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Gloger's rule in plants: The species and ecosystem levels

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Gloger's rule posits that darker birds are found more often in humid environments than in arid ones, especially in the tropics. Accordingly, desert-inhabiting animals tend to be light-colored. This rule is also true for certain mammalian groups, including humans. Gloger's rule is manifested at 2 levels: (1) at the species level (different populations of the same species have different pigmentation at different latitudes), and (2) at the species assembly level (different taxa at a certain geography have different pigmentation than other taxa found at different habitats or latitudes). Concerning plants, Gloger's rule was first proposed to operate in many plant species growing in sand dunes, sandy shores and in deserts, because of being white, whitish, or silver colored, based on white trichomes, because of sand grains and clay particles glued to sticky glandular trichomes, or because of light-colored waxes. Recently, Gloger's rule was shown to also be true at the intraspecific level in relation to protection of anthers from UV irradiation. While Gloger's rule is true in certain plant taxa and ecologies, there are others where "anti-Gloger" coloration patterns exist. In some of these the selective agents are known and in others they are not. I present both Gloger and "anti-Gloger" cases and argue that this largely neglected aspect of plant biology deserves much more research attention.

Gloger's rule, one of several zoological rules that identify patterns of adaptations at a global scale (rules that do have exceptions), posits that darker birds are found more often in humid environments than in arid ones, especially in the tropics.[1] This rule was later demonstrated to be true also in certain mammalian groups including humans.[2,3] Accordingly, desert-inhabiting animals tend to be light-colored.[4] Gloger's rule in animals is manifested at 2 levels, (1) at the species level (different populations of the same species have different pigmentation at different latitudes), and (2) at the species assembly level (different taxa have different pigmentation than other taxa found at different habitats or latitudes). It is not easy to pinpoint the reasons for the operation of Gloger's rule in animals. It seems, however, that 3 factors, (1) crypsis via background matching, (2) resistance to keratin-degrading micro-organisms in hair or feathers rich in eumelanin, and (3) thermoregulation are involved.[5,6]

Concerning plants, Gloger's rule was first proposed to operate in many plant species growing in sand dunes, sandy shores and in deserts. These are white, whitish, or silver colored, based on white trichomes, because of sand grains and clay particles glued to sticky glandular trichomes, or because of light-colored waxes.[7] The common classic explanations for light coloration of such plants were that it protects them from sun irradiation (including UV),[8] and that the glued sand defends them from abrasion by sand particles moving in strong wind, and by camouflage from herbivores.[9] Lev-Yadun[7] concluded that light-colored plant surfaces have several additional functions: (1) they can undermine the camouflage of herbivorous insects of other colors and expose them to predation, (2) since dust is a strong insect repellent and is lethal to insects, attached soil particles (especially clays) may defend plants with sticky glandular trichomes from insect herbivory, (3) the attached sand may defend from herbivory by mammals and arthropods by causing teeth or mouth part wear as do phytoliths (silica bodies) of grasses, and (4) white coloration of leaves and branches may mimic fungal infestation to reduce herbivory. Lev-Yadun[7] also proposed that since many desert animals tend to be paler than other members of the same taxa that inhabit wetter environments, according to Gloger's rule,[4] the above-mentioned light-colored plant species are a good indication that Gloger's rule applies to plants. Recently it was elegantly demonstrated that Gloger's rule applies at the intraspecific level concerning UVB absorption via dark areas in flowers to defend their anthers and pollen from exposure to UV light reflected from petals,[10] this being the second system where Gloger's rule operates in plants. In both cases, flowers[10] and coastal/sand dune/desert plants,[7] the characters involved in the operation of Gloger's rule in plants belong to complex functions, the probable outcome of several simultaneous selective agents that together resulted in the Gloger's rule phenomenon.

In addition to the numerous, complicated and not well-defined and sometimes unknown factors involved in the evolution of types of pigmentation of both animals and plants that commonly complicate the study of functional coloration, there are various exceptions to Gloger's rule. A common exception is of dark (melanic) animal morphs in certain temperate animals selected for because their dark color allows for better

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warming.[11-14] Being darker at higher latitudes for warming was also proposed to be important for various plant taxa. For instance, in *Collinsia parviflora* and *Mimulus guttatus* plants, growing in the Flat Top Islands, British Columbia, plants with upper-epidermis anthocyanin pigmentation are found more frequently in cold, exposed habitats.[15] Similarly, the immature female cones of European larch (*Larix decidua*) and Norway spruce (*Picea abies*) growing in Austria were red in high altitudes with low temperatures, while green cones dominated lower and warmer habitats.[16] On the other hand, there are plant taxa in which light-colored morphs are found in more northern and humid habitats. A good example for this is the Mediterranean species *Anemone coronaria*, in which flower color is only red in the drier habitats of southern Israel, while in the much more humid and colder habitats of the north, white, light bluish and pink morphs grow alongside the red morph.[17] Some of this "anti-Gloger" pattern can be explained by edaphic issues,[18] but a close inspection of *A. coronaria* populations in the field indicates that there are many populations where the edaphic factor is not exclusive. The complexity of patterns of selection and evolution in flower color was further demonstrated when the selection and evolution of flower color polymorphism was studied in wild radish (*Raphanus sativus*). In wild radish, pollinators select for yellow and white flowers, while herbivores select for pink and bronze flowers.[19] The selection for plant crypsis by herbivores over short distances irrespective of latitude, but according to the level of apparency, was found for plants inhabiting harsh soils.[20] An even stronger "anti-Gloger" pattern was demonstrated by Lev-Yadun and Ne'eman,[21] who found that in *Pinus halepensis*, which disperses its seeds either on hot dry days or after fires and which suffers very high seed predation rates by birds, ants, and rodents, many seeds have a bi-modal color pattern. One of the seed's sides is light-brown or gray and the other side is black, exposing only one color when lying on the ground. The seeds are dispersed by wind, fall to the ground, and are commonly exposed to secondary dispersal by wind before losing their conspicuous wings. One side of seeds with bimodal color pattern provides better camouflage than the other on any light or dark background.

I conclude that Gloger's rule operates in many plant taxa at both the habitat level as an interspecific strategy[7] and the intraspecific level.[10] However, there are many cases that show opposite patterns because of specific local or regional selective agents. Since very little attention has been given to Gloger's rule in plants, we still do not know the extent of its significance in plant biology.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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