Title: Temperature-dependent developmental plasticity and its effects on Allen's and Bergmann's Rules in endotherms

Running title: Phenotypic plasticity and ecogeographical rules

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Abstract

Ecogeographical rules, describing common trends in animal form across space and time, have provided key insights into the primary factors driving species diversity on our planet. Among the most well-known ecogeographical rules are Bergmann's Rule and Allen's rule, with each correlating ambient temperature to the size and shape of endotherms within a species. These two rules have recently attracted renewed research attention, largely with the goal of understanding how they emerge (e.g. via natural selection or phenotypic plasticity), and thus, whether they may emerge quickly enough to aid adaptations to a warming world. Yet despite this attention, the precise proximate and ultimate drivers of Bergmann's and Allen's rules remain unresolved. In this conceptual paper, we articulate novel and classic hypotheses for understanding whether and how plastic responses to developmental temperatures might contributed to each rule. Next, we compare over a century of empirical literature surrounding Bergmann's and Allen's Rules against our hypotheses to uncover likely avenues by which developmental plasticity might drive temperature-phenotype correlations. Across birds and mammals, studies strongly support developmental plasticity as a driver of Bergmann's and Allen's rules, particularly with regards to Allen's rule and responses to heat. However, these plastic contributions toward each appear largely non-linear and dependent upon: (1) efficiency of energy use at given ambient temperatures (Bergmann's rule), and (2) thermal advantages at given ambient temperatures (Allen's Rule). These findings suggest that, among endotherms, rapid changes in body shape and size will continue to occur, but generalizing the direction of responses across populations is likely naive.

Keywords: Allen's Rule, Bergmann's Rule, James' Rule, Thermoregulation, Phenotypic Plasticity, Energy Expenditure

Introduction

Phenotypic variation, both within and among species, is a key contributor to the beauty and resilience of life. In their theories of evolution, both Darwin and Wallace recognized this importance of variation (Wallace, 1855; Darwin, 1859; Darwin,1868) but lacked a formal understanding of how it might first arise. However, Darwin speculated that traits within individuals – or otherwise identical individuals – were likely malleable and varied according to environmental context (reviewed in Winther, 2000). Today, this speculated process is best known as "phenotypic plasticity" and is widely understood as a strategy to cope with, or even exploit, novel or changing environments (see, for example, Bradshaw, 1965; West-Eberhard, 1989; Brooker at al, 2021).

Some of the most striking displays of phenotypic plasticity occur in response to temperature. In the Chinese primrose (*Primula sinensis*), flowers that develop red at 20°C emerge white at 30°C, regardless of parentage (Baur, 1919). Similarly, five-spotted hawkmoth larvae (*Manduca quinquemaculata*) from the same brood develop black when raised at mild ambient temperature (< 20°C) but bright green when raised in the warmth (>28°C; Suzuki and Nijhout, 2006). In fish, Atlantic halibut (*Hippoglossus hippoglossus*) raised in warmer waters (>10°C) accelerate growth so rapidly that they can weigh more than twice that of their conspecifics held in cooler waters (6°C) by six months of age (Jonassen et al, 1999). These examples not only highlight the profound consequences of phenotypic plasticity on life, but also that the thermal environment during development can, and often does, play a direct role in mediating its occurrence.

Across natural environments, whether plastic responses to temperature can explain variations in species form has been questioned for decades but remains debated (Hansson, 1985; Sebens, 1987; Teplitsky et al, 2008; discussed in Yom-Tov and Geffen, 2011). However, correlations between the thermal environment and both the size and shape (specifically extremity length) of endothermic animals have been known since the nineteenth century (Bergmann, 1847; Allen, 1877), providing provocative fodder for speculation. These correlations, now known as Bergmann's rule (or sometimes "James' Rule" intra-specifically; Blackburn et al, 1999) and Allen's rule, have since been observed at both inter-specific (e.g. Ashton et al, 2000; Meiri and Daya, 2003; Rodríguez et al, 2008; Symonds and Tattersall, 2010; Alhajeri et al, 2020; Benítez-López et al, 2021; McQueen et al, 2022; Weeks et al, 2023) and intra-specific levels (e.g.

James, 1970; Ashton 2002; Freckleton et al, 2003; Benítez-López et al, 2021; McQueen et al, 2022). Although traditional explanations for both rules are generally genetic (i.e., with natural selection favouring body sizes and shapes that reduce heat-loss in the cold and increase heat-loss in the warmth; Mayr, 1956), that each are sometimes evident *within* species suggests that phenotypic plasticity, in addition to fixed genetic effects, may also contribute to their occurrence. Unfortunately, however, the majority of studies pertaining to Bergmann's and Allen's rules have focused on their validity and physiological implications (see e.g. Scholander 1955; Mayr 1956; Geist, 1987; Meiri and Daya, 2003; McNab, 2010; Gutiérrez-Pinto et al 2014), thus leaving knowledge about their mechanistic drivers comparatively less developed (but see Serrat, 2007).

In this conceptual paper, we first review over a century of empirical literature testing the hypothesis that plastic responses to the thermal environment, specifically during post-natal development, give rise to intra-specific variants of Bergmann's rule and/or Allen's rule. While we recognize that plasticity during adulthood - or "phenotypic flexibility" (Piersma and Drent, 2003) - may also contribute to the manifestation of these rules (e.g. Gosler, 1987), we have chosen to focus our discussion on plastic effects during development owing to evidence supporting this life stage as a critical window for shaping final structure and size in many vertebrates (see Wells, 2014). We base our discussion around both novel and traditional hypotheses describing *how* this plasticity might operate, and which precise phenotypes might be expected across temperatures under each. Our intent is not to exhaustively test how the thermal environment during development impacts body size (similar to Weeks et al, 2022) and extremity length; rather, our goal is to create a theoretical framework with which: (1) an influence of the thermal environments on endotherm size and shape across space and time, as they are understood through ecogeographical rules, might be critically evaluated, and (2) future empirical studies may be best oriented.

Bergmann's Rule

Bergmann's rule, that endotherms living in warm environments are usually smaller than their congeners in cold environments, is arguably the most well-known and hotly-disputed of all ecogeographical rules. While some of this disputation surrounds the validity of the rule itself (see above), much is also semantic, and reduces to disagreements about how Bergmann's ideas should be correctly interpreted (see Watt et al, 2010; Meiri, 2011). Bergmann himself reported that a negative correlation between body size and environmental temperature (proxied by latitude) was most apparent when observed *across* species of closely related endotherms, despite first predicting a more obvious trend within species (Bergmann, 1847; discussed in Watt et al, 2010). Several decades later, Rensch (1932) argued that Bergmann's ultimate explanation – viz. that larger animals have higher capacities for heat retention – should have equal relevance within species. Although both inter- and intra-specific variants of Bergmann's Rule could be explained by selective responses to temperature, or even range shifts in animal populations over time and space, intra-specific variants present the possibility that temperature-body size correlations are also explained by plastic responses to the environment. Given our interest in plasticity as a driver of ecogeographical rules, we have therefore chosen to focus our paper on intra-specific versions of Bergmann's Rule in phenotype.

A framework for how temperature-dependent, developmental plasticity affects body size

Arguably the most parsimonious route by which ambient temperature might directly influence body size, and thus give rise to Bergmann's Rule, is by shaping rates and durations of growth during post-natal development (together, "cumulative growth"). In ectotherms, such an effect – known as the "temperature-size rule" – is well supported (Walters and Hassall, 2006) and its mechanistic drivers are becoming clearer (Verberk et al, 2021). Whether and how a similar effect may arise in endotherms, however, is currently unknown. In line with classic mechanisms proposed by Bergmann (1847) and Rensch (1932), increases in cumulative growth in the cold and decreases in cumulative growth in the warmth may reflect selection on the efficiency of heat exchange at a given temperature (henceforth, the "Thermal Advantage Hypothesis"; Box 1). A likely alternative, however is that changes in cumulative growth across ambient temperatures occur to increase efficiency of energy use during post-natal development (henceforth, the "Energy Efficiency Hypothesis"; Box 1; refer to Parsons, 2005 for the fitness value of energy efficiency). This distinction between mechanisms is critical, since precisely how body size should vary across ambient temperatures is likely to differ under each. Under the Thermal Advantage Hypothesis, cumulative growth, and ultimately, relative body size, should correlate linearly and negatively with ambient temperature, regardless of concurrent thermogenic or thermolytic costs, until constraints imposed by other fitness-related traits emerge (e.g. fecundity and locomotion; Alisauskas and Ankney, 1990; Shaeffer and Lindstedt, 2013; see Boyer at al., 2010; Fig. 1A). Under the Energy Efficiency Hypothesis, however, correlates between cumulative growth (or relative body size) and ambient temperature should instead represent a right-skewed quadratic with maximum values (i.e. the apex) occurring at, or near, the temperature at which maximum energy assimilation rate is achieved (Fig. 1B). The temperatures at which net growth or relative size becomes negative (i.e., *x*-intercepts) should then lay where either the energetic costs of thermoregulation begin to compete with, and compromise, those of growth, or where growth is stunted by heat-induced cellular damage (Fig. 1; see Ørstedt et al, 2022).

If Bergmann's rule is explained by plastic responses to ambient temperature, and such plastic responses occur to confer thermal advantages, one may predict that increases in ambient temperature during development should cause unanimous decreases in body size and vice versa, until constraints on size are imposed by other fitness-related traits (discussed above; Fig. 1A). However, if plastic responses occur to increase efficiency of energy use, a more complex pattern in response to warming temperature should emerge. More specifically, if ambient temperatures are usually high during development (relative to range of developmental temperatures that are the most conducive for growth), then further increases in temperature should impose a decrease in body size. By contrast, if ambient temperatures are usually low during development (again, relative to the optimal range of developmental temperatures), increases in temperature should instead impose an increase in body size (Fig. 1B). In the context of a warming climate, these two hypotheses present very different responses with respect to species phenotype.

Below, we interpret empirical literature within this theoretical framework and question whether there is: (1) evidence of a plastic origin to Bergmann's rule in endotherms, and (2) indication that any plastic origin to Bergmann's rule conforms more closely with the Thermal Advantage Hypothesis or the Energy Efficiency Hypothesis. To facilitate these ends, findings are discussed qualitatively and with a focus on effect sizes (in percent change). Thermal effects imposing <5% changes in body size are arbitrarily considered weak.

Evidence for direct effects of developmental temperature on body size across endotherms

Controlled experiments, whereby ambient temperature alone is varied during development, remain the gold standard for evaluating a plastic origin to ecogeographical rules. In one of the first of its kind, Sumner (1909) reared newly weaned, captive-born mice (*Mus musculus*) in either cold environments (approximately 6°C) or warm environments (approximately 26°C) while monitoring body mass throughout development. In contrast to

Bergmann’s rule, the average mass of cold- and warm-reared mice was strikingly similar at 6 weeks of age (i.e. at the end of maximum growth velocity; Kurnianto et al, 1997), with cold-reared mice being less than 0.5 grams (2%), heavier than their warm-reared conspecifics. Many years later, Ashoub (1958) corroborated these findings, showing that, albeit subjectively, wild-origin mouse pups reared at 10°C appeared to develop “normally”. Among more modern research, similarly limited effects of cold exposure on body size development have been well supported. Ballinger and Nachman (2022), for example, found that the average mass of wild-derived house mice reared at 5°C was within 0.3 g (again, 2%) of those reared at 21°C, even when compared between full siblings of the same sex. Still lower ambient temperatures (-3°C) did little to change this effect, with masses of adult, cold-reared mice being only 4% higher than warm-reared mice (23°C; Barnett and Dickson, 1984). Even more surprisingly, Serrat et al (2008) reported a *decrease* in body mass (6%) among cold-reared mice (7°C) relative to warm-reared mice (27°C) at 12 weeks of age. Such findings (i.e., those of Serrat et al, 2008) are not only inconsistent with expectations of Bergmann’s rule, but directly oppose them. Beyond mice, still other mammalian studies have repeatedly shown negligible to weak effects of developmental cold exposure on mature body mass, suggesting that enhanced growth in these conditions – vis-à-vis classic interpretations of Bergmann’s rule – is hardly universal (pigs, *Sus scrofa*: Weaver and Ingram, 1969; domestic rats, *Rattus norvegicus*, Quinn, 1978; Albustanji et al, 2019; fat-tailed dunnarts, *Sminthopsis crassicaudata,* Riek and Geiser, 2012; yellow-footed antechinuses, *Antechinus flavipes*, Stawski and Geiser, 2020; see Heath 1984 for an in-depth review of early literature).

In birds, a similar picture of how developmental cold exposure, relative to thermoneutral conditions, influences adult phenotype is emerging. In Japanese quail (*Coturnix japonica*), Burness et al (2013) reported a negligible (ca. 1%) effect of rearing young at 15°C throughout early development (5-51 days of age) on body mass at maturity (56-84 days) when compared with 30°C controls, despite subtle differences in mass earlier on. Likewise, exposure to post-natal cooling bouts (20°C, relative to 30°C) led to no detectable changes in adult mass of domestic chickens (*Gallus gallus;* Mujahid and Furuse, 2009; but see May and Lot 2001). Further lowering ambient temperatures in cold exposure treatments, however, appear to elicit slightly different results in both species. In Japanese quail, for example, we recently observed that rearing young at 10°C from hatching onward leads to *negative* effects on adult body mass, not positive, with cold-reared birds weighing 7% less at maturity than those reared in the warmth (30°C; Persson, E., Tabh, J. K. R., Nord, A., et al., *unpublished*). Snedecor (1971) reported a similar end with the body mass of domestic chickens being 10% higher when reared at intermediate (25°C) rather than cool (15°C) temperatures. Such negative effects of developmental cold exposure have also been supported in at least two other avian species (Muscovy ducks, *Cairina moschata,* and great tits, *Parus major;* Rodríguez and Barba, 2016a; Teulier et al, 2014; but see negligible effects of cycling cold temperature on body size in chickens; Swain and Farrell, 1975).

Contrasting results from cold-exposure studies, those obtained from experimental heat exposures (again, relative to thermoneutral conditions) generally support expectations of Bergmann's rule. In mice, for example, young raised at 35°C after weaning were 11% lighter than those reared at 25°C in otherwise similar environments (Sundstroem; 1922a, 1922b). Similarly, guinea pigs (*Cavia porcellus*) raised at 36°C were 9% smaller at one week of age than those raised at 21°C (Adamsons et al, 1969), and domestic pigs exposed to cycling heat stressors within their second week (between 32°C and 38°C) were 0.4 kg (8%) lighter at weaning than controls (25.4°C; Johnson et al, 2018). In birds, a recent review of literature published over the last half-century reported that 9 of 15 relevant studies revealed a negative effects of heat exposure during development on the body size of young at fledging or maturity (Weeks et al, 2022). While intriguing, the varied nature of metrics used to measure "body size" (e.g., tarsus length, wing length, body mass) may limit the study's interpretability in the context of Bergmann's rule, particularly since some metrics may have greater relevance to Allen's rule (e.g., tarsus length; discussed below). Regardless, experimental studies monitoring body mass of birds throughout post-hatch development often show a negative effect of heating on growth or final mass (e.g. May and Lot, 2001; Rodríguez and Barba, 2016a, albeit non-significant; Marchini et al, 2011; Andreasson et al, 2018; but see Ernst et al, 1984). As with cold-exposure studies, however, this negative effect is not always evident, and is, in some case, reversed (see, for example, Herrington and Nelbach, 1942; Dawson et al, 2005; Pérez et al, 2008; Ton et al, 2021), even among observational studies (Teplitsky et al 2008; Shipley et al, 2022). Nevertheless, such directional inconsistencies appear less common among experimental warming studies than experimental cooling studies.

Bergmann's rule in light of developmental plasticity literature

Although the precise timing of heat- or cold-exposures during development may generate some noise in the findings discussed above (see Knudsen, 1962; Serrat, 2013; Nord and Giroud, 2020), evidence across both birds and mammals generally support an effect of post-natal heat exposure, but less so cold exposure, on final body size. Still, when viewed across a sufficiently broad range of ambient temperatures, it is nonetheless likely that the thermal sensitivity of body size during development does contribute to Bergmann's rule-like patterns. Perhaps more interestingly, however, the varying and non-linear responses of endotherms to experimentally cooled or heated environments highlight that plastic contributions to Bergmann's rule are unlikely to be explained by selection for thermal benefit alone (i.e. the Thermal Advantage Hypothesis). Instead, these findings better align with the hypothesis that plastic contributions to Bergmann's rule are driven by selection to increase efficiency of energy use in a given thermal environment (i.e., the Energy Efficiency Hypothesis; Fig. 1B). Indeed, under this hypothesis, body size responses to a temperature challenge should not be linear and should depend on the degree to which the challenge shifts development within, or outside temperature zones that are prescriptive for growth (*sensu* Mitchell et al, 2018; Fig. 1B). Supporting this prediction, the body mass of tree swallow (*Tachycineta bicolor*) nestlings increased when experimental heating raised developmental temperatures to within thermoneutrality (i.e., 30°C*;* Williams, 1988). Moreover, pushing developmental temperatures into ranges that likely increased costs of heat dissipation and decreased energy assimilation rates led to *decreases* in body mass of other avian species (observed in Andreasson et al., 2018, and Johnson et al. 2018, where experimental heating raised developmental temperatures well above thermoneutrality for their study species; O'Connor, 1975; Huynh, 2005). It is possible that variations in resource abundance under natural conditions may constrain the possibilities for phenotypic responses in contribute to some variation in outcomes of field studies, contributing to variations in outcomes such as those described above. Nevertheless, with these observations in mind, we speculate that temperature-mediated plasticity should not induce unanimous decreases in body size when temperatures rise (e.g. Fig. 1A), as is often predicted for endotherms in a climate warming scenario (e.g. Sheridan and Bickford, 2011; Youngflesh et al, 2022). Rather, we propose that plastic responses to a warming world should manifest in a more complex and nuanced manner, with high-latitude or otherwise cold-exposed populations increasing in cumulative growth and body size (consistent with Meiri et al, 2009 and Boutin and Lane, 2014), and already heat-exposed populations decreasing in final size. We recognise that other selective processes (e.g. relaxed selection on body size in warm winters) probably influences how body size might respond to warming or changing climates (Ozgul et al, 2009; Ballinger and Nachman, 2022; but see Teplitsky et al 2008). However, widespread support for plastic responses to developmental temperature indicate that such should not be ignored when seeking to understand the emergence of Bergmann's rule and species-level responses to climatic change.

Allen's rule

Allen's rule states that endotherms living in colder environments tend to have shorter bodily extremities than those living in warmer environments. Unlike Bergmann's rule, the intra- or inter-species specificity of this particular rule has been subject to relatively little debate. Although Allen restricted his observations to phenotypic trends within species, his original writings did not exclude the possibility or similar trends emerging across species of a phylogenetic grouping (see Allen, 1877). This possibility has now been supported with several broad-scale studies on birds and mammals (e.g., Nudds and Oswald, 2007; Symonds and Tattersall, 2010; Alroy, 2019; Alhajeri et al, 2020; but see Gohli and Voje, 2016). Functionally, Allen's rule is understood as a mechanism to reduce the loss of costly body heat in the cold and increase the loss of damaging body heat in the warmth (i.e., by reducing or increasing relative body surface area respectively). However, whether this function is achieved through natural selection on, or plasticity of, extremity length is unclear (see Mayr 1956; Gohli and Voje, 2016).

Models for how developmental temperature and plasticity affect extremity length in endotherms

Allen himself speculated that variations in extremity length within species were caused by plastic responses to their local environments – a quite different view from that held by Bergmann. In the introduction of his seminal work, Allen (1877; p. 1-2) states: "*…[my conclusions] show that other influences than natural selection operate powerfully in the differentiation of specific forms, and that geographical causes share more largely in the work than naturalists have heretofore been prepared to admit*". Although no empirical evidence is provided to support his hypothesis, the observation that the pelage of domestic sheep thickens in response to cooler climates is offered for allegorical rationale. This deduction is notable since it reveals that selection favouring plastic responses to temperature, or *adaptive phenotypic plasticity*, is arguably best aligned with Allen's conclusions. More specifically, plasticity to reduce extremity length in the cold and increase extremity length in the warmth may have been selected to decrease and increase heat loss in each environment respectively (i.e. the "Thermal Advantage Hypothesis" under Allen's rule; Box 2). An alternative hypothesis is that any plastic changes in extremity length induced by the thermal environment are merely byproducts of other adaptive, or non-adaptive, responses to cold or warmth. Under this hypothesis (henceforth, the “Exaptation Hypothesis”; Box 2), temperature-mediated plasticity of extremity length is not a result of natural selection for thermal advantages *per se*, but nevertheless still provides energetic benefits within some thermal environments (similar to an evolutionary spandrel; Gould and Lewontin, 1979).

There are likely several routes by which temperature might influence extremity length indirectly, or as a byproduct. One of the simplest and best described is through q10 effects on cellular metabolic process and cell proliferation. For example, the rate of chondrocyte division (and, hence, bone elongation), have been shown to increase with increasing tissue temperatures, even *ex vivo* when housing temperatures are fixed above expected body temperatures (Serrat et al, 2008). While some of this correlation may still be explained by adaptive adjustments in, for example, the cellular machinery responsible for nutrient uptake and delivery, mere q10 effects are nonetheless also probable (reviewed in Serrat, 2014). Such effects would have important implications for phenotypic responses at high ambient temperatures where extremity elongation could become exacerbated beyond that advantageous for dry heat loss (i.e., further lengthening even once ambient temperature exceeds body temperature), unless the lengthening response is constrained by accumulation of cellular damage in the heat (see Ørsted et al, 2022). In this way, the Thermal Advantage and Exaptation Hypotheses should yield different predictions regarding the effect of ambient temperature on extremity length. Specifically, under the Thermal Advantage Hypothesis, elongation of extremities in the warmth should only occur insofar as advantages to dry heat loss are provided (i.e., when ambient temperature is below body temperature and heat can be lost non-evaporatively) and should diminish thereafter (Fig. 2). By contrast, under the Exaptation Hypothesis, where q10 effects are likely contributors to extremity growth, elongation of extremities in the heat should continue as temperatures rise regardless of whether advantages to heat loss exist or not (Fig. 2) and will be truncated only when selection against extremity length for non-thermoregulatory reasons appear. In response to cold, predictions under both hypotheses are similar since stunting of extremity growth should continue to provide thermal advantages even at extreme low temperatures (Fig. 2). Although responses to temperature under each hypothesis are likely to be bound by functional constraints (e.g., locomotion or feeding), differences in their expected consequences nonetheless paint unique pictures of how endotherms may change in a warming world.

Below, we review empirical literature seeking to uncover a role of developmental plasticity in dictating Allen's rule within species and discuss these findings in light of the Thermal Advantage and Exaptation Hypotheses to the ontogeny of temperature-extremity length relationships across endotherms.

Evidence for plastic effects of developmental temperature on extremity lengths

In mammals, exposure to cold during development often elicits dramatic effects on growth of the tail, limbs, and other bodily appendages (e.g., ears and antlers). In one of the most remarkable examples of this, Thorington (1970) observed a 32% decrease in the tail lengths of white-footed mice (*Peromyscus leucopus*) reared at 16°C relative to 27.5°C by 12 weeks of age, independent of cold-induced changes in body size. Similar cold-induced reductions in tail growth have also been observed in studies of domestic mice. Knudsen (1962), for example, reported a 30% reduction in tail length among eight-week-old mice reared at 18°C relative to 32°C. Moreover, Sumner (1909), Barnett (1964), and Barnett and Dickson (1984) each observed reductions in tail length exceeding 5% among mature mice that were reared below 10°C relative to near-room temperatures (23°C-25°C). In one of these cases (Barnett, 1964), stunting effects of the cold correlated with a decrease in both the absolute number of caudal vertebrae and their individual length. Thus, temperature-effects on extremity growth may extend beyond modifications to cartilaginous or muscular tissues (see Serrat et al, 2014 for an in-depth review of this topic). At the level of the limbs and ears, cold-induced growth restrictions are equally well supported, Lowering ambient temperatures to 5°C after weaning elicited a 10% reduction in femur length and 25% reduction in ear surface area of domestic pigs at 88 days of age when compared with warm-raised controls (35°C; Weaver and Ingram, 1969). In rats, raising young from weaning at 3-5°C relative to 18-28°C also led to 5% reductions in tibial length, 7% reductions in third metatarsal length, and other significant but unquantified declines in radial, ulnar, and ear length at maturity (Lee et al, 1969; Riesenfeld, 1973; see Villarreal et al, 2007 for similar findings). Further findings in domestic mice are also comparable (Serrat et al, 2008). These lesser reductions in limb length, relative to those reported for tails and ears, are notable, but can probably be explained by an earlier emergence of functional constraints when key constituents of the locomotory apparatus are modified, leaving fewer possibilities for developmentally plastic changes in some appendages compared to others.

In birds, empirical studies evaluation a role of ambient temperature on extremity growth are comparatively few. In great tits (*Parus major*), cooling of nests by 5°C after hatching led to a weak 4% reduction in tarsus length at 15 days of age (Rodríguez and Barba, 2016a), and in Japanese quail, rearing at 7°C relative to 24°C led to a 2.5% reduction in tarsus length by maturity (Krijgsveld et al, 2003). Although the bill is recognised as a potentially important structure for avian thermoregulation (Tattersall et al, 2017) and known to follow Allen's rule (Symonds and Tattersall, et al 2010; Fan et al, 2019; Romano et al, 2020), we are only aware of two studies using experimental methods to test an effect of rearing temperatures on adult bill length (NeSmith, 1985, as discussed in James, 1991; Burness et al, 2013). In one study cold temperatures during development reportedly caused a qualitative reduction in bill length near fledging (in Red-winged blackbirds, *Agelaius phoeniceus*; NeSmith, 1985), while in the other, rearing temperature elicited a negative but weak effect (~3% reduction) on bill length at maturity (in Japanese quail; Burness et al, 2013). Most observations among mammals, but less so birds therefore appear to indicate a negative effect of low developmental temperatures on elongation of extremities, which could contribute to morphometric clines recognised as Allen's rule.

Studies measuring how extremity lengths respond to heat exposure in both birds and mammals are also scarce, particularly with heat treatments nearing or exceeding body temperature. However, in one early study (Przibram, 1925), 11-week-old rats that had been reared in ambient temperatures between 5°C and 40°C showed an almost linear increase in relative tail length with increasing temperature, even when ambient temperatures exceeded body temperatures typical for this species (i.e., 37°C-39°C; Poole and Stephenson, 1977). In another study, unilateral surface heating at 40°C throughout development led to significant increases in limb and ear length of 5-week-old mice when compared with mice unilaterally heat-treated at 30°C (Serrat et al, 2015). These findings suggest that plastic contributions to extremity length hold even at ambient temperatures above body temperature (i.e., as predicted by the Exaptation Hypothesis; Fig. 2). In stark contrast, however, three studies in birds reported no effect of experimental heating in the nest on tarsus length near fledging (Dawson et al, 2005; Rodríguez and Barba 2016b; Andreasson et al, 2018). Additionally, although domestic chickens raised at 35°C displayed longer legs than those raised at 15°C, leg lengths were still comparable to those raised at 25°C by 5 weeks of age, indicating that cold stunts, but heat does not affect, extremity length in this species (Snedecor, 1971). These studies suggest that plastic changes in extremity length following heat exposure are reduced, or even negated above a certain threshold temperature (predicted by the Thermal Advantage Hypothesis to Allen's rule, Fig. 2). Although possibly confounded by parental behaviour, that several field observations have supported such a conclusion (e.g. a lack of extremity elongation in extreme heat) is intriguing (see Cunningham et al, 2013; Pipoly et al, 2013; Andrew et al, 2017).

Allen's rule in light of developmental plasticity literature

Findings from experimental literature strongly support an effect of ambient temperature during post-natal development on the elongation, or shortening, of bodily extremities in birds and mammals. This effect, in most cases, is consistent with intra-specific correlations between ambient temperature and extremity length known as "Allen's rule", particularly in response to low and moderate developmental temperatures (in keeping with both the Thermal Advantage and Exaptation Hypotheses). However, although empirical studies are limited, available evidence most commonly indicates a reduced, and even negated effect of high heat load on the lengthening of extremities during development. These observations are not consistent with the Exaptation Hypothesis, but do support the Thermal Advantage Hypothesis (Fig. 2). Such findings are notable since they suggest that: (1) plastic changes in extremity length consistent with Allen's rule may well be adaptive responses to minimize heat loss in the cold and maximize heat loss in the warmth and, (2) species developing in hot environments may already display maximal extremity lengths for their body sizes and change little in response to further warming. Although we recognise that extremity lengths may, in part, be explained by inheritance of, and selection on, fixed phenotypes (e.g., Cheung and Parker 1974; Alatalo and Lundberg, 1986), our qualitative assessment of the literature suggests that the contributions of such to Allen's rule need not be in isolation, in view of substantial phenotypic plasticity in extremity length when parental and offspring thermal environments differ. Interestingly, studies in mice have arrived at similar conclusions (e.g., Serrat, 2007; Ballinger and Nachman, 2022). This lack of fixity among extremity lengths implies that, for many endothermic species, changes in response to warming climate are likely to occur rapidly (consistent with Ryding et al, 2021). Similar to plastic responses driving Bergmann's rule (discussed above), however, evidence also suggests that the extent to which these shifts occur will probably depend upon the range at which ambient temperature is raised in a species' breeding environment, and whether extremity lengths are already maximized for a given species.

Outlook

Numerous empirical studies across endotherms indicate that the development of both body size and extremity length are labile and can differ according to the post-natal thermal environment. This lability often recapitulates the classic phenotypic clines known as Bergmann's and Allen's rule. However, a wide body of evidence suggests that the precise shapes of these labile responses are not linear. Instead, our qualitative review indicates that phenotypic responses to developmental temperature are much more nuanced and dependent on both environmental context (i.e., range-specific ambient temperatures) and individual-level factors (i.e., intrinsic temperature tolerance and energy available for growth). Accordingly, while data across numerous empirical studies show that increases in ambient temperature often cause plastic reductions in body size and increases in extremity length (following Bergmann's and Allen's rules respectively), these changes may be lost or even reversed at relatively low and extremely high ambient temperatures, respectively. With this in mind, we argue that although warming climates may well lead to rapid changes in the morphology of endotherms, consistent and generalized responses of shrinking body sizes and elongating extremities are doubtful.

Although supported by decades of empirical literature, we recognise that our mechanistic hypotheses and conclusions remain largely theoretical. To better interrogate each, we suggest that future research emphasis be placed in three main areas:

1. *The functional or adaptive significance of Bergmann's and Allen's rule:* Adjustments in body size and extremity length that both recapitulate Bergmann's and Allen's Rules and track a warming climate are expected to: (i) endow individuals with thermal/ energetic benefits and, (ii) carry implicit fitness advantages (e.g. Youngflesh et al. 2022). Nevertheless, both the precise thermal advantages of conforming with Bergmann's and Allen's rules, and their links to organismal fitness, remain surprisingly understudied and may even be insignificant when compared from those obtained by acutely changing thermoregulatory behaviours, blood flow patterns, thermogenesis, and evaporative cooling (Scholander, 1955; McNab, 1971, 2010; Briscoe et al, 2015; but see Steudel, 1994). For this reason, we recommend that future studies evaluate empirically the thermoregulatory benefit of each rule, either in the laboratory using respirometry, or in the wild by combining infrared

thermography and biophysical modeling (McCafferty et al. 2011), and attempt to put these insights into a context of survival and reproductive performance within a changing world. Doing so will inform on the evolutionary meaning of climate change-induced changes in body size and shape. In this context, it will also be important to address whether developmental temperature to size/shape correlations are broadly generalizable across males and females of a species with references to any sex-linked variation in the strength of selection for size or shape for non-thermoregulatory reasons (e.g., fecundity- or propagule size-selection in females; cf. Ronget et al. 2018).

2. *The relative contributions of environmental, genetic, and genotype-by-environment effects toward Bergmann's and Allen's rule:* Our review highlights that environmental effects contribute to the emergence of temperature-to-phenotype relationships known as Bergmann's and Allen's rule. However, genetic contributions toward each are also well supported (Teplitsky et al, 2008; Ozgul et al, 2009; Ballinger and Nachmann, 2022) and some studies have even elucidated a combination of genetic and the environmental contributions (i.e., genotype-by-environment effects; Harrison et al, 1955; Barnett, 1965). To help disentangling the precise contributions of each of these effects — and thus understand how matching of body size and shape to a given thermal environment might evolve — more studies leveraging full-sib breeding designs (e.g., Ballinger and Nachmann, 2022), particularly in wild taxa, are needed. Such studies could either be undertaken on wild-caught subjects reared in controlled and varying environments (see Ballinger & Nachman, 2022), or could be based on reciprocal transplant experiments (e.g., as is possible over wide latitudinal ranges in birds; Broggi et al, 2005). Captive models can still be highly useful in this endeavor, however, only on the premise of retained thermal plasticity of phenotypic traits (Morgan et al, 2022).

3. *The proximate underpinnings of plastic responses to developmental temperature:* Our study sought to evaluate: (i) evidence backing plastic contributions toward Bergmann's and Allen's rule, and (ii) support for key hypotheses describing how, at the whole animal level, such plastic contributions might emerge. As such, the precise physiological or molecular drivers behind any temperature-dependent plasticity that might recapitulate Bergmann's and Allen's rule fell beyond the scope of our study. Nevertheless, uncovering these drivers

is critical if we wish to fully appraise our whole animal level hypotheses raised above. With respect to Bergmann's rule, Weeks et al (2022) recently speculated that temperature dependence of insulin-like growth factors (namely IGF1) may influence the emergence of temperature-size relationships within avian species. Understanding how IGFs respond quantitatively and qualitatively to ambient temperature would provide valuable insight on the likelihood of our Thermal Advantage or Energy Efficiency Hypotheses toward Bergmann's rule (Fig. 1). With respect to Allen's rule, *in vitro* experiments by Serrat et al (2008) have shown that heat exposure may directly increase elongation of extremities by speeding rates of endochondral ossification (discussed above). Assessing the strength of this effect *in vivo*, and whether it breaks down or plateaus at ambient temperatures where dry heat loss is no longer useful for thermoregulation would strongly enable comparative evaluations of the Exaptation and Thermal Advantage Hypotheses, but will require experimental approaches that separate the direct, emergent effects of temperature on tissue temperature and cell growth rate from any indirect effects of temperature perception by the animal.

Evaluating the functional significance, genetic contributions, and fine-scale mechanistic drivers of Bergmann's and Allen's rule are critical next steps to understanding how quickly these rules might emerge and whether they may do so adaptively. More importantly, doing so will be essential if we wish to generate accurate forecasting models for animal morphology in a warming world. We hope that the points raised in this commentary, and the practical framework concluding it, will be inspiring for future research into animals, temperature, and morphological change within and beyond global warming contexts.

Figures and Text Boxes

Please note that each box is to contain one figure; box 1 contains figure 1, and box 2 contains figure 2.

Box 1 | How may plastic responses to developmental temperatures explain Bergmann's rule in endotherms? Intra-specifically, Bergmann's rule states that the body size (and thus, surface-area to volume ratios) of conspecific endotherms is typically larger in cooler ambient temperatures than in warmer ambient temperatures. This negative correlation between size and ambient temperature is generally thought to reduce the costs of thermoregulation by slowing rates of heat loss in the cold, and increase the rates of heat loss in the warmth.

We contrast two hypotheses explaining how plastic responses to temperature during post-natal development may lead to Bergmann's rule-like patterns within endothermic species: the Thermal Advantage Hypothesis, and the Energy Efficiency Hypothesis. The Thermal Advantage Hypothesis posits that cooler temperatures lead to increases in cumulative growth during development, thus increasing adult body size and decreasing total costs of thermoregulation at maturity. Here, increases in growth in the cold (and, therefore, final body size) occur despite, and concurrent with, higher energetic costs of heat production (Fig 1A). A seldom-discussed nuance to this hypothesis, and Bergmann's rule, is that correlations between body size and ambient temperature should diminish at extreme temperatures, when constraints from other fitness-related traits (e.g. fecundity and locomotion) are imposed on body size (Fig. 1A). Contrasting the Thermal Advantage 'Hypothesis, the Energy Efficiency Hypothesis posits that ambient temperature influences cumulative growth during development by: (1) setting limitations on the amount of resources available for growth by dictating the energy cost of thermoregulation, and (2) determining energy assimilation rates. Under this hypothesis, the relationship between body size (via cumulative growth) and ambient temperature is best represented by a skewed-quadratic, with apex at the temperature of maximal energy assimilation and x-intercepts *near* the upper and lower inflection points of a species' prescriptive or thermoneutral zone (Mitchel et al. 2018; Fig. 1B). The term "near" is emphasized to acknowledge that other physiological parameters, including heat substitution from growth, parental care strategies, and strategies for mass deposition (i.e., muscle vs. fat; see Heath, 1983) are likely to influence their true locations. In Fig. 1B, this uncertainty is indicated by light-grey bands. Skewness of this temperature-growth relationship is negative, with decreases in growth occurring faster at high ambient temperatures, since: (1) endotherms are often heterothermic or poikilothermic during development (see Whittow and Tazawa, 1991; Geiser, 2008), and (2) the rates of metabolic processes increase most rapidly with increasing tissue/body temperatures (see Mundim et al, 2020).

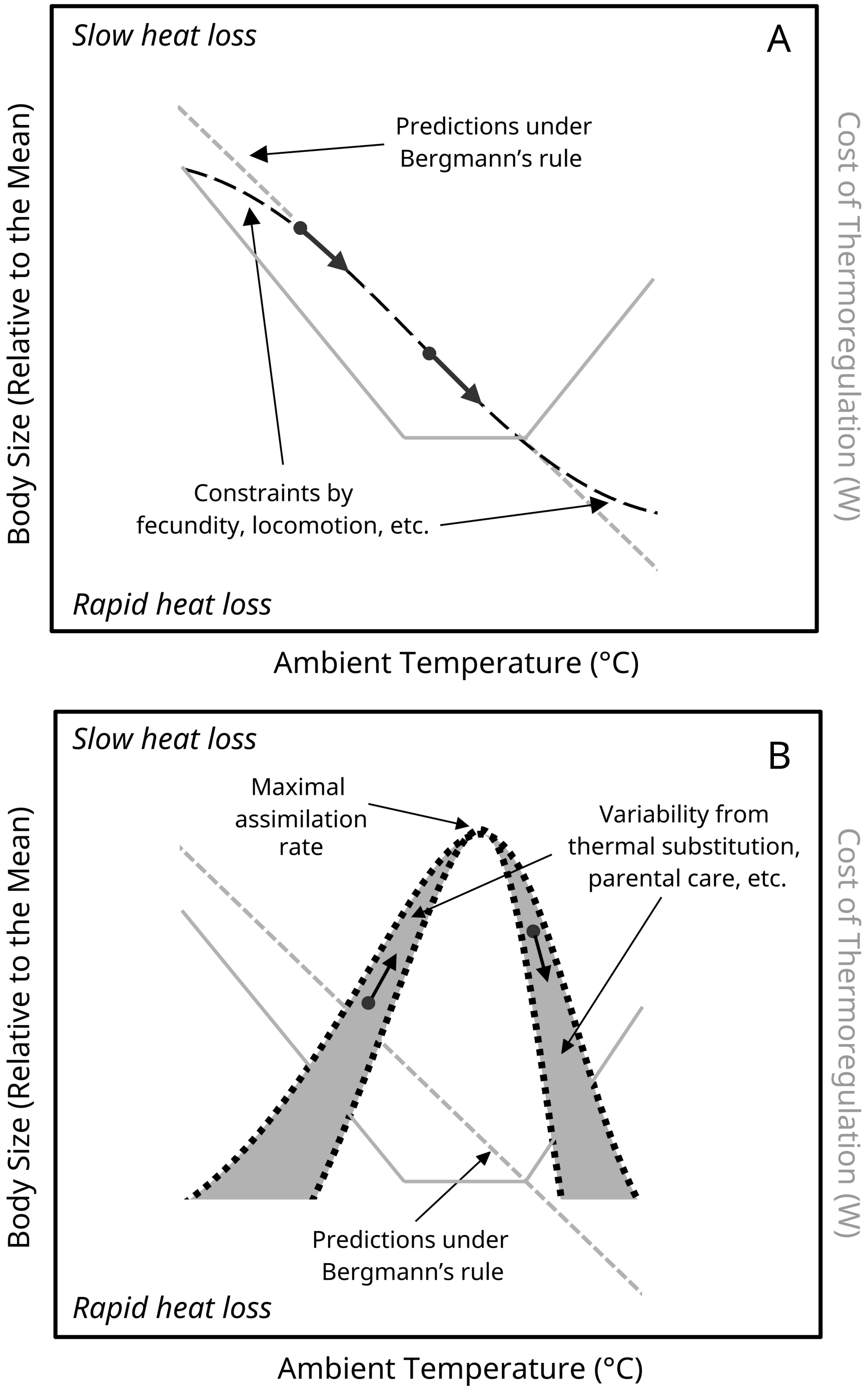

Figure 1 | Predicted effects of ambient temperature on body size of developing endotherms under two plastic hypotheses of Bergmann's rule. Panel **A** outlines predicted effects under the Thermal Advantage Hypothesis, and panel **B** outlines predicted effects under the Energy Efficiency Hypothesis. Black lines indicate patterns of relative body size (left *y*-axis) for a model endotherm, and grey lines indicate expected costs of thermoregulation (right *y*-axis) for the same species. Black dots represent two conspecific endotherms and arrows leading from dots represent predicted changes in their body size in response to a warming environment. The classic prediction of Bergmann's rule (i.e., a negative linear correlation between ambient temperature and body size) is displayed with dashed grey lines and expected rates of heat loss for a given relative body mass (e.g. rapid or slow) are indicated on each panel. Conformation with Bergmann's Rule is likely constrained by numerous biological processes at extreme small and large body sizes; a select set of examples (i.e., fecundity and locomotion) of which are provided in the figure panel. The thermoneutral zone (TNZ), where costs of thermoregulation are minimal and independent of ambient temperature, are intentionally narrow to emphasise predictions at temperatures both below and above the lower- and upper critical temperatures respectively (delimiting the TNZ), where most endotherms are likely to reside (see Škop et al, 2020, for an example). Note that the exact shape of curves and position of inflection points are hypothetical and will likely vary between both species and environments.

Box 2 | How may temperature-dependent, developmental plasticity explain Allen's rule in endotherms? Allen's rule states that the bodily extremities of both conspecific and heterospecific endotherms are usually shorter in cooler ambient temperatures than in warmer ambient temperatures (Allen, 1877). Like Bergmann's rule, Allen's rule is typically explained in thermoregulatory terms, with shortened extremities enhancing heat retention in the cold and elongated extremities enhancing heat loss in the warmth.

Most parsimoniously, increasing ambient temperatures may lead to plastic elongation of extremities throughout development via either: (1) adaptive plasticity to reduce heat loss in the cold and increase heat loss in the warmth (the Thermal Advantage Hypothesis), or (2) direct and not-always-adaptive temperature effects on cell proliferation and metabolism(the Exaptation Hypothesis). Under the Thermal Advantage Hypothesis, elongation of extremities is expected to slow, stop, or even reverse when benefits to heat dissipation are no longer evident (indicated by a zero body-to-ambient temperature gradient on the secondary *x*-axis in Fig. 2). By contrast, under the Exaptation Hypothesis, extremities should elongate with increasing ambient temperatures regardless of any heat dissipation benefits. In the cold, both hypotheses predict a continuous decrease in extremity length since such decreases may occur either as a direct effect of ambient heat loss or an indirect effect of selection to decrease extremity surface area and, thus, heat loss. As such, phenotypic trends at these temperatures should not be informative when seeking to distinguish between each hypothesis. Limits to extremity lengths under both hypotheses, and in both temperature extremes of the range, are determined by constraints from other fitness-related traits such as locomotion and feeding.

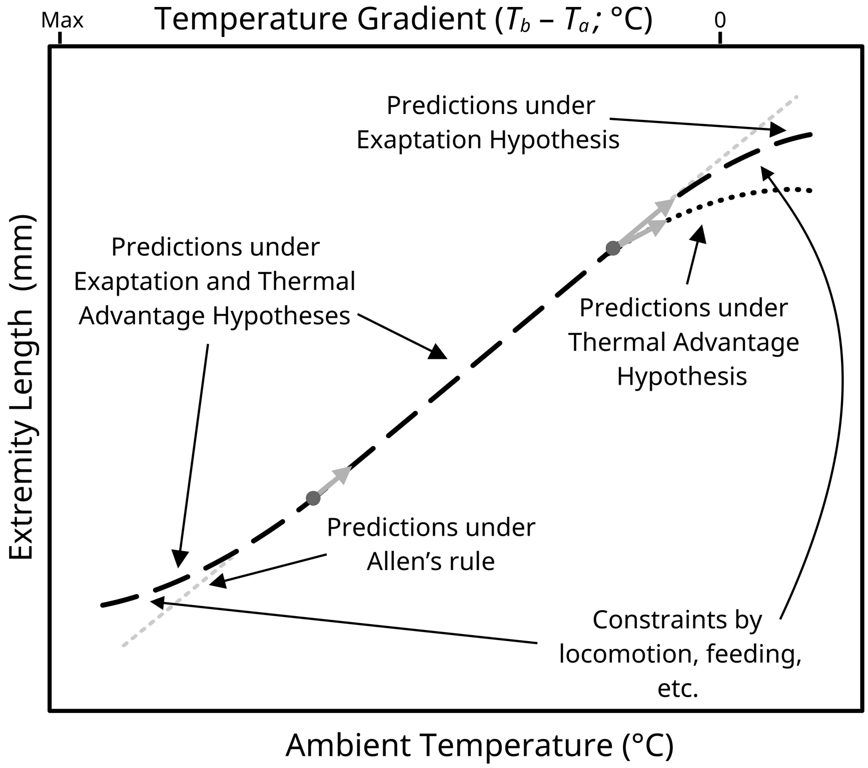

Figure 2 | Predicted effects of ambient temperature on the developmental elongation of bodily extremities in endotherms. The dotted grey line indicates the classic expectation under Allen's rule, that there is a positive linear correlation between ambient temperature and extremity length. Similar to Bergmann's rule, complete conformation with Allen's rule is likely to be constrained by certain biological processes at size extremes; two relevant examples (i.e., locomotion and feeding) are provided. Black dots represent two model endotherms and grey arrows leading from dots represent predicted changes in their extremity lengths in a warming environment. These dots highlight difference growth trajectories depending on whether appendage elongation follows predictions under the Thermal Advantage Hypothesis or the Exaptation Hypothesis. Distinctions between these trajectories are predicted to manifest at high ambient temperatures alone, when dry heat loss to the environment becomes less significant and ultimately reversed (i.e. when the environment is warmer than the animal). For example, if extremities lengthen in the warmth under the Thermal Advantage Hypothesis, then there should be no further increase in length when ambient temperature (T_a) surpasses body temperature (T_b) and dry heat loss becomes negative (indicated by 0 on the secondary *x*-axis).

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