

Bergmann and Converse Bergmann Latitudinal Clines in Arthropods: Two Ends of a Continuum?¹

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SYNOPSIS. Two seemingly opposite evolutionary patterns of clinal variation in body size and associated life history traits exist in nature. According to Bergmann's rule, body size increases with latitude, a temperature effect. According to the converse Bergmann rule, body size decreases with latitude, a season length effect. A third pattern causally related to the latter is countergradient variation, whereby populations of a given species compensate seasonal limitations at higher latitudes by evolving faster growth and larger body sizes compared to their low latitude conspecifics. We discuss these patterns and argue that they are not mutually exclusive because they are driven by different environmental causes and proximate mechanisms; they therefore can act in conjunction, resulting in any intermediate pattern. Alternatively, Bergmann and converse Bergmann clines can be interpreted as over- and undercompensating countergradient variation, respectively. We illustrate this with data for the wide-spread yellow dung fly, *Scathophaga stercoraria* (Diptera: Scathophagidae), which in Europe shows a Bergmann cline for size and a converse Bergmann cline (*i.e.*, countergradient variation) for development time. A literature review of the available evidence on arthropod latitudinal clines further shows a patterned continuum of responses. Converse Bergmann clines due to end-of-season time limitations are more common in larger species with longer development times. Our study thus provides a synthesis to the controversy about the importance of Bergmann's rule and the converse Bergmann rule in nature.

INTRODUCTION

Large-scale systematic patterns of variation lie at the heart of organismic biology and have interested biologists ever since the beginning. They are most obvious as regards body size, probably the single most important quantitative trait of an individual. This is because body size severely affects virtually all physiological (*e.g.*, metabolic rate) and fitness traits (*e.g.*, fecundity or mating success), producing strong but not necessarily well understood allometric relationships within and among organisms (Wootton, 1979; Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Shine, 1988; Reiss, 1989; Honek, 1993; Andersson, 1994; Blanckenhorn, 2000a). Starting with Bergmann in the mid 19th century, a number of ecological and evolutionary patterns or "rules" dealing with body size have been described over the years, the most prominent being Bergmann's rule (Bergmann, 1847; Atkinson and Sibly, 1997; Ashton *et al.*, 2000; Ashton, 2002a, b, 2004; Ashton and Feldman, 2003), the converse Bergmann rule (Park, 1949; Mousseau, 1997), countergradient variation (Conover and Present, 1990), Cope's rule (McLain, 1993; Jablonski, 1997), and Rensch's rule (Rensch, 1950; Abouheif and Fairbairn, 1997; Kraushaar and Blanckenhorn, 2002). Surprisingly, the mechanisms underlying many of these patterns remain enigmatic, so they continue to interest organismic biologists to this day. We here focus on patterns of latitudinal or altitudinal (*i.e.*, geographic) variation in body size and associated life history traits, which are

common in animals (Atkinson, 1994; Ashton *et al.*, 2000; Ashton, 2002a, b, 2003, 2004).

A few years ago, a paper published by Van Voorhies (1996) spurred a discussion in the journal *Evolution* about whether ectotherms follow Bergmann's or the converse Bergmann rule (Mousseau, 1997; Partridge and Coyne, 1997; Van Voorhies, 1997; Fig. 1). The point seemed moot, as obviously both patterns exist in nature (Ashton, 2002a, b, 2003, 2004 see examples listed in Table 1), but the controversy was not resolved. We here argue that both patterns are not mutually exclusive, since they are effected by different environmental causes (temperature and season length, respectively) and have different underlying mechanisms. They thus form two ends of a continuum, with all intermediate clinal patterns possible in principle. While this has been pointed out before, in a somewhat overlooked paper in this context (Chown and Gaston, 1999; see also Chown and Klok, 2003), we here discuss two lines of empirical evidence to support the argument. We first present common-garden laboratory data on the yellow dung fly *Scathophaga stercoraria* (Diptera: Scathophagidae) demonstrating an intermediate pattern for European populations. Second, we review available studies on latitudinal body size clines in arthropods that show a patterned variety of responses. We begin by briefly explaining both Bergmann's and the converse Bergmann rule, as well as countergradient variation, the three major hypotheses put forward in the context of latitudinal body size clines.

Bergmann's rule

Bergmann's rule originally referred to clinal geographic variation among endothermic (warm-blooded) species only, which tend to be bigger in colder cli-

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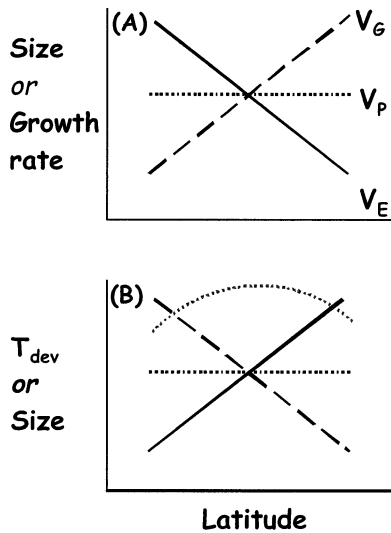


FIG. 1. Two non-exclusive explanations for the observation of a continuum of body size clines with latitude. (A) Countergradient variation occurs when higher latitude populations of a given species compensate for an environmental decrease in season length with latitude, resulting in slower growth (solid line; V_E), by evolving (genetically) faster growth (hatched line; V_G) compared to their lower latitude conspecifics to reach the same phenotypic body size (dotted line; V_P). Assuming perfect compensation, no size cline results, as depicted. However, growth rate may be under- or overcompensated, resulting in converse Bergmann or Bergmann clines, respectively (not depicted). (B) As Bergmann (increasing solid line) and converse Bergmann (decreasing hatched line) clines are presumably caused by different environmental variables (temperature and season length, respectively) and proximate mechanisms (cf. Fig. 1), they can act independently in conjunction. If they act additively (dotted line), any slope can result depending on the relative strength of either underlying mechanism (perfect cancellation is depicted); if they act multiplicatively (dotted curve), a hump-shaped pattern can result.

mates (Cushman *et al.*, 1993; Barlow, 1994; Hawkins and Lawton, 1995; Blackburn *et al.*, 1999). The adaptive explanation originally suggested by Bergmann (1847) was that larger individuals possess smaller surface-to-volume ratios more conducive to conserving heat in cold climates. However, evidence for birds and mammals is inconsistent, so the generality of this supposed cause, and in fact Bergmann's rule itself, continues to be contended (Geist, 1987, 1990; Paterson, 1990; Blackburn *et al.*, 1999; Ashton *et al.*, 2000; Ashton, 2002a). Nevertheless, about one hundred years after Bergmann it transpired that the rule extends to ectothermic (cold-blooded) organisms (Ray, 1960), for which the cause must be different, as especially small ectotherms acclimate to ambient temperature almost instantly (Stevenson, 1985). A unifying explanation for this phenomenon is still lacking, although there is agreement in that Bergmann's rule seems to be effected by temperature per se (Atkinson and Sibly, 1997). Ectothermic Bergmann clines in nature can be shown to be genetic when they are expressed not only in nature but also at common garden laboratory conditions. As they evolve repeatedly (and predictably), they are presumed by many to be an adaptation (Partridge and Coyne, 1997; Huey *et al.*, 2000; but see below). Ad-

ditionally, there is a strong environmental component: a majority of ectotherms grow larger at lower temperatures (also known as the temperature-size rule: reviewed by Atkinson, 1994; Angilletta and Dunham, 2003).

There is much debate about whether ectothermic Bergmann clines are adaptive or whether they are a mere consequence of physiological processes at the cellular level (*i.e.*, a constraint: van der Have and de Jong, 1996; Atkinson and Sibly, 1997; Partridge and Coyne, 1997; Blanckenhorn, 2000b; Huey *et al.*, 2000; Blanckenhorn and Hellriegel, 2002). Environments constraining growth (*e.g.*, food shortage) typically produce smaller body sizes. Low temperatures are a notable exception, however, as they constrain growth but nevertheless result in larger body sizes (Taylor, 1981; Atkinson and Sibly, 1997). This has been termed a life history puzzle by Berrigan and Charnov (1994). Evolutionary ecologists favor adaptive explanations for Bergmann's rule at the whole-organism level (Partridge and Coyne, 1997; Huey *et al.*, 2000), even though there is no general theory available demonstrating the adaptive nature of Bergmann clines (Atkinson and Sibly, 1997). In particular, while in many animal species large body size is typically favored by fecundity selection (*e.g.*, Wootton, 1979; Shine, 1988; Honěk, 1993), sexual selection (Andersson, 1994) and even viability selection (Peters, 1983; Calder, 1984; Reiss, 1989; but see Blanckenhorn, 2000a), there is no evidence or argument for why this should generally be less the case at warm temperatures or in warm climates. The fact that Bergmann clines evolve rapidly and repeatedly even when species are transferred to other continents is, at best, indirect evidence (*e.g.*, *Drosophila subobscura*: Huey *et al.*, 2000; Gilchrist *et al.*, 2000), as this may be equally well explained by fundamental underlying physiological processes (discussed below). Direct evidence for the adaptive nature of Bergmann clines requires that the fitness optimum lies at smaller body sizes at warm temperatures (or in warm habitats), typically involving demonstration of temperature dependent trade-offs. Such demonstrations are rare. The best, but by no means conclusive evidence to date in this regard has been presented by McCabe and Partridge (1997) and Reeve *et al.* (2000).

In contrast, physiologists and developmental biologists emphasize mechanisms to explain Bergmann's rule. Bertalanffy (1960) argued that physical processes affecting energy assimilation, such as foraging activity at the whole organism level and nutrient absorption or diffusion at the cellular level, are less affected by temperature than chemical processes driving energy dissipation (*i.e.*, metabolism). This implies relatively less energy available for somatic growth at higher temperatures, and consequently smaller size (formalized by Perrin, 1995). Analogously, van de Have and de Jong (1996) argued that the rate of growth is primarily affected by protein synthesis, which largely depends on diffusion and is thus less limited by temperature, whereas the rate of cell differentiation and cell division (*i.e.*, development) is highly temperature dependent.

This implies that at higher temperatures organisms reach maturity much more rapidly while at the same time growth increases less rapidly, resulting in smaller size. Both arguments can be understood as non-adaptive hypotheses due to physiological constraints, although both may ultimately still be grounded in (adaptive) energetic trade-offs at the physiological (*e.g.*, ATP) level (Atkinson and Sibly, 1997).

These mechanistic arguments apply generally to all parts of the body such as eggs, sperm or individual cells, so that Bergmann clines in whole-organism body size can be seen as a result of processes at the cellular level (Partridge *et al.*, 1994; James *et al.*, 1995, 1997; Stevenson *et al.*, 1995; van de Have and de Jong, 1996; Van Voorhies, 1996). Bergmann clines in egg size have been shown in *Drosophila melanogaster* (Azevedo *et al.*, 1996) and the pitcher-plant mosquito (Armbruster *et al.*, 2001), and smaller egg (and cell) sizes at higher temperatures have been experimentally demonstrated in a few insect species (Ernsting and Isaaks, 1997, 2000; Blanckenhorn, 2000b; Fox and Czesak, 2000; Fischer *et al.*, 2003). In this context, Bradford (1990) and Woods (1999) provided a third physiological mechanism possibly explaining why eggs and cells should be smaller at higher temperatures: while oxygen diffusion depends only weakly on temperature, oxygen consumption depends strongly on it, so large cells may suffer from hypoxia at high temperatures. Similar effects of temperature on body, cell and gamete size suggest a unifying physiological mechanism underlying Bergmann's rule extended to ectotherms (van de Have and de Jong, 1996; Van Voorhies, 1996). In contrast, there is essentially no empirical evidence to date that temperature-mediated egg, cell or sperm sizes are adaptive. Of the few direct experimental tests available (Ernsting and Isaaks, 1997, 2000; Blanckenhorn, 2000b), only one (Fischer *et al.*, 2003) found support for the hypothesis that eggs laid at a particular temperature performed best at that temperature (*i.e.*, the beneficial acclimation hypothesis: Huey *et al.*, 1999). On the other hand, Blanckenhorn and Hellriegel (2002) recently found that sperm length of the yellow dung fly *Scathophaga stercoraria* increases (rather than decreases) with temperature. Furthermore, Angilletta and Dunham (2003) recently refuted the generality of the hypothesized underlying physiological mechanism of Berthalanffy (1960) and Perrin (1995). These two lines of evidence therefore also question the generality of the physiological constraint hypothesis.

The converse Bergmann rule

Somewhat paradoxically, so-called converse Bergmann clines also exist in a number of ectothermic species, describing the phenomenon that body size decreases towards the poles (first reported by Park, 1949; Masaki, 1967; Brennan and Fairbairn, 1995; Mousseau, 1997; *fig. 1*). At least in insects, these converse Bergmann clines are often genetic, as smaller sizes and shorter development times of high latitude populations

are also expressed in common-garden laboratory settings (*e.g.*, Masaki, 1967, 1972, 1978; Mousseau and Roff, 1989; Blanckenhorn and Fairbairn, 1995). Contrary to Bergmann's rule, this effect is mediated by season length, as opposed to temperature per se. Shorter seasons at higher latitudes progressively limit the time available for foraging, growth and development and hence the phenotypic body size that can be attained, resulting in a pattern of decreasing body size towards the poles. Analogous seasonal time constraints can be caused by altitude (*e.g.*, Berven, 1982a, b; Dingle *et al.*, 1990; Blanckenhorn, 1997; Fischer and Fiedler, 2002; Chown and Klok, 2003). This outcome is predicted by optimality theory based on a trade-off between body size (and thus ultimately reproductive success), which increases with the time available to grow, and survival to adulthood, which correspondingly decreases with the time available to attain maturity (Roff, 1980; Rowe and Ludwig, 1991). Therefore, converse Bergmann clines are adaptive, as this trade-off can (and must) be demonstrated (*e.g.*, as for water striders *Aquarius remigis*: Blanckenhorn, 1994; Blanckenhorn and Fairbairn, 1995).

Countergradient variation

A third prominent hypothesis related to latitudinal variation in body size is that of countergradient variation, also known as the latitudinal compensation hypothesis (Levinton and Monahan, 1983; Conover and Present, 1990). The underlying cause is the same as for converse Bergmann clines. Countergradient variation is exhibited when high latitude (or altitude) populations of a given species compensate for seasonal time constraints by evolving (genetically) faster growth compared to their low latitude (or altitude) conspecifics. As in the simplest case growth rate is body size per unit development time, perfect compensation of season length limitations at a given latitude (the environmental component) would be indicated if growth rate (the genetic component) evolved such that the resulting phenotypic body size is the same at all latitudes. In this case no size cline results (*Fig. 1*). However, growth rate can be, for whatever reason, perfectly compensated (*e.g.*, common frog development times: Laugen, 2003; Laugen *et al.*, 2003), under- (*e.g.*, water striders: Blanckenhorn and Fairbairn, 1995; Brennan and Fairbairn, 1995) or overcompensated (*e.g.*, wood frogs: Berven, 1982a, b), resulting in converse Bergmann or Bergmann clines, respectively.

These three hypotheses or rules describing clinal body size variation are obviously interrelated. While Bergmann's and the converse Bergmann rule share the same name (probably unduly so) and merely phenomenologically describe opposite patterns, their environmental cause, and probably also their underlying proximate mechanism, are quite different. Countergradient variation actually describes the same phenomenon as the converse Bergmann rule, albeit from a different perspective, as it specifically refers to the genetic response involved. *Figure 1* illustrates how a continuum

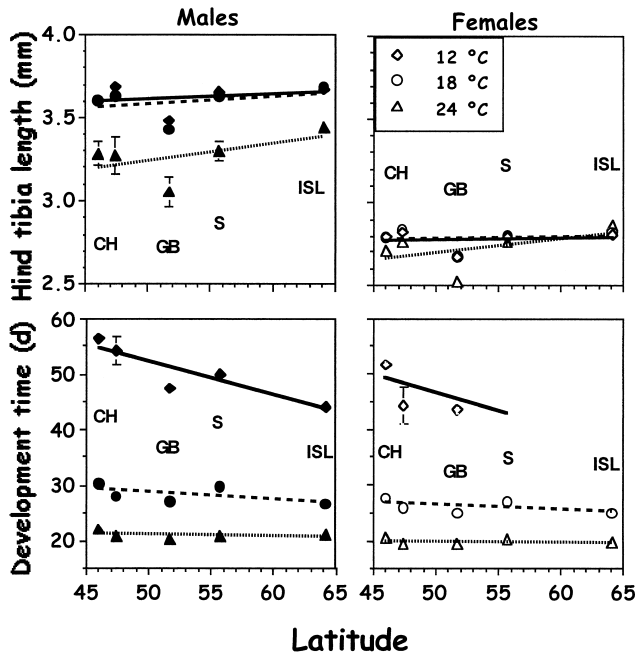


FIG. 2. Mean \pm SE body size (top) and egg to adult development time (bottom) as a function of latitude for lab-reared families of yellow dung fly males (left) and females (right) from five different latitudinal populations in Europe, at three different temperatures in the simultaneous experiment (CH: Switzerland; GB: England; S: Sweden; ISL: Iceland).

of clinal body size patterns can be theoretically obtained from the hypothesis of countergradient variation alone, as well as from a combined action of the presumably different mechanisms underlying Bergmann's and the converse Bergmann rule. We now present the results of a study showing such an intermediate pattern. A subsequent literature review of the available evidence on arthropod latitudinal clines further reveals a continuum of responses depending on body size and development time.

METHODS

Laboratory common garden rearing of yellow dung flies

The study animal. The yellow dung fly, *Scathophaga stercoraria* (L.; Diptera: Scathophagidae; sometimes *Scatophaga*), occurs in north-temperate regions of the Old and the New World (Stone *et al.*, 1965; Gorodkov, 1984). Larvae of this species are coprophagous, meaning they feed on the dung of large mammals, which they thereby decompose, together with many other species of primarily earthworms, beetles and flies (Hammer, 1941). Adult yellow dung flies, in contrast, are sit-and-wait predators of small insects and lick nectar from flowers in addition to fresh dung (Hammer, 1941; Foster, 1967). Adult flies require feeding on prey (primarily protein and lipids) beyond the nutrients they acquire during the larval stage in order to produce eggs and sperm, *i.e.*, they are nutritionally anautogenous (Foster, 1967). The distribution of

Scathophaga stercoraria up to places like Iceland and high elevations reveals a preference for colder temperatures (Gorodkov, 1984; Sigurjónsdóttir and Snorrason, 1995; Blanckenhorn, 1997). Towards the south its distribution appears to be limited by hot temperatures, which this species is susceptible to and evidently avoids (Hammer, 1941; Parker, 1970; Gibbons, 1987; Ward and Simmons, 1990; Blanckenhorn, 1998; Blanckenhorn *et al.*, 2001). In north-central Europe, *Scathophaga stercoraria* is one of the most abundant and widespread insect species associated with cow dung, probably relating to human agricultural practices, as this species is considered a cow dung specialist.

After copulation with a male at the dung, females lay clutches of 30–70 eggs into fresh dung, which the developing larvae feed on and thereby deplete. Individuals have to complete larval development in order to overwinter as pupae (Blanckenhorn, 1998), at which point adult body size has been fixed, but pupal development (*i.e.*, metamorphosis) still requires time to be completed. Body size and development time in this species are greatly influenced by the amount of dung individuals feed on as larvae (Amano, 1983; Sigurjónsdóttir, 1984; Blanckenhorn, 1998), but they are also heritable (Simmons and Ward, 1991; Blanckenhorn, 2002). Males are larger than females on average (Borgia, 1981, 1982; Jann *et al.*, 2000; Kraushaar and Blanckenhorn, 2002). Large size confers a mating advantage to males (Borgia, 1982; Jann *et al.*, 2000; Kraushaar and Blanckenhorn, 2002) and a fecundity advantage to females (Borgia, 1981; Jann *et al.*, 2000; Kraushaar and Blanckenhorn, 2002).

Laboratory rearing experiments. We obtained flies from five European countries, spanning a wide latitudinal range: Reykjavik, Iceland (ISL: 64°11'N/21°54'W; about the northernmost extent of their distribution); Lund, Sweden (S: 55°40'N/13°30'E); Oxford, England (GB: 51°45'N/1°15'W); Bielefeld, Germany (D: 52°02'/8°30'E); plus two populations from Switzerland (CH), Fehraltorf (north of the Alps: 47°23'N/8°41'E) and Lugano (south of the Alps: 46°00'/8°55'E), from about the southern edge of their distribution (except at higher altitudes). Flies from these populations were collected in the field at different times between autumn 2000 and summer 2002, either as live adults or eggs. Populations of at least 30 males and 30 females were thereafter maintained in the laboratory for a varying number of generations (2–11).

Two sets of common garden laboratory rearings were performed. The first rearing was performed soon after collection, always using second laboratory generation individuals. These experiments were performed separately for all populations (because they were collected at different times) but at identical climatic conditions of constant 15°C, 60% relative humidity and 13 hr photoperiod (henceforth called the sequential experiment). In a second common garden experiment conducted later (henceforth called the simultaneous experiment), all populations (except D) were reared simultaneously at the same climatic conditions (see be-

low), using third (ISL, CH) up to eleventh (GB) generation individuals. In both experiments statistical units refer to family means.

For the simultaneous experiment, individual clutches laid in the laboratory (*i.e.*, full-sib families) were split among three environments differing in temperature only. The larvae were allowed to develop at 60% relative humidity, constant 12°, 18° or 24°C, and 12 hr, 13 hr and 14 hr photoperiod (respectively), in plastic containers with overabundant (*i.e.*, >2 g per larva; Amano, 1983) defrosted fresh and uniform cow dung. Temperature/photoperiod combinations were chosen not to deviate too much from natural conditions. There were $N = 12$ –18 replicate families per population and rearing temperature combination. We checked the containers for emerged adults at least every other day, until no more individuals emerged for four weeks. We thus obtained egg to adult development times for all emerged individuals, from which mean development times per family and temperature treatment were calculated separately for males and females (because they differ). We also measured the hind tibia length (HTL) of three randomly picked emerging males and females per family using a binocular microscope at 16 \times magnification, from which mean HTLs (*i.e.*, body sizes) per family and temperature treatment were computed. We conducted the sequential experiment using essentially the same methods, except that families were not split among different temperature environments.

Literature review on clinal body size variation in arthropods

We collected available data on latitudinal body size variation from the literature. We included only those studies for which an estimate of the change in body size with latitude (measured by various traits) could be extracted, typically from (regression) plots of body size on latitude, but sometimes from tables or the text. Body mass data (rarely used) were cube-root-transformed to bring them to the same scale as the more typical linear length measurements. All estimates were standardized as percent length change per degree latitude (*cf.* Ray, 1960). This number was positive if size increased and negative if size decreased with latitude. We differentiated between field data (reflecting genetic and environmental variation) and laboratory common garden data (reflecting genetic variation only).

Ideally, we required body size data that can be directly compared among species. As a variety of morphological traits are typically used, this was not possible. However, most studies used either wing length or total body length (Table 1). For those studies of species not using either of these two traits, we obtained rough wing or body length estimates from other sources. In the end, we based our analyses on mean wing length estimates for each species, whereby wing length was (arbitrarily) set as 80% of body length for unwinged species and those species for which only body length could be obtained. Additionally, because across species body size correlates well with development

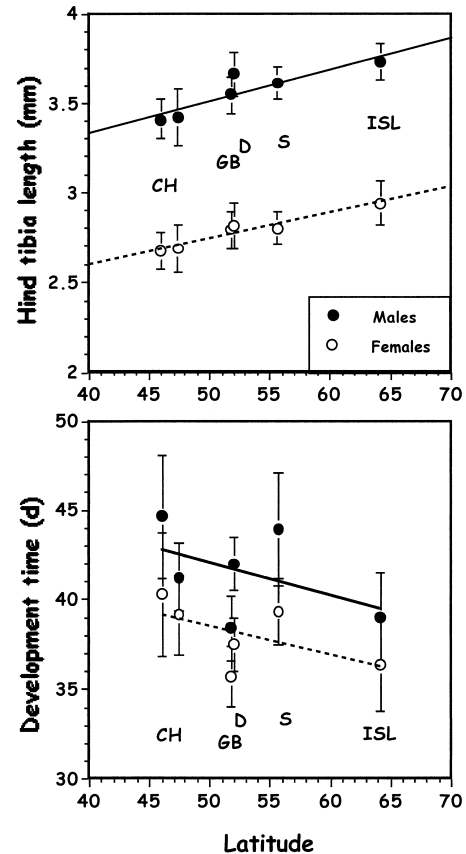


FIG. 3. Mean \pm SE body size (top) and egg to adult development time (bottom) as a function of latitude for lab-reared families of yellow dung fly males and females from six different latitudinal populations in Europe, at 15°C in the sequential experiment (CH: Switzerland; GB: England; D: Germany; S: Sweden; ISL: Iceland).

time and because development time is the prime mediator of seasonal time limitations on body size (Roff, 1980), we attempted to obtain corresponding rough estimates of real-time (egg to adult) development times, at whatever conditions in the field or the laboratory. These data sometimes stem from the same study, but often from other studies on the same species. Development time data were not available for all species, thus substantially reducing the data set that could be analyzed.

We analyzed the data in two ways. In a first analysis, we subdivided the data into those studies following Bergmann's rule (positive slope with latitude) and those following the converse Bergmann rule (negative slope with latitude), and compared mean wing lengths or development times between the two groups using non-parametric Mann-Whitney U -tests (because data were highly skewed). In a second analysis, we regressed the estimated percent size change per degree latitude on the estimated wing length or development time. To at least partly correct for the strong correlation of body size and development time with taxon, we used independent contrasts (CAIC: Purvis and Rambaut, 1995). A phylogeny for the arthropods in our data set was constructed from the tree of life web site www.phylogeny.arizona.edu/tree/phylogeny.html, with

TABLE 1. Summary statistics of all arthropod studies on latitudinal clines reviewed.

Species	Order	Rule	Latitudinal change (% per degree latitude)		Length ¹ (mm)	Trait measured	Development time (d)	Reference
			Field	Lab				
<i>Haemaphysalis leporis-palustris</i>	Acari	B	0.6		1	Scutum width		Thomas, 1968
<i>Scottoloana canadensis</i>	Copepoda	B		1.95	0.8	Body length	12	Lonsday and Levinton, 1985
<i>Enallagma cyathigerum</i>	Odonata	CB	-0.66		22	Wing length	120	Johansson 2003; Macan, 1974
<i>Pemphigus populitransversus</i>	Homoptera	B	0.17		2	Wing length		Sokal and Rinkel, 1963
<i>Aquarius remigis</i>	Hemiptera	CB	-3.4	-1.6	13	Body length	53	Brennan and Fairbairn, 1995; Blanckenhorn and Fairbairn, 1995
<i>Myrmeleon immaculatus</i>	Neuroptera	B	0.17	2	36	Wing length	180	Arnett and Gotelli, 1999a,b
<i>Dicaelus purpuratus</i>	Coleoptera	CB	-1.56		16	Elytra length		Park, 1949
<i>Carabus nemoralis</i>	Coleoptera	CB	-0.8		14.5	Elytra length		Krummbiegel, 1936
<i>Phyllotreta striolata</i>	Coleoptera	B	0.3		2	Elytra length		Masaki, 1967
<i>Apis mellifera</i>	Hymenoptera	B	2		10	Wing length	17	Alpatov, 1929; Harbo, 1992
<i>Leptothorax acervorum</i>	Hymenoptera	B	0.33	0.59	3	Thorax length	77	Heinze <i>et al.</i> 2003; A. Buschinger, pers. comm.
<i>Myrmica rubra</i>	Hymenoptera	CB		-0.22	4	Body mass	45	Elmes <i>et al.</i> , 1999
<i>Teleogryllus emma</i>	Orthoptera	CB	-2.8		17.5	Head width	90	Masaki, 1967, 1972, 1978
<i>Teleogryllus yezoemma</i>	Orthoptera	CB	-3.8		18	Head width	80	Ohmachi and Masaki, 1964
<i>Pteronemobius fascipes</i>	Orthoptera	CB	-1.4		7	Head width	50	Masaki, 1972
<i>Allonemobius socius</i>	Orthoptera	CB	-1.5		13	Femur length	70	Mousseau and Roff, 1989; Bradford and Roff, 1993
<i>Acheta pennsylvanicus</i>	Orthoptera	CB	-1.9		20	Body length	45	Bigelow, 1962
<i>Acheta veletis</i>	Orthoptera	CB	-2.3		17	Body length	56	Alexander and Bigelow, 1960
<i>Chorthippus brunneus</i>	Orthoptera	CB		-0.85	19	Body mass	24	Telfer and Hassall, 1999
<i>Papilio canadensis</i>	Lepidoptera	CB		-0.5	45	Wing length	60	Ayres and Scriber, 1991
<i>Polyommatus icarus</i>	Lepidoptera	CB	0.1	-1.7	15	Wing length	31	S. Nylin, pers. comm.; Leimar, 1996
<i>Palaeocrysophanus hippothoe</i>	Lepidoptera	CB	-0.27		16	Wing length	39	Nylin and Svärd, 1991; Fischer and Fiedler, 2002
<i>Heodes virgaureae</i>	Lepidoptera	CB	-1		16	Wing length		Nylin and Svärd, 1991
<i>Lycaena helle</i>	Lepidoptera	CB	-0.3		13	Wing length		Nylin and Svärd, 1991
<i>Lycaena phlaeas</i>	Lepidoptera	B	0.25		14.5	Wing length		Nylin and Svärd, 1991
<i>Coenonympha tullia</i>	Lepidoptera	CB	-1.4		17.5	Wing length		Nylin and Svärd, 1991
<i>Coenonympha arcania</i>	Lepidoptera	CB	-1.49		16.5	Wing length		Nylin and Svärd, 1991
<i>Coenonympha hero</i>	Lepidoptera	CB	-1.41		16	Wing length		Nylin and Svärd, 1991
<i>Coenonympha pamphilus</i>	Lepidoptera	CB	-0.2		15.5	Wing length	45	Nylin and Svärd, 1991; Goverde <i>et al.</i> , 2002
<i>Aphantopus hyperantus</i>	Lepidoptera	CB	-0.88		21	Wing length		Nylin and Svärd, 1991

TABLE 1. *Continued.*

Species	Order	Rule	Latitudinal change (% per degree latitude)		Length ¹ (mm)	Trait measured	Development time (d)	Reference
			Field	Lab				
<i>Maniola jurtina</i>	Lepidoptera	CB	-0.23		23	Wing length		Nylin and Svård, 1991
<i>Erebia ligea</i>	Lepidoptera	CB	-0.87		23	Wing length		Nylin and Svård, 1991
<i>Hipparchia semele</i>	Lepidoptera	CB	-0.25		26	Wing length		Nylin and Svård, 1991
<i>Lasiommata megera</i>	Lepidoptera	CB	-1.18		22	Wing length	37	Nylin and Svård, 1991; Wiklund and Forsberg, 1991
<i>Lasiommata maera</i>	Lepidoptera	CB	-1.2		24.5	Wing length	33	Nylin and Svård, 1991; Wiklund and Forsberg, 1991
<i>Lasiommata petropolitana</i>	Lepidoptera	B	0.23		20.5	Wing length	28	Nylin and Svård, 1991; Wiklund and Forsberg, 1991
<i>Pararge aegeria</i>	Lepidoptera	CB	-0.49		21.5	Wing length	42	Nylin and Svård, 1991; Wiklund and Forsberg, 1991
<i>Lymantria dispar</i>	Lepidoptera	CB		-1.9	35	Wing length	50	Goldschmidt, 1933
<i>Scathophaga stercoraria</i>	Diptera	B		0.185	8	Wing length	21	This study
<i>Musca domestica</i>	Diptera	B		1.4	2.6	Wing length	14	Bryant, 1977; Sullivan and Sokal, 1963
<i>Drosophila melanogaster</i>	Diptera	B		0.175	1.2	Wing length	10	David and Bocquet, 1975; James <i>et al.</i> , 1995; van t'Land <i>et al.</i> , 2000
<i>Drosophila subobscura</i>	Diptera	B		0.27	2.5	Wing length	27	Huey <i>et al.</i> , 2000; Gilchrist <i>et al.</i> , 2001; Budnik <i>et al.</i> , 1991
<i>Drosophila robusta</i>	Diptera	B		0.29	2	Wing length		Stalker and Carson, 1947
<i>Drosophila buzzatti</i>	Diptera	B		0.1	1.9	Wing length	18	Loeschcke <i>et al.</i> , 2000
<i>Drosophila alduchi</i>	Diptera	B		0.1	2	Wing length	18	Loeschcke <i>et al.</i> , 2000
<i>Drosophila kikkawai</i>	Diptera	B		0.89	2.4	Wing length	9.7	Karan <i>et al.</i> , 1998; P. Gilbert, pers. comm.
<i>Drosophila simulans</i>	Diptera	B		0.095	1.8	Wing length	9.1	David and Bocquet, 1975; Tantawy and Mallah, 1961; Petavy <i>et al.</i> , 2001
<i>Zaprionus indianus</i>	Diptera	B		0.4	2.3	Wing length		Karan <i>et al.</i> , 2000

¹ Wing length or equivalent.

additional information on the Lepidoptera from S. Nylin, Stockholm University (personal communication).

RESULTS

Laboratory common garden rearing of yellow dung flies

For both experiments, we analogously analyzed the family mean body size and development data using

repeated-measures ANOVA with rearing temperature as a (discrete) fixed factor (omitted in the sequential experiment), sex as a repeated factor (because brothers and sisters are related), and latitude as a continuous covariate. In the simultaneous experiment, body size was greater for males ($F_{1,155} = 28.49$; $P < 0.001$) and at colder temperatures ($F_{2,155} = 3.95$; $P = 0.021$), as is typical in this species (Blanckenhorn, 1997, 1998).

Importantly, body size overall increased with latitude slightly but significantly ($F_{1,155} = 4.16$; $P = 0.043$), following Bergmann's rule (Fig. 2). All interactions were not significant ($P > 0.2$). Analogously, development time increased at colder temperatures ($F_{2,118} = 82.55$; $P < 0.001$), equally for both sexes (sex effect $F_{1,118} = 0.80$; $P = 0.373$). Interestingly, however, development time decreased with latitude ($F_{1,118} = 92.66$; $P < 0.001$), more strongly at lower temperatures (temperature by latitude interaction $F_{2,118} = 41.09$; $P < 0.001$), following the converse Bergmann rule (Fig. 2). All other interactions were not significant ($P > 0.2$). Note that at 12°C there are few if any data for the northern populations (S, ISL) because most flies entered winter pupal diapause.

Results of the sequential experiment (at 15°C, and including the German [D] population) were qualitatively identical (Fig. 3), so no further statistics are given. Most crucially, our data show that while body size increases with latitude, development time decreases with latitude, a mixed pattern. This implies faster growth rates of the more northern populations, and reveals slightly overcompensating countergradient variation (*cf.* Fig. 1).

Literature review on clinal body size variation in arthropods

Table 1 lists all arthropod studies we could find describing latitudinal body size trends. The data show a variety of responses ranging from 2% increase in body size per degree latitude, indicative of Bergmann's rule, to a -3.8% decrease in size, indicative of the converse Bergmann rule. Bergmann clines were apparent for 19 species and converse Bergmann clines for 29 species. This is not significantly different from an even distribution (binomial test $P > 0.1$).

Furthermore, there is a pattern in this variation. Larger species with relatively long development times tend to decrease in size with latitude, *i.e.*, follow the converse Bergmann rule (B in Table 1: mean \pm SD wing length 18.9 ± 7.7 mm, median 17.5 mm; mean \pm SD development time 53.9 ± 23.5 days, median 47.5 days), whereas small species with short development times tend to increase in size with latitude, *i.e.*, follow Bergmann's rule (B in Table 1: mean \pm SD wing length 6.1 ± 8.9 mm, median 2.3 mm; mean \pm SD development time 33.9 ± 47.3 days, median 27.2 days). These differences in wing length and development time between the two groups are significant (Mann-Whitney U -tests: $Z = -4.62$ and 3.29 , respectively; both $P < 0.001$). Figure 4 plots the data in a bivariate fashion, showing a negative relationship between square-root-transformed wing length ($r = -0.50$, $N = 48$) or development time ($r = -0.43$, $N = 32$) and the percent size change per degree latitude (both $P < 0.02$). This relationship is strongly confounded by taxon (Fig. 4; Table 1). Nevertheless, the negative correlations remain when analyzing the data using independent contrasts (CAIC), but become non-significant: $r = -0.25$ ($P < 0.1$, $N = 47$) and $r =$

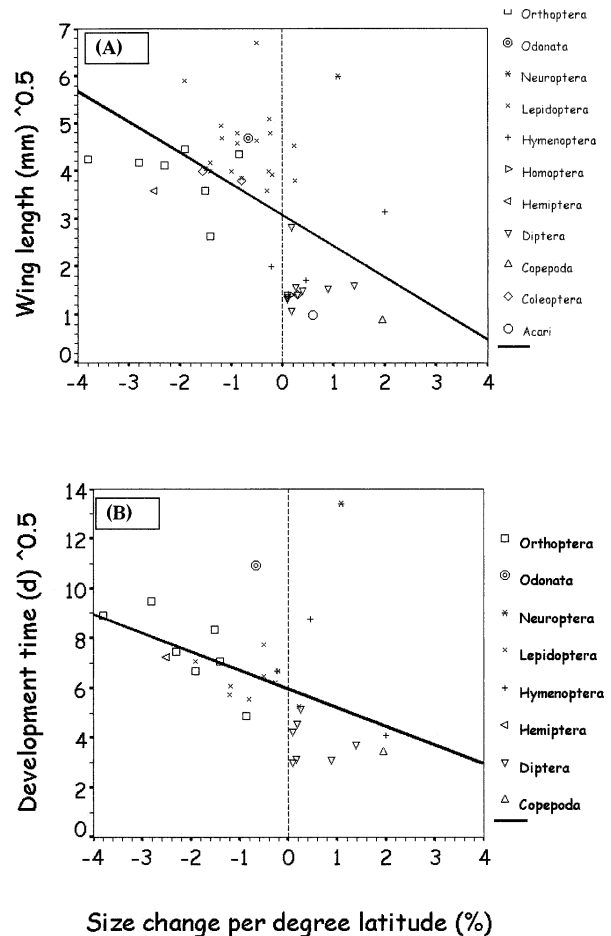


FIG. 4. Relationship between square-root transformed (A) wing length and (B) egg to adult development time and the percent size change per degree latitude in the field for numerous arthropod species.

-0.23 ($P > 0.2$, $N = 30$), respectively. However, when excluding one outlier, the ant lion (Neuroptera in Fig. 4), the correlations are again significant: $r = -0.41$ ($P < 0.01$, $N = 46$) and $r = -0.38$ ($P < 0.05$, $N = 29$), respectively.

DISCUSSION

Our comparative study shows that arthropod species, as well as other taxa (Belk and Houston, 2002; Ashton, 2004), feature a range of relationships of body size with latitude within species. Both Bergmann size clines, showing increased body size at higher latitudes (Atkinson and Sibly, 1997), and converse Bergmann clines, showing decreased body size at higher latitudes (Park, 1949; Masaki, 1967; Mousseau, 1997), are about equally common. Moreover, the slope (*i.e.*, the strength) of the latitudinal body size change varies in a continuous fashion among species. Which type of cline is evident, and how strong the effect is, depends crucially on the body size and/or development time of the species in question: larger species with typically longer development times tend to show converse Bergmann clines, whereas smaller species with shorter de-

velopment times tend to show Bergmann clines. This lends empirical support to the original suggestion of Chown and Gaston (1999) that generation time relative to season length is a crucial parameter in determining which rule applies. That is, species with long development times relative to season length that consequently have often only one generation per year, such as the water strider *Aquarius remigis* (Blanckenhorn and Fairbairn, 1995), are more prone to experience end of season time constraints (and thus exhibit converse Bergmann clines) than multivoltine species with short generation times and many generations per year, such as *Drosophila melanogaster* (James *et al.*, 1995). Bergmann's rule (Bergmann, 1847; Atkinson and Sibly, 1997) and the converse Bergmann rule (Park, 1949; Mousseau, 1997), the two seemingly opposite rules long described, thus appear to be two ends of a continuum.

Our common garden laboratory comparison of various European yellow dung fly populations along a latitudinal gradient further shows different clines for body size and development time: body size slightly increased with latitude (thus showing a Bergmann cline), whereas development time decreased with latitude (thus showing a converse Bergmann cline). This was also found in at least one other insect species, the ant lion (Arnett and Gotelli, 1999a). This mixed response is unexpected because the theory predicting converse Bergmann clines under seasonal time constraints (Roff, 1980; see Introduction) assumes both traits to be positively correlated, as it takes time to get large. And indeed, in yellow dung flies there is an albeit low positive genetic correlation between body size and development time (Blanckenhorn, 1998). Our result implies faster growth rates of higher latitude populations, which face shorter seasons, a case of adaptive countergradient variation (Conover and Present, 1990). In this light, heritable growth rates of yellow dung flies can be interpreted to be overcompensated, resulting in the slight increase in body size with latitude (*i.e.*, the Bergmann cline) obtained here, as the null-expectation of perfect compensation of latitudinal changes in season length and temperature would predict no phenotypic change in body size (*cf.* Fig. 1A). However, this null model of countergradient variation implicitly assumes that the target (*i.e.*, presumably optimal) body size be the same for all populations across the latitudinal gradient. It is unclear why this should be so, as it is well known that the costs and benefits of, and hence selection on, body size vary spatio-temporally due to a variety of ecological variables (Kingsolver *et al.*, 2001; *e.g.*, Jann *et al.*, 2000 for yellow dung flies). Moreover, there is a dearth of evidence for optimizing selection on body size even though it is generally postulated (Schluter *et al.*, 1991; Blanckenhorn, 2000a). So over- or, in fact, undercompensating countergradient variation of varying degrees could be quite common in nature and may explain the continuous variation in latitudinal body size cline slopes evident in our comparative study (Fig. 4).

Another interpretation of the results obtained here would be that Bergmann and converse Bergmann size clines are not at all mutually exclusive, as they are driven by different causes and mechanisms, temperature and season length respectively (Chown and Gaston, 1999). Thus in principle they can operate in conjunction and may cancel each other to varying degrees if they interact additively (Fig. 1B). By the same reasoning as above, the proximate mechanisms ultimately producing converse Bergmann clines in response to end of season time constraints are likely to dominate in univoltine species with long development times, whereas the growth mechanisms causing Bergmann size clines in response to temperature are more likely dominant in species with short generation times in which the constraining effects of season length are diluted and thus negligible. Any slope of a linear relationship conceivable may be the net result, potentially explaining our results in Figure 4. Furthermore, if the different proximate mechanisms causing Bergmann and converse Bergmann clines instead interact multiplicatively, at least theoretically dome-shaped clines could also occur, as *e.g.*, in the ant *Myrmica rubra* or the damselfly *Enallagma cyathigerum* (Elmes *et al.*, 1999; Johansson, 2003).

Although we here identified body size and development time of a species as major determinants explaining which type of latitudinal cline should be expected, there surely are other important environmental factors. For example, as noted early on by Masaki (1967, 1972) for crickets and later formalized by Roff (1980), a change from one to two generations per year will produce complex, sawtooth body size clines. If such voltinism changes remain undetected or ignored, the resulting overall pattern may be flat and quite different, as found *e.g.*, for some butterfly species by Nylin and Svärd (1991). Furthermore, systematic latitudinal or altitudinal changes in food availability may affect clines as well (Chown and Klok, 2003).

The crucial effect of body size and development identified here for arthropods may not be as important in more long-lived taxa. For example, when we plotted the data of Belk and Houston (2002) on fish as in Figure 4, no relationship resulted (not shown). Ashton (2004) also did not find a relationship between the strength of the cline and body size in various vertebrate species. This is perhaps unsurprising, because for organisms growing continuously over several years, the effects of end of season time constraints during any particular year will get diluted as well, just as in organisms featuring many generations per year, and may hence not strongly affect the overall growth strategy and final body size of the species in question.

In conclusion, our study provides a synthesis to the controversy about the importance of Bergmann's rule and the converse Bergmann rule in nature (Van Voorhies, 1996, 1997; Mousseau, 1997; Partridge and Coyne, 1997). Apparently both phenomena are about equally common in arthropods. The different mechanisms presumably producing one or the other phenom-

enon are thus not mutually exclusive and can act simultaneously, possibly canceling each other. The work of Ashton and colleagues (Ashton *et al.*, 2000; Ashton, 2002a, b, 2003, 2004) also shows that both rules are common in many vertebrate taxa, although there are clear patterns (*e.g.*, Bergmann clines are more common in birds; converse Bergmann clines are more common in squamates). We here also demonstrated a pattern in arthropods dependent on the size and development time of a species relative to generation time, as originally suggested by Chown and Gaston (1999; see also Chown and Klok, 2003). Nevertheless, we must emphasize that our study does not elucidate at all the underlying cause of Bergmann's rule, the mystery of which must therefore continue (Atkinson and Sibly, 1997; Angilletta and Dunham, 2003).

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