Are latitudinal clines in body size adaptive?

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Body size of animals often increases with increasing latitude. These latitudinal clines in body size have interested biologists for over 150 years. However, the mechanisms that generate these clines in size are still unclear, though latitudinal gradients in temperature appear to play an important role. More importantly, many studies that examine latitudinal clines in body size and the mechanisms responsible for these clines use phenotypic data, confounding genetic (adaptive) and non-genetic (plasticity) sources of variation. Yet, most of these studies make adaptive conclusions based on phenotypic measures of size. Here I show the dangers of making adaptive inferences from phenotypic measures of size. In addition, I use a specific form of plasticity in body size of ectotherms, called the temperature–size rule, to illustrate how confusion about genetic and non-genetic contributions to phenotypic variation has hampered progress in understanding the evolution of latitudinal clines in size. Field-based measurements of body size can no doubt be influenced by plasticity, but demonstrating that latitudinal clines have a genetic basis is necessary to show that these patterns are adaptive.

Many traits of animals often vary geographically. For instance, one of the most widely observed patterns in nature is that body size of animals increases with increasing latitude (and thus presumably in colder environments) (Bergmann 1847, Partridge and Coyne 1997, Blanckenhorn et al. 2006, Stillwell et al. 2007). This pattern was first recognized in endothermic animals by Carl Bergmann (Bergmann 1847), but it has since been found in several different taxa of animals including ectothermic animals (Blanckenhorn and Demont 2004, but see Ashton and Feldman 2003, Adams and Church 2008). For over 150 years, a plethora of studies have explored these latitudinal clines in body size. However, latitude itself is not of interest as it merely represents a geographic location on a map (Hawkins and Diniz-Filho 2004). Rather, it is the environmental and ecological variables that change with latitude (or any geographic location) that are of interest. A historic focus on using latitude as a proxy for other variables (e.g. temperature) has led to numerous studies (including many recent studies) that simply test for the pattern (whether size increases with increasing latitude) without examining the potential mechanisms involved (Watt et al. 2010). While it is useful to use latitude to document geographic variation in size, it is necessary to examine the mechanisms that generate these patterns to understand how broad-scale geographic variation in body size evolves (Stillwell et al. 2007, Olalla-Tárraga et al. 2009, Terribile et al. 2009, Wilson 2009, Ho et al. 2010).

Because temperature changes systematically with latitude, a gradient in temperature is assumed to create the increase in body size with increasing latitude. This hypothesis was first proposed by Carl Bergmann (this pattern of increasing size with declining temperatures is commonly referred to as Bergmann's rule), who suggested that endothermic animals were generally larger in colder environments because they have a reduced surface area-to-volume ratio compared to small animals and can thus conserve heat better (Bergmann 1847). However, it is not entirely clear that this mechanism explains latitudinal clines in some endotherms (Ashton et al. 2000, Ashton 2002, Olson et al. 2009, Watt et al. 2010). In addition, latitudinal clines in body size exist in many ectothermic animals, including small ectotherms such as insects which acclimate to ambient temperature very quickly (Stevenson 1985, Blanckenhorn and Demont 2004, Blanckenhorn et al. 2006). However, many ectothermic animals do not exhibit these latitudinal clines (Hawkins and Lawton 1995, Pincheira-Donoso et al. 2008), so it is not clear if a general pattern exists. Even so, there is strong evidence that temperature generates latitudinal clines. For example, body size of the fruit fly, *Drosophila melanogaster*, increases with increasing latitude on several continents (Coyne and Beecham 1987, Capy et al. 1993, Imasheva et al. 1994, James et al. 1995, Van't Land et al. 1995) and these clines evolve rapidly after invasion onto new continents (Huey et al. 2000), suggesting there is strong selection for these clines. Furthermore, body size of *Drosophila* spp. evolves in laboratory thermal selection experiments (natural selection experiments in which experimental populations are subjected to different thermal regimes for several generations; Anderson 1966, 1973, Cavicchi et al. 1985, 1989, Partridge et al. 1994) in directions consistent with the pattern of increasing size with increasing latitude. In addition, artificial selection experiments (flies selected for large and small sizes)

with *D. melanogaster* show that selection favors larger size at lower temperatures (McCabe and Partridge 1997, Reeve et al. 2000), consistent with the hypothesis that temperature-mediated variation in selection favors larger size in cooler climates and thus at higher latitudes. It is thus likely that temperature is responsible for generating latitudinal clines in body size in both endothermic and ectothermic organisms, but perhaps in a more complex way than Bergmann originally thought. For example, the balance between heat gain and heat loss is largely dependent on size and may explain why some groups show increases in size with increasing latitude while other groups show decreases in size with increasing latitude (Olalla-Tárraga et al. 2006).

Nevertheless, numerous ecological and environmental variables change systematically with latitude and could be responsible for producing latitudinal clines in body size (Blackburn et al. 1999, Ashton et al. 2000, Stillwell et al. 2007, 2008). However, only recently have studies begun to explore the impact of these other ecological and environmental variables on selection, and thus their potential to generate latitudinal clines. For example, the length of the growing season decreases with increasing latitude. Several studies have found that seasonality best explains clines in body size (Boyce 1978, Lindstedt and Boyce 1985, Murphy 1985, Cushman et al. 1993, Arnett and Gotelli 1999), probably because of greater starvation resistance of large individuals at higher latitudes. In addition, desiccation resistance and body size often increase with increasing latitude (Hoffmann and Harshman 1999, Gilchrist et al. 2001). It is likely that gradients in moisture will generate variation in selection on body size via variation in desiccation resistance due to greater desiccation resistance of large individuals; large individuals have a reduced surface-to-volume ratio and overall higher absolute water content compared to small individuals (Schoener and Janzen 1968, Le Lagadec et al. 1998, Chown and Gaston 1999, 2010, Olalla-Tárraga et al. 2009). In the seed-feeding beetle *Stator limbatus*, body size increases with increasing latitude (Stillwell et al. 2007), but no single environmental/ecological variable adequately explains the variation in body size; host plant seed size, seasonality and moisture availability best explains the size variation. Therefore, it is likely that many environmental and ecological variables interact to generate geographic clines in body size (Jones et al. 2005, Stillwell et al. 2007, 2008).

Understanding the mechanisms underlying latitudinal clines in body size is essential to studies of geographic variation in size (Watt et al. 2010), but whether latitudinal clines are adaptive is much less clear. Numerous studies that evaluate whether latitudinal clines are adaptive often measure phenotypic variation in body size (e.g. using field-collected museum specimens), such that genetic and non-genetic sources (i.e. environmental) of variation are confounded (Gienapp et al. 2008, Teplitsky et al. 2008). This is a critical issue for studies of geographic clines in body size of both endotherms (Bergmann's rule) and ectotherms (also sometimes referred to as Bergmann's rule although this is not technically correct). Although this may seem like an obvious point (especially to evolutionary geneticists), many studies continue to make adaptive conclusions from phenotypic data (Gienapp et al. 2008). For example, some recent studies have shown that body size of birds and

mammals (phenotypic measures of size) is declining over time as global temperatures rise, evidence that is interpreted as showing how a classic biological rule (Bergmann's rule) is being affected by global climate change (Smith et al. 1995, Yom-Tov 2001, Millien 2004, Yom-Tov and Yom-Tov 2004, Yom-Tov et al. 2006, Van Buskirk et al. 2010). However, Teplitsky et al. (2008) showed that the response in birds is a result of temperature-induced plasticity, illustrating the dangers of inferring adaptive explanations from phenotypic data.

The importance of examining the genetic basis of latitudinal clines when inferring adaptation is best illustrated with a particular form of plasticity that occurs in ectothermic animals. Body size of ectothermic animals typically increases with decreasing developmental temperatures, a phenomenon known as the temperature–size rule (Atkinson 1994, 1996, Angilletta and Dunham 2003, Kingsolver and Huey 2008). Consequently, this pattern of temperature-induced plasticity in body size (which comes from laboratory studies) mirrors the latitudinal clines found in some ectothermic animals. Indeed, there is much confusion over the temperature–size rule and latitudinal clines in size; historically, the popular view that ectotherms exhibit latitudinal clines seems to come from laboratory studies that demonstrate the temperature–size rule and extrapolate to geographic patterns (Belk and Houston 2002). For example, Van Voorhies (1996) claimed that this temperature-induced plasticity in size provides a non-adaptive explanation for the occurrence of latitudinal clines in body size of ectotherms, which caused a fierce debate on the adaptive significance of these clines in ectotherms (Mousseau 1997, Partridge and Coyne 1997, Van Voorhies 1997). However, making inferences about latitudinal clines in size based on laboratory experiments that manipulate developmental temperatures is not appropriate. Studies that examine latitudinal clines in size and the temperature–size rule refer to variation at different scales; studies that test for latitudinal clines typically examine large-scale variation in size among populations of a species (or among different species), whereas studies that examine the temperature–size rule explore whether genotypes within populations produce different phenotypes when raised at various temperatures (Kingsolver and Huey 2008, Watt et al. 2010). More importantly, genotypes/populations from different geographic locations can even vary in the degree of plasticity in body size they exhibit in response to temperature (Angilletta 2009); e.g. some populations of the cabbage white butterfly *Pieris rapae* exhibit the temperature–size rule, whereas other populations break the rule (Kingsolver et al. 2007). While there is no doubt that field-based measurements are influenced by plasticity (see example on birds above), it is not clear what role, if any, the temperature–size rule plays in generating latitudinal clines in body size of ectotherms.

Ultimately, for latitudinal clines in size to be the result of adaptation, the differences among populations along a latitudinal gradient must be genetic. Indeed, several studies have shown that geographic clines in body size do have a genetic basis; clines in body size persist after populations are raised in common laboratory conditions (Partridge and Coyne 1997, Gilchrist and Partridge 1999, Stillwell et al. 2007). However, most of this evidence comes from *Drosophila melanogaster*. Few studies have conducted the necessary common

garden or reciprocal transplant experiments needed to disentangle genetic (adaptation) and non-genetic (phenotypic plasticity) contributions to the phenotype in animals other than insects. It is thus unclear whether latitudinal clines in size generally have a genetic basis. One obvious reason for a lack of studies exploring the genetic basis of latitudinal clines is that it is often not practical to conduct common-garden or reciprocal transplant experiments with organisms such as birds or mammals due to the large number of samples that are needed or due to the need to do long-term monitoring of individuals (Van Buskirk 2010). However, alternative methods can be used to demonstrate that latitudinal clines have a genetic basis. For example, recent studies have measured current selection on body size (Van Buskirk et al. 2010), assessed past nutritional conditions during growth using ptilochronology (Gardner et al. 2009) and used the 'animal model' (Teplitsky et al. 2008) to explore whether latitudinal clines in size were genetically based and thus adaptive. Regardless of the approach, it is essential to establish that geographic clines in body size are at least partially genetically based to show that they are a result of adaptation.

Conclusions

In summary, latitudinal clines in body size of animals has fascinated biologists for over a century (Angilletta et al. 2004). However, many studies do not distinguish between genetic and environmental contributions to phenotypic variation in size, leading to confusion about the role plasticity plays in creating these geographic clines in size and whether these clines are adaptive. For latitudinal clines in size to be adaptive, studies must show that they have an underlying genetic basis using common-garden experiments, reciprocal transplant experiments or other alternative methods.

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