

Exploring Gloger's ecogeographic rule

Why organisms are darker in wetter & warmer environments



R. van Mazijk

VMZRUA001@myuct.ac.za

2017-08-15

BSc Hons Biological Sciences

Critical theory essay

For Dr A. Amar & Dr P. Sumasgutner

Gloger's rule is an ecogeographic trend wherein organisms possess darker pigmentation in warmer, more humid environments (Gloger 1833; Lev-Yadun 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"

Theory vs empiricism of "rules" ...

Lomolino et al. (2006) outline the study of observed patterns or trends of organismal traits across geographical space. These ecogeographic "rules" (i.e. observations) highlight examples of pattern 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. As such, Lomolino et al. (2006) says, 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.

Gaston et al. (2008) (has a def for Gloger's rule too) (also d/d's betw intrasp. traits, intersp. traits, and assemblage patterns (e.g. Bishop 2016 on ants) (in community properties or community trait avgs))

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

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, need not be without exception, as they are "correlative generalisations". Though, mechanistic understandings of the processes that generate these law-defining 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.

Ontogenetic level too! (Booth, C.L. 1990)

Origins of the rule

See Roulin & Randin (2015) for a good def of the rule in the abstract (e.g. fitness benefits of melanin in warm and environments). Roulin & Randin (2015) also compare this to fitness in warm/humid climes is conferred via alternative phenotypic adaptations (owls) (see their results—*it's complicated*)

Manifestations of Gloger's rules

Intrasp. Gloger's rule manifestations (= "ecotypic", sensu Millien et al. (2006)) vs intersp./community level manifestations (Lev-Yadun 2015)

Where does this idea come from? What's the logic?

- Gloger's observations
 - Gloger noted bird plumage darkness ~ warmth, humidity (Miksch; Burt & Ichida 2004)
- His contemporaries' thoughts
- Theoretical reasoning behind the rule

Evidence & examples

Gloger vs anti-Gloger patterns (sensu Lev-Yadun 2015), e.g. "negative Gloger's rule" in invertebrates, e.g. Collembolates (Rapoport 1969)

Does the pattern exist? Is it observed in the first place? Dissect the observations at the intrasp., intersp., and assemblage levels

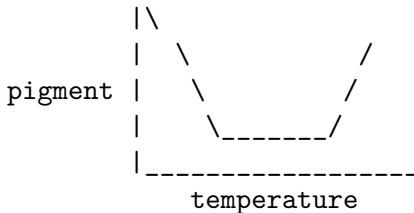
Kamilar & Bradley (2011) primate *interspecific* coat colour follows Gloger's rule -> little mechanistic work in this paper though! They speculate about 1) background matching, 2) anti-bacterial stuff, and 3) maybe thermoregulation (#FutureStudies). Unlikely to be UV, because primates live in trees! (not even in the upper-canopy, where UV is strong—primates do not spend tonnes of time up there)

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!), Gloger's rule was supported, and with "smoothly clinal distributions" [sic] (as a function of the few dispersal barriers *and* steep environmental gradients).

Bishop et al. (2016) ant *assemblage* work (ECTOTHERMAL):

- organismal darkness as a modal pattern
- at low temperatures for thermoregulatory need
- at higher temperatures for UV-B protection
- also darkness incr with smaller body size
- these patterns are evident at the *assemblage* level



(~confound rainfall, sexual selection)

Plants vs endothermic animals vs ectothermic animals; 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?

Mechanisms behind the pattern

Burt & Ichida (2004) found that dark plumage is resistant to bacterial degradation (~ pigments), a common problem in humid climates; methods: measure intrasp. Δ colour 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 described 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

Concluding remarks

- ...

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

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