh and make  
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30 265 their choice of which bucket to flip open. The first trials allowed gibbons to learn the association  
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32 266 between the color cue and their preferred food item. The three colored buckets were baited out of  
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34 267 direct sight of the gibbons and the apparatus presented with the three food items concealed under  
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36 268 each one. On the first few presentations, the choice made would be inevitably random as the  
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38 269 gibbons did not know where their favorite food item was hidden. However, with repeated trials,  
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40 270 it was possible for the apes to acquire all the necessary knowledge to learn the association  
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42 271 between the color cue and the value of the reward beneath it. If they learned this association,  
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44 272 they should selectively choose the high value (preferred) food as their first choice on subsequent  
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46 273 trials. For example, during the first trial block, if 'green' was designated as the color cue that  
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48 274 would yield the highest reward, the preferred food item for the test subject (identified during  
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50 275 Phase 1) would be concealed under the green bucket for all trials in that block a block consists of  
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3 276 all trials needed to reach criterion before moving to a new color association to a maximum of  
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6 277 100). For the first trials, the position of the green bucket was held constant to allow the  
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8 278 association between 'green' and the high value reward to be learned. Once the gibbon had  
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10 279 selected the green bucket as their first choice, the position of the green cue on all remaining trials  
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12 280 in the block was randomized; that is, the high value reward was always under the green bucket,  
13  
14 281 however, the position of the green cue varied on each trial.

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16  
17 282 The subject was considered to have learned the color-reward association when they  
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19 283 reached criterion performance set at 10 consecutive choices (out of a maximum 100 trials) of the  
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21 284 preferred food type. Once criterion had been reached, presentations continued of the same color-  
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23 285 reward association until all 100 trials had been given. Trials that occurred after criterion had been  
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25 286 reached were referred to as 'post-criterion' trials.

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29 287 Once gibbons had completed the required trials in the first block (learning and post-  
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31 288 criterion  $N = 100$ ) with the first color/reward pairing, they moved to the second block of testing  
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33 289 where a new color/reward association had to be learned. Thus, individuals had to suppress the  
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35 290 previously learned rule and make a new association between a colored signal and reward. Three  
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37 291 blocks were presented (for each of the three color-reward associations to be learned) with each  
38  
39 292 block consisting of 100 presentations (learning and post-criterion trials) in total. The order of  
40  
41 293 presentation of each color-reward pairing was consistent across subjects. The trial was only  
42  
43 294 scored if the subject showed direct interest, measured by approaching the feeding platform  
44  
45 295 within 30 seconds. Trials were considered 'correct' if the gibbon chose the preferred item as their  
46  
47 296 first choice, however, they were allowed to continue lifting buckets until all rewards were  
48  
49 297 obtained (to maximize their motivation to take part). The trial was complete once all food items  
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51 298 has been consumed or after one minute elapsed. Any additional activity after one minute was  
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3 299 considered “play” and the feeding platform was then taken away from the subject. If no choice  
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6 300 was made within the minute of exposure time, the trial was marked as incomplete and would be  
7  
8 301 resumed on the next day of testing. Similarly, if the subject lost interest during the trials, the  
9  
10 302 experiment was stopped and resumed at a later date, continuing where the subject left off until  
11  
12 303 100 presentations were completed. The inter-trial duration was approximately three minutes.  
13  
14  
15 304 This was the time needed to change the location of the buckets into a random order and bait the  
16  
17 305 buckets with the food items. Most subjects needed four sessions to complete 100 successful trial  
18  
19 306 presentations; however Reg and Truman (*Hylobates sp.*) needed five sessions.

20  
21  
22 307 *Data analysis*

23  
24 308 Data were not normally distributed and so non-parametric statistics were used to evaluate  
25  
26  
27 309 the effect of color on learning speed. Friedman’s tests assessed differences in number of trials  
28  
29 310 needed to reach criterion performance (10 consecutive choices of preferred food first) for each  
30  
31 311 ‘color-preferred food’ association (3 levels – Yellow, Green and Red). An extension of  
32  
33 312 generalized linear models (GZLM), generalized estimating equations (GEE) that accommodates  
34  
35 313 small, correlated within-subjects data sets and allows for comparisons between subjects [Garson  
36  
37 314 2013], determined how subject parameters (sex and genus) influenced learning the color-food  
38  
39 315 association. As data comprised counts of trials, Poisson loglinear regression with a log link  
40  
41 316 function was specified for all models with number of trials to criterion (as the response variable).  
42  
43 317 Genus, sex and food-color association (consecutive choices of preferred food first) were factors  
44  
45 318 in the model, with main effects tested. *Hylobates* was always the referent category for GEE  
46  
47 319 parameter estimates.

48  
49  
50 320 For the post-criterion performance analyses (trials that occurred after the initial  
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52  
53 321 association had been learned), the number of trials varied across individuals due to differences in  
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3 322 the acquisition of criterion performance and the maximum of 100 trials per individual summed  
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5  
6 323 across learning and post-criterion trials (Post-criterion trial number = Maximum number of trials  
7  
8 324 (100) – number of trials to criterion). Counts were therefore transformed into percentages for the  
9  
10 325 main analyses. Friedman's tests assessed differences in number of trials where preferred food  
11  
12 326 was selected first once learning had taken place for each color/preferred food association (3  
13  
14  
15 327 levels – Yellow, Green and Red). GEE was again used to assess the retention of the color-reward  
16  
17 328 association across trials in the post-criterion stage with the same factors and covariates as  
18  
19  
20 329 previously described; however, as data were no longer counts, a linear model was specified with  
21  
22 330 an identity link function. Again, *Hylobates* was the reference genus for the parameter estimates.  
23  
24 331 An additional Wilcoxon analysis was performed comparing the first ten trials post-criterion to  
25  
26  
27 332 the last ten to evaluate whether performance was consistent throughout trials presented. Alpha  
28  
29 333 was set at 0.05 throughout and all tests were 2-tailed.

## 30 31 32 334 **RESULTS FOR EXPERIMENT 1**

### 33 34 335 *Learning trials to criterion*

35  
36 336 All subjects tested demonstrated a preference for banana in the initial food choice trials  
37  
38 337 with nine of the 13 subjects choosing this food item first on 100% of presentations. The  
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40  
41 338 remaining four subjects selected the banana first on the majority of preference trials in Phase 1  
42  
43 339 (86.67 – 93.33%) with cucumber being the occasional first choice. No subject selected monkey  
44  
45  
46 340 biscuits as first choice in the preference tests. Therefore, banana was selected as the primary  
47  
48 341 color/reward referent for all subjects and responses scored as correct when the first choice made  
49  
50 342 on test trials was to select the location of this food type.

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52  
53 343 The number of trials needed to learn the primary food/reward association varied across  
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55 344 individuals (range 16-100); however, all subjects were able to reach criterion performance in all  
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3 345 conditions within the 100-trial maximum. The color paired with the preferred food did not  
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6 346 influence learning speed across all individuals (Median (Yellow) = 26.00(IQR = 15.5), Median  
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8 347 (Green) = 25.00(13.50), Median (Red) = 28.00(18.00), Freidman's test:  $\chi^2(2) = 0.840$ ,  $p =$   
9  
10 348 0.657). However, there were significant differences between the genera on acquisition of the  
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12  
13 349 color/reward association.

14  
15 350 In general, *Hylobates* gibbons needed more presentations to learn the 'color-preferred  
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17 351 food' association than either *Hoolock* or *Symphalangus* (Table III). There was a significant effect  
18  
19  
20 352 of genus on learning speed with *Hoolock* and *Symphalangus* needing significantly fewer trials  
21  
22 353 than *Hylobates* to learn the color associations (GEE: *Hoolock* B = -0.677,  $\chi^2(1) = 124.87$ ,  $p <$   
23  
24 354 0.001; *Symphalangus* B = -0.854,  $\chi^2(1) = 33.94$ ,  $p < 0.001$ ) (Figure 3a). There were no  
25  
26  
27 355 significant differences between sexes on number of trials to criterion (GEE: B = -0.216,  $\chi^2(1) =$   
28  
29 356 2.854,  $p = 0.091$ ). Color paired with the preferred reward remained insignificant in this analysis  
30  
31  
32 357 (GEE:  $\chi^2(2) = 1.965$ ,  $p = 0.374$ ).

### 33 34 358 *Post-criterion trials*

35  
36 359 One subject did reach criterion in the all color-reward associations, however, only on the  
37  
38  
39 360 final presentation of the green-reward configuration. This individual was therefore removed from  
40  
41 361 the post-criterion performance analyses. Selection of preferred food item was generally high  
42  
43 362 across all post-criterion trials (Mean (Yellow) = 91.56(SE = 1.35)%, Mean (Green) =  
44  
45 363 78.71(7.39)%, Mean (Red) = 88.51(1.88)%), with no significant differences in performance  
46  
47  
48 364 across color cues (GEE:  $\chi^2(1) = 1.941$ ,  $p = 0.379$ ). Sex was also non-significant as a predictor of  
49  
50 365 post-criterion performance (GEE:  $\chi^2(1) = 0.001$ ,  $p = 0.970$ ). Genus however, did significantly  
51  
52 366 impact performance with *Symphalangus* performing significantly better than *Hylobates* (B  
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55 367 =10.184,  $\chi^2(1) = 10.468$ ,  $p < 0.01$ ). *Hoolock* also obtained fewer rewards than *Symphalangus*,

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3 368 although performance was not significantly different from that of *Hylobates* subjects ( $B = 4.961$ ,  
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5 369  $\chi^2(1) = 1.838$ ,  $p = 0.175$ ) (Figure 3b). No color/preferred food association showed diminished  
6  
7  
8 370 persistence in the first block post-criterion compared to the last block (Wilcoxon matched pairs:  
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10 371 Yellow  $Z = 0.00$ ,  $p = 1.00$ ; Green  $Z = -0.905$ ,  $p = 0.366$ ; Red  $Z = -0.707$ ,  $p = 0.480$ ).

## 12 372 **DISCUSSION FOR EXPERIMENT 1**

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15 373 We were able to determine the rank order of food items and the most preferred for all  
16  
17 374 subjects was banana. We also determined that gibbons could successfully select their preferred  
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20 375 food when colored buckets covered it, suggesting they could use the color as a signal to the high  
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22 376 value food's location. There were no differences across color-reward associations, indicating  
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25 377 learning was not affected by the particular color/reward.

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27 378 There was no evidence the gibbons tested here generalized from their learning in the first  
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29 379 round to other rounds as there were no differences between number of trials to reach criterion  
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31  
32 380 performance with each successive color-reward association to be learned. Effectively, they  
33  
34 381 seemed to be learning each new association from scratch – as if they had not seen or experienced  
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36 382 the task before. This could be the result of multiple food items being used that distracted the  
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39 383 gibbons and obscured the intended question of whether gibbons can generalize and use  
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41 384 information learned in the first association to inform their learning in subsequent novel  
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43 385 associations.

## 44 386 **INTRODUCTION FOR EXPERIMENT 2**

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48 387 Since we found the gibbons tested showed no evidence of generalizing from their  
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50 388 learning, we changed the methods and feeding platform in a second experiment where only one  
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53 389 food item would be searched for with three possible locations cued by a colored background that  
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55 390 we hoped would provide a more salient cue to the rewards location. We aimed to further  
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3 391 investigate the flexibility of learning by assessing whether there was any evidence of gibbons  
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5 392 generalizing from the first color/reward association learned to other, novel associations.  
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8 393 In Experiment 1, gibbons were required to learn an association between a preferred food  
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10 394 and specific color while simultaneously presented with two further possible color choices that  
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12 395 would also provide a reward, all be it of lower value. In Experiment 2, we reduced the cognitive  
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14 396 load by removing the secondary food items and the competing color cues in an attempt to focus  
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16 397 the gibbon's attention on a single preferred food reward (banana). We hypothesized that by  
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18 398 simplifying the cues presented, the gibbons tested may be better able to extract information from  
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20 399 their initial learning experience that would aid them in subsequent novel associations: that is,  
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22 400 they should be able to generalize from their learning in the first presentations and show improved  
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24 401 performance in subsequent similar learning situations.  
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## 29 402 **METHODS FOR EXPERIMENT 2**

30  
31 403 The feeding platform for Experiment 2 required the gibbons to reach through doors to  
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33 404 select a hidden food item. Only one door was baited with a piece of banana and the position was  
34  
35 405 determined by the color cue on the front of the platform that measured 1.2 meters long, 0.3  
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37 406 meters wide and 0.6m high. It was large enough for the experimenter to hide behind and "reload"  
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39 407 the food item between trials without subjects seeing where the food item was placed. The  
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41 408 experimenter also wore dark sunglasses during the trials to avoid giving inadvertent gaze cues to  
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43 409 the subject.  
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48 410 The front of the feeding platform had three doors located at the base – on the left, center  
49  
50 411 and right. The doors were six inches long and six inches wide – large enough for the animals to  
51  
52 412 easily reach through (Figure 2). On the back of the doors was secured a sheet of heavy fabric that  
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54 413 prevented the animals seeing through to the reward. Thus, in order to retrieve a reward, the  
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3 414 subject had to move aside the fabric and reach through the door. Wooden dividers acted as  
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5 415 barriers on the offside of the feeding platform, between the three possible feeding locations, to  
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7 416 prevent the animals from reaching in one door and stretching their arms to the location of a food  
8  
9 417 item behind another door. Three laminated color boards were inserted onto the front of the  
10  
11 418 feeding platform behind a Plexiglas screen. The reason for the Plexiglas was because it is easily  
12  
13 419 cleaned between trials and provided a mechanism to hold the interchangeable laminates in place  
14  
15 420 (Figure 2). The laminates provided the color cue and varied dependent on the trial block between  
16  
17 421 red, blue and yellow.  
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22 422 A video that illustrates the animals' behavior as well as visually displaying the  
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24 423 experimental design of Experiment 2 can be viewed by clicking the following link: (AJP  
25  
26 424 Production Team – Please Create Link to Video 2)  
27  
28

29 425 *Desensitization and Learning Trials*  
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31 426 Similar to Experiment 1, desensitization trials were conducted before experimental trials  
32  
33 427 began. This was to desensitize the subjects to using the new feeding platform. The experimenter  
34  
35 428 placed pumpkin seeds in front of the closed doors and blueberries behind the closed doors. The  
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37 429 feeding platform was then presented to the subjects by positioning it outside the enclosure,  
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39 430 within direct reach of the gibbons. This feeding platform set-up was exactly the same on every  
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41 431 presentation.  
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44

45 432 Identical to Experiment 1, the platform was in this position until all of the food items  
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47 433 were consumed or for a maximum of five minutes if only a portion of the food was eaten. The  
48  
49 434 gibbons were assumed to have learned to associate the presence of the platform with a reward  
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51 435 when they readily approached, investigated and ate the food items. If the subject did not  
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53 436 approach the platform at all, the presenter would try again later that same day with a gap of two  
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3 437 hours between desensitization trials. The desensitization period continued on consecutive days  
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6 438 until the subjects were comfortable using the feeding platform.

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8 439 The gibbons were recorded as associating the presence of the platform with a reward  
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10 440 when they completed two steps: 1) readily approached, investigated and ate the pumpkin seeds  
11  
12 441 and 2) reached through the doors and ate the blueberries. It took slightly longer for the gibbons in  
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14  
15 442 Experiment 2 to make this association with as many as seven presentations of the feeding  
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17 443 platform required before there was evidence of an associative connection between the feeding  
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19  
20 444 platform and the potential for reward in all gibbons. Once all subjects were consistently using the  
21  
22 445 new platform, we began trials to provide an opportunity for the gibbons to learn the task  
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24  
25 446 requirements for Experiment 2.

26  
27 447 During the initial learning trials, a food reward (piece of banana) was concealed behind  
28  
29 448 one of the doors which the gibbon was given the opportunity to retrieve. The location of the food  
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31  
32 449 reward was determined by the color background (laminated) that was held constant to allow  
33  
34 450 gibbons to make the association between the reward's position and the color cue. Each subject  
35  
36 451 was initially presented with the red background which signified the reward (banana) was located  
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38  
39 452 behind the left door. This configuration was repeatedly presented until the gibbon reliably chose  
40  
41 453 the left door, and retrieved the banana on their first selection for three consecutive trials  
42  
43 454 (criterion for the learning phase). Once criterion was reached for this color/position association,  
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45  
46 455 the background color and the position of the reward were changed to a blue background with the  
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48 456 banana behind the center door, and finally a yellow background with the banana behind the right  
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51 457 door (Table II) with criterion being three consecutive correct choices for each color/reward  
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53 458 association.

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3 459 Similar to Experiment 1, a trial was only scored if the subject showed direct interest,  
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6 460 measured by approaching the feeding platform within 30 seconds. The trial was marked as  
7  
8 461 correct if the subjects' first choice was for the rewarded location and a trial was considered  
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10 462 complete once the food item had been consumed or after one minute elapsed (if no choice was  
11  
12 463 made). Any additional activity after one minute was considered "play" and the feeding platform  
13  
14 464 was then taken away from the subject. If the food item was not consumed within the minute of  
15  
16 465 exposure time, the trial was marked as incomplete and would be resumed on the next day of  
17  
18 466 testing. Similarly, if the subject lost interest during the trials, the experiment was stopped and  
19  
20 467 resumed at a later date, continuing where the subject left off until all possible presentations were  
21  
22 468 completed. The inter-trial duration for all trials (learning and experimental) was approximately  
23  
24 469 three minutes.  
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27  
28  
29 470 Once criterion was reached for all three possible positions in block 1 (all trials where  
30  
31 471 position of reward was always placed in accordance with the color/reward associations learned in  
32  
33 472 the training trials), the subject moved on to the experimental trials (see below). On completion of  
34  
35 473 the first round of testing in block 1 (learning and experimental trials), the learning trials for block  
36  
37 474 2 commenced following the same protocol as for block 1, where the position of the reward  
38  
39 475 changed dependent on the color background association (block 2 - Red/Center, Blue/Right,  
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41 476 Yellow/Left). Thus, the subject experienced a series of learning trials followed by the  
42  
43 477 experimental trials for block 1, and then returned to learning trials for block 2. Once the  
44  
45 478 experimental trials for block 2 were completed, the learning trials for block 3 commenced (Block  
46  
47 479 3 – Red/Right, Blue/Left, Yellow/Center).  
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53 480 *Experimental Trials*  
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3 481           Once the subject completed the learning trials for each block, they progressed to the  
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6 482   experimental phase where 30 trials were presented with all three possible color/position  
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8 483   associations for that block were presented an equal number of times across in a randomized  
9  
10 484   pattern. Between each trial, the background color was changed and this determined where the  
11  
12 485   reward would be placed dependent on the block. There was a similar constraint as in Experiment  
13  
14 486   1 that the position could not be the same for two consecutive trials.

15  
16  
17 487           For example, in block 1, the blue background signaled the food item (banana) was behind  
18  
19 488   the center door, the red background, the food item was behind the left door and the yellow  
20  
21 489   background, the food item behind the right door. Once all 30 experimental trials were completed,  
22  
23 490   the subject went back to the learning trials for block 2 after which the experimental trials for the  
24  
25 491   second block were presented. This procedure was then repeated for block 3. Overall, each  
26  
27 492   individual experienced 90 experimental trials (30 for block 1, 30 for block 2 and 30 for block 3)  
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29 493   interspersed with the relevant learning trials as described above. Scoring was the same as the  
30  
31 494   learning trials.

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33  
34 495   *Data analysis*

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37 496           Trials were scored as correct if the gibbon retrieved the food reward with their first  
38  
39 497   choice when presented with the apparatus. For the learning trials, the number of trials needed to  
40  
41 498   reach criterion (three consecutive correct choices) were analyzed using Friedman's repeated  
42  
43 499   measures test to assess whether any background color association was more difficult to learn.  
44  
45 500   GEE models were used to evaluate whether performance on the learning trials differed across  
46  
47 501   genera or by sex. As data were counts, Poisson distribution with a log function was specified,  
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49 502   genus and sex being factors in the model.  
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3 503 Performance on the experimental trials was evaluated at the group and individual level.

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5 504 To determine the effects of learning on subsequent color/position associations, a GEE was  
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7  
8 505 conducted with a binomial distribution and logit link function. Events in trials data were  
9  
10 506 specified with a fixed value of 30 (number of experimental trials per block). Genus and sex were  
11  
12 507 added as factors in the model with *Hylobates* as the referent category for the former.

13  
14 508 Whether the gibbons were using the color cues to guide their choices was assessed by  
15  
16 509 determining whether they were selectively choosing the correct door significantly above chance.  
17  
18 510 Binomial tests with the test proportion set at 0.33 (as there were three possible choices) were  
19  
20 511 conducted at the group and individual level. During the observations, a location bias seemed  
21  
22 512 possible. Therefore, Chi square goodness of fit tests were used to evaluate whether the gibbons  
23  
24 513 as a group and individually, were selecting any particular door (center, left or right) more that  
25  
26 514 would be expected. Alpha for all tests was set at 0.05.

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31 515 **RESULTS FOR EXPERIMENT 2**

32  
33 516 *Learning trials*

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35 517 Eight gibbons cooperated enough to engage in experimental trials and generate useable  
36  
37 518 data. Although it was planned to include representatives from all four genera, none of the  
38  
39 519 northern white-cheeked gibbons (*Nomascus leucogenys*) would participate in the experiment.  
40  
41 520 Only one female white-cheeked gibbon would approach the feeding platform and remove the  
42  
43 521 food items in the training trials. However, this gibbon was apprehensive to reach through the  
44  
45 522 doors to remove the hidden food items in the learning or experimental trials. The male white-  
46  
47 523 cheeked gibbons would not approach the feeding platform. This could be due to the daily feeding  
48  
49 524 routine that involves feeding each gibbon separately with some food being handed directly or  
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51 525 gently tossed to them to catch. They do not typically approach a feeding platform, hesitated  
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3 526 doing so in these experiments, which made them unwilling participants. Therefore, the final  
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6 527 sample consists of subjects from three genera (Table I).

7  
8 528 The number of trials needed to learn each background color/reward association ranged  
9  
10 529 from 3 to 11 with most individuals reaching criterion in 5 or less trials for each color-reward  
11  
12 530 configuration. There were no significant differences between number of trials to criterion for  
13  
14 531 each background color association in the learning trials (Median (Yellow background) =  
15  
16 532 14.50(IQR = 6.0), Median (Blue background) = 13.00(9.0), Median (Red background) =  
17  
18 533 15.00(9.00), Freidman's test:  $\chi^2(2) = 2.769$ ,  $p = 0.250$ ). There was a main effect of genus on  
19  
20 534 number of trials to criterion with *Hoolock* and *Symphalangus* needing fewer presentations than  
21  
22 535 *Hylobates* (GEE: *Hoolock* B = -0.529,  $\chi^2(1) = 99.887$ ,  $p < 0.001$ ; *Symphalangus* B = -0.493,  
23  
24 536  $\chi^2(1) = 31.124$ ,  $p < 0.001$ ) (Figure 4). Sex was not a significant predictor of performance in the  
25  
26 537 learning trials (GEE:  $\chi^2(1) = 2.971$ ,  $p = 0.085$ ).

### 32 33 538 *Experimental trials*

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35  
36 539 Consistent with the learning trials, there was no evidence that the gibbons were  
37  
38 540 generalizing from the learned association in block 1 to the novel associations in block 2 and 3  
39  
40 541 (GEE:  $\chi^2(2) = 0.719$ ,  $p = 0.698$ ). The effect of genus on performance in the experimental trials  
41  
42 542 was significant with *Symphalangus* gaining significantly more rewards than *Hylobates*  
43  
44 543 (*Symphalangus* Mdn = 57.00, *Hylobates* Mdn = 43, B = 0.658,  $\chi^2(1) = 65.161$ ,  $p < 0.001$ ).  
45  
46 544 *Hoolock* did gain more rewards than *Hylobates*, however this did not reach significance  
47  
48 545 (*Hoolock* Mdn = 46, B = 0.290,  $\chi^2(1) = 2.771$ ,  $p = 0.096$ ). Sex was again non-significant in this  
49  
50 546 analysis ( $\chi^2(1) = 0.791$ ,  $p = 0.372$ ).

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3 547 As a group, gibbons were selectively choosing the correct reward location above chance  
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6 548 levels gaining 378 out of 720 possible rewards collectively (Binomial:  $p < 0.001$ ). Individual  
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8 549 performance is shown in Table IV, with six gibbons selecting the rewarded door significantly  
9  
10 550 above chance overall. Within this group, three gibbons dropped below chance level on one set of  
11  
12 551 the three with the remaining three performing above chance in all sets. Developing a bias for one  
13  
14 552 location over the others may have influenced performance. Five of the eight gibbons showed a  
15  
16 553 positional bias (Table V) selectively favoring the center door in general. This bias did not  
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18 554 however emerge consistently across all blocks.  
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## 20 555 **GENERAL DISCUSSION**

21  
22 556 In Experiment 1, we found no evidence the gibbons tested generalized from their learning  
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24 557 and we cautioned this could be the result of multiple food items and competing color cues being  
25  
26 558 used that distracted the gibbons. Therefore, we changed the experimental design to a more  
27  
28 559 specific task in Experiment 2 to focus the gibbon's attention on a single food/color association to  
29  
30 560 see if the gibbons were able to use information from their first learning experience of the task to  
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32 561 facilitate future learning of novel color/reward associations. Despite making these changes, the  
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34 562 data show they learned each new association from scratch – as if they had not seen or  
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36 563 experienced the task before as in Experiment 1. Our findings are similar to other studies  
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38 564 [Rumbaugh & McCormack, 1967] that found gibbons struggle with learning set formation and  
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40 565 do not show the learning to learn pattern as found in other species. However, once the learning  
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42 566 association was made, the gibbons performed well above chance. We found no differences  
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44 567 across color associations indicating learning was not affected by the particular color / reward  
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46 568 association  
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3 569           The results reported here could be due to the small sample size and because of the captive  
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5  
6 570 environment in which these gibbons were raised. Karenina and Marlow, siamang gibbons  
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8 571 (*Symphalangus syndactylus*) who performed quite well in the tasks reported here, had a lot of  
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10 572 human interaction from a young age. Perek, a Javan gibbon (*Hylobates moloch*) who did not  
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12 573 perform as well in these experiments, was born at Howlets Wild Animal Park, UK, and did not  
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14 574 have as much human interaction.

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17 575           The Gibbon Conservation Center provided a unique opportunity being the only institution  
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19 576 in the world to house and breed all four genera of gibbon [Mootnick, 1997]. However, obtaining  
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21 577 large sample sizes is very challenging as there are very few gibbons (particularly of the *Hoolock*  
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23 578 genus) in captivity. Another possibility for these results is the low criterion level set for  
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25 579 Experiment 2. We lowered the number of consecutive correct learning trials to compensate for  
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27 580 the gibbons short attention spans but this may not have given them sufficient time to really learn  
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29 581 the association. Results from previous experiments where hundreds of trials have been presented  
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31 582 in the learning phase [Rumbaugh & McCormack, 1967] suggest performance may have been  
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33 583 much better had they been given more opportunity to learn. Despite such a low criterion, many  
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35 584 of the gibbons did perform well above chance in the experimental trials although they may not  
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37 585 have had the opportunity to learn the rules of the task that could then be generalized to future  
38  
39 586 novel presentations.

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41 587           We found a key difference in the learning and association rates between male and female  
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43 588 gibbons with the males learning at a faster rate than females. Reproductively active females may  
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45 589 be highly motivated to explore potential resources due to the additional energy requirements of  
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47 590 pregnancy and lactation; however, increased investment in developing offspring could make  
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49 591 them more guarded in their investigations and so reluctant to engage with unknown objects such  
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3 592 as our testing equipment [Cunningham et al., 2011]. Males, without the investment in offspring,  
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5 593 may be more devoted to the search of potential resources and more willing to explore novel  
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8 594 objects.

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10 595 We have shown that when given provisioned food items, the subjects tested have  
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12 596 preferred foods and can associate color signals with these foods. However, there were no  
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15 597 differences across color associations and the rate of learning was no different from the colors red,  
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17 598 green, yellow, blue, or if the food item was on the left, center or right. This suggests the subjects  
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20 599 can associate each of the colors tested to the food items at the same rate and accuracy with no  
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22 600 particular preference to a specific color or location.

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24 601 The *Hylobates sp.* had the slowest learning rate before they made the association between  
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26 602 their preferred foods and the color cue in Experiment 1 and 2. *Hoolock* learned the association  
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28 603 significantly quicker, needing fewer trials in all color/preferred food association learning phases.  
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31 604 For all gibbons tested, males learned faster than the females, however age did not impact  
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33 605 learning rate although younger gibbons did show more inconsistencies in their performance,  
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35 606 selecting other food items as their first choice on some trials in Experiment 1, especially in the  
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37 607 post-criterion phase. This however did not have a significant impact on results with all subjects  
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39 608 selecting their preferred food item with a high level of accuracy in all post-criterion trials.

#### 40 41 42 43 609 *Possible Foraging Implications*

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45 610 This ability to associate colors to preferred foods can be an advantage in a changing  
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47 611 environment. For instance, *Hoolock* gibbons, which performed well compared to the lar-group in  
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49 612 this study, are from an environment that is variable and resources can be scarce. The lar-group  
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51 613 gibbons, who performed the poorest, live in an area where the climate is more stable and food is  
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53 614 likely to be plentiful year round [Brockman & van Schaik CP, 2005; Curran & Leighton, 2000].  
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3 615 This suggests that animals required to search more vigorously for high quality food items due to  
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6 616 environmental variability are more flexible in their learning than animals that do not have the  
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8 617 same foraging pressures.  
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11 618 There have been previous investigations that support the assumption that trichromatic  
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13 619 color vision provides an advantage related to foraging [Caine & Mundy, 2000; Nagle & Osorio,  
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15 620 1993; Osorio & Vorobyev, 1996; Regan et al., 1998, 2001; Lucas et al., 1998]. However, these  
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17 621 investigations did not take into account using colors as visual landmarks or make the direct  
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19 622 connection between preferred foods and how animals can associate colors to these foods.  
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22 623 To consider possible foraging implications as well as the ecological validity of the  
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24 624 experimental design and results reported here, the fact that color is an ephemeral cue in the  
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26 625 environment must be taken into account. In general, forests retain a homogenous set of colors  
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28 626 with changes in accordance with fruit ripening and leave leaf maturation across time. Mostly,  
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30 627 animals focus on more permanent environmental cues while navigating such as the size and  
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32 628 shape of trees. However, if an animal can take advantage of the changing colors in the  
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34 629 environment and learn to make the association of these new color cues to the location of ripe  
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36 630 fruit, they will have a foraging advantage over animals that do not possess this ability.  
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41 631 Resource availability is rarely ideal. Research has found yearly fluctuations in the  
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43 632 availability of resources which has a significant impact on the demography, foraging ecology,  
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45 633 life history patterns, population density, anti-predator strategies, and social behaviour of  
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47 634 nonhuman primates [Brockman & van Schaik, 2005]. When preferred foods are scarce, optimal  
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49 635 foraging theory predicts primates should attempt to maintain the net energy intake required for  
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51 636 physiological maintenance by either increasing their ranges to continue utilizing preferred foods  
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53 637 or relying on alternative foods [e.g., MacArthur & Pianka, 1966; Stephens & Krebs, 1986; van  
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3 638 Schaik & Brockman, 2005]. Thus, primates may act as “energy maximizers,” increasing their  
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6 639 day journey length (DJL) or home range size to consume as many scarce preferred resources as  
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8 640 possible, or “energy minimizers,” decreasing their DJL and home range size while consuming  
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10 641 more low-quality resources [e.g., Clutton-Brock, 1977; Boinski, 1987; Barton et al., 1993;  
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12 642 Barton, 1998, 1999; Overdorff, 1993; Hemingway & Bynum, 2005; Riley, 2007].

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15 643       Given a gibbon’s body size, morphological and physiological adaptations, grouping  
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17 644 patterns and social organization, they fit the description of energy maximizers. They spend a  
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19 645 great deal of energy searching for and traveling between patches of foods. They use their  
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21 646 adaptations, expand their ranges, and continue to search for preferred foods that are usually high-  
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23 647 energy fruits that are bright in color. In order understand the foraging advantages conferred by  
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25 648 the ability to associate ephemeral color cues to preferred food items in relation to resource  
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27 649 distribution, further testing is needed in both captivity and nature.

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32 650 *Conclusions and Future Study*

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34 651       Since we have shown the gibbons tested had difficulty generalizing from their learning in  
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36 652 one context and using it to facilitate learning in a similar situation, we must conclude that these  
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38 653 apes are capable of making color/reward associations but cannot use their learning flexibly. This  
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40 654 makes it unlikely that they would, with further testing, demonstrate learning set formation  
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42 655 consistent with results from earlier research [Rumbaugh & McCormack, 1967]. However, the  
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44 656 emergence of learning to learn patterns may occur with the use of more structured small steps to  
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46 657 facilitate learning of the rules of the task in an incremental way. For example, repeated  
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48 658 presentations of one color cue that signifies a reward presented with a neutrally colored  
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50 659 unreinforced cue before changing the color cue but not the rule (color would still indicate the  
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52 660 position of the reward) after the subject experienced many more trials than used here may allow  
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3 661 gibbons to extract the general rule that can be used to solve future novel presentations rather than  
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6 662 just a simple stimulus-reward association. With this more intensive training regime, they may be  
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8 663 able to apply their learning in a more flexible way.  
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19  
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25

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**Figure Legends**

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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.

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.

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 (b). Error bars represent  $\pm 1SE$ . \*\* denotes significance at  $p < 0.001$

Figure 4: Adjusted means for number of trials to reach criterion performance in the learning trials of Experiment 2 by genus. Error bars represent  $\pm 1SE$ . \*\* denotes significance at the 0.001 level.

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**Tables:**

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

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

863 Table II: Experimental sets used in Experiment 1 and 2.

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Sets	Experiment 1 <sup>1</sup>	Experiment 2 <sup>2</sup>
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 <sup>1</sup>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 <sup>2</sup>In Experiment 2, the color refers to the background and the position to the location of the food  
 870 reward.

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902 Table III: Unadjusted means for number of trials to criterion performance.

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904 905 906 907 908	Preferred food color association <sup>1</sup>	<i>Hoolock</i> (n = 7) mean(SE)	<i>Hylobates</i> (n = 4) mean(SE)	<i>Symphalangus</i> (n = 2) mean(SE)
909	YELLOW	22.29(1.782)	50.25(11.161)	29.50(10.500)
910	GREEN	28.57(2.277)	48.50(19.294)	23.00(0.000)
911	RED	27.14(2.064)	48.75(11.116)	21.00(0.000)

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<sup>1</sup>Ten consecutive correct choices for three genera of gibbon for each color-preferred food association in Experiment 1

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

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Subject	S1		S2		S3		Total	
	<i>Correct</i>	<i>p</i>	<i>Correct</i>	<i>p</i>	<i>Correct</i>	<i>p</i>	<i>Correct</i>	<i>p</i>
Marlow	19	0.001***	19	0.001***	18	0.002**	56	0.001***
Khin	15	0.001***	12	0.002	11	0.001	38	0.042
Maung Win								
U Myint	16	0.017*	21	0.001***	19	0.002**	56	0.001***
Swe								
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**

944  
945 Across each set (maximum correct is 30 trials per set), and in total (maximum score is 90 trials)  
946 and binomial test results. Values noted as significant represent performance above chance level.  
947 P values that are significant but not annotated represent performance below chance levels.

948  
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	
	$\chi^2(2)$	<i>p</i>	$\chi^2(2)$	<i>p</i>	$\chi^2(2)$	<i>p</i>	$\chi^2(2)$	<i>p</i>
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*	- <sup>a</sup>	- <sup>a</sup>	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.

981  
 982 <sup>a</sup> 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)

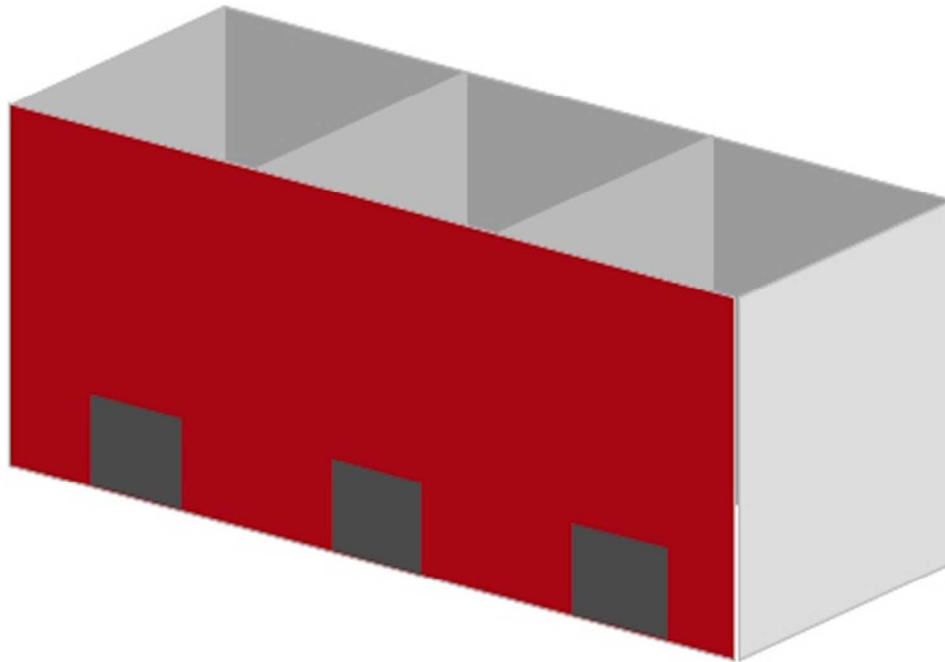


Figure 2. Feeding platform used for Experiment 2. This platform required the gibbons to reach through doors to select the hidden food item. Three laminated color boards were inserted onto the front of the feeding platform behind a Plexiglas screen.  
246x166mm (72 x 72 DPI)

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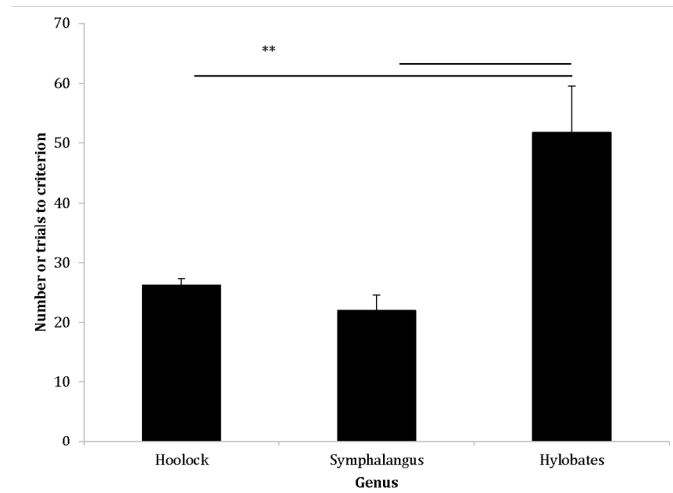
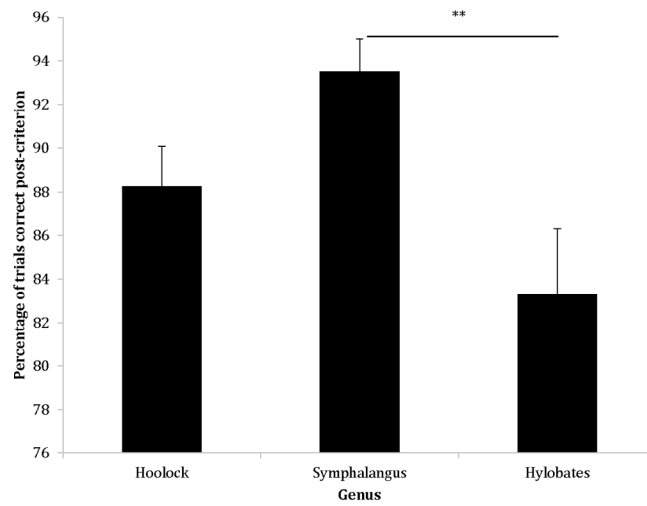


Figure 3: Adjusted means for number of trials needed to reach criterion performance (10 consecutive first choices of preferred food type) by genus (a) and percentage of correct responses by genus in the post-criterion phase  
215x279mm (200 x 200 DPI)



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

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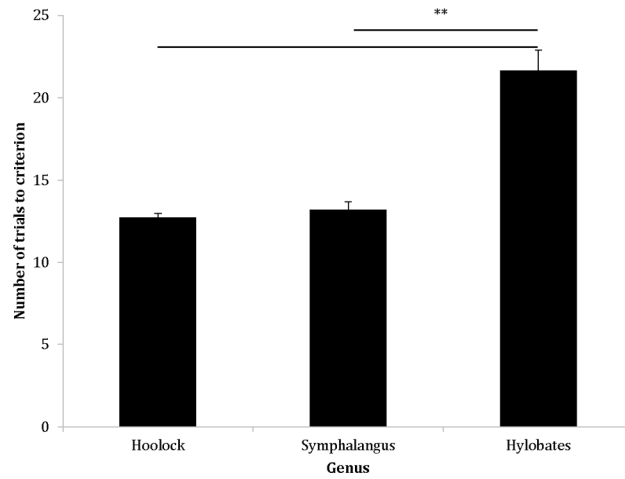


Figure 4: Adjusted means for number of trials to reach criterion performance in the learning trials of Experiment 2 by genus. Error bars represent  $\pm 1SE$ . \*\* denotes significance at the 0.001 level.  
215x279mm (200 x 200 DPI)