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No evidence of social learning in a socially roosting butterfly in an associative learning task

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1 Insects may acquire social information by active communication and through inadvertent
2 social cues. In a foraging setting, the latter may indicate the presence and quality of resources.
3 Although social learning in foraging contexts is prevalent in eusocial species, this behaviour
4 has been hypothesised to also exist between conspecifics in non-social species with
5 sophisticated behaviours, including *Heliconius* butterflies. *Heliconius* are the only butterfly
6 genus with active pollen feeding, a dietary innovation associated with a specialised, spatially
7 faithful foraging behaviour known as trap-lining. Long-standing hypotheses suggest that
8 *Heliconius* may acquire trap-line information by following experienced individuals. Indeed,
9 *Heliconius* often aggregate in social roosts, which could act as 'information centres', and
10 present conspecific following behaviour, enhancing opportunities for social learning. Here, we
11 provide a direct test of social learning ability in *Heliconius* using an associative learning task
12 in which naïve individuals completed a colour preference test in the presence of demonstrators
13 trained to feed randomly or with a strong colour preference. We found no evidence that
14 *Heliconius erato*, which roost socially, used social information in this task. Combined with
15 existing field studies our results add to data which contradict the hypothesised role of social
16 learning in *Heliconius* foraging behaviour.

17

18 **Keywords:** *Heliconius*. Pollen feeding. Foraging decision. Social information. Cognitive
19 ecology. Lepidoptera.

20 Introduction

21 Learning to find food, mates, and to avoid danger by observing others is often advantageous
22 in vertebrate societies [1-3]. Social learning can also be achieved by organisms with less
23 expansive nervous systems, such as insects [4-19]. In insects, social learning has been
24 observed when individuals actively pass on acquired information in eusocial species, such as
25 the waggle dance in honeybees [4-6] and the tandem-running recruitment system in ants [7].
26 It has also been reported as a by-product of copying an animal's behaviour, known as
27 inadvertent social information [8], and is chiefly obtained in contexts of foraging [9-13], mate
28 [14] and oviposition choices [15-17], and predation avoidance [18,19].

29 When foraging, inadvertent social information via location, visual and chemosensory
30 cues [20] may indicate the presence and quality of resources [8]. Observer bumblebees, for
31 example, use location cues when feeding sites are unfamiliar [9,21]. They also switch flower
32 preference more easily in the presence of a conspecific demonstrator [10,12], and develop a
33 preference for a flower colour after observing a demonstrator [11]. Thus, location and visual
34 cues may increase the probability that the observer will be attracted to a particular location
35 (local enhancement) or to a specific object or colour (stimulus enhancement) [3,11,12].

36 Although social learning in foraging contexts is more likely in more social species
37 [22,23], it does occur outside these contexts. For example, in *Gryllus bimaculatus*, a subsocial
38 cricket with relatively solitary lives but with sophisticated communication among conspecifics,
39 naïve individuals prefer the odour of drinking stations which a demonstrator previously
40 occupied [24]. *Heliconius* butterflies, have also long been hypothesised to use social
41 information [25] in the context of a novel foraging specialisation [26-28]. *Heliconius* are the
42 only butterflies to actively collect and digest pollen [29-31], a behaviour associated with
43 increased longevity [32] and delayed reproductive senescence [33], but one that requires
44 specialised foraging behaviours, known as trap-lining, to learn the location of pollen resources
45 [27,32,34,35]. Trap-lining involves learning spatially and temporally faithful foraging routes;
46 and provides an efficient strategy for repeated visitation of reliable resources [32,34]. Many
47 *Heliconius* exhibit nocturnal gregarious roosting, with butterflies returning to the same sites

48 from dusk to dawn, from which they start their trap-lines [25-28]. *Heliconius* also have
49 overlapping generations which is suggested to enhance opportunities for social learning [22].

50 Consequently, social learning has been hypothesised to be important for *Heliconius* in
51 the context of information-sharing of food sources via nocturnal gregarious roosting sites
52 [26,34], which may function as 'information centres' [36]. According to this view, new roost
53 mates learn the location of food sources by following experienced individuals [26,34].
54 However, a key prediction of the information-sharing hypothesis, that younger individuals
55 should follow more experienced individuals out of the roost, was not supported in field
56 experiments, with only one of 256 recorded foraging bouts involving a roost mate following
57 another individual from the roost site to a food source [37]. Furthermore, roost mates have
58 only partially overlapping home ranges, and visit different floral resources [27]. Instead, data
59 support the adaptive value of gregarious roosting as enhancing aposematic signals [37].
60 Nevertheless, following behaviour occurs regularly in butterflies from neighbouring roost sites
61 between food sources [26,28,38], suggesting that opportunities for social learning may still
62 occur.

63 In this study, we provide the first experimental assessment of social learning ability in
64 *Heliconius*. We focus on *H. erato*, a socially roosting species [39] that has been the focus of
65 field studies on gregarious roosting and social following, as these behaviours were previously
66 believed to act as mechanisms of information transfer [36]. While social learning of foraging
67 routes has been investigated in a small number of species, typically ants [7], the less
68 stereotyped behaviour of *Heliconius*, combined with the complexity and scale of their native
69 habitats, makes this approach more challenging in these butterflies. We therefore adapted
70 well-established associative learning protocols [40], focused on colour preference assays, to
71 assess whether naïve butterflies that acted as observers would adjust their initial preference,
72 or more rapidly learn a foraging task, when exposed to older, experienced individuals.

73

74 **Materials and methods**

75 *Experimental subjects and arena*

76 Experimental subjects originated from first-generation insectary-reared stock populations of
77 *Heliconius erato phyllis*, descended from multiple wild-caught females collected in Mata do
78 Jiqui, Natal, Brazil (5°55'39"S, 35°10'59"W). We maintained stock populations in outdoor
79 cages (3 x 3 x 2.5m) in which free-flying butterflies were able to engage in natural social and
80 flight behaviours, including chasing, mating and following. At night, individuals were observed
81 to form roosts of 2-22 individuals. Stock butterflies had access to hostplants (*Passiflora misera*
82 and *P. galbana*) and rewarding artificial white flowers. All butterflies were individually labelled
83 with unique IDs. The test arena was composed of purple and yellow artificial flowers. These
84 colours were chosen given that they are, on average, both relatively unpreferred [41].
85 Rewarding flowers contained a ~20% sugar solution mixed with bee-pollen supplement while
86 unrewarding flowers were empty. Twelve flowers of each colour were placed on a grid of 24,
87 with randomised positions (Figure S1).

88

89 ***Selection of demonstrators***

90 Butterflies were randomly assigned to one of two demonstrator groups, each collectively
91 subjected to four days of training (Figure S2). For one group, only purple flowers were
92 positively reinforced to strengthen preference for purple. For the other, the colour of the
93 rewarding flower was randomly determined for each trial. Training was run between 08:00-
94 16:00. In the following day, a final 5-minute test was conducted to determine demonstrators'
95 colour preferences. Preference was calculated as the proportion of landings on purple and
96 yellow flowers out of 20 landing events. Demonstrators with a $\leq 60\%$ purple preference were
97 assigned to the control group, whereas demonstrators with a $\geq 80\%$ purple preference were
98 assigned to the knowledgeable group, creating two demonstrator groups with non-
99 overlapping, unbiased and biased preferences respectively (Figure 1)

100

101 ***Social learning experiment***

102 The social learning experiment consisted of two phases (Figure S3). (1) During *pre-training*,

103 naïve butterflies, hereafter 'observers', fed on artificial white flowers between 08:00-16:00 to
104 get accustomed to artificial flowers. (2) In the *trailing phase*, which lasted for four days,
105 butterflies were randomly assigned to either the control or the knowledgeable demonstrator
106 groups. Observers were released in pairs along with 10 demonstrators to ensure that most of
107 individual-level feeding attempts were by the demonstrators. During trials, we scored the
108 number of feeding attempts made by each observer on purple rewarding flowers and yellow
109 unrewarding flowers for 15 minutes. A choice was scored when the butterfly landed on a
110 flower.

111

112 ***Statistical analysis***

113 Data were analysed using generalised linear mixed models in R using lme4 [42]. First, we
114 asked whether demonstrators from different groups preferred the rewarding colour, using a
115 binomial GLM with response variable 'preference for rewarding colour' (proportion of landings
116 on purple flowers) and fixed factor 'group' (control and knowledgeable). Then, for observers,
117 we examined whether there were intergroup differences in preference for rewarding colour
118 over time, using a binomial GLMM with response variable 'preference for rewarding colour'
119 and fixed factors 'group' and 'trial day' (1-4), with identity set as a random effect. Finally, we
120 analysed whether observers preferred flowers occupied by demonstrators using a binomial
121 GLMM with response variable 'local preference' (0= no; 1= yes) and fixed factors 'group' and
122 'trial day' (1-4), with identity set as a random effect.

123

124 **Results**

125 ***Demonstrators differ in colour preference after training***

126 Demonstrators were clearly differentiated based on the strength of their colour preferences,
127 with those assigned to the knowledgeable group preferring purple flowers significantly more
128 than those assigned to the control group (Figure 1, $z=10.13$, $df=57$, $n=60$ individuals,
129 $p<0.001$). Prior to the social learning experiment, demonstrator groups therefore had different

130 preferences for purple and yellow colours.

131

132 ***Social context does not alter observers' initial preferences***

133 Most individual-level feeding attempts were made by demonstrators (75.7%). Observer
134 preferences were similar with regards to flower colour in individuals foraging alongside
135 knowledgeable and control butterflies in the first day of the trialling phase (Figure S4, $z=-0.44$,
136 $df=27$, $\sigma^2_1=0.08$, $n=30$, $p=0.66$). This result shows that observer colour preferences did not
137 match demonstrator preferences with both observer groups preferring purple. Furthermore,
138 observers avoided flowers that were occupied by experienced conspecifics, landing
139 preferentially on unoccupied flowers. This behaviour was observed throughout the trials and
140 did not change over time ($z=-0.19$, $df=126$, $\sigma^2_1=0.59$, $n=35$, $p=0.85$).

141

142 ***Social context does not alter learning rate in observers***

143 Overall, observers' preferences for the rewarding colour increased over time ($z=3.61$, $df=127$,
144 $\sigma^2_1=0.46$, $n=35$, $p<0.001$, Figure S5). However, there was no significant effect of the
145 demonstrator group on colour preference ($z=0.50$, $df=126$, $\sigma^2_1=0.46$, $n=35$, $p=0.61$, Figure 2).
146 In fact, observers from the control group tended to show a better overall performance (control:
147 $z=3.02$, $df=62$, $\sigma^2_1=0.34$, $n=17$, $p<0.01$; knowledgeable: $z=1.96$, $df=62$, $\sigma^2_1=0.59$, $n=18$, $p=0.05$).
148 Specifically, 65% of these individuals increased their preference for purple over time, with only
149 6% showing a decrease, compared to 44% and 22%, respectively, of individuals from the
150 knowledgeable group. It is possible that the high mean naïve preference for the positively
151 rewarded colour masks the potential for social learning. To explore this effect, we conducted
152 two analyses: First, we sub-sampled the data to only include individuals with naïve
153 preferences outside the range of the knowledgeable demonstrators (<70%). We again found
154 no effect of group ($t=-1.897$, $df=12$, $n=14$, $p=0.08$). Second, we compared the relationship
155 between naïve preference and the shift in preference after training (trial 4-trial 1). We predicted
156 that if individuals with weaker preferences more readily learn social information, we would

157 expect this relationship to differ between the two treatment groups. This prediction was not
158 met ($t=-0.761$, $df=12$, $n=14$, $p=0.46$).

159

160 Discussion

161 Using a classic paradigm for learning through observation, we found no evidence that
162 *Heliconius erato* feeding preferences are influenced by social cues. Neither the colour
163 preference nor learning rate of naïve butterflies was affected by the behaviour of experienced
164 conspecifics that had a strong preference for the rewarding colour. Naïve individuals also
165 showed no preference for feeding from resources recently visited by conspecifics. Our study
166 therefore shows that conspecifics are not attracting others to a specific flower colour (stimulus
167 enhancement) or to a particular flower (local enhancement).

168 Our study was motivated by a long-held hypothesis that naïve *Heliconius* butterflies
169 learn foraging routes between pollen resources by social following of experienced individuals.
170 Given the difficulty of testing this hypothesis directly, we focused on the general capacity of
171 *H. erato* to use social information in a simpler assay. However, we argue this test has
172 biological relevance for the following reasons: First, in our cages free-flying individuals still
173 engage in social interactions, providing the opportunity for following to the feeders. Second,
174 for social learning of foraging behaviour to occur in the wild, naïve individuals must follow
175 experienced individuals to the point where they feed, otherwise there is no obvious
176 reinforcement of the locality cues; as such, our experiment focuses on a key point in this
177 interaction. Finally, floral colour cues do have significance in the wild, with most *Heliconius*
178 collecting pollen from a restricted, but variable range of plant species [43], which may be used
179 in the context of external cues, such as time of day [44]. As such, if *H. erato* pays attention to
180 conspecific foraging behaviours, we argue the current experiment should capture this ability.
181 One potential limitation of our data is the relatively biased naïve preference for the rewarded
182 colour. It is possible that this preference renders asocial learning an efficient strategy, with
183 social learning being solely deployed in contexts where asocial learning is ineffective [45].
184 However, we do not see evidence of this effect in our data, when exploring the interaction

185 between the naïve individual preference and the social treatment.

186 While we cannot formally rule out the possibility that *Heliconius* use social cues in other
187 contexts, we suggest our results support the conclusion that the impact of conspecific
188 behaviour on learned foraging behaviours may be overestimated in *Heliconius* [27,28].
189 Consistent with this interpretation, previous descriptions of following behaviour suggest this
190 does not regularly lead to feeding resources [38]. Arguably, conspecifics could still play a role
191 by attracting others to a general location, such as a pollen source, and indeed co-roosting
192 individuals can have overlapping foraging routes [27,28]. However, this result can also be
193 explained by a preference for resources in proximity to their roosting sites [27,28] within a
194 relatively small, and stable home range [25,27,46], and field data suggest very low levels of
195 conspecific following on leaving the roost [28].

196 In the absence of social learning, foraging decisions in *Heliconius* butterflies may be
197 influenced by innate biases, and individual experience. If our results generalise, *Heliconius*
198 either do not learn the links between social context and reward or may not need to because
199 social information is less reliable or more costly than direct experience. Of potential relevance,
200 is the generally patchy distribution of pollen resources [34]. Social information is potentially
201 inefficient in this context because of increased competition and depletion of limited resources.
202 Indeed, in our experiment, observer butterflies from the knowledgeable group tended to show
203 a lower learning rate, perhaps due to a competition effect. In this case, knowledgeable
204 demonstrators were more likely to feed on purple flowers expelling the observers, which
205 preferred unoccupied flowers.

206 Social information is, nevertheless, prevalent in a range of insects with complex
207 foraging needs for which many of the arguments above would also apply. This includes
208 bumblebees, for example, a social species that not only copy feeding techniques of
209 conspecifics but are also able to improve on them [47], suggesting behavioural flexibility [48].
210 For non-colonial insects, especially aggregating solitary insects, the use of inadvertent social
211 information has been observed in contexts of i) mate choice, with females exploiting public
212 information to select mates [14]; ii) oviposition choice, with females preferring to lay eggs on

213 food substrates associated with female conspecifics [15,16] or other social cues [49]; and iii)
214 predator-avoidance behaviours mediated by chemical cues [18] and by the observance of
215 conspecific hiding behaviour [19]. Although, in foraging contexts, social learning has been
216 reported only in a cricket species [24], the use of inadvertent social information is not as widely
217 reported, suggesting it may be less prevalent among foraging solitary insects. Consistent with
218 this interpretation, our experiment provides no evidence of social learning in *H. erato*. This,
219 together with field data contradicting the information centre hypothesis and the hypothesis that
220 following leads to floral resources [27,28], casts doubt on the role of social learning in
221 supporting the specialised foraging behaviour of *Heliconius*.

222

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226

227 **References**

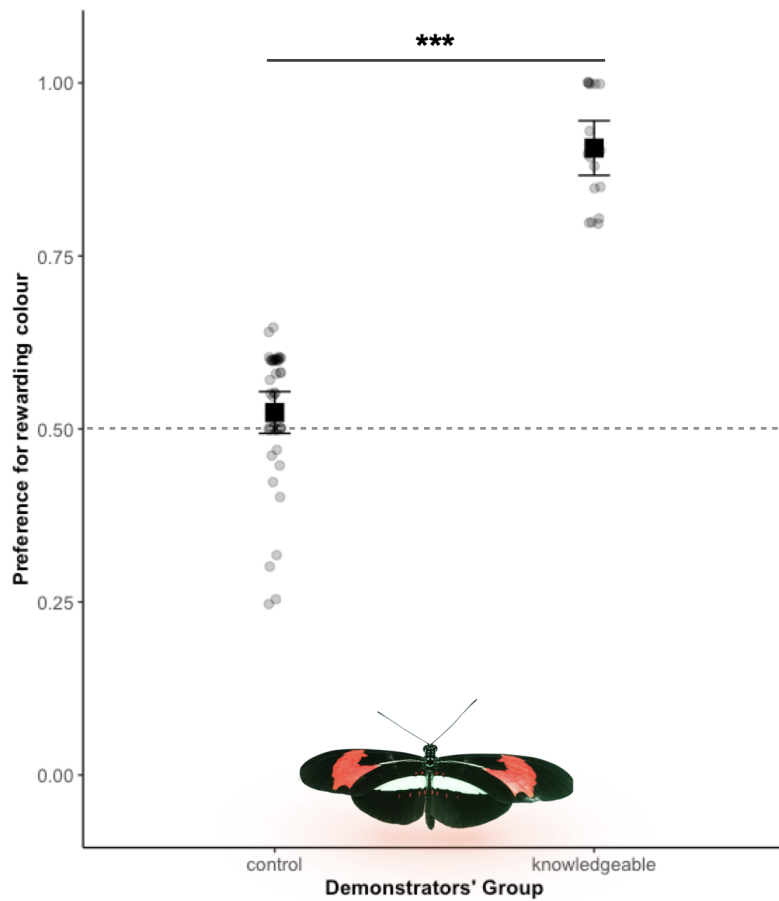
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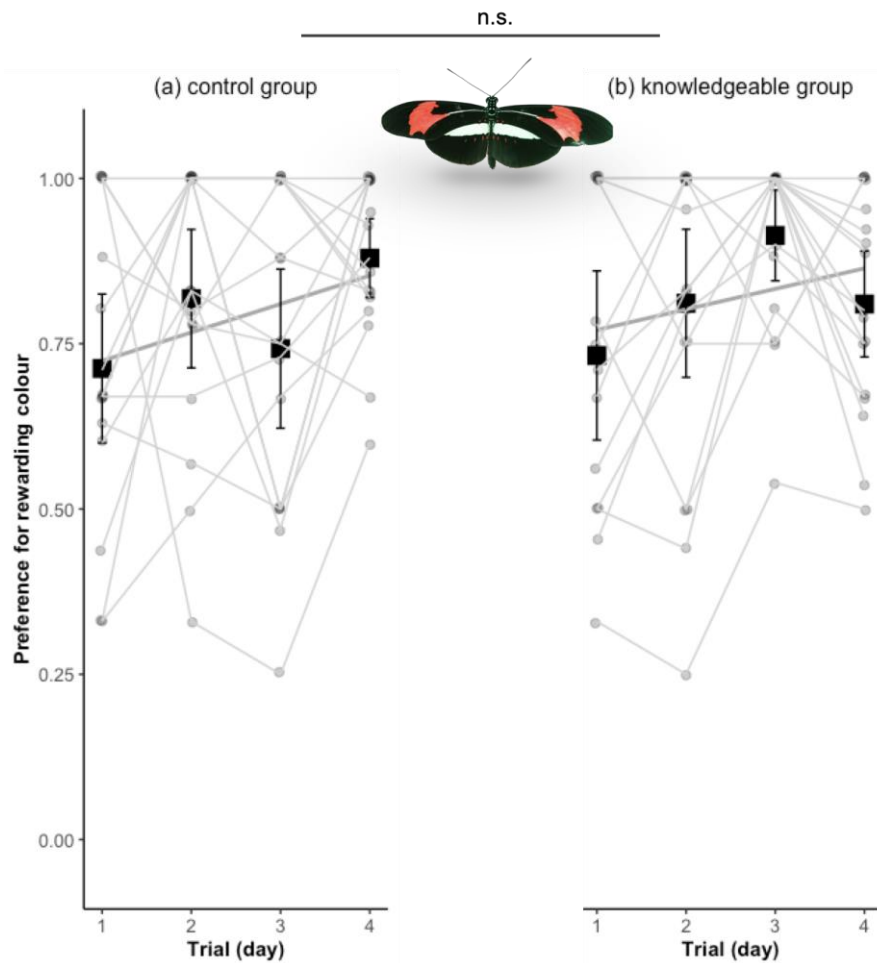
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348

349 **Figure 1.** Data from colour preference tests of *H. erato* demonstrators from control and
 350 knowledgeable groups following training. Squares and whiskers are means of individuals'
 351 preference \pm 95% CI. *** $p < 0.001$.



352

353 **Figure 2.** Preference for the rewarding colour in preference trials of *H. erato* observers in (a)
 354 control and (b) knowledgeable groups during the social learning experiment. Points are
 355 individual observations. Light grey lines connect the same individual. Squares and whiskers
 356 represent means of individuals' preference \pm 95% CI.

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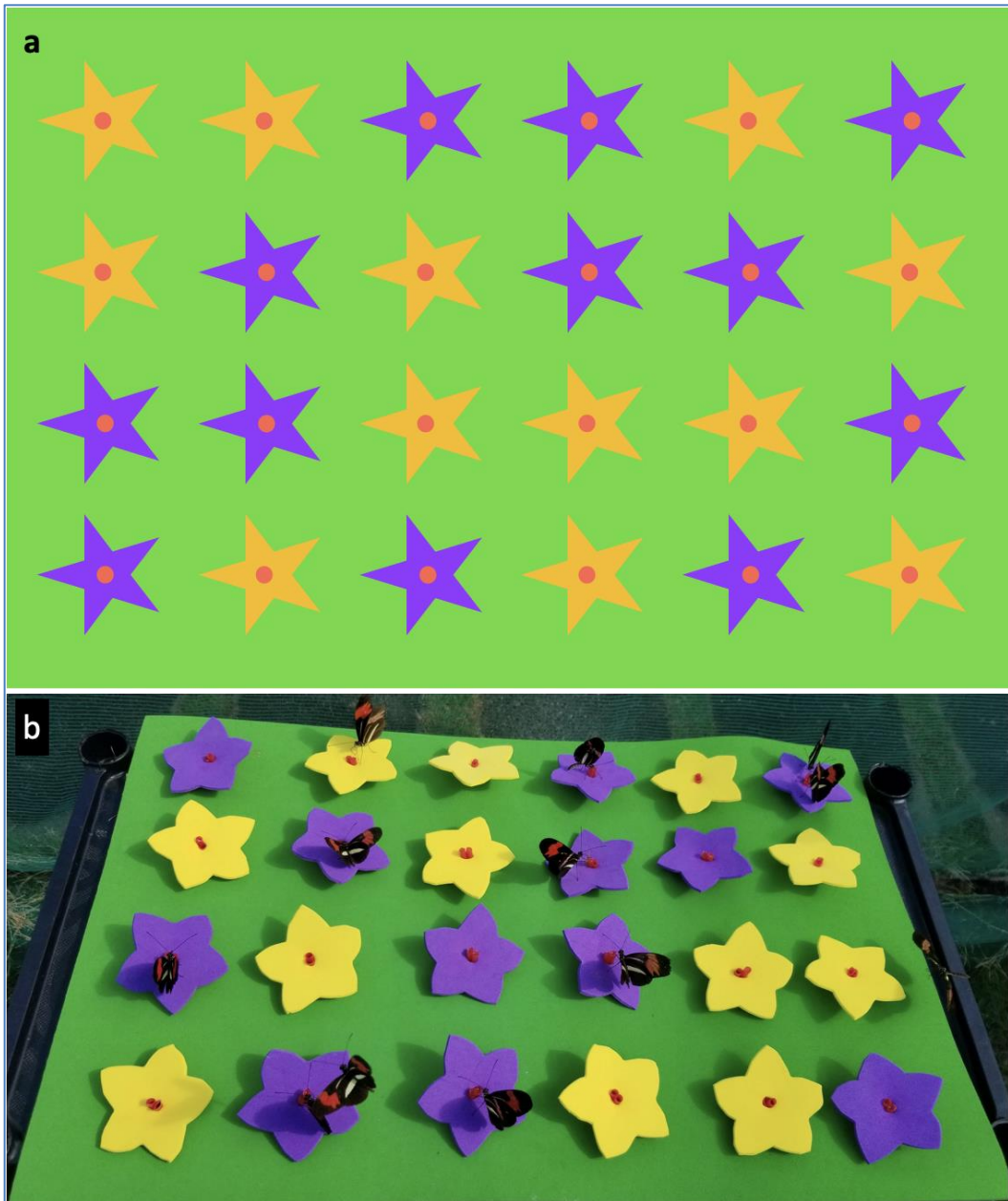
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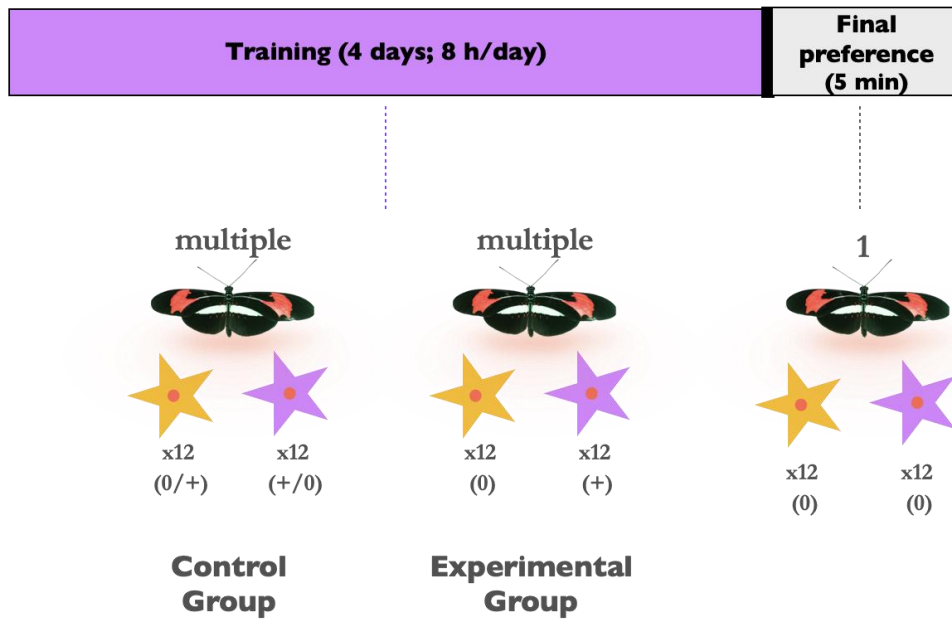


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368 **Figure S1.** Grid of 24 artificial flowers composed of 12 purple (rewarding) and 12 yellow

369 flowers (unrewarding) with randomised positions. **a.** Illustration of the grid. **b.** Experimental

370 butterflies exploring the grid of flowers.



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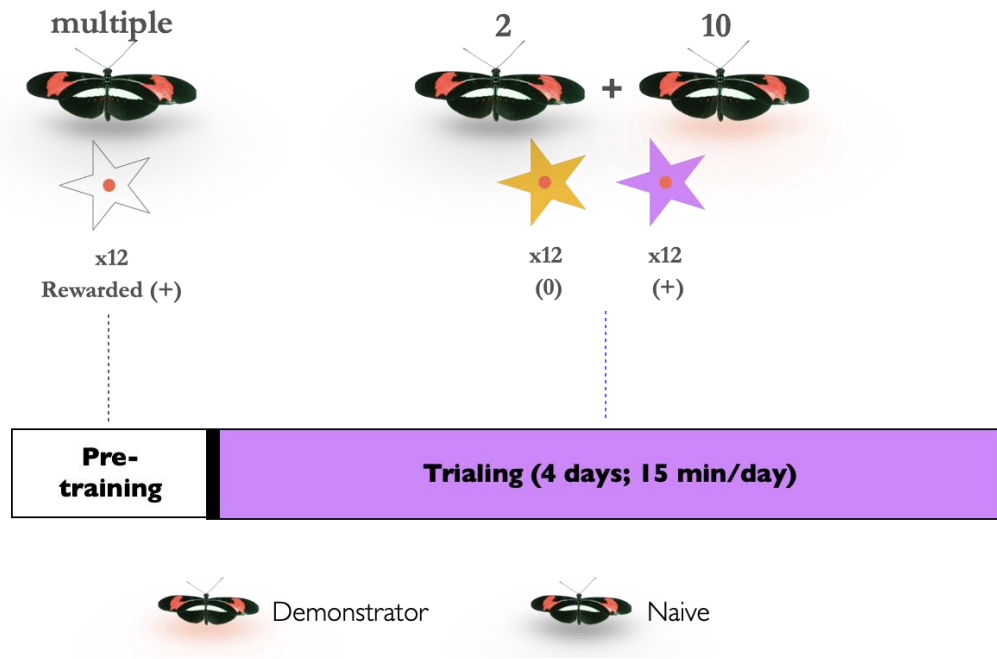
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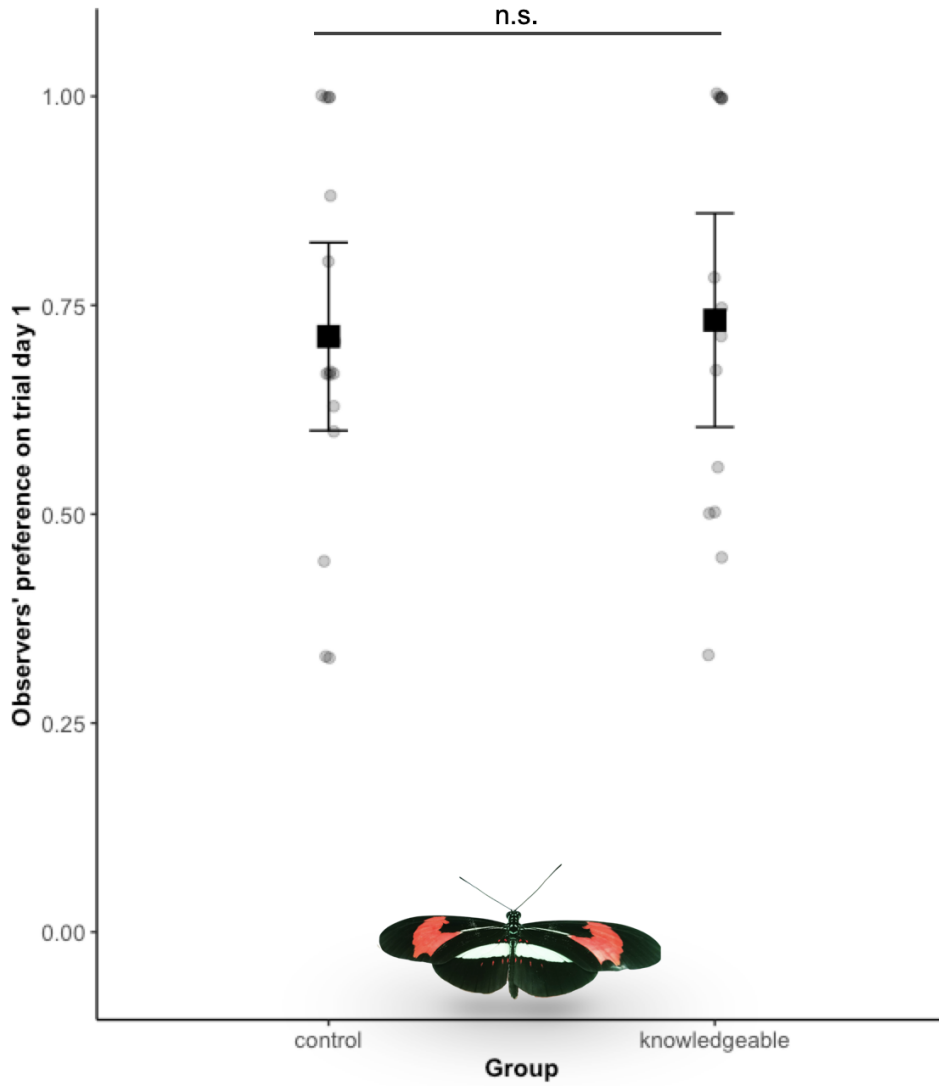
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Figure S2. Scheme for selecting demonstrators. During training, butterflies were split into two groups (control and knowledgeable) and trained with a grid of rewarding artificial flowers. For the first group, either purple or yellow flowers were rewarding. For the other, only purple flowers were rewarding. To check for final preference, butterflies were tested individually with unrewarding artificial flowers.



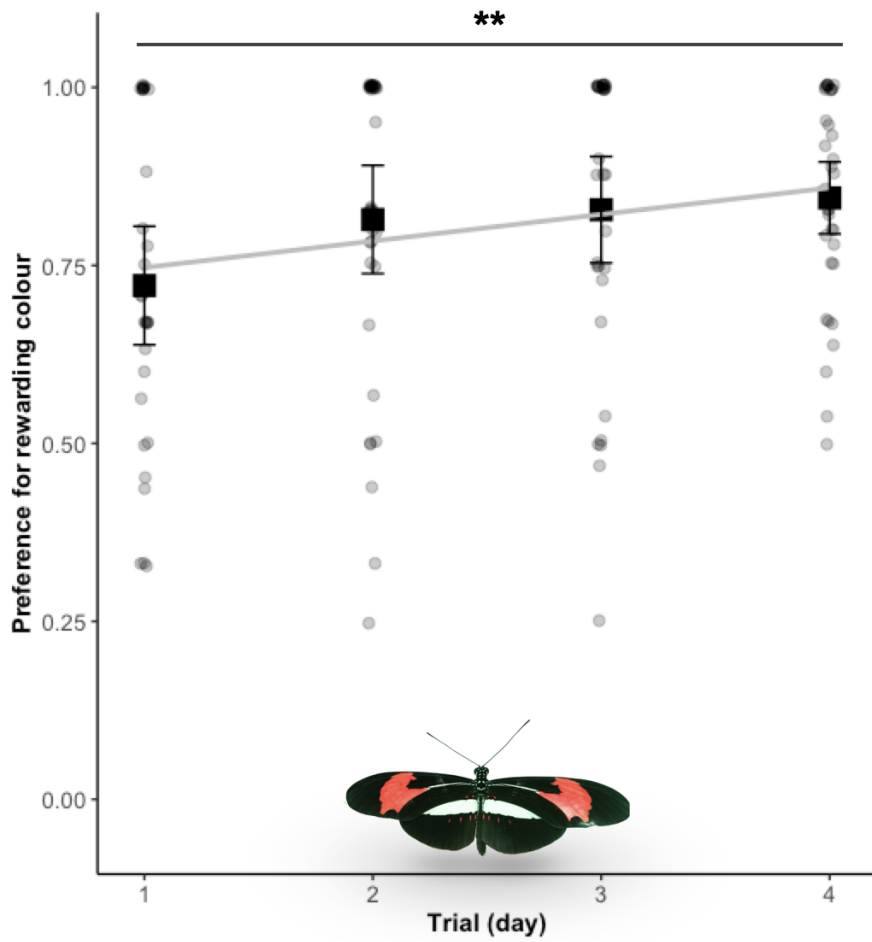
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378 **Figure S3.** Scheme for the social knowledgeable approach. During pre-training, observers
 379 from both groups were kept together. During trialing, butterflies were split into two groups
 380 (control and knowledgeable) with a pair of observers exploring the grid of flowers along with
 381 10 demonstrators.



382

383 **Figure S4.** Preference for purple colour for *H. erato* observers assigned either to control or
 384 knowledgeable groups on the first day of the social learning experiment. Flowers used in the
 385 naive preference test were devoid of rewards. Squares and whiskers are means of individuals'
 386 preference \pm 95% CI.



387

388 **Figure S5.** Preference for rewarding colour as a function of trial day in *H. erato* observers
 389 during the social learning experiment. Points are individual observations. Squares and
 390 whiskers are means of individuals' preference \pm 95% CI. **p < 0.01.

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