

## Unidirectionality of floral colour changes

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**Abstract:** Many angiosperms have arranged their flowers in inflorescences forming a distinct signalling unit to flower visitors. In some species, the flowers of inflorescences undergo a temporal colour change corresponding exactly to a change in the reward status. Based on information obtained from the spectral reflection curves of pre-change and post-change colours of flower corollas and/or floral guides, it was possible to demonstrate that the colour phase associated with reward closely corresponds to the visual stimuli which trigger behavioural responses of inexperienced flower visitors, and that the colour phase associated with less reward corresponds to visual stimuli less attractive to naïve flower visitors. Reciprocal colour changes were not observed. It is to be assumed that the unidirectionality of floral colour changes is an adaptation of angiosperms aimed at the guidance of first-time flower visitors. Signalling reward to inexperienced flower visitors is an additional function of floral colour changes. The main function of floral colour changes, however, is to provide cues with which the flower visitors can learn to associate one colour phase with reward.

The display of colourful flowers is one way angiosperms attract animal pollinators. Some angiosperm species undergo distinct colour changes of either corollas or floral guides. The colour phases are accurately attuned to the reward status of the flowers (DELPH & LIVELY 1985; GORI 1989; WEISS 1991 a, b). It is known that the flower visitors quickly learn to associate a distinct colour phase with food and to probe flowers of the colour phase associated with food significantly more often than would be expected based on the abundance of flowers of this colour phase (KUGLER 1936, WEISS 1991 a).

Freshly emerged, flower visitors also use colour signals to initially detect flowers and to locate their rewarding sites (LUNAU & MAIER 1995). In behavioural experiments, freshly emerged, inexperienced flower visitors exhibit innate colour preferences at artificial flowers. It is thus tempting to ask whether one of the two colour phases provides colour stimuli which fit more closely to the innate colour preferences of the flowers visitors. This study intends to analyse the pre-change colour and the post-change colour of flowers in order to test the correlation of the two colours with the initial colour preferences in naïve flower visitors.

Three kinds of innate preferences towards colour stimuli are known in insect flower visitors:

1. Brightness vision. Results from behavioural tests do not provide direct evidence about how inexperienced nocturnal flower visitors use visual cues to detect flowers. Training experiments with sphingid moths (*Sphingidae*) and noctuid moths (*Noctuidae*) showed that these animals can discriminate colour stimuli even in dim light (KNOLL 1925, 1927, 1956). Testing innate colour preferences in the diurnal sphingid moth, *Macroglossum stellatarum*, showed that these animals exhibit a preference in which the brightness of colours, colours corresponding to distinct wavebands, and the spectral purity of colours play a role (KELBER & PFAFF, pers. comm.). In addition, the prevalence of white flowers in species pollinated by nocturnal moths is evidence of the hypothesis that these animals use brightness cues to locate flower colours against natural backgrounds. In contrast to white melittophilous flowers, some white psychophilous and sphingophilous flowers even reflect ultraviolet light (DAUMER 1958; KUGLER 1963, 1966; BURR & BARTHOLOTT 1993; LUNAU 1993; LUNAU & MAIER 1995).

2. Wavelength-specific behaviour. Freshly emerged hoverflies, *Eristalis tenax* (*Syrphidae*, *Diptera*), preferably approach human yellow artificial flowers (ILSE 1949, KUGLER 1950, LUNAU 1988). After landing the hoverflies extend their proboscis only towards deep human-yellow artificial floral guides. The proboscis reaction is released by green monochromatic light stimuli on the waveband of 520–610 nm. Small quantities of ultraviolet and blue light admixed to green light stimuli strongly inhibit the releasing of the proboscis reaction (LUNAU & WACHT 1994, 1995; WACHT & LUNAU 1995). Inexperienced butterflies also exhibit behaviour specifically related to wavelength. The feeding behaviour in the butterfly, *Pieris brassicae* (*Pieridae*, *Lepidoptera*), is released by monochromatic light stimuli in the blue (420–500 nm) and red (590–610 nm) region (SCHERER & KOLB 1987). Wavelength-specific behaviour is strongly intensity dependent and triggered with small ranges of wavelengths.

3. Colour vision. Bumble bee workers, *Bombus terrestris* (*Apidae*, *Hymenoptera*), do not exhibit an innate preference for colours corresponding to any distinct waveband (LUNAU 1990). Instead, naïve bumble bees are attracted by colours of high purity showing strong reflection in one or two out of the three wavebands (ultraviolet, blue, green) each corresponding to a particular type of photoreceptor. Stimuli showing a constant reflection in the bumble bees' visible range of wavelengths were the least attractive. Brightness cues are unlikely to play a role in the initial flower detection of bumble bees (LUNAU 1990, 1992 b; see also BACKHAUS & MENZEL 1987). Calculation with the quantum flux values showed that the preference behaviour was correlated with the spectral purity of the tested stimuli (LUNAU 1990): The frequency of distant approaches towards artificial flowers depended on the distance between the colour locus of the corolla colour and the locus of achromatic stimuli. At close range, the bumble bees make antennal contact with either the corolla or the floral guide. The percentage of cases in which the approach flight concluded with an antennal contact with the floral guide depended on the spectral purity of the floral guide colour minus that of the corolla colour, i.e., higher, positive differences caused a higher frequency of antennal contacts with the floral guide than lower or negative differences. The contrast between the two col-