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; Gaston et al. 2008; 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" …

It is important to consider what is mean 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 *eco*geographic 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 across levels of organisation

Gaston et al. (2008) differentiate between *intra*specific, *inter*specific, and *assemblage* patterns in organismal traits across environmental gradients. Bishop et al. (2016), for example, describe community trait averages in order to describe the extent of Gloger's rulein ants.

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

Booth (1990): Ontogenetic level too!

Gloger's rule—evidence & examples

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 warma 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)) svs 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 (Burtt & Ichida 2004; Miksch 2015)
- His contemporaries' thoughts
- Theoretical reasoning behind the rule (if any??)

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 *inter*specific 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 closesly 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 thew few dispersal barries *and* steep environmental gradients.

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

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

```
        |\
        |  \           /
pigment |   \         /
        |    \_______/
        |__________________
            temperature
            (~^confound rainfall,
                        sexual selection)
```

Plants vs endothermic animals vs ectothermic animals; UV-B protection (Gloger's rule) vs thermal hypothesis vs dessication 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

Burtt & Ichida (2004) found that dark pluamge is resistant to bacterial degradation (~ pigments), a common problem in humid climes; 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 populations 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 habs 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 cliamte change!

References

Bishop, T.R., Robertson, M.P., Gibb, H., Rensburg, B.J. van, Braschler, B., Chown, S.L., Foord, S.H., Munyai, T.C., Okey, I., Tshivhandekano, P.G., Werenkraut, V. & Parr, C.L. 2016. Ant assemblages have darker and larger members in cold environments. *Global Ecology and Biogeography*. 25(12):1489–1499. DOI: 10.1111/geb.12516.

Booth, C.L. 1990. Evolutionary significance of ontogenetic colour change in animals. *Biological Journal of the Linnean Society*. 40(2):125–163. DOI: 10.1111/j.1095-8312.1990.tb01973.x.

Burtt, E.H. & Ichida, J.M. 2004. Gloger's Rule, Feather-Degrading Bacteria, and Color Variation Among Song Sparrows. *The Condor*. 106(3):681. DOI: 10.1650/7383.

Dominy, N.J. & Lucas, P.W. 2004. Significance of color, calories, and climate to the visual ecology of catarrhines. *American Journal of Primatology*. 62(3):189–207. DOI: 10.1002/ajp.20015.

Gaston, K.J., Chown, S.L. & Evans, K.L. 2008. Ecogeographical rules: Elements of a synthesis. *Journal of Biogeography*. 35(3):483–500. DOI: 10.1111/j.1365-2699.2007.01772.x.

Gloger, C. 1833. Das Abändern der Vögel durch Einfluss der Klima's. 1833. Breslau, Germany: A. Schulz.

Kamilar, J.M. & Bradley, B.J. 2011. Interspecific variation in primate coat colour supports Gloger's rule. *Journal of Biogeography*. 38(12):2270–2277. DOI: 10.1111/j.1365-2699.2011.02587.x.

Koski, M.H. & Ashman, T.-L. 2015. Floral pigmentation patterns provide an example of Gloger's rule in plants. *Nature Plants*. 1(1):14007. DOI: 10.1038/nplants.2014.7.

Lev-Yadun, S. 2007. Defensive functions of white coloration in coastal and dune plants. *Israel Journal of Plant Sciences*. 54(4):317–325. DOI: 10.1560/IJPS_54_4_317.

Lev-Yadun, S. 2015. Gloger's rule in plants: The species and ecosystem levels. *Plant Signaling & Behavior*. 10(12):e1040968–1–e1040968–2. DOI: 10.1080/15592324.2015.1040968.

Lomolino, M.V., Sax, D.F., Riddle, B.R. & Brown, J.H. 2006. The island rule and a research agenda for studying ecogeographical patterns. *Journal of Biogeography*. 33(9):1503–1510. DOI: 10.1111/j.1365-2699.2006.01593.x.

Miksch, J. 2015. An Ecological Rule for Animals Applies to Flowers. *University of Pittsburgh News Services*. Available: http://www.news.pitt.edu/news/ecological-rule-animals-applies-flowers.

Millien, V., Kathleen Lyons, S., Olson, L., Smith, F.A., Wilson, A.B. & Yom-Tov, Y. 2006. Ecotypic variation in the context of global climate change: Revisiting the rules. *Ecology Letters*. 9(7):853–869. DOI: 10.1111/j.1461-0248.2006.00928.x.

Olalla-Tárraga, M.Á. 2011. "Nullius in Bergmann" or the pluralistic approach to ecogeographical rules: A reply to Watt et al. (2010). *Oikos*. 120(10):1441–1444. DOI: 10.1111/j.1600-0706.2011.19319.x.

Pinkert, S., Brandl, R. & Zeuss, D. 2016. Colour lightness of dragonfly assemblages across North America and Europe. *Ecography*. DOI: 10.1111/ecog.02578.

Rapoport, E.H. 1969. Gloger's rule and pigmentation of Collembola. *Evo-*

lution. 23(4):622–626. DOI: 10.2307/2406857.

Roulin, A. & Randin, C. 2015. Gloger's rule in North American Barn Owls. *The Auk*. 132(2):321–332. DOI: 10.1642/AUK-14-167.1.

Tate, G.J., Bishop, J.M. & Amar, A. 2016. Differential foraging success across a light level spectrum explains the maintenance and spatial structure of colour morphs in a polymorphic bird. *Ecology Letters*. 19(6):679–686. DOI: 10.1111/ele.12606.

VanderWerf, E.A. 2012. Ecogeographic patterns of morphological variation in Elepaios (Chasiempis spp.): Bergmann's, Allen's, and Gloger's rules in a microcosm. *Ornithological Monographs*. 73(1):1–34. DOI: 10.1525/om.2011.73.1.1.1.