Exploring Gloger's ecogeographic rule

Why organisms are darker in wetter & warmer environments

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Gloger's rule is an ecogeographic trend wherein organisms possess darker pigmentation in warmer, more humid environments, as opposed to drier environments (Gloger 1833; James 1991; Lev-Yadun 2007, 2015; Gaston et al. 2008; 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. However, there is evidence for the pattern's applicability to ectotherms (Bishop et al. 2016), to which the opposing Bogert's rule (the "thermal melanism hypothesis") is usually thought to apply (Bogert 1949; Rapoport 1969; Pinkert et al. 2016). Plants, too, can display patterns predicted by Gloger's rule (Lev-Yadun 2007; Koski & Ashman 2015). There may be different processes in different taxa that result in this pattern (and other patterns) of organismal pigmentation across these 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 is 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"

It is important to consider what is meant by the term "rule" in biology. There are many biogeographic and ecogeographic patterns that are referred to as rules, e.g. Bergmann's rule, Allen's rule. Gloger's rule, the focus here, is also often grouped with these. Like many other other ecogeographic rules, Gloger's rule has gained renewed research interest in the 21st century. Lomolino et al. (2006) outline the study of observed patterns or trends of organismal traits across geographical space. Here, ecogeographic rules are employed to generalise 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. There are exceptions, such as Bogert's rule (Bogert 1949), wherein organisms are darker in colder climates, which is almost always attributable to the thermal melanism hypothesis (discussed below). Furthermore, due to the tendency of ecological relationships to be non-linear, studying these ecogeographic patterns must be assisted and informed by theory (Lomolino et al. 2006).

Olalla-Tárraga (2011) discusses approaches to studying rules too. Olalla-Tárraga (2011) advocates a pluralist approach, wherein the manifestations of ecogeographical rules at multiple 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. Gloger's rule is often found to be a result of multiple mechanisms (see cases below). Contrast this with Bogert's rule (see ectotherm cases below), which is formally mechanistic (Bogert 1949; Delhey 2017). Though mechanistic understanding of the processes that generate pattern is desirable, and indeed often the aim of such research, this does not imply that correlative ecogeographic rules are not useful. 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 *intra*specific, *inter*specific, 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 when pigmentation is darker in populations of a 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 anaylyses of Gloger's rule are investigating interspecific comparisons of greater quantities. Besides this, communities and assemblages can convey meaningful groupings of species and habitats together. Questions at these scales aim to discern patterns between species, but

also between groups of species.

The level of organisation at which Gloger's rule is observed is an important consideration when discussing evidence for the rule, as it changes the suite of possible mechanisms one can attribute to the pattern. For example, mechanisms driving differences in average pigmentation in assemblages of species are likely not to apply to differences between morphs of a single species. 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

How ubiquitous is Gloger's rule? I will now discuss empirical evidence and mechanisms for the rule, or patterns similar to it, for three major groups of terrestrial biota: endothermic animals, ectothermic animals, and plants, though the majority of studies concerning Gloger's rule appear to concern birds and mammals. I will then discuss these mechanisms with regards to the level of biological organisation at which they were observed.

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 than the plumage of conspecific birds in more arid areas (Burtt & Ichida 2004; Miksch 2015). 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, see below). The implication of *fitness* in a given habitat allows one to see the *evolutionary* aspect to Gloger's *eco*geographic rule (a sentiment Lomolino et al. (2006) highlights). Colouration is indeed an important aspect to animal evolution. In mammals, predator-prey interactions (e.g. concealment), communication, and ecophysiology drive body and hair colour (Caro 2005, 2013). It is easy to see how these same properties drive avian plumage evolution, as animal colour is often an evolutionarily labile trait-suite (Friedman & Remeš 2017).

There is well studied evidence of Gloger's rule at the intraspecific level in birds: e.g. Song Sparrows (*Melospiza melodia*) in North America (Burtt & Ichida 2004), North American Barn Owls (*Tyto alba pratincola*) (Roulin & Randin 2015), Hawaii Elepaios (*Chasiempis sandwichensis*) (VanderWerf 2012), Oahu Elepaios (*C. ibidis*) (in the same study by VanderWerf (2012)), Black Sparrowhawks (*Accipiter melanoleucus*) (Tate et al. 2016), and Shiny Cowbirds (*Molothrus bonariensis*) (Mahler et al. 2010). Mechanistically, Song Sparrows in humid contexts appear to be under greater pressure from feather-degrading bacteria (Burtt & Ichida 2004), as humid environments support a greater abundance of bacteria (Shawkey & Hill 2004). Consequently darker-morphs are more fit there, as melanin increases the resistance of feathers to bacterial degradation (Burtt & Ichida 2004; Shawkey & Hill 2004; Gunderson et al. 2008). Gunderson et al. (2008), in particular, note that although the evidence for the bacterial resistance afforded to feathers by greater concentrations, controlled field experiments are still needed in order to verify this process outside of laboratory conditions. Notably, Mahler et al. (2010) did not find differences in bacterial degradation between light and dark morphs of female Shiny Cowbirds. As is discussed by Roulin & Randin (2015) concerning Barn Owls, there are multiple seletive pressures that relate to pigmentation, specifically melanin-based darkness. Indeed, Burtt & Ichida (2004) describe their findings as "simply another pressure that selects for dark feathers", and outline the myriad other causes (see Table 2 in Burtt & Ichida 2004). It is interesting, though, that many of these pressures can align to produce patterns predicted by Gloger's rule—e.g. background matching (i.e. concealment), thermoregulation, and indeed resistance to bacterial degradation. These mechanisms (Table 2 in Burtt & Ichida 2004) are reported to be responsible for interspecific differences in plumage darkness, but are easily extensible to intraspecific differences, in evolutionary terms.

Concealment and crypsis related mechanisms in particular are often demonstrated, as darker colouration aligns with moist, tropical habitats—which contrasts with pale/white colouration in high latitude habitats (Millien et al. 2006). This facilitates less predation pressure on prey species, and may also conceal predators from their prey, enabling them to hunt more succesfully. Relating to the latter, Tate et al. (2016) found support for the "light level-detectability hypothesis" (Galeotti et al. 2003) in Black Sparrowhawks. Persistent colour polymorphism within populations of Black Sparrowhawk suggests equivalent fitnesses of the morphs in a heterogeneous habitat. They found that darker morphs forage better in darker habitats, as they are better concealed. As mentioned above for mammals (Caro 2005, 2013), predator-prey interactions such as these evidently affect organismal colour. Here, dealt with explicitly is the relationship between environmental lightness and organismal colour. Since darker habitats are more likely to be wetter and more humid, the findings of Tate et al. (2016) can relate to

Gloger's rule. Indeed, Amar et al. (2014) demonstrate that Black Sparrowhawk dark morphs are more common (but not the exclusive morph) in wetter regions.

VanderWerf (2012) looked at plumage, among other things, within populations of two closely related birds across environmental gradients in Hawaii. In this regard, Gloger's rule was supported, such that pigmentation was darker for birds of either species in areas of high rainfall. VanderWerf (2012) eliminated thermoregulatory and bachground-matching mechanisms for the case of Elepaios, however. This was because of the observed independence of Elepaio plumage on temperature, and little differential predation upon Elepaios along mositure or temperature gradients, respectively.

Explicitly *inter*pecific comparisons of organismal darkness also demonstrate Gloger's rule in birds: e.g. Australasian meliphagids and acanthizids (Friedman & Remeš 2017). Friedman & Remeš (2017) found contrasting patterns in dorsal and ventral plumage darkness. Though Gloger's rule *seems* to apply, it is contingent on their proposed explanations of this discrepancy: that countershading and the signalling-importance of ventral plumage preclude ventral colouration from following Gloger's rule in these bird families. The background matching mechanism for Gloger's rule, for example, may impose weaker selective pressure on ventral plumage than dorsal plumage. Gloger's rule has been described in-part across many Australian bird species (Delhey 2017). The study by Delhey (2017) in particular dealt both with between-species and between-assemblage comparisons. They found that bird species and species assemblages are darker in wetter and *colder* regions. The concordance of Australian bird species and assemblages with Gloger's rule in terms of humidity is likely a function of the mechanisms mentioned so far: bacterial resistance and/or crypsis. The darkness of these bird species and assemblages follows *Bogert's rule* in terms of *temperature*, however (Delhey 2017). Bogert's rule (Bogert 1949; Delhey 2017) is typically applied to ectotherms (see ectotherm cases below), wherein organisms are darker in order to gain more heat in cold climates, and paler in order to reflect more heat in hot climates.

Gloger's rule has also been documented within mammal species. House mice (*Mus musculus*) coat colour in Asia follow Gloger's rule, likely due to some combination of background mathcing, bacterial resistance, and thermoregulatory benefits (Lai et al. 2008). Blind mole rat dorsal colour has been found to follow Gloger's rule as a function of thermoregulatory need and crypsis (Singaravelan et al. 2013). Primate coat colour (Kamilar & Bradley 2011; Caro 2013) and some facial colour patterns (Santana et al. 2012) have also been observed to follow the rule. Kamilar & Bradley (2011) had little mechanistic conclusions, and speculate towards the usual plausible set of mechanisms (background matching,

bacterial resistnace, and possibly thermoregulation). Notably, they conclude that primate coat darkness is unlikely to be for protection from ultraviolet radiation, as the vast majority of primates are arboreal, generally spending most of their time shaded in the lower canopy. Santana et al. (2012) argue that all these ecological mechanisms, *including* protection from ultraviolet rays, are at play in determining the darkness of primate facial patterns, though more research is needed. Carnivores, artiodactyls, and rodent species have also been found to follow Gloger's rule (Caro 2013).

It can be said, then, that thermoregulatory considerations tend not to produce Gloger's rule patterns in endotherms, if not the opposite (sensu Bogert's rule). This will be explored more with ectotherms below. The extent to which endothermic animal darkness is determined by climate is thus the combined result of humid-arid (Gloger's rule) and hot-cold gradients (Bogert's rule; sometimes Gloger's rule). These cases exemplify the way in which different, non-mutually exclusive mechanisms combine, with varying strengths, to produce patterns in accrodance with Gloger's rule. Each specific case need not follow the rule as a consequence of all, nor some specific process (Olalla-Tárraga 2011). Predator-prey interactions, resistance to bacterial degradation, and protection from ultraviolet radiation seem to to be the most common mechanisms among endotherms.

Ectotherms

Concerning the applicability of Gloger's rule to ectotherms (viz. terrestrial invertebrates), an "inverse" of Gloger's rule is often reported (Rapoport 1969; Lev-Yadun 2015)—also known as the thermal melanism hypothesis, or Bogert's rule (Bogert 1949; Delhey 2017). Here, organisms are lighter in hotter regions, and darker in colder regions, in order to reflect and gain heat in those environments respectively (Bogert 1949; Rapoport 1969; Delhey 2017). Indeed, the major mechanistic explanations for geographic patterns in organismal pigmentation in endotherms can be reversed in ectotherms.

Suppose some mechanistic explanation for an ectothermic population demonstrating a Bogert's rule pattern. Here, the importance of Gloger's rule mechanisms is outweighed by the thermoregulatory concerns of Bogert's rule. 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, inuitively, because they require greater degrees of melanism in order acrue heat from the environment more easily in these typically colder regions (Rapoport 1969).

North American and European dragonly assemblages have been found to follow Bogert's rule, being paler in warmer areas and darker in colder areas (Pinkert et al. 2016). These results, however, are cautioned to only extend to non-tropical regions. In the case of ant assemblages (Bishop et al. 2016), a mixture of the class Gloger's rule

and its inverse has been demonstrated. Ant assemblages tended to be darkest in regions of higher and lower temperatures, and paler in colour in intermediate regions. At lower temperatures, ant assemblages tended to be darker for thermoregulatory reasons (Bogert 1949), 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 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 therma inertia. Here, the relative strengths of Gloger's and Bogert's rules mechanisms differ across an environmental gradient, such that each rule predominantly governs pigmentation darkness at either environmental extreme. This contrasts with the case of dragonfiles (Pinkert et al. 2016) and collembolates (Rapoport 1969), wherein only Bogert's rule is found.

There is clearly a difference between the applicability of Gloger's rule to ectotherms as opposed to endotherms. Gloger's rule can apply (Bishop et al. 2016), but is sometimes overrun by ecogeographic rules typical to ectotherms—namely Bogert's rule.

Plants

Extending the generality of Gloger's rule to another Kingdom of organisms, the plant species *Argentina anserina* has been found to follow the rule in its floral pigmentation (in pigments pertaining to ultraviolet wavelengths) (Koski & Ashman 2015). Stronger ultraviolet pigement "bullseye" markings are found when occuring nearer the equator. The bullseye marking is for pollinator attraction, but is also shown to protect against radiation (Koski & Ashman 2015). This follows the ultraviolet protection mechanism shown in ants (Bishop et al. 2016), primate facial markings (Santana et al. 2012), and the avian examples above.

Lev-Yadun (2007) also demonstrated foliar plant traits that follow Gloger's rule, primarily in arid/desert flora. Here, as the rule does predict, plants are pale in an arid context, likely in order to reflect incident radiation (i.e. a thermoregulatory mechanism) (Lev-Yadun 2007).

The distinction between mechanisms generating Gloger's rule patterns in animals and plants is important, though not obvious. Here, plants appear to be subject to thermoregulatory and radiation protection mechanisms. Ectothermal animal pigmentation is also consequence of thermoregulatory concerns, but usually result in Bogert's rule patterns, and only sometimes Gloger's rule patterns. This contrasts with the predation-related and bacteria-related mechanisms in *endo*therms. To summarise, the ecogeographic patterns in organismal pigmentation can

differ between taxa. When a pattern is shared between two taxa, it need not be as a result of the same process (e.g. Gloger's rule in birds vs plants). When patterns differ, the underlying mechanism can be the same, but still resulting in those two different patterns depending on the taxon (e.g. thermoregulation-borne Gloger's rule in plants vs Bogert's rule in dragonflies).

Scales of organisation and evolutionary process

Studies concerning Gloger's rule, and indeed most patterns in nature, must ideally consider the historical, evolutionary context to organismal form (Lomolino et al. 2006)—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 pigementation 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, a sufficient amount evolutionary time must pass in order for this pattern to arise.

Conversely, with respect to interspecific and community ecogeographic patterns, environmental filtering (Cavender-Bares et al. 2009) 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 strictly be adaptations (sensu Baum & Larson 1991), having evolved elsewhere.

Distinguishing between whether organismal pigmentation following the Gloger's rule pattern is governed by deterministic (i.e. environmental filtering) or historical (i.e. adaptation) processes would be insightful. Research 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, in combination or isolation, govern these patterns. Lev-Yadun (2015) identifies these complexities in Gloger's rule across scales, and its need for investigation in plants (exemplified by the brevity of its discussion above).

Mayr (1956) seems to say that ecogeographic rules only operate within species. There has been evidence to the contrary (e.g. Bishop et al. 2016). Note, there are more exceptions to these rules at higher levels of organisations (such as assemblages), as the systems become necessarily more complex. That is not to say that there are no exceptions at instraspecific levels either (e.g. the inapplicability of Gloger's rule to rare melanistic coyotes in Florida, U.S.A (Caudill & Caudill 2015)), but as Mayr (1956) suggests:

> The fact that "cold climates do not produce a fauna tending towards large-sized globular forms with small protruding parts" (Scholander, 1955) is not in the least in conflict with Bergmann's or Allen's rule.

In other words, ecogeographic rules have been treated as having more predictive power *within* species, not between. But, this should not preclude these ecogeographic patterns from being manifest at higher levels of organisation too—even if the original rule was describing instraspecific patterns.

Regarding higher levels of organisation, it is worth noting the welcome and impressive amount of phylogenetic context applied to many of the assemblage-level cases discussed here (Kamilar & Bradley 2011; Santana et al. 2012; Bishop et al. 2016; Pinkert et al. 2016; Friedman & Remeš 2017). These evolutionary perspectives are important, as they allow us to distinguish ecogeographic patterns from those produced by the relatedness of biota alone (Cavender-Bares et al. 2009). This is important, as Friedman & Remeš (2017) points out, because animal colour is often an evolutionarily labile—but one must verify that this is the case. A good example of this is coccolithophore pigmentation (Van Lenning et al. 2004), which is largely historically determined. Here, ecogeographic rules are not needed to explain the pattern.

Concluding remarks

Millien et al. (2006) discuss intraspecific variation in the context of global climate change. Traits can vary with geography, as we have seen. Accordingly, so too can they with anthropogenic modifications of geography and climate. Identified are ways in which ecogeographic rules could be an invaluable tool in predicting the effects of climate change on biota. Indeed, Roulin (2014) recapitulates this mechanistically, in that melanisation may likely represent a key aspect in organismal success under climate change (due to its radiation protection role). These important applied aspect, and the basic research motivation to study ecogeographic patterns themselevs, are founded in the reality of such patterns. Here, I have discussed reasonable evidence of Gloger's rule in multiple taxa, and across various scales of biological organisation. Consequently, complexities to the rule do emerge. Gloger's rule varies in importance and strength between taxa, and interacts with other ecogeographic patterns. Historical and phy-

logenetic community (Cavender-Bares et al. 2009) contexts to ecogeographic studies represent a wealth of research opportunity, especially in regard to Gloger's rule.

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