## Short Communication

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# Larger insects in a colder environment? Elevational and seasonal intraspecific differences in tropical moth sizes on Mount Cameroon

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## Abstract

Bergmann's Rule describes an increase in the body size of endothermic animals with decreasing environmental temperatures. However, in ectothermic insects including moths, some of the few existing studies investigating size patterns along temperature gradients do not follow the Bergmann's Cline. Intraspecific differences in moth sizes along spatiotemporal temperature gradients are unknown from the Palaeotropics, hindering general conclusions and understanding of the mechanism responsible. We measured intraspecific forewing size differences in 28 Afrotropical moth species sampled in 3 seasons along an elevational gradient on Mount Cameroon, West/Central Africa. Size increased significantly with elevation in 14 species but decreased significantly in 5 species. Additionally, we found significant inter-seasonal size differences in 21 species. Most of these variable species had longer forewings in the transition from the wet to dry season, which had caterpillars developing during the coldest part of the year. We conclude that environmental temperature affects the size of many Afrotropical moths, predominantly following prevailingly following Bergmann's Cline. Nevertheless, the sizes of one-third of the species demonstrated a significant interaction between elevation and season. The responsible mechanisms can thus be assumed to be more complex than a simple response to ambient temperature.

## Introduction

Bergmann's Rule describes a negative correlation between environmental temperature and endotherms' body size (Bergmann 1847): endothermic animals are smaller in warm environments than in cold climates. The smaller surface:mass ratio of larger endotherms reduces heat loss in colder environments. The body temperature of ectotherms depends on environmental temperature (and therefore Bergmann's Rule were not defined for ectotherms; Vinarski 2014), and their size might therefore depend on the length of the warm season, which is usually shorter at higher altitudes and/or latitudes (Mousseau 1996). Consequently, the opposite of Bergmann's Clines (i.e. the same pattern as predicted by Bergmann's Rule for endotherms) is often observed in ectotherms (*e.g.,* Mousseau 1996; Vinarski 2014): body size decreases with decreasing environmental temperature. However, numerous studies have showed Bergmann's Clines in ectotherms. Larger bodies absorb more heat through basking in colder environments, are a useful barrier against cold weather (*e.g.,* Vinarski 2014; Beck *et al.* 2016; Brehm *et al.* 2019), and function as a buffer to aid survival through seasonal unavailability of resources (Horne *et al.* 2017).

Studies of elevational patterns in insect body sizes have predominantly focused on interspecific patterns in communities, with both positive and negative relationships between body size and elevation detected (Shelomi 2012). Body size and elevation have been positively correlated in geometrid and arctiine moths in the Costa Rican mountains (Brehm *et al.* 2019), arctiine moths in the Ecuadorian Andes (Fiedler & Brehm 2021), and macromoths in the Swiss Alps (Beck *et al.* 2016). However, no significant relationship between elevation and geometrid body size was found in the Ecuadorian Andes (Brehm & Fiedler 2004). Although temperature and other mechanisms are thought to be responsible for these interspecific trends (*e.g.,* Shelomi 2012, Beck *et al.* 2016), the phylogenetic complexity of multispecies communities makes the

results difficult to interpret (Mungee et al. 2021). Intraspecific changes in insect body size along elevation have rarely been studied (16% of 676 datasets included in Shelomi 2012), but such studies are instrumental for understanding the responsible mechanisms. Most of these uncommon, intraspecific datasets mostly showed Bergmann's Clines (Shelomi 2012), including four tortricids in North America (Miller 1974, 1991), four geometrids and one noctuid in North Carolina (Sullivan & Miller 2007), and one geometrid moth in Costa Rica (Sullivan & Miller 2007). Brehm et al. (2019) found intraspecific Bergmann's clines among most of 84 Costa Rican geometrid and arctiine moths they examined, and Mungee et al. (2021) found significant but weak Bergmann's clines in 24 sphingid species in the eastern Himalayas.

Individual generations of multivoltine ectotherms can differ in their body sizes (Chown & Gaston 2010; Horne et al. 2015; Horne et al. 2017). Although availability of food, water and humidity, along with predation and pathogen risk can differ seasonally (Chown & Gaston 2010), the main drivers of multivoltine insect body size are expected to be ambient environmental temperature and—at higher latitudes—photoperiod (Chown & Gaston 2010; Horne et al. 2017). Seasonal intraspecific differences in the body size of insects and other arthropods have been recently meta-analysed, and the body sizes of 86% of 102 species decreased in warmer seasons (Horne et al. 2017). This pattern was demonstrated in a North American tortricid moth Epiphyas postvittana (Danthanarayana 1976) and in 8 of 10 butterfly species studied (Horne et al. 2017). The opposite trend of larger specimens developed during warmer period was shown in 10 European moth species (Teder et al. 2010). Zeuss et al. (2017) found a negative relationship between voltinism (i.e., number of generations per year) and body size in European lepidopterans, whilst Seifert et al. (2022) showed the opposite trend for European moths. Nevertheless, the knowledge of intraspecific seasonal changes in lepidopteran size is limited, and no study on intraspecific seasonal differences in body sizes in tropical moths is available.

Our study examines intraspecific changes in sizes of 28 moth species (Lepidoptera) along an elevational gradient and in different seasons in Afrotropical rainforests on Mount Cameroon, an important biodiversity hotspot (Ustjuzhanin et al. 2018, 2020). Forewing length is strongly correlated with body size in lepidopterans (Brehm et al. 2019; Mertens et al. 2021), and we hypothesised that the forewing length generally increases with elevation. Additionally, we analysed inter-seasonal differences in forewing length, hypothesising that individuals will be larger in wetter seasons with less sunshine. We analysed relationships between size and elevation separately for males and females, as this is known to play a role (Baranovská & Knapp 2018; Brehm et al. 2019).

## Methods

We analysed moths sampled along the elevational gradient of Mount Cameroon, the highest mountain (4095 m a.s.l.) in West/Central Africa. Moths were attracted by light at six elevations: 350, 650, 1100, 1450, 1850 and 2200 m a.s.l. Sampling was repeated in three seasons: transition from wet to dry seasons: November/December; dry season: January/February; and transition from dry to wet seasons: April/May (Maicher et al. 2018). See Maicher et al. (2020) for more details on the sampling and sites. All specimens were identified by comparison with a large reference collection of identified material and confirmed by genitalia dissection; morphospecies are therefore considered to be taxonomically valid species.

From 17,598 moths (Lepidoptera: Heterocera) of 561 morphospecies from Maicher et al. (2020), we selected 28 moth species (13 Erebidae: Arctiinae, 10 Erebidae: Lymantriinae, 2 Notodontidae, 2 Lasiocampidae and 1 Sphingidae; Table 1; Fig. S1) with at least 5 specimens at each of at least 2 elevations and seasons. Altogether, 3223 specimens were photographed with a scale, and their right forewing length was measured from the base to its apex using ImageJ 1.46r (Ferreira & Rasband 2012). Forewing lengths were analysed separately for each species, and wherever possible (eight species; Table 1) also for both sexes. Relationships between forewing length (continuous response variable) and elevation (continuous explanatory variable), season (factorial explanatory variable), and their interactions were tested with generalised linear models (GLMs) in glm2 package (Marschner 2011) in R 4.0.2 (R Core Team 2020). In several cases, the number of specimens from individual elevations or seasons was not sufficient to include one of the response variables or their interaction in the particular model. Based on the visual inspection, Poisson or quasi-Poisson distributions were applied (Table 1).

## Results and discussion

Of the 28 moth species, the forewing lengths of 14 species increased significantly with elevation in at least one sex and decreased significantly in 5 species. There was no significant relationship in the remaining nine species (Table 1; Fig. S2). Intersexual differences were highly variable, although no moth species showed opposite trends in males and females (Table 1; Fig. S2). Significantly positive relationships between forewing length and elevation in both sexes was observed in three species (Asythosia velutina, Galtara sp. "1" and Palaeugoa camerunensis). In two species (Afrasura cf. numida and Eilema cf. fletcheri), significantly positive trends were found only in males, and significantly negative sex-specific trends were observed in males of Ligulosia costimaculata and females of Mylantria xanthospila.

Our results are consistent with results affirming Bergmann's Clines in moths from other biogeographic areas (Miller 1974, 1991; Sullivan & Miller 2007; Brehm et al. 2019; Fiedler & Brehm 2021; Mungee et al. 2021), as well as for some other insects (Shelomi 2012). Although some adult moths, such as sphingids, can increase their temperature by vibrating their wing muscles (Heinrich 2013), we do not expect the relationship between body surface area and thermal metabolism as predicted by Bergmann (1847). Nor can we expect that improved solar basking influences the size of these nocturnal animals (Vinarski 2014; Tammaru et al. 2018). Therefore, some other mechanisms, such as the hypothesised balancing of resource supply and demand (Horne et al. 2017), may be responsible for widespread intraspecific Bergmann's Cline. Additionally, we hypothesise that longer wings may enable greater mobility at higher elevations with scarcer resources. A similar relationship between forewing length and mobility was already shown for intraspecific differences for some lepidopterans (e.g., Fric et al. 2006). This hypothesis is supported by the negative elevational trends for both lasiocampid species with non-feeding adults. An alternative explanation could be related to the necessity of larger wings in less dense air at higher elevations (Brehm et al. 2019); although such evolutionary mechanism has not been studied in moths to our knowledge, it was repeatedly demonstrated in hummingbirds (e.g., Altshuler et al. 2004).

The forewing lengths of 21 moth species were significantly different among the three seasons. In nine of these, there was an interaction between elevation and season affecting forewing lengths

**Table 1.** Summary of measured moths along the elevational gradient of Mount Cameroon, together with details and results of GLM models, with separated effects of elevation, season and their interaction on the forewing length of the 28 moth species. Significance – p < 0.001: ***, p < 0.01: **, p < 0.05: *, p > 0.05: n.s. Values of F-tests for models with quasi-Poisson distribution, and values of $\chi^2$ tests for models with Poisson distribution. Elevational trends – significantly positive: ↗, significantly negative: ↘, insignificant: n.s. Seasonal trends – WD: transition from wet to dry seasons, D: dry season, DW: transition from dry to wet seasons; the seasonal differences were checked visually by comparison of trends (Fig. S1), where > means that moth forewings were larger in one or two seasons than in the other one or two seasons, and ≈ means no apparent inter-seasonal difference.

| | | | | GLM details and results | | | | | | | |
| | | | | Elevation | | | Season | | | Elevation*Season | |
| Species | Sex | No. specimens | Distribution | F/$\chi^2$ | p | trend | F/$\chi^2$ | p | trend | F/$\chi^2$ | p |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Erebidae: Arctiinae** | | | | | | | | | | | |
| *Afrasura* cf. *numida* | F | 46 | Poisson | 0.3 | 0.743 | n.s. | 7.1 | **0.002** | WD>DW | 8.8 | 0.250 |
| | M | 73 | Poisson | 21.7 | **<0.001*** | ↗ | 4.7 | **<0.001*** | D>(DW≈WD) | 19.3 | **<0.001*** |
| *Afrasura* cf. *peripherica* | M | 155 | Poisson | 112.5 | **<0.001*** | ↗ | 4.7 | **0.003** | WD>(DW≈D) | 1.7 | 0.227 |
| *Anapisa* sp. "2" | M | 118 | Poisson | 102.7 | **<0.001*** | ↗ | 0.6 | **<0.001*** | (DW≈WD)>D | 7.9 | **0.021*** |
| *Asura* cf. *craigii* | M | 121 | Poisson | 113.1 | **0.002** | ↗ | <0.1 | **<0.001*** | (D≈WD)>DW | 4.0 | **<0.001*** |
| *Asythosia velutina* | F | 22 | Poisson | 4.7 | **<0.001*** | ↗ | 10.2 | **<0.001*** | (WD≈D)>DW | 22.3 | **0.021*** |
| | M | 259 | quasi-Poisson | 327.1 | **<0.001*** | ↗ | 13.4 | **<0.001*** | (WD≈D)>DW | 4.2 | **0.017*** |
| *Cyana* sp. "2" | M | 117 | Poisson | 12.7 | **<0.001*** | ↘ | 25.0 | **<0.001*** | WD>(DW≈D) | 25.0 | 0.274 |
| *Eilema* cf. *fletcheri* | F | 15 | Poisson | 10.3 | 0.683 | n.s. | 4.8 | **<0.001*** | (WD≈D)>DW | | *not analysed* |
| | M | 114 | Poisson | 131.7 | **<0.001*** | ↗ | 0.6 | **<0.001*** | (WD≈D)>DW | 15.9 | **0.012*** |
| *Galtara* sp. "1" | F | 15 | Poisson | 19.2 | **<0.001*** | ↗ | | | *not analysed* | | |
| | M | 90 | Poisson | 34.9 | **<0.001*** | ↗ | 5.3 | 0.725 | n.s. | 14.3 | 0.474 |
| *Lamprosiella* sp. "1" | M | 138 | Poisson | 22.1 | 0.199 | n.s. | 0.3 | **<0.001*** | (WD≈D)>DW | 0.5 | **<0.001*** |
| *Ligulosia costimaculata* | F | 50 | quasi-Poisson | 1.5 | 0.230 | n.s. | 24.8 | **<0.001*** | (WD≈D)>DW | | *not analysed* |
| | M | 92 | Poisson | 1.6 | **0.034*** | ↘ | 5.6 | 0.198 | n.s. | 19.7 | 0.408 |
| *Palaeugoa camerunensis* | F | 15 | Poisson | 2.8 | **<0.001*** | ↗ | 5.2 | **0.038*** | WD>D | 12.3 | 0.338 |
| | M | 71 | Poisson | 31.2 | **0.014*** | ↗ | 8.0 | **<0.001*** | WD>(DW≈D) | 19.4 | 0.941 |
| *Phasmatilema* sp. "1" | M | 82 | Poisson | 22.9 | 0.306 | n.s. | 65.9 | **<0.001*** | WD>(DW≈D) | 18.6 | 0.465 |
| *Rhipidarctia postrosea* | M | 87 | Poisson | 28.4 | **<0.001*** | ↗ | 6.7 | 0.055 | n.s. | 25.0 | 0.230 |
| **Erebidae: Lymantriinae** | | | | | | | | | | | |
| *Euproctis* sp. "1" | M | 49 | quasi-Poisson | 0.3 | 0.590 | n.s. | 2.4 | 0.101 | n.s. | 0.3 | 0.619 |
| *Leucoma* sp. "7" | M | 46 | quasi-Poisson | 0.1 | 0.812 | n.s. | 3.2 | 0.051 | n.s. | 0.3 | 0.559 |
| Lymantriinae sp. "5" | M | 113 | Poisson | 3.3 | 0.071 | n.s. | 8.8 | **<0.001*** | (D≈DW)>WD | 3.1 | 0.050 |
| Lymantriinae sp. "54" | M | 92 | quasi-Poisson | 25.7 | **<0.001*** | ↗ | 1.1 | 0.323 | n.s. | 2.4 | 0.093 |
| Lymantriinae sp. "55" | M | 88 | Poisson | 79.4 | **<0.001*** | ↗ | 8.8 | **<0.001*** | DW>(WD≈D) | 14.8 | 0.057 |
| Lymantriinae sp. "58" | M | 79 | Poisson | 47.6 | **<0.001*** | ↗ | 9.1 | **<0.001*** | D>(WD≈DW) | 5.5 | **<0.001*** |
| Lymantriinae sp. "65" | M | 69 | Poisson | 51.2 | 0.263 | n.s. | 9.4 | 0.080 | n.s. | 6.5 | 0.524 |

**Table 1.** (*Continued*)

| | | | | GLM details and results | | | | | | | |
| | | | | Elevation | | | Season | | | Elevation*Season | |
| Species | Sex | No. specimens | Distribution | F/χ² | p | trend | F/χ² | p | trend | F/χ² | p |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Lymantriinae sp. "75" | M | 48 | Poisson | 44.1 | <0.001*** | ↗ | 2.4 | <0.001*** | (WD≈D)>DW | not analysed | |
| Mylantria xanthospila | F | 74 | Poisson | 91.3 | <0.001*** | ↘ | 9.1 | <0.001*** | (WD≈DW)>D | 5.1 | 0.542 |
| | M | 219 | quasi-Poisson | <0.1 | 0.987 | n.s. | 8.3 | <0.001*** | (D≈DW)>WD | 25.9 | <0.001*** |
| Stracena cf. bananae | M | 69 | Poisson | 90.3 | 0.674 | n.s. | 1.0 | <0.001*** | WD>D | 6.7 | 0.576 |
| **Notodontidae** | | | | | | | | | | | |
| Desmeocraera sp. "1" | M | 106 | Poisson | 42.2 | 0.768 | n.s. | 4.3 | <0.001*** | (D≈DW)>WD | 8.6 | 0.342 |
| Eurystaura sp. "1" | M | 97 | Poisson | 74.1 | 0.610 | n.s. | 0.8 | <0.001*** | (D≈DW)>WD | 2.7 | 0.087 |
| **Lasiocampidae** | | | | | | | | | | | |
| Mallocampa audea | M | 122 | Poisson | 64.1 | <0.001*** | ↗ | 14.3 | <0.001*** | (WD≈DW)>D | **24.3** | **0.046*** |
| Mariaeia spargatana | M | 62 | Poisson | 18.1 | <0.001*** | ↗ | 58.1 | not analysed | | | |
| **Sphingidae** | | | | | | | | | | | |
| Polyptychus nigriplaga | M | 210 | quasi-Poisson | 5.8 | **0.017*** | ↗ | 2.4 | 0.090 | n.s. | 0.7 | 0.475 |

([Table 1](#)). Although no consistent trends in the inter-seasonal differences of forewing length were found among the species, females from all 7 species with enough female specimens and males from 12 species analysed had longer forewings in the transition from wet to dry seasons than in one or both other studied seasons. Although their phenology and voltinism are largely unknown, most of these specimens probably developed during the wet season, *i.e.*, the coldest months on Mount Cameroon (Maicher *et al.* 2020), because all moth individuals grow during their larval stages. This suggests that the intraspecific differences in insect size results from climatic effects on physiological processes during development and may not be an adaptation for adult life (Meister *et al.* 2018). However, the seasonal intraspecific differences in moth body size may also be related to differences in the accessibility and quality of food during larval development (Atkinson & Sibly 1997; Rodrigues & Moreira 2004). Unfortunately, the larval food plants of Afrotropical moths are largely unknown.

We confirmed that environmental temperature is a key factor determining insect size along an elevational gradient and among seasons (Atkinson & Sibly 1997, Chown & Gaston 2010; Horne *et al.* 2017). Nevertheless, since there were interactions between the effects of elevation and season on size of one-third of the moth species we studied, we assume the relationship and its causality could be more complex and requires more attention.

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