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[Ontology terms]

Biological sciences / Plant sciences / Plant reproduction / Flowering

Biological sciences / Plant sciences / Natural variation in plants

Biological sciences / Evolution

Biological sciences / Plant sciences / Plant evolution

Flower colour: Gloger's Rule isn't just for the Birds

Innes C. Cuthill

A 180 year-old "law" in zoology has found its best support to date in a study of floral colour. This not only documents darker plants growing closer to the equator but also supports the idea that it all stems from ultraviolet protection.

As long ago as 1833 the German ornithologist Constantin Lambert Gloger noted that birds from warmer regions (usually interpreted as the tropics) tend to be darker than related species from cooler areas¹. Since then "Gloger's Rule" has been observed in several bird and mammal species as well as humans. In this issue Koski and Ashman breathe new life into this old idea by investigating the phenomenon in plants². Observing 35 populations of the silverweed cinquefoil, *Argentina anserine*, across a range of latitudes in both hemispheres they saw a clear trend towards greater dark pigmentation in populations from lower latitudes. This pattern is not visible to the casual observer, being due to pigments that observe ultraviolet light.

Gloger's Rule has had a venerable history, rife with conjectures as to its cause. One explanation is that it arises as an adaptation against feather degradation by bacteria in moister climates³. The pigment responsible for much of the variation in darkness, eumelanin, improves feathers' resistance to both physical and chemical damage. Other zoologists have noted that various mammal groups also adhere to Gloger's Rule, at least using latitude as a proxy for climate^{4,5}, but have tended to favour different explanations.

The direct overhead solar illumination of the tropics also produces more intense dorso-ventral shadowing. This is thought to favour stronger countershading (darker back, lighter belly) to counteract the self-shadowing and aid camouflage, as supported by data from a comparative study of ungulates⁶. Conversely, the favoured explanation for the variation in skin colour in humans is a trade-off between the benefits of protection from UV damage and need for UV for vitamin D₃ synthesis^{7,8}. In the tropics the balance is in favour of UV protection and dark skin, at higher latitudes the weaker sun favours reduced pigmentation to allow vitamin D₃ synthesis⁹. Since Koski and Ashman observed variation in UV pigmentation they could directly test the UV protection hypothesis as it applies to flowers².

A "bullseye" pattern is common in many flowers, often with the petal bases absorbing UV and the petal tips strongly reflective (see figure). Although attracting and/or guiding pollinating insects is a likely function, a role has been suggested in the protection of pollen from UV light reflected on to the anthers by the disk of petals. Koski and Ashman measured the size of the UV bullseye in their populations of *A. anserine*. Across four latitudinal transects, bullseye size

increased towards the equator. Crucially for the proposed function, the level of UV-B irradiance at each location was the best predictor of bullseye size, followed by temperature but not rainfall.

But does a larger bullseye really protect the flower from UV? Kloski and Ashman took *A. anserine* plants into the lab and exposed half the flowers of each plant to ecologically realistic levels of UV-B irradiation, with the other half unexposed. In the absence of UV, pollen germination was actually higher in flowers with smaller bullseyes, but in the presence of UV-B the relationship changed, with higher pollen viability from flowers in which they were larger, but not too large. In a second lab experiment, with artificial flowers surrounding the anthers from real plants, flowers with large bullseyes had pollen germination levels similar to that in the absence of UV, while that from flowers with small bullseyes had 28% lower germination rates. These two lab experiments demonstrate that UV-absorbing petal tissue does enhance pollen viability, consistent with the latitudinal variation being the result of selection for UV protection.

This an important conclusion about the causes of floral colour variation, although it does not rule out other factors from being as (or more) significant, including the effects of UV on other plant functions. Nevertheless it is somewhat ironic that, after 180 years of research on Gloger's rule by zoologists, some of the strongest evidence for the driver of that latitudinal pattern comes from research on plants. It is of course possible that Gloger's rule has no single explanation and that different groups are responding to different selective agents, all correlated with latitude. After all, Gloger's original observation was of a relationship between pigmentation and "warmth" as much as latitude. Also, although for both *A. anserine* and humans UV-B irradiance is a stronger correlate of pigmentation than humidity or latitude per se, in humans it may be UV-B-induced folate photolysis that is the major selective agent⁸. What is clear is that, nearly 200 years on, the observations of Constantin Lambert Gloger are still providing inspiration for innovative research.

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Figure 1. *A. anserine* flowers showing enlarged UV bullseyes at lower latitudes.

Although similar to the naked eye (left) the upper bloom shows a larger area of dark pigmentation under UV light (right). The flowers come from the extreme north (upper) and south (lower) of New Zealand. Image by Matthew Koski.

