

Exploring Gloger's ecogeographic rule

Why organisms are darker in wetter & warmer environments



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Critical theory essay

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Gloger's rule is an ecogeographic trend wherein organisms possess darker pigmentation in warmer, more humid environments (Gloger 1833; James 1991; Gaston et al. 2008; Lev-Yadun 2015; Roulin & Randin 2015; Bishop et al. 2016). Gloger (1833) first described this pattern in birds, and consequently the rule is largely treated as applying to endothermic animals (Bishop et al. 2016). However, evidence mounts for the pattern's applicability to ectotherms (e.g. Rapoport 1969; Bishop et al. 2016), and plants (e.g. Lev-Yadun 2007; Koski & Ashman 2015). Though, there may be different processes in different taxa that result in this pattern of organismal pigmentation across climatic gradients.

Herein, I discuss the treatment of ecogeographic rules in ecological and evolutionary science, and within this context discuss the degree to which Gloger's rule has merit as a genuine pattern in nature. I discuss insights into possible mechanisms that generate the Gloger's rule pattern, and how these vary between taxa, and across levels of biological organisation. I argue that there is sufficient evidence to support Gloger's rule as a useful and true generalisation.

Ecogeographic & biogeographic "rules"

The theory vs empiricism of "rules" ...

It is important to consider what is meant by the term "rule" in biology. There are many of biogeographic and ecogeographic patterns that are referred to as rules, e.g. Bergmann's rule, Allen's rule, etc. Gloger's rule, the focus here, is also often grouped with these.

Lomolino et al. (2006) outline the study of observed patterns or trends of organismal traits across geographical space with ecogeographic rules (i.e. observations). They highlight examples of *patterns* at broad ecological scales as consequence of *processes* at a range of scales. Indeed, the patterns themselves are also manifest at a variety of scales and levels of organisation. As such, Lomolino et al. (2006) notes, underlying causal mechanisms behind these patterns are difficult to ascertain.

Lomolino et al. (2006) also talk about theory vs empirical evidence, and varying scales, and also the *evolutionary* side to ecogeographic rules.

Olalla-Tárraga (2011) discusses approaches to studying rules too, with focus on Bergmann's rule. Olalla-Tárraga (2011) advocates a pluralist approach, wherein the manifestations of ecogeographical rules at multiple scales and

levels of biological organisation are considered. He also outlines that "laws" and "rules" in ecology, and in science generally, need not *always* contain mechanistic statements, and need not be without exception, as they are "correlative generalisations". Though, mechanistic understandings of the processes that generate patterns is desirable, and indeed often the aim of research, this does not imply that correlative ecogeographic rules are not useful intrinsically. Not least, these rules are often the starting point of research. Thus, these rules represent interesting observed patterns that can motivate research, *and* useful generalisations that can be employed in other work.

Ecogeographic rules operate across various levels of biological organisation. Gaston et al. (2008) differentiate between *intraspecific*, *interspecific*, and *assemblage* patterns in organismal traits across environmental gradients. In the context of Gloger's rule, the pattern would manifest at intraspecific (= "ecotypic" sensu Millien et al. 2006) levels in that pigmentation would generally be darker in populations, of some species, in more humid habitats. The operative question here is whether individuals (or individuals of certain genotypes) are darker in more humid habitats.

At the interspecific level, the organismal pigmentation darkness values measured to vary across a humidity gradient would be derived from populations of *different* species. Here, the question of concern is whether species in humid habitats are generally darker than species in more arid habitats. Similarly, assemblage and community analyses of Gloger's rule are investigating interspecific comparisons of greater quantities. Besides this, communities and assemblages are also meaningfully large units of interspecific comparison. Questions at these scales aim discern Gloger's rule patterns between species, but also between groups of species. Bishop et al. (2016), for example, describe community trait averages in order to describe the extent of Gloger's rule in ants.

The scale and levels of organisation at which Gloger's rule is an important consideration when discussing case studies and evidence for the rule, as it evidently entails nuances to the questions. Note, Gloger's rule does not appear to concern ontogenetic colour change—that is, colour change within the development and lifespan of an individual organism (Booth 1990). This is because the primary aim of Gloger's rule is to demonstrate trends in the evolutionary and ecological significance of the environment to organismal colour, assuming organismal colour is relatively fixed through out an organism's lifespan.

Gloger's rule—evidence & explanations

[Endotherms]

As stated above, Gloger's rule stems from his observations of bird plumage darkness across climatic moisture gradients (and, by the simplest extension, pigmentation in endothermic animals too) Gloger noted bird plumage was darker in warmer, more humid areas (Burt & Ichida 2004; Miksch 2015) than the plumage of conspecific birds in more arid areas (Burt & Ichida 2004). Roulin & Randin (2015) describe the logic of Gloger's rule lucidly:

The rule is based on the assumption that melanin pigments and/or dark coloration confer selective advantages in warm and humid regions.

They investigate animal fitness in warm, humid environments as conferred via alternative phenotypic adaptations (viz. in owls). The implication of *fitness* in a given habitat allows one to see the *evolutionary* aspect to Gloger's *ecogeographic* rule (a sentiment Lomolino et al. (2006) highlights).

Like many other other ecogeographic rules, Gloger's rule has gained renewed research interest in the 21st century (Lomolino et al. 2006).

Millien et al. (2006) discuss ecotypic (i.e. intraspecific, i.e. between populations) variation in terms of ecogeographic rules, too.

Manifestations of Gloger's rules across various scales and levels of organisation [...] intrasp. Gloger's rule manifestations (= "ecotypic", sensu Millien et al. (2006)) vs intersp./community level manifestations (Lev-Yadun 2015)

How ubiquitous is Gloger's rule? I will now discuss empirical evidence for the rule, or patterns similar to it. First, there is well studied evidence of Gloger's rule at the intraspecific level in birds. E.g. Song Sparrows (*Melospiza melodia*) in North America (Burt & Ichida 2004), North American Barn Owls (*Tyto alba pratincola*) (Roulin & Randin 2015), Hawaii Elepaos (*Chasiempis sandwichensis*) (VanderWerf 2012), Oahu Elepaos (*C. ibidis*) (in the same study by VanderWerf (2012)), and Gloger's rule has also been documented within mammal species. E.g. house mice (*Mus musculus*) in Asia (Lai et al. 2008). Notably, extending the generality of the rule (Koski & Ashman 2015), the plant species *Argentina anserina* has been found to follow the rule in its floral pigmentation (in ultraviolet wavelengths) (Koski & Ashman 2015), having stronger "bullseye" markings when occurring nearer the equator.

In interspecific comparisons of organismal darkness, Gloger's rule patterns have been observed in birds (...), mammals (e.g. primate coat colour (Kamilar & Bradley 2011) ...), insects (e.g. ant assemblages (Bishop et al. 2016)).

[Ectotherms]

Concerning the applicability of Gloger's rule to ectotherms (viz. invertebrates), an "inverse" of Gloger's rule is often reported (Rapoport 1969; Lev-Yadun 2015). Indeed, the major mechanistic explanations for Gloger's rule in endotherms (below) can be reversed in ectotherms—should

they deal with temperature—or outweighed by processes more important to ectotherm fitness in a given environment. Collembolates—interspecifically—follow this inverse Gloger's rule pattern (Rapoport 1969), such that the proportion of darker species is greater at higher latitudes. This is likely as they require greater degrees of melanism in order accrue heat from the environment more easily in these typically colder regions (Rapoport 1969). In the case of ant assemblages (Bishop et al. 2016), a mixture of the class Gloger's rule and its inverse was demonstrated. Ant assemblages tended to be darkest in regions of high and low temperatures, and paler in colour in intermediate regions. At lower temperatures, ant assemblages tended to be darker for thermoregulatory reasons (as found with Collembolates (Rapoport 1969)), while in regions of higher temperature ant assemblages were more melanised also, in order to increase fitness in the high levels of ultraviolet radiation in warmer regions (Bishop et al. 2016). The resulting patterns (see Fig. 2b in Bishop et al. 2016) were also interacting with ant assemblage mean body size, in that assemblages typified by smaller ants were also darker (see Fig. 2a in Bishop et al. 2016). This was concluded to be because smaller ectotherms more strongly require the thermoregulatory benefits of darker colouring, due to their relatively little thermal inertia..

[Plants]

[Across scales]

[Evolution-rant]

Studies concerning Gloger's rule, and indeed most patterns in nature (Lomolino et al. 2006), must ideally consider the historical, evolutionary context to organismal form—not just local deterministic mechanisms. Though, it must be noted, the extent to which historical and deterministic processes govern organismal pigmentation largely depends on the scale of investigation. Ontogenetic changes in pigmentation are a-historical. Intraspecific patterns may represent micro-evolutionary fitness benefits to certain genotypes. Interspecific and assemblage patterns, however, would be indicative of more long-term, persistent selection pressures—e.g. ant species *assemblages* follow Gloger's rule in humid environments, implying that there may be long-standing, consistent strength to Gloger's rule in ants. In other words, enough evolutionary time must pass [...].

Conversely, with respect to interspecific and community ecogeographic patterns, environmental filtering could conceivably produce trait patterns over shorter, ecological time-scales. In this case, if the traits in taxa that follow an ecogeographic rule (e.g. Gloger's rule) *do* confer a fitness benefit as the rule would predict, they would not be adaptations (sensu Baum, Mayr, [...]), having evolved elsewhere.

Distinguishing between whether organismal pigmentation follows the Gloger's rule pattern (if and when it does) is governed by deterministic (i.e. environmental filtering) or historical (i.e. adaptation) processes would be insightful. Re-

search concerning this distinction would further allow one to ascertain the degree to which Gloger's rule is a consequence of multiple processes (at multiple spatio-temporal scales), and the number and relative strength of processes that partake therein. In such a case that these patterns have, say, historical drivers in one system at one scale, and deterministic drivers in another, this would emphasise the complexity of ecogeographic patterns. It would also mirror the notion Olalla-Tárraga (2011) puts forward, wherein correlative generalisations, such as Gloger's rule, need not encapsulate one, if any, mechanisms. Though, it is unlikely that there is *no* mechanisms behind Gloger's rule patterns. Instead, it is interesting and insightful that multiple mechanisms, combined or in isolation, govern these patterns.

- Van Lenning et al. (2004) -> evolutionary, not deterministic, pattern to coccolithophore pigment
- VanderWerf (2012) looked at bird body size, bill size, and plumage in populations two closely related birds across environmental gradients in Hawai'i. With regards to plumage, bird individuals (N.B. this is basically intraspecific-scale work! Not just b.c. the two species are closely related, but b.c. they only seem to actually DO intrasp. comparisons anyway), Gloger's rule was supported, and with "smoothly clinal distributions" [sic] (as a function of the few dispersal barriers *and* steep environmental gradients).
- Plants vs endothermic animals vs ectothermic animals (for animals see highlighted § in James (1991)); UV-B protection (Gloger's rule) vs thermal hypothesis vs desiccation hypothesis (Pinkert et al. 2016); Plants foliarly (sensu Lev-Yadun 2007) vs florally (sensu Koski & Ashman 2015)
- Animal vs plant e.g. -> differences in meaning and interpretation. Also consider Dominy & Lucas (2004) food colour and primates—could THIS connect to an environmental pattern in plant colour?
- Kamilar & Bradley (2011) -> little mechanistic work in this paper though! They speculate about 1) background matching, 2) anti-bacterial stuff, and 3) maybe thermoregulation (#FutureStudies). Unlikely to be UV, because primates live in trees! (not even in the upper-canopy, where UV is strong—primates do not spend tonnes of time up there)
- Burt & Ichida (2004) found that dark plumage is resistant to bacterial degradation (~ pigments), a common problem in humid climates; methods: measure intrasp. Δcolour vs bacterial activity.
- cf Koski & Ashman (2015) -> UV role (in plants)
- Tate et al. (2016) found persistent colour polymorphism within a population of a species -> equivalent fitness of the morphs in heterogeneous habitats; results: darker species forage/hunt better in darker habitats (~ hiding in the ambient background). Since (Ruan says) darker habitats are wetter (ish), this relates to Gloger's rule.
 - Connect evidence above to mechanisms de-

- scribed in their respective papers (if applicable)
- & mechanisms from other papers concerning pigment and environment (e.g. Tate et al. 2016)
- Dissect the observations at the intrasp., intersp., and assemblage levels MECHANISTICALLY
- Animal vs plant e.g. -> differences in meaning and interpretation for MECHANISM
- & Shawkey & Hill (2004) microbial feather shit! read more...
- VanderWerf (2012) background matching maybe too??

Concluding remarks

- ...
- Millien et al. (2006) traits vary with geography, but also with global climate change!

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