Title: Temperature-dependant, developmental plasticity and its effects on Allen's and James' rule in endotherms

Running title: Phenotypic plasticity and ecogeographical rules

Authors: Joshua K.R. Tabh[1]*, Andreas Nord[1]

Affiliations: [1] Department of Biology, Section for Evolutionary Ecology, Lund University, Lund, Sweden

* Indicates primary contact

Email: joshua.tabh@biol.lu.se

Author Contributions: JKRT and AN conceptualised the paper, JKRT wrote the first draft of the manuscript, AN and JKRT contributed to manuscript revisions.

Acknowledgments: We thank Elin Persson, Elisa Thoral, Sofie Mohlin, Emma Hammarlund, Cecilia Lundberg, Luis Quintino, and all member of Lunds Universitets Tissue Development and Evolution (TiDE) group for their insights into the development of this manuscript.

Funding: JKRT was supported by a postdoctoral grant from the Wenner-Gren Foundation (UPD2021-0038). AN was supported by the Swedish Research Council (2020-04686).

Abstract

Ecogeographical rules, describing common trends in animal form across space and time, have provided key insights into the primary factors driving species persistence on our planet. Among the most well-known ecogeographical rules are James' rule (an intraspecific variant of 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 gained 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 facilitate species persistence in a warming world. Yet despite this attention, the precise proximate and ultimate drivers of James' and Allen's rules remain unresolved. In this paper, we review over a century of empirical literature surrounding these rules and ask whether each could be explained by plastic effects of developmental temperature on adult phenotype among endotherms. Across birds and mammals, studies strongly support developmental plasticity as a driver of James' and Allen's rules, particularly with regards to Allen's rule and responses to heat. However, we find that plastic contributions toward each are non-linear and probably depend on: (1) efficiency of energy use at given ambient temperatures (James' 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 generalising the direction of responses across populations (e.g. as "shrinking" or "shape-shifting") 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 an organism’s first line of defense in a novel or changing environment (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 body 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 intraspecifically, James’ rule;

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 could indeed 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 paper, we first review over a century of empirical literature to evaluate the hypothesis that plastic responses to the thermal environments, specifically during post-natal development, give rise to intra-specific variants of Bergmann's rule (henceforth, James' rule) and Allen's rule. Next, using novel theoretical frameworks, we compare this literature against specific hypotheses about *how* such developmental plasticity might operate. With these objectives, our goal is to generate a lense through which: (1) an influence of the thermal environments on endotherm size and shape might be understood, and (2) effects of a changing climate on endotherm phenotype may be predicted.

James' rule (Bergmann's rule within species)

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 hottly-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 its interpretation (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 at the species level. However, given that the drivers (both proximate and ultimate) of body size clines probably differ within and among species, some have called for a division in nomenclature, with intra-specific trends being referred to as James' rule rather than Bergmann's rule (in honor of Frances James; Blackburn et al, 1999). Indeed, although both "rules" could be explained by selective responses to temperature, or even range shifts in animal populations over time and space, James' rule alone permits the possibility that temperature-body size correlations are explained by phenotypic plasticity.

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 James' 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 body size, should correlate linearly 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; Box 1; Fig. 1a). Under the Energy Efficiency Hypothesis, however, correlates between cumulative growth 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 (Box 1; Fig. 1b). The points at which net growth becomes negative (i.e., y-intercepts) should then lay at ambient temperatures where energetic costs of thermoregulation begin to compete with, and compromise, those of growth (Box 1; Fig. 1b).

If James’ 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 James’ rule in endotherms, and (2) indication that any plastic origin to James’ rule conforms more closely with the Thermal Advantage Hypothesis or the Energy Efficiency Hypothesis.

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

Controlled experiments, whereby ambient temperature 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 James’ rule, the average mass of cold- and warm-reared mice was strikingly similar at 6 weeks of age (the end of maximum growth; 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. Lower still 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 subtle *decrease* in body mass (6%) among cold-reared mice (7°C) relative to warm-reared mice (27°C) at 12 weeks of age. These findings are not only inconsistent with expectations of James’ 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 James' 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 similarly complicated picture of how developmental cold exposure influences adult phenotype is emerging. In Japanese quail (*Coturnix japonica*), Burness et al (2013) reported no effect of rearing young at 15°C from 5 days of age on body mass at maturity when compared with 30°C controls. 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 onwards leads to *negative* effects on adult body mass, not positive, with cold-reared birds weighing 7% smaller at maturity than those reared in the warmth (30°C; Persson, E., et al., *unpublished*). Snedecor (1971) and Swain and Farrell (1975) reported similar ends, with body masses of domestic chickens being higher when rearing temperatures were intermediate (25°C) or cycled around intermediate (between 5°C and 20°C) rather than cold (15°C or 5°C respecively). 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, 2006a; Teulier et al, 2014).

Contrasting results from cold-exposure studies, those obtained from experimental heat exposures generally support expectations of James' 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 purported 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 James’ 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, 2006a; 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.

James’ 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 ranges of ambient temperatures, it is nonetheless-likely that the thermal sensitivity of body size during development does contribute to James’ 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 James’ rule are unlikely to be explained by selection for thermal benefit alone (i.e. the Thermal Advantage Hypothesis; Box 1; Fig. 2).

Instead, these findings better align with the hypothesis that plastic contributions to James' rule are driven by selection to increase efficiency of energy use in a given thermal environment (i.e., the Energy Efficiency Hypothesis; Box 1; 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; Box 1; Fig. 1b). More specifically, if experimental heat exposures push developmental temperatures into ranges that decrease costs of thermogenesis and increase energy assimilation rates, then plastic *increases,* not decreases, in body mass should be expected. Such an increase was observed byDawson et al.(2005), where heating of tree swallow (*Tachycineta bicolor*) nests raised developmental tempeartures to within thermoneutrality (i.e., 30°C*;* Williams, 1988) during development. By contrast, if heat exposures push developmental temperatures into ranges that increase costs of heat dissipation and decrease energy assimilation rates, then plastic *decreases* in body mass should be expected (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). With these observations in mind, we argue 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 James' rule and species-level responses to climatic change.

Allen's rule

Allen's rule stats 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, the original writing 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

Interestingly, 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 as 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 minimize and maximize heat loss in each environment respectively (i.e. the "Thermal Advantage Hypothesis" under Allen's rule; Box 2; Fig. 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, temperature-mediated plasticity of extremity length is not a result of natural selection for thermal advantage, but still provides energetic benefits (similar to an evolutionary spandrel; Gould and Lewontin, 1979).

There are likely several routes in which temperature-extremity length relationships might emerge as byproducts. However, one that has attracted particular attention implicates a role of peripheral vasculature (the "Vascularity Hypothesis"; Serrat et al, 2008; Serrat, 2014). Under this hypothesis, vasoconstriction in the cold limits the capacity of peripheral vasculature to delivery oxygen, nutrients, growth factors, and even heat, to growing extremities, thus limiting their rates at which elongation can occur. Likewise, by vasodilation in the warmth, the capacity of the peripheral vasculature to deliver the same nutrients, growth factors, and heat is enhanced, thus spurring their elongation (Box 2; Fig. 2). A critical yet subtle aspect of this hypothesis is that the effects of ambient temperature on total growth of extremities is both indirect via stimulation of vasomotor responses, and direct via influence over the local temperature of growth sites (see Serrat et al 2008; Serrat, 2014). Thus, the Thermal Advantage and Vascularity Hypotheses yield different predictions for 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 (Box 2; Fig. 2). By contrast, under the Vascularity Hypothesis, elongation of extremities in the heat should continue as temperatures rise regardless of whether advantages to heat loss exist or not (Box 2; 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 should be similar since stunting of extremity growth should continue to provide thermal advantages even at extreme low temperatures (Box 2; 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 respond 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 Vascularity 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, for example, 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).

Despite a comparative lack of studies, an effect of developmental cold exposure on the elongation of bodily extremities is also emerging in birds. In great tits (*Parus major*), cooling of nests by 5°C after hatching led to a 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 reduction in bill length near fledging (in Red-winged blackbirds, *Agelaius phoeniceus*; NeSmith, 1985), while in the other rearing temperature elicited no effect on bill length at maturity (in Japanese quail; Burness et al, 2013). Most observations among both birds and mammals, therefore, point toward a negative effect of low developmental temperatures on elongation of extremities, which could well explain morphometric clines recognized as Allen’s rule.

Studies measuring how extremity lengths respond to heat exposure are scarce, particularly with heat treatments nearing or exceeding body temperature. 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 Vascularity 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 intruiging (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 intraspecific 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 Vascularity 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 Vascularity 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 large, 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 James’ 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

Phenotypic plasticity is often implicated as the first line of defense in novel or changing environments (Bradshaw, 1965; West-Eberhard, 1989; Brooker at al, 2021). In the context of development, empirical studies across numerous endotherm taxa indicate that both body size and the lengths of bodily extremities are labile and can differ according to thermal environments experienced during post-natal development. Further, this lability often recapitulates the classic phenotypic clines known as James’ 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 lead to plastic reductions in body size and increases in extremity length (following James' 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 significance of James' and Allen's rule:* Both James' and Allen's rule are often assumed to provide thermal advantages by reducing either costs of thermoregulation or risk of heat stress in a given thermal environment (discussed above). By extension, changes in both extremity length and body size that recapitulate each rule and track a warming climate are commonly thought to endow individuals with thermal and energetic advantages (e.g. Youngflesh et al. 2022). Nevertheless, the precise thermal advantages of conforming with James' and Allen's rules 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 modelling (McCafferty et al. 2011). 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 James' and Allen's rule:* Our review clearly highlights that environmental effects contribute to the emergence of temperature-to-phenotype relationships known as James' 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 supported 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 James' 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 James' 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 James' rule, Weeks et al (2022) recently speculated that temperature dependance of insulin-like growth factors may influence the emergence of temperature-size clines within avian species. Understanding whether these growth factors respond linearly or curvilinearly to declining ambient temperatures would provide valuable insight on the likelihood of our Thermal Advantage or Energy Efficiency Hypotheses toward James' rule (Fig. 1). Further, 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. Assessing the strength of this effect *in vivo* would strongly enable comparative evaluations of the Vascularity 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 James' 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 James' rule in endotherms? James' 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. Similar to Bergmann's rule (Bergmann, 1847), 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.

In this conceptual study, we contrast two hypotheses explaining how plastic responses to temperature during post-natal development may lead to a James' rule-like patterns in endotherms: 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 James' 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 y-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 emphasised 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).

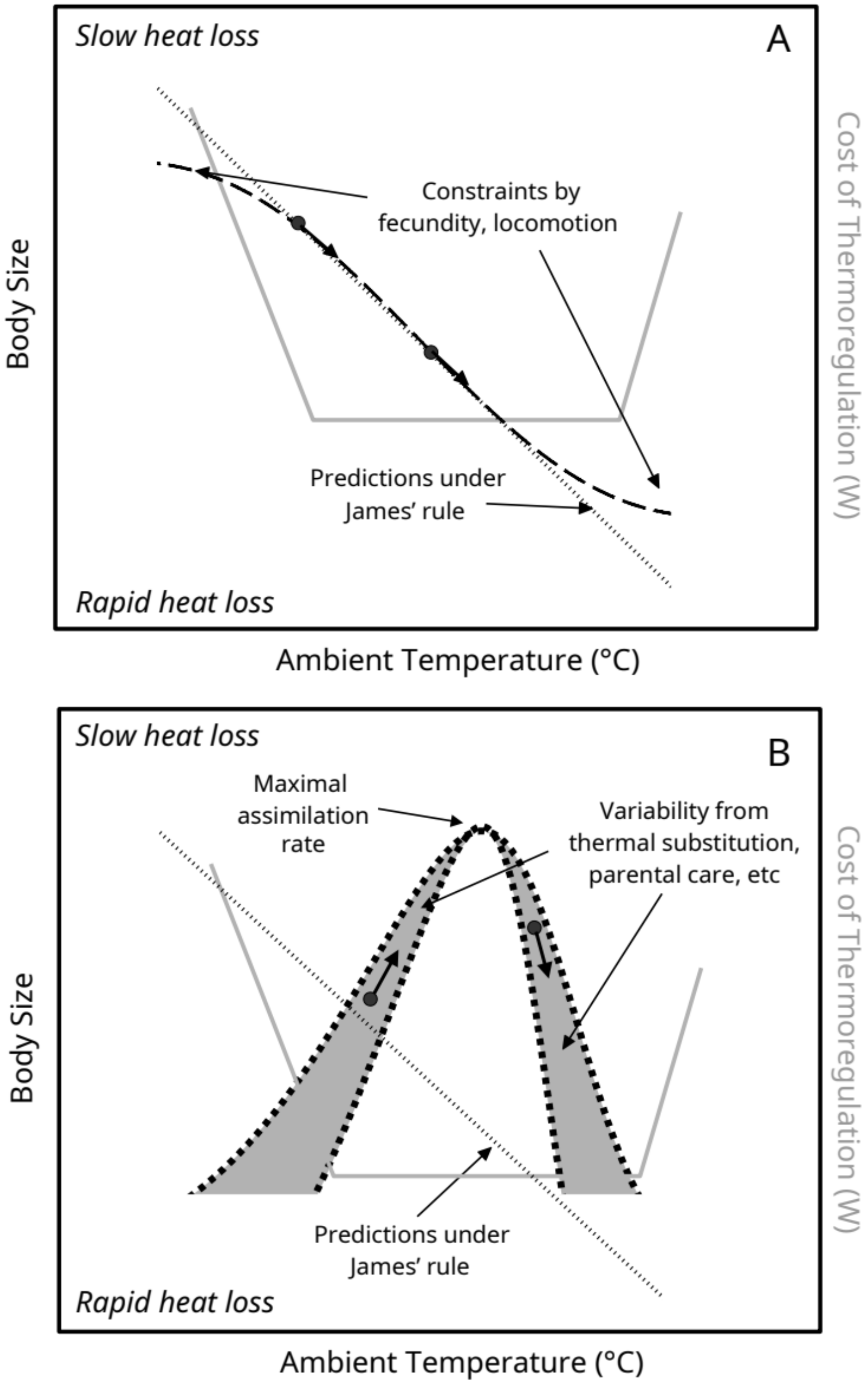

Figure 1 | Predicted effects of ambient temperature on body size of developing endotherms under two plastic hypotheses of James' rule. Panel **A** outlines predicted effects under the Thermal Advantage Hypothesis, and panel **B** outlines predicted effects under the Energy Efficiency Hypothesis. Black lines indicate patterns of 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 James' rule (i.e., a negative linear correlation between ambient temperature and body size) is displayed with dotted lines.

Box 2 | How may temperature-dependant, 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 both James' and 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 temperature effects on cell proliferation and metabolism, mediated by changes in peripheral blood flow and local tissue temperature (the Vascularity Hypothesis). Under the Thermal Advantage Hypothesis, elongation of extremities is expected to slow or stop when benefits to heat dissipation are no longer evident (indicated by a zero body to ambient temperature gradient [upper x-axis] in Fig 2). By contrast, under the Vascularity 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.

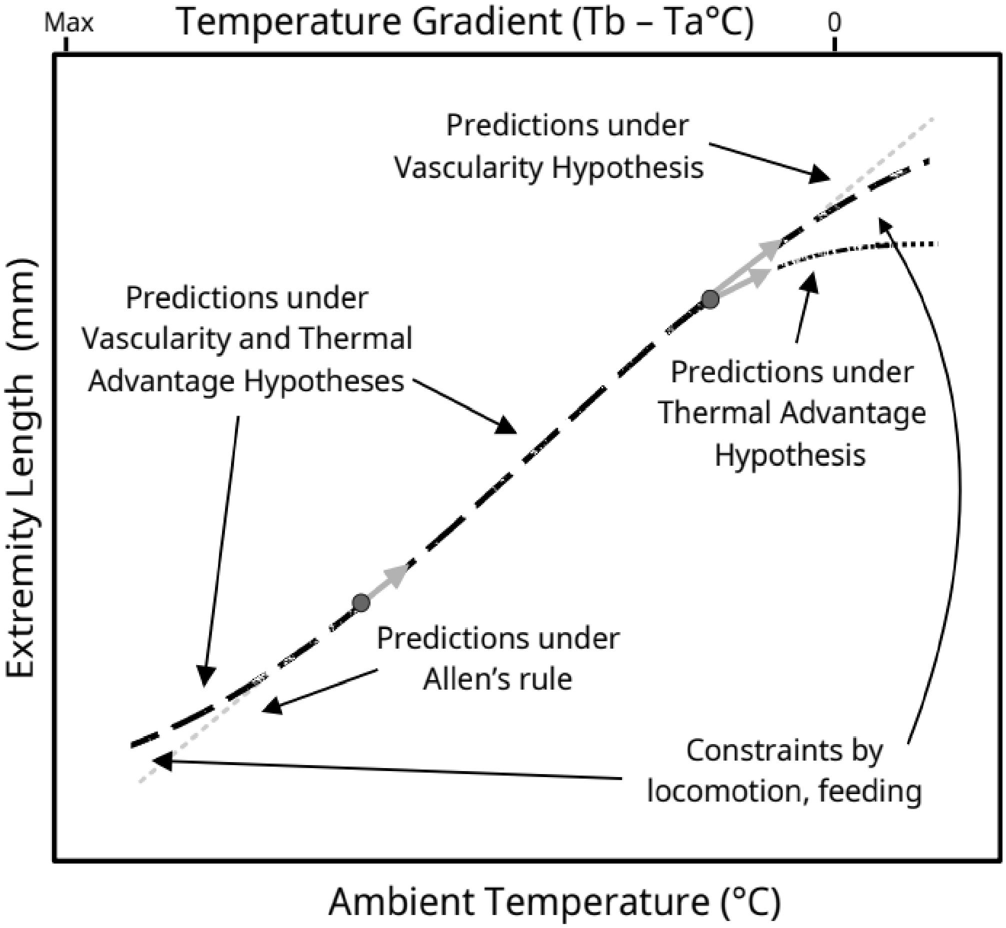

Figure 2 | Predicted effects of ambient temperature on the developmental elongation of bodily extremities in endotherms. The dotted grey line indicates the classic expectation under Allen's rule, that there is a positive linear correlation between ambient temperature and extremity length. Black dots represent two model endotherms and grey arrows leading from dots represent predicted changes in their extremity lengths in a warming environment. These show different growth trajectories depending on whether appendage elongation follows predictions under the Thermal Advantage Hypothesis or Vascularity Hypothesis 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 surpasses body temperature (and dry heat loss becomes negative; indicated by 0 on the secondary x-axis).

References

Abreu-Vieira G, Xiao C, Gavrilova O, Reitman ML. 2015. Integration of body temperature into the analysis of energy expenditure in the mouse. *Mol Metab.* 4:461-470.

Adamsons K, Blumberg E, Joelsson I. 1969. The effect of ambient temperature upon post-natal changes in oxygen consumption of the guinea-pig. *J Physiol.* 202:261-269.

Alatalo RV, Lundberg A. Heritability and selection on tarsus length in the pied flycatcher (*Ficedula hypoleuca*). *Evol.* 40:574-583.

Albustanji L, Perez GS, Alharethi E, Aldiss P, Bloor I, Barreto-Medeiros JM, Budge H, Symonds ME, Dellschaft N. 2019. Housing temperature modulates the impact of diet-induced rise in fat mass on adipose tissue before and during pregnancy in rats. *Front Physiol.* 10:209.

Alhajeri BH, Fourcade Y, Upham NS, Alhaddad H. 2020. A global test of Allen’s rule in rodents. *Glob Ecol Biogeogr.* 29:2248-2260.

Al-Hilli F, Wright EA. 1983. The effects of changes in the environmental temperature on the growth of tail bones in the mouse. *Br J Exp Pathol.* 64:34-42.

Alisauskas RT, Ankney CD. 1990. Body size and fecundity in Lesser Snow Geese. *Auk.* 107:440-443.

Allen JA. 1877. The influence of physical conditions in the genesis of species. *Radic Rev.* 1:108-140.

Alroy J. 2019. Small mammals have big tails in the tropics. *Glob Ecol Biogeogr.* 28:1042-1050.

Andreasson F, Nord A, Nilsson JÅ. 2018. Experimentally increased nest temperature affects body temperature, growth and apparent survival in blue tit nestlings. *J Avian Biol.* 49:jav-01620.

Andrew SC, Hurley LL, Mariette MM, Griffith SC. 2017. Higher temperatures during development reduce body size in the zebra finch in the laboratory and in the wild. *J Evol Biol.* 30:2156-2164.

Ashoub MER. 1958. Effect of two extreme temperatures on growth and tail-length of mice. *Nature.* 181:284-284.

Ashton KG. 2002. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Glob Ecol Biogeogr.* 11:505-523.

Ashton KG, Tracy MC, Queiroz AD. 2000. Is Bergmann's rule valid for mammals?. *Am Nat.* 156:390-415.

Barnett SA. 1965. Genotype and environment in tail length in mice. *Q J Exp Physiol Cogn Med Sci.* 50:417-429.

Barnett SA, Dickson RG. 1984. Changes among wild house mice (*Mus musculus*) bred for ten generations in a cold environment, and their evolutionary implications. *J Zool.* 203:163-180.

Baur E. 1919. Einführung in die experimentelle Vererbungslehre. Gebrüder Borntraeger, Berlin.

Benítez-López A, Santini L, Gallego-Zamorano J, Milá B, Walkden P, Huijbregts M. A, Tobias JA. 2021. The island rule explains consistent patterns of body size evolution in terrestrial vertebrates. *Nat Evol Ecol.* 5:768-786.

Bergmann K. 1847. Über die Verhältnisse der wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien.* 3:595-708.

Blackburn TM, Gaston KJ, Loder N. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. *Divers Distr.* 5*:*165-174.

Bonsall M, Charlesworth B. 2010. Genetics and the causes of evolution: 150 years of progress since Darwin. *Philos Trans R Soc.* 365:2427-2429.

Boutin S, Lane JE. 2014. Climate change and mammals: evolutionary versus plastic responses. *Evol Appl.* 7*:*29-41.

Boyer AG, Cartron JLE, Brown JH. 2010. Interspecific pairwise relationships among body size, clutch size and latitude: deconstructing a macroecological triangle in birds. *J Biogeogr.* 37:47-56.

Bradshaw AD. 1965. Evolutionary significance of phenotypic plasticity in plants. *Adv Genet.* 13:115-155.

Briscoe NJ, Krockenberger A, Handasyde KA, Kearney MR. 2015. Bergmann meets Scholander: geographical variation in body size and insulation in the koala is related to climate. *J Biogeogr.* 42:791-802.

Broggi J, Hohtola E, Orell M, Nilsson JÅ. 2005. Local adaptation to winter conditions in a passerine spreading north: A common-garden approach. *Evol.* 59:1600-1603.

Brooker R, Brown LK, George TS, Pakeman RJ, Palmer S, Ramsay L, Schöb C, Schurch N, Wilkinson MJ. 2021. Adaptive plasticity - its definition, measurement, and importance. *OSF Preprints.* doi: https://doi.org/10.31219/osf.io/6veyu.

Burness G, Huard JR, Malcolm E, Tattersall GJ. 2013. Post-hatch heat warms adult beaks: irreversible physiological plasticity in Japanese quail. *Proc R Soc B: Biol Sci.* 280:20131436.

Cheung TK, Parker RJ. 1974. Effect of selection on heritability and genetic correlation of two quantitative traits in mice. *Can J Genet Cytol.* 16:599-609.

Cunningham SJ, Martin RO, Hojem CL, Hockey PA. 2013. Temperatures in excess of critical thresholds threaten nestling growth and survival in a rapidly-warming arid savanna: a study of common fiscals. *PLoS One.* 8:e74613.

Darwin C. 1859. The origin of species; and, the descent of man. Modern Library, New Yok, USA.

Darwin C. 1868. The variation of animals and plants under domestication. John Murray, London, UK.

Dawson RD, Lawrie CC, O'Brien EL. 2005. The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. *Oecologia.* 144:499-507.

Ernst RA, Weathers WW, Smith, J. 1984. Effects of heat stress on day-old broiler chicks. *Poult Sci.* 63:1719-1721.

Fan L, Cai T, Xiong Y, Song G, Lei F. 2019. Bergmann's rule and Allen's rule in two passerine birds in China. *Avian Res.* 10:1-11.

Geiser F. 2008. Ontogeny and phylogeny of endothermy and torpor in mammals and birds. *Comp Biochem Physiol A: Mol Integr Physiol.* 150:176-180.

Geist V. 1987. Bergmann's rule is invalid. *Can J Zool.* 65:1035-1038.

Geist V. 1990. Bergmann's rule is invalid: a reply to JD Paterson. *Can J Zool.* 68(7):1613-1615.

Gohli J, Voje KL. 2016. An interspecific assessment of Bergmann’s rule in 22 mammalian families. *BMC Evol Biol.* 16:1-12.

Gould SJ, Lewontin RC. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc R Soc B: Biol Sci.* 205:581-598.

Gutiérrez-Pinto N, McCracken KG, Alza L, Tubaro P, Kopuchian C, Astie A, Cadena CD. 2014. The validity of ecogeographical rules is context-dependent: testing for Bergmann's and Allen's rules by latitude and elevation in a widespread Andean duck. *Biol J Linn Soc.* 111:850-862.

Freckleton RP, Harvey PH, Pagel M. 2003. Bergmann’s rule and body size in mammals. *The American Naturalist*, *161*(5), 821-825.

Hansson L. 1985. Geographic differences in bank voles Clethriononys glareolus in relation to ecogeographical rules and possible demographic and nutritive strategies. *Ann Zool Fenn.* 22*:*319-328.

Harrison GA, Morton RJ, Weiner JS. 1959. The growth in weight and tail length of inbred and hybrid mice reared at two different temperatures i. Growth in weight ii. Tail length. *Phil Trans R Soc B; Biol Sci.* 242:479-516.

Heath ME. 1983. The effects of rearing-temperature on body composition in young pigs. *Comp Biochem Physiol A: Physiol.* 76:363-366.

Heath ME. 1984. The effects of rearing-temperature on body conformation and organ size in young pigs. *Comp Biochem Physiol B: Comp Biochem.* 77:63-72.

Herrington LP, Nelbach JH. 1942. Relation of gland weights to growth and aging processes in rats exposed to certain environmental conditions. *Endocrinol.* 30:375-386.

Huynh TTT. 2005. Heat stress in growing pigs. PhD Dissertation, Wageningen University.

James FC. 1970. Geographic size variation in birds and its relationship to climate. *Ecol.* 5:365-390.

James FC. 1991. Complementary descriptive and experimental studies of clinal variation in birds. *Am Zool.* 31:694-706.

Johnson JS, Aardsma MA, Duttlinger AW, Kpodo KR. 2018. Early life thermal stress: Impact on future thermotolerance, stress response, behavior, and intestinal morphology in piglets exposed to a heat stress challenge during simulated transport. *J Anim Sci.* 96:1640-1653.

Jonassen TM, Imsland AK, Stefansson SO. 1999. The interaction of temperature and fish size on growth of juvenile halibut. *J Fish Biol.* 54:556-572.

Knudsen B. 1962. Growth and reproduction of house mice at three different temperatures. *Oikos*. 13:1-14.

Krijgsveld KL, Visser GH, Daan S. 2003. Foraging behavior and physiological changes in precocial quail chicks in response to low temperatures. *Physiol Behav.* 79:311-319.

Kurnianto E, Shinjo A, Suga D. 1997. Comparison of the three growth curve models for describing the growth patterns in wild and laboratory mice. *J Vet Epidemiol.* 1:49-55.

Lee MM, Chu PC, Chan HC. 1969. Effects of cold on the skeletal growth of albino rats. *Am J Anatom.* 124:239-249.

Marchini CFP, Silva PL, Nascimento MRBM, Beletti ME, Silva NM, Guimarães EC. 2011. Body weight, intestinal morphometry and cell proliferation of broiler chickens submitted to cyclic heat stress. *Int J Poult Sci.* 10:455-460.

May JD, Lott BD. 2001. Relating weight gain and feed: gain of male and female broilers to rearing temperature. *Poult Sci.* 80:581-584.

Mayr E. 1956. Geographical character gradients and climatic adaptation. *Evol.* 10:105-108.

McNab BK. 1971. On the ecological significance of Bergmann's rule. *Ecol.* 52:845-854.

McNab BK. 2010. Geographic and temporal correlations of mammalian size reconsidered: a resource rule. *Oecologia.* 164:13-23.

McQueen A, Klaassen M, Tattersall GJ, Atkinson R, Jessop R, Hassell CJ, Christie M, Victorian Wader Study Group, Australasian Wader Studies Group, Symonds MR. 2022. Thermal adaptation best explains Bergmann's and Allen's Rules across ecologically diverse shorebirds. *Nat Comm.* 13:4727.

Meiri S. 2011. Bergmann's Rule–what's in a name?. *Glob Ecol Biogeogr.* 20:203-207.

Meiri S, Dayan T. 2003. On the validity of Bergmann's rule. *J Biogeogr.* 30:331-351.

Meiri S, Guy D, Dayan T, Simberloff D. 2009. Global change and carnivore body size: data are stasis. *Glob Ecol Biogeogr.* 18:240-247.

Mitchell D, Snelling EP, Hetem RS, Maloney SK, Strauss WM, Fuller A. 2018. Revisiting concepts of thermal physiology: predicting responses of mammals to climate change. *J Anim Ecol.* 87:956-973.

Morgan R. Andreassen AH, Åsheim ER, Finnøen MH, Dresler G, Brembu T, Loh A, Miest JJ, Jutfelt F., 2022. Reduced physiological plasticity in a fish adapted to stable temperatures. *Proc Nat Acad Sci USA.* 119:2201919119.

Mujahid A, Furuse M. 2009. Oxidative damage in different tissues of neonatal chicks exposed to low environmental temperature. *Comp Biochem Physiol A: Mol Integr Physiol.* 152(4):604-608.

Mundim KC, Baraldi S, Machado HG, Vieira FM. 2020. Temperature coefficient (Q10) and its applications in biological systems: Beyond the Arrhenius theory. *Ecol Modell.* 431*:*109127.

NeSmith CC. 1985. The effect of the physical environment on the development of red-winged blackbird nestlings. Msc. Thesis. Florida State University, Tallahassee.

Nord A, Giroud S. 2020. Lifelong effects of thermal challenges during development in birds and mammals. *Front Physiol.* 11:419.

Nudds RL, Oswald SA. 2007. An interspecific test of Allen's rule: evolutionary implications for endothermic species. *Evol.* 61:2839-2848.

O’Connor RJ. 1975. Growth and metabolism in nestling passerines. – In: Peaker M. (ed.), *Avian physiology, Symposia of the Zoological Society of London, vol. 35*. Academic Press, pp. 277– 306.

Ogle C. 1934. Climatic influence on the growth of the male albino mouse. *Am Physiol.* 107:635-640.

Ozgul A, Tuljapurkar S, Benton TG, Pemberton JM, Clutton-Brock TH, Coulson T. 2009. The dynamics of phenotypic change and the shrinking sheep of St. Kilda. *Science.* 325:464-467.

Parsons PA. 2005. Environments and evolution: interactions between stress, resource inadequacy and energetic efficiency. *Biol Rev.* 80:589-610.

Pérez JH, Ardia DR, Chad EK, Clotfelter ED. 2008. Experimental heating reveals nest temperature affects nestling condition in tree swallows (*Tachycineta bicolor*). *Biol Lett.* 4:468-471.

Pipoly I, Bókony V, Seress G, Szabó K, Liker A. 2013. Effects of extreme weather on reproductive success in a temperate-breeding songbird. *PLoS One.* 8:e80033.

Poole S, Stephenson JD. 1977. Body temperature regulation and thermoneutrality in rats. *Q J Exp Physiol Cog Med Sci: Transl Integr.* 62:143-149.

Przibram H. 1925. Direkte Temperaturabhängigkeit der Schwanzlänge bei Ratten, Mus (Epimys) decumanus Pall. und M.(E.) rattus L. Die Umwelt des Keimplasmas. XI. *Arch Mikroskop Anat Entwicklungsmech.* 104:434-496.

Quinn DE. 1978. The effect of developmental temperature on morphology, energy metabolism, growth hormone and thyroid stimulating hormone in Long-Evans rats. Phd Thesis, Portland State University, USA.

Rensch B. 1938. Some problems of geographical variation and species-formation. *Proc Linn Soc London.* 150:275-285.

Riek A, Geiser F. 2012. Developmental phenotypic plasticity in a marsupial. *J Exp Biol.* 215:1552-1558.

Riesenfeld A. (1973). The effect of extreme temperatures and starvation on the body proportions of the rat. *Am J Phys Anthropol.* 39:427-459.

Rodríguez MÁ, Olalla-Tárraga MÁ, Hawkins BA. 2008. Bergmann's rule and the geography of mammal body size in the Western Hemisphere. *Glob Ecol Biogeogr.* 17:274-283.

Rodríguez S, Barba E. 2016a. Effects of cool nest microclimates on nestling development: an experimental study with Mediterranean great tits *Parus major*. *Ardeola.* 63:251-260.

Rodriguez S, Barba E. 2016b. Nestling growth is impaired by heat stress: an experimental study in a Mediterranean great tit population. *Zool Stud.* 55:e40.

Romano A, Séchaud R, Roulin A. 2020. Geographical variation in bill size provides evidence for Allen’s rule in a cosmopolitan raptor. *Glob Ecol Biogeogr.* 29:65-75.

Ryding S, Klaassen M, Tattersall GJ, Gardner JL, Symonds MR. 2021. Shape-shifting: changing animal morphologies as a response to climatic warming. *TREE.* 36:1036-1048.

Schaeffer PJ, Lindstedt SL. 2013. How animals move: comparative lessons on animal locomotion. *Comp Physiol.* 3:289-314.

Scholander PF. 1955. Evolution of climatic adaptation in homeotherms. *Evol.* 9:15-26.

Sebens, KP. 1987. The ecology of indeterminate growth in animals. *Ann Rev Ecol Syst.* 18:371-407.

Serrat MA. 2007. Environmentally-determined tissue temperature modulates extremity growth in mammals: A potential comprehensive explanation of Allen's rule. PhD Dissertation. Kent State University, USA.

Serrat MA, King D, Lovejoy CO. 2008. Temperature regulates limb length in homeotherms by directly modulating cartilage growth. *Proc Natl Acad Sci USA.* 105:19348-19353.

Serrat MA. 2013. Allen's rule revisited: temperature influences bone elongation during a critical period of postnatal development. *Anat Rec.* 296:1534-1545.

Serrat MA. 2014. Environmental temperature impact on bone and cartilage growth. *Comp Physiol.* 4:621-655.

Serrat MA, Schlierf TJ, Efaw ML, Shuler FD, Godby J, Stanko LM, Tamski HL. 2015. Unilateral heat accelerates bone elongation and lengthens extremities of growing mice. *J Orthopaed Res.* 33:692-698.

Sheridan JA, Bickford D. 2011. Shrinking body size as an ecological response to climate change. *Nat Clim Change.* 1:401-406.

Shipley JR, Twining CW, Taff CC, Vitousek MN, Winkler DW. 2022. Selection counteracts developmental plasticity in body-size responses to climate change. *Nat Clim Change.* 12: 863-868.

Snedecor JG. 1971. Responses of normal and goitrogen-fed cockerels to different environmental temperatures. *Poult Sci.* 50:237-243.

Stawski C, Geiser F. 2020. Growing up in a changing climate: how temperature affects the development of morphological, behavioral and physiological traits of a marsupial mammal. *Front Physiol.* 11:49.

Steudel K, Porter WP, Sher D. 1994. The biophysics of Bergmann's rule: a comparison of the effects of pelage and body size variation on metabolic rate. *Can J Zool.* 72:70-77.

Sumner FB. 1909. Some effects of external conditions upon the white mouse. *J Exp Zool.* 7:97-155.

Sundstroem ES. 1922a. Studies on the adaptation of albino mice to an artificially produced tropical climate: I. Effect of the various factors composing a tropical climate on growth and fertility of Mice. *Am J Physiol.* 60:397-415.

Sundstroem ES. 1922b. Studies on the adaption of albino mice to an artificially produced tropical climate: II. Relations of the body form and especially the surface area to the reactions released by and the resistance to a tropical climate. *Am J Physiol.* 60:416-424.

Suzuki Y, Nijhout HF. 2006. Evolution of a polyphenism by genetic accommodation. *Science.* 311:650-652.

Swain S, Farrell DJ. 1975. Effects of different temperature regimens on body composition and carry-over effects on energy metabolism of growing chickens. *Poult Sci.* 54:513-520.

Symonds MR, Tattersall GJ. 2010. Geographical variation in bill size across bird species provides evidence for Allen's rule. *Am Nat.* 176:188-197.

Tattersall GJ, Arnaout B, Symonds MR. 2017. The evolution of the avian bill as a thermoregulatory organ. *Biol Rev.* 92:1630-1656.

Teulier L, Rouanet JL, Rey B, Roussel D. 2014. Ontogeny of non-shivering thermogenesis in Muscovy ducklings (*Cairina moschata*). *Comp Biochem Physiol A: Mol Integr Physiol.* 175:82-89.

Teplitsky C, Mills JA, Alho JS, Yarrall JW, Merilä J. 2008. Bergmann's rule and climate change revisited: Disentangling environmental and genetic responses in a wild bird population. *Proc Natl Acad Sci USA.* 105:13492-13496.

Thorington Jr RW. 1970. Lability of tail length of the white-footed mouse, *Peromyscus leucopus noveboracensis*. *J Mammol.* 51:52-59.

Ton R, Stier A, Cooper CE, Griffith SC. 2021. Effects of heat waves during post-natal development on mitochondrial and whole body physiology: an experimental study in zebra finches. *Front Physiol.* 554.

Verberk WC, Atkinson D, Hoefnagel KN, Hirst AG, Horne CR, Siepel H. 2021. Shrinking body sizes in response to warming: explanations for the temperature–size rule with special emphasis on the role of oxygen. *Biol Rev.* 96:247-268.

Villarreal JA, Schlegel WM, Prange HD. 2007. Thermal environment affects morphological and behavioral development of *Rattus norvegicus*. *Physiol Behav.* 91:26-35.

Wallace AR. 1855. XVIII - On the law which has regulated the introduction of new species. *Ann Mag Nat.* 16*:*184-196.

Walters RJ, Hassall M. 2006. The temperature-size rule in ectotherms: may a general explanation exist after all?. *Am Nat.* 167:510-523.

Watt C, Mitchell S, Salewski V. 2010. Bergmann's rule; a concept cluster?. *Oikos.* 119:89-100.

Whittow GC, Tazawa H. 1991. The early development of thermoregulation in birds. *Physiol Zool.* 64:1371-1390.

Williams JB. 1988. Field metabolism of tree swallows during the breeding season. *Auk.* 105:706-714.

Winther RG. 2000. Darwin on variation and heredity. *J Hist Biol.* 33:425-455.

Weaver ME, Ingram DL. 1969. Morphological changes in swine associated with environmental temperature. *Ecol.* 50:710-713.

Webster AF. 1981. The energetic efficiency of metabolism. *Proc Nutr Soc.* 40:121-128.

Weeks BC, Klemz M, Wada H, Darling R, Dias T, O'Brien BK, Probst CM, Zhang M, Zimova M. 2022. Temperature, size and developmental plasticity in birds. *Biol Lett.* 18:20220357.

Weeks BC, Harvey C, Tobias JA, Sheard C, Zhou Z, Fouhey DF. 2023. Bird wings are shaped by thermoregulatory demand for heat dissipation. *Biorxiv Preprint,* doi: https://doi.org/10.1101/2023.02.06.527306.

West-Eberhard MJ. 1989. Phenotypic plasticity and the origins of diversity. *Ann Rev Ecol Syst.* 20(1):249-278.

Yom-Tov Y, Geffen E. 2011. Recent spatial and temporal changes in body size of terrestrial vertebrates: probable causes and pitfalls. *Biol Rev.* 86:531-541.

Youngflesh C, Saracco JF, Siegel RB, Tingley MW. 2022. Abiotic conditions shape spatial and temporal morphological variation in North American birds. *Nat Evol Ecol.* 6:1860-1870.