

More than colour attraction: behavioural functions of flower patterns

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Abstract

Flower patterns are thought to influence foraging decisions of insect pollinators. However, the resolution of insect compound eyes is poor. Insects perceive flower patterns only from short distances when they initiate landing or search for reward on the flower. From further away flower displays jointly form larger-sized patterns within the visual scene that will guide an insect's flight behaviour. Chromatic and achromatic cues in such patterns may help insects to find, approach and learn rewarded locations in a flower patch, bringing them close enough to individual flowers. Flight trajectories and the spatial resolution of chromatic and achromatic vision in insects determine the effectiveness of floral displays, and both need to be considered in studies of plant-pollinator communication.

Highlights

1. Insects perceive separately chromatic and achromatic aspects of colour patterns.
2. Flowers present colour patterns as individual or shared displays.
3. Visual appearance of flowers changes considerably with viewing distance.
4. Pollinators use close-up views for landing and handling of flowers.
5. Further away shared displays within the visual scene guide approach trajectories.

Introduction

1 Visual information is indispensable for insect pollinators to locate, choose and
2 interact with flowers. However, insect vision is constrained by the poor optical
3 resolution of their small compound eyes, which is about a hundred times lower
4 than that of our single-lens eye [1]. Unlike single-lens eyes, which are able to
5 focus on objects at different distances, insect eyes have the same angular
6 resolution at far and close distances. Therefore, insects are unable to resolve
7 spatial details of distant objects, however they can use vision at extremely close
8 distances. Theoretical analysis of the optical resolution of insect eyes
9 demonstrates that most flower patterns can be resolved only when the insect is
10 millimeters away [2](Fig.1). Hence small-sized flower patterns do not play a role
11 during approach to the flowers, as spatial details simply cannot be optically
12 resolved. Resolution of chromatic vision is predicted to be lower than the eye's
13 optical resolution. Different spectral types of photoreceptors that contribute to
14 colour coding are randomly located across the eye [3]. Hence, chromatic vision
15 requires that signals from more than one ommatidium are integrated which
16 reduces the resolution beyond the limits set by the optics of the eye [4].
17
18 Under dim light conditions the spatial and temporal resolution of insect vision is
19 decreased further in order to increase contrast sensitivity. Many nocturnal
20 insects, such as moths and beetles, have light-sensitive compound eyes with

21 superposition optics and therefore lower spatial resolution than diurnal insects.
22 Several species of bees, however, have the less sensitive diurnal-type apposition
23 eyes and are nevertheless able to forage in dim light, during twilight or even
24 during the night [5**]. The contrast sensitivity of such eyes can be enhanced by
25 neural mechanisms, and anatomical evidence suggests that nocturnal bees sum
26 signals from many ommatidia [6]. Consequently this also reduces the spatial
27 resolution of their eyes. Furthermore, due to temporal summation of receptor
28 and neural signals that can occur in both types of eyes, vision becomes slower as
29 light levels decrease, which affects the insect's flight speed and trajectories
30 [7,8,9**]. Interestingly, some nocturnal insects have not sacrificed colour vision
31 in order to increase their visual sensitivity and can identify flowers on the basis
32 of their colours even during moonless nights [10,11].

33
34 Insect views of flowers differ fundamentally from ours, and human observers
35 usually overestimate the signalling distance range and functions of floral
36 displays [e.g. 12]. The low spatial resolution of insect eyes defines their
37 perception of flower colours, shapes and patterns. Behavioural experiments
38 confirm that insects cannot resolve small objects or small-scaled variations of
39 shapes and patterns over long distances. For instance, the detection limit for
40 single-coloured discs is 5° of angular size in honeybees, around 2° in large-sized
41 bumblebees and 1° in swallowtail butterflies, which can be related to differences
42 in eye size [13,14,15*]. For a 1cm flower, this corresponds to a viewing distance
43 of 11 to 57 cm, respectively. Dissectedness of the outline shape in flower-like
44 targets impairs the detection range [16], as predicted by the optical model of the
45 honeybee eye. The behavioural resolution of chromatic vision is even worse –
46 honeybees cannot detect and discriminate targets on the basis of chromatic cues
47 if they subtend a visual angle less than 13-15° [17,18]. As an insect moves, the
48 appearance of flowers will change considerably, and consequently the insect
49 must be able to rely on different visual cues when foraging and navigating in
50 flower patches. To evaluate the functions of floral displays it is therefore not only
51 important to know how they are resolved and processed by the visual system but
52 to also consider an insect's flight trajectory at different distances from flowers.

53 54 **Why are flower patterns so widespread and diverse?**

55
56 It is usually assumed that flower patterns increase the diversity of floral displays
57 and help pollinators to discriminate between flowers and to identify the best-
58 rewarding ones. However, when taking into account the poor resolution of
59 compound eyes and typically small sizes of individual floral displays, it is evident
60 that flower patterns can be seen by an insect and influence its behaviour only
61 when it is already close to the flower, initiating a sequence of motor actions that
62 lead up to landing and interactions with the flower. In that phase flowers can use
63 patterns to exploit visuo-motor responses guiding an insect's movement [19,20]
64 to optimise pollen transfer and reduce potential damage from handling of the
65 flower by the insect.

66
67 To communicate with insect pollinators over a distance, flowers must increase
68 individual display sizes considerably or contribute to shared displays in
69 inflorescences, mass displays or multi-species patches (Fig.2). Shared displays in

70 a scene can produce effective signals with variable features, suited to influence
71 the insect's approach behaviour when it moves through the environment,
72 deciding where to go and which flowers to inspect and visit. Foraging decisions
73 are not limited to the final stage of a floral visit. As the insect moves between
74 flowers, the success of its foraging efforts is influenced by spatial memory
75 processes and the cost of flight and interactions with flowers [21-23], and thus
76 also by the effective visual guidance of the pollinator's movements. It is therefore
77 important to consider the spatial scales, over which flower signals engage with
78 visual and learning mechanisms, to understand the selective pressures that
79 insect behaviour exerts on colour and pattern features of floral displays.

80

81 **Chromatic and achromatic processing in insect vision**

82

83 The perception of colour patterns depends on the spatial distribution of contrast
84 edges in an individual or shared display. These are processed by colour-blind
85 edge detection and pattern discrimination mechanisms [24] that are segregated
86 from a low-resolution chromatic system in insect vision [25,26**,27]. Achromatic
87 and chromatic neural pathways operate in parallel and process, respectively,
88 high and low-frequency components of visual scenes and objects.

89

90 Repetitive elements in pattern design found across angiosperms [28] point
91 towards evolutionary selection of feature-dependent functions that target
92 visually-guided behaviours of insects. Such behaviours are mediated in different
93 ways by chromatic and achromatic visual mechanisms. For example, many
94 flowers display a concentric (or 'bull's-eye') pattern that consists of a central disc
95 surrounded by a contrasting outer ring. Patterns that have a bright (for bees)
96 outer ring surrounding a dim disc can be detected from further distances than
97 those having a bright disc surrounded by an outer dim ring. It appears that
98 flowers with a bright outer ring are more common and tend to be smaller than
99 those having a bright central disc and dim outer ring, suggesting that this
100 arrangement may have been selected by insect vision [29]. Nevertheless, the
101 overall detectability of both types of concentric patterns is worse than that of
102 single-coloured discs (see Box 1), which suggests that these patterns have not
103 evolved to simply attract pollinators. Instead they may be effective for flight
104 control and stabilisation during landing and at the same time direct the insect
105 towards the centre of the flower that contains the nectar and pollen rewards.

106

107 It is well known that insects discriminate a wide range of patterns and shapes,
108 from simple to complex, artificial and naturalistic patterns in objects or visual
109 scenes [e.g. 24,30,31]. After extensive training, bees can learn to perform difficult
110 tasks such as pattern grouping and categorisation [32]. Pattern vision is
111 predominantly mediated by achromatic mechanisms; in bees by the L (long-
112 wavelength sensitive or 'green') photoreceptor [e.g. 24]. Motion vision in insects
113 is also colour-blind. Movement-derived visual information helps the insect to
114 avoid collisions, negotiate narrow gaps, land on a surface, or locate the nest and
115 foraging sites [recently viewed by 33]. Motion parallax and looming cues can
116 improve the detection range for an object placed in front of a background [34],
117 facilitate landing manoeuvres at flowers with shapes of distinct depths, or
118 positioning of the proboscis [35].

119

120 Movement causes motion blur, but its effect on pattern vision is negligible in
121 visual systems that acquire visual information by fixating on objects. Although
122 theoretically, it is plausible that insects reconstruct the image from temporal
123 variations of the signal caused by motion, insects, such as flies and bees, fixate on
124 objects, i.e. acquire visual information in a similar way to vertebrates. To
125 stabilize gaze they control the orientation of their body, which sometimes can
126 deviate from their flight direction, and display saccadic movements which
127 include fast body turns when changing the direction of gaze. Gaze stabilization is
128 supported by head movements [36,37]; however, these are minute and
129 extremely fast as the mobility of the head is limited by the insect's morphology.

130

131 **Flight trajectories influence foraging responses and learning**

132

133 Since gaze direction is closely coupled with body orientation in insects, the
134 viewing conditions, e.g. distances and directions, during approach and landing on
135 flowers will strongly depend upon the flight behaviour and navigational
136 decisions. Thus, flight trajectories influence the perception and learning of
137 sensory information by insects. When foraging insects navigate, their routes and
138 approach trajectories are largely determined by the availability of suitable visual
139 cues [38,39]. Insects can, to some degree, flexibly adjust their flight behaviour for
140 solving navigational and spatial orientation tasks by actively acquiring specific
141 visual cues for spatial learning [40,41]. This flexibility is influenced by the cost of
142 efficiently executing flight and landing movements. Flying insects obey the laws
143 of aerodynamics, hence approach and landing manoeuvres during a flower visit
144 require a number of well-coordinated actions [42*]. To initiate a landing
145 sequence at short distance from the flower the flying insect has to adjust the
146 height of the flight trajectory and reduce its speed significantly. It has to maintain
147 a good balance of its body to withstand aerodynamic drag downwards [43].
148 Sophisticated motor mechanisms rely on visual guidance allowing the insect to
149 land elegantly [44**], rather than to crash into a flower, which is not a trivial task
150 as flowers often move [45].

151

152 Flowers exploit the tight connection between vision and flight trajectory
153 throughout the different phases of the approach flight and landing sequence. For
154 example, field observations commonly describe the strong directionality of
155 bumblebees foraging on vertical inflorescences, starting at the bottom and
156 moving upwards [22,46]. Flower orientation varies, and vertically-presented
157 flowers on slopes tend to adaptively face down-slope, receiving more visitation
158 as they offer convenient petal orientation for landing of bees moving
159 preferentially upwards [47]. Observations on flowers reveal that flower
160 orientation influences the landing behaviour of pollinators [48]. It is beneficial
161 for flowers to guide pollinator movement in a way that enhances pollen transfer
162 [49**], and field observations suggest that small patterns ('nectar-guides') help
163 pollinators to orient on flowers [50-52].

164

165 **Colour and multimodal learning at the flower**

166

167 The presence of colour in flower patterns is often suggested to attract insects
168 towards the flower based on innate colour preferences and reflexive feeding
169 responses [e.g. 52,53]. However, experience may be equally if not more
170 important: insect pollinators quickly learn positive associations between food
171 rewards and colour cues [for reviews see 54,55,56]. The ability to memorise and
172 discriminate diverse colour and pattern cues is well established for many insect
173 pollinators, and consequently flower choices are strongly influenced by the
174 sensory experience acquired during foraging and previous flower visits [e.g.
175 57,58-62]. Once the insect arrives at the flower and is able to see and recognise
176 the contrasting colours of pattern elements, chromatic cues are likely to
177 reinforce the decision to finalise a landing sequence or to follow contrast
178 contours. Some colour elements in flower patterns may however present little or
179 no chromatic contrast to the insect eye (Fig.1), and examples are best found
180 among orchids which evolved an extreme diversity of colour patterns to
181 accurately manipulate the insect's movements at the flower for a single
182 opportunity to deposit pollinia on a specific body part of the insect.

183

184 Whilst at the flower, insects may combine cues for multimodal guidance, such as
185 sensory information provided by the shape of the surface, texture, odours, and
186 electrostatic forces [e.g. 63*,64-66]. As visual patterns help to make landing and
187 reward localisation on a flower easier (alone or in combination with multimodal
188 cues), the perceived reward value will be enhanced and learning improved; and
189 consequently pollinators will show preferences for flowers with patterns.

190

191 **Conclusions**

192

193 Pollinating insects forage in a three-dimensional environment and look at
194 flowers from different distances and directions. What they see depends on the
195 spatial resolution of the compound eye and visual mechanisms that process
196 object information, however, it is also influenced by their flight trajectories and
197 viewing conditions. What they choose depends on their vision and visual
198 learning capabilities and is strongly influenced by navigation and spatial learning
199 mechanisms. It remains to be understood how decisions are made and
200 behavioural responses coordinated at far and near distances, as a pollinator
201 moves between flowers, approaches and visits them. The underlying neural
202 mechanisms involve basic sensory and motor systems that are shared across
203 different taxonomic groups of insects. A wide range of flower search and choice
204 behaviours adopted by insects can be explained by mechanistic models that take
205 into account constraints imposed by the optics of insect eyes and aerodynamics
206 of insect flight, rather than by models based on the assumptions of higher order
207 cognitive processing of visual information.

208

209 **Box 1**

210

211 Bees use colour (chromatic cues) to discriminate single-coloured discs and two-
212 coloured concentric patterns, but only from close viewing distances (Fig.3). Bees
213 are colour-blind while detecting and discriminating objects from further away,
214 when those subtend small visual angles [13,17,18,67]. In this case they rely on
215 achromatic (brightness) cues, the signals of the L receptor alone. However, the

216 detection threshold does not depend on the magnitude of L-receptor contrast. A
217 critical parameter for the detectability of patterns is the distribution of L-
218 receptor contrasts within the target [17,67] (Fig.3). An outer ring with a strong
219 L-receptor contrast (bright) surrounding a central disc with weak contrast (dim)
220 is detected over a shorter distance than a single-coloured disc of the same colour
221 and diameter. The detection distance is even shorter for patterns composed of a
222 dim ring surrounding a bright disc [67]. When viewed through bee eyes such
223 pattern has blurred edges; the impaired detectability is therefore likely to be a
224 consequence of processing visual information by detector neurons with centre-
225 surround organisation of their receptive fields [67]. Such neurons are found in
226 visual pathways of many animals. The consequences of detecting objects through
227 such detectors vary for flowers of different sizes. Plants with smaller-sized
228 flowers could have evolved compensatory strategies by sharing displays, without
229 necessarily growing dense inflorescences or high densities of conspecific flowers.
230 Sharing displays can also occur when different species grow in mixed patches
231 next to each other (Fig.2), by offering large-sized visual features that inform an
232 insect's navigational decisions and guide it towards a reward location with
233 several flowers. In detection experiments honeybees and bumblebees showed a
234 slightly improved detectability for groups of three discs that were placed at
235 sufficiently large inter-disc distances to prevent optical merging when seen from
236 a long distance [68]. This suggests that detector neurons interact in various ways
237 to evoke differential responses towards extended distributions of objects across
238 the visual scene.

239

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241

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246

247 **Figure captions**

248

249 **Figure 1: Flowers through bee eyes.** Shown are pattern displays of small
250 flowers (1cm scale) in human colours (first row) and 'bee colours' (second row,
251 high spatial resolution) [for methods see 2,29]. From left to right: *Traunsteinera*
252 *globosa*, *Viola biflora*, *Helianthemum nummularia*, *Geranium robertianum*.
253 Spectral sensitivities of the S, M and L-receptors of honeybees (peak sensitivities
254 344nm, 436nm, 556nm) were used to calculate quantum catches in each pixel of
255 the multispectral images. To show 'bee colours' (second row) quantum catches
256 were converted into RGB values for the three primary monitor colours (see
257 inset). The third row shows the images of single flowers projected onto the
258 ommatidial lattice of the honeybee eye at a close distance (2cm). Images in the
259 fourth and lowest row simulate views at distances where the flower subtends a
260 visual angle of 16°, which is above the chromatic threshold, or 7°, which is below
261 the chromatic threshold and approximately at the detection limit within the
262 range of the achromatic (brightness) visual system. Note that above the
263 chromatic threshold, at short distances, only larger-sized patterns are optically
264 resolved. Visually contrasting small ornaments or flower parts are visible when

265 the insect is on the flower. They are invisible during its approach flight, shown
266 here for a distance of 2 cm at which a bee prepares for landing.

267

268 **Figure 2: Shared floral displays through bee eyes.** Shown is a simulated
269 flower patch. The single-coloured target flower (1 cm in diameter) is in the
270 centre. When the bee views the target flower from a distance of 11.4cm it
271 subtends a visual angle of 5°, the minimum angle for it to be detected. Its
272 individual colour cannot be resolved at this distance. At a distance of 32cm the
273 target flower and other individual flowers in this patch are too small to be
274 individually detected, but the whole group forms a shared display which
275 subtends a visual angle of 15°. The colour of this shared display will be visible to
276 the approaching bee. From further away, at a distance of 50cm, the colour of this
277 shared display cannot be resolved. It is integrated with surrounding groups of
278 flowers in the visual scene contributing to chromatic and brightness pattern cues
279 that the bee can use.

280

281 **Figure 3 (to be placed in Box 1): Spatial resolution of the honeybee's**
282 **chromatic and achromatic visual system.** Two parallel visual systems in the
283 honeybee are tuned to objects of different sizes [13,17,18,67]. At short distances
284 when coloured discs subtend large visual angles, bees predominantly use
285 chromatic cues to detect and discriminate coloured targets. The colour vision
286 system receives input from all three receptor types (S, M, L). At longer distances,
287 the achromatic visual system mediates detection and discrimination through the
288 L-receptor contrast (achromatic or brightness contrast). The detection limit for a
289 single-coloured disc presented individually is 5°. It does not vary with contrast
290 strength. Signals from several adjacent ommatidia are processed, presumably by
291 detector units with centre-surround receptive fields [68]. When the bee
292 approaches the target, the angular size increases; above the chromatic threshold
293 of 13-15° the target's colour will be resolved and chromatic cues determine the
294 visual perception of bees. There is sensitivity for achromatic L-contrast but it is
295 low; from short distances bees are able to detect very bright [69], but not less
296 bright [68] achromatic discs. The detection range for concentric patterns is
297 lower than for single-coloured discs and varies depending on the spatial
298 arrangement of the pattern elements with different brightness contrast.

299

300

301 **Reference annotations**

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343 nectar. Response times are increased under dim light conditions, but not
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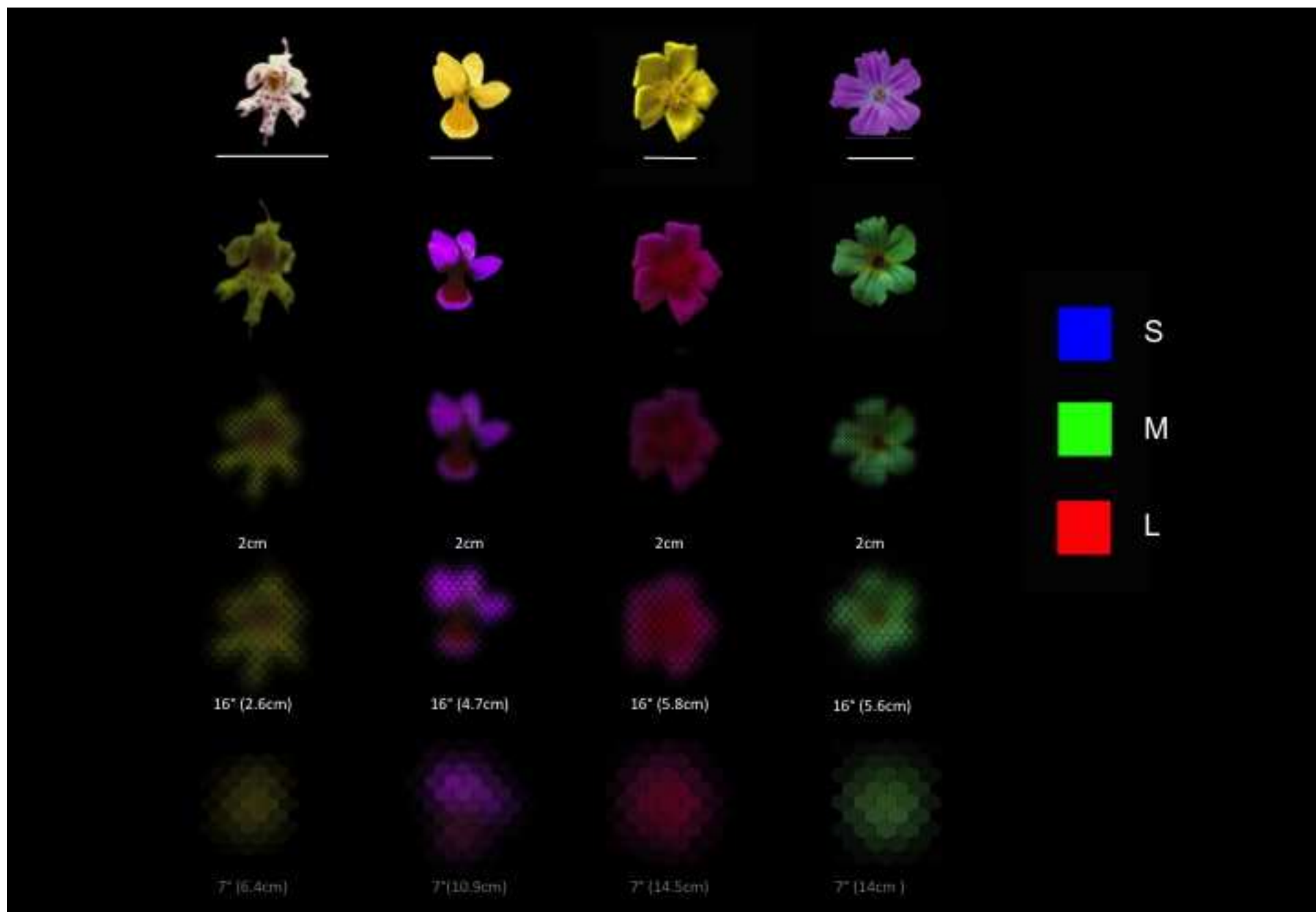
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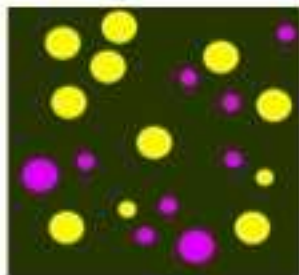
Figure

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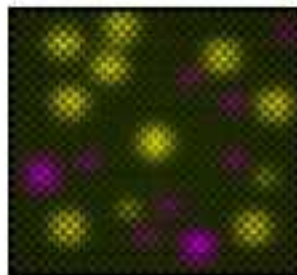


Figure

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Distance



11cm



32cm



50cm

Figure

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