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PAPER



# Bergmann's rule does not apply to geometrid moths along an elevational gradient in an Andean montane rain forest

Gunnar Brehm and Konrad Fiedler

Department of Animal Ecology I, University of Bayreuth, 95440 Bayreuth, Germany. E-mail: [gunnar\\_brehm@yahoo.com](mailto:gunnar_brehm@yahoo.com)

## ABSTRACT

**Aim** Bergmann's rule generally predicts larger animal body sizes with colder climates. We tested whether Bergmann's rule at the interspecific level applies to moths (Lepidoptera: Geometridae) along an extended elevational gradient in the Ecuadorian Andes.

**Location** Moths were sampled at 22 sites in the province Zamora-Chinchi in southern Ecuador in forest habitats ranging from 1040 m to 2677 m above sea level.

**Methods** Wingspans of 2282 male geometrid moths representing 953 species were measured and analysed at the level of the family Geometridae, as well as for the subfamily Ennominae with the tribes Boarmiini and Ourapterygini, and the subfamily Larentiinae with the genera *Eois*, *Eupithecia* and *Psaliodes*.

**Results** Bergmann's rule was not supported since the average wingspan of geometrid moths was negatively correlated with altitude ( $r = -0.59$ ,  $P < 0.005$ ). The relationship between body size and altitude in Geometridae appears to be spurious because species of the subfamily Larentiinae are significantly smaller than species of the subfamily Ennominae and simultaneously increase in their proportion along the gradient. A significant decrease of wingspan was also found in the ennomine tribe Ourapterygini, but no consistent body size patterns were found in the other six taxa studied. In most taxa, body size variation increases with altitude, suggesting that factors acting to constrain body size might be weaker at high elevations.

**Main conclusions** The results are in accordance with previous studies that could not detect consistent body size patterns in insects at the interspecific level along climatic gradients.

## Keywords

Andes, Bergmann's rule, body size, elevational gradient, Geometridae, insects, macroecology, mountains, rain forest, wingspan.

\*Correspondence: Gunnar Brehm, Department of Animal Ecology I, University of Bayreuth, 95440 Bayreuth, Germany. E-mail: [gunnar\\_brehm@yahoo.com](mailto:gunnar_brehm@yahoo.com)

## INTRODUCTION

Changes in body sizes of animals along environmental gradients have attracted the attention of ecologists since Bergmann's famous publication (Bergmann, 1847). He found that endothermic ('homiothermic', 'gleichwarme') vertebrate species tend to be smaller in warmer climates and larger under cooler conditions. According to his hypothesis, animals with larger body masses suffer smaller losses of energy due to their more favourable relationship between body volume and surface area. Since then, several redefinitions of his rule have been formulated.

For example, Rensch (1938) restricted the rule to intraspecific body size variations of endothermic animals, while Blackburn *et al.* (1999) redefined it as 'the tendency for a positive association between the body mass of species in a monophyletic higher taxon and the latitude inhabited by those species'. The latter concept explicitly included ectothermic animals ('poikilothermic', 'wechselwarme' animals according to Bergmann), yet excluded all gradients other than latitudinal ones. This restriction to latitudinal gradients as suggested by Blackburn *et al.* might be questioned, because climatic changes, as mentioned by Bergmann, occur not only along latitudinal gradients. On a smaller

geographical scale, climatic conditions also change significantly along elevational gradients. Body size changes along these gradients have been investigated in a number of studies (e.g. Hawkins & DeVries, 1996; Smith *et al.*, 2000), and we see no convincing reason why elevational gradients should be excluded from Bergmann's concept.

For endothermic mammals and birds the available evidence clearly supports Bergmann's rule (Meiri & Dayan, 2003). In contrast, no convincing general hypothesis that explains insect body size patterns along climatic gradients is currently available. A number of factors can be responsible for changing insect body sizes, including developmental temperature (Mousseau, 1997), starvation resistance, as well as the relationship between growing season length and generation time (Partridge & French, 1996; Chown & Gaston, 1999).

Given this multitude of selective forces, there are serious doubts as to whether a consistent phenomenon of changing insect body sizes along environmental gradients exists at all (Blackburn *et al.*, 1999). Previous studies, both at the intra-specific and interspecific level, revealed no consistent overall trends. Some studies showed an increase in body size with increasing altitude or latitude (e.g. Cushman *et al.*, 1993), whereas other studies found a decrease in body size (e.g. Sota, 1996), or inconsistent patterns (Hawkins & Lawton, 1995; Hawkins & DeVries, 1996; Krasnov *et al.*, 1996).

We chose geometrid moths as a model group for our study. The diversity of this very species-rich family has been investigated along an altitudinal gradient in a montane rain forest in southern Ecuador (Brehm, 2002; Brehm & Fiedler, 2003, 2004; Brehm *et al.*, 2003a,b). In contrast to many previous studies on tropical arthropods, analyses were carried out on a fine taxonomical scale. With a total of 13,938 specimens representing 1010 nocturnal species, the large data set offered the unique chance to analyse body size patterns of a highly diverse monophyletic group of herbivorous insects along an elevational gradient in their natural habitat. According to Bergmann's rule, we tested the prediction that body size of geometrid moths increases with increasing elevation at the interspecific level. Moreover, we tested for a change of body size variability without an *a priori* prediction.

Analyses were not restricted to the family level but were also carried out at the level of the seven largest subordinated taxa (> 60 species in the study area: Ennominae with the tribes Boarmiini and Ourapterygini, and Larentiinae with the genera *Eupithecia*, *Eois* and *Psaliodes*). We used this approach in order to detect phylogenetic effects on the results. As in previous comparable studies (e.g. Hawkins & Lawton, 1995; Hawkins & DeVries, 1996), we did not apply phylogenetic comparative methods (Harvey & Pagel, 1991) because of large uncertainties with regard to the actual phylogenetic relationships within geometrid moths. These relationships are still unresolved even at subfamily level (Abraham *et al.*, 2001; Pitkin, 2002). Monophyly is clearly supported for Geometridae and the subfamily Larentiinae (Holloway, 1997), but uncertainties exist in respect of most other taxa investigated in this study.

## METHODS

### Study area and sampling

The study area in southern Ecuador is situated within the East Cordillera of the Andes and belongs to the province Zamora-Chinchi (vicinity of Reserva Biológica San Francisco, 3°58' S, 79°5' W). Most parts are covered with undisturbed or slightly disturbed montane rain forest. The vegetation of the upper part of the study area was described by Bussmann (2001) and Paulsch (2002). Twenty-two sampling sites were selected at 11 elevational levels between 1040 m and 2677 m above sea level. Annual precipitation ranges from some 2000 mm at the lowest elevations to c. 5500 mm at the highest altitudes (P. Emck, personal communication). The mean monthly temperature ranges from 20–22 °C to 10–12 °C across the gradient. Moths were sampled manually between 18.30 and 21.30 hours using portable weak light traps (2 × 15 W, UV-emitting light tubes). Traps consisted of a white gauze cylinder (height 1.60 m, diameter 0.60 m) and were placed at the forest floor. A more detailed description of the sites and a discussion of the sampling methods was provided by Brehm (2002) and Brehm & Fiedler (2003). Specimens were first sorted to morphospecies level and later determined in the Zoologische Staatssammlung, Munich and the Natural History Museum, London. Fifty-two percent of the morphospecies (67% of the specimens) were identified at species level. Local diversity was very high: Fisher's alpha ranged between 69 and 131 per site, and the extrapolated species number ranged between 244 and 445 species. A detailed analysis of diversity patterns was provided by Brehm *et al.* (2003b).

We used wingspan as a measure of body size because it is highly correlated with other measures such as body length and forewing length (Loder *et al.*, 1998), and can rapidly be obtained from spread specimens. Measures were performed with a calliper rule (Mitutoyo CD-15CP) at a degree of accuracy of 1 mm. In total, 2282 male specimens were measured (Table 1). Analysis was restricted to males because sexes are often dimorphic in body size (Hawkins & Lawton, 1995), and males were much more abundant in the samples than females. In 94% of all geometrid species sampled, males were available for analysis (Table 1). However, the data set contains many rare species. Since this is a

**Table 1** Numbers of species sampled, and numbers of species in which males were available for analysis of the three largest taxa analysed (Geometridae, and the two large subfamilies Ennominae and Larentiinae). Total numbers and proportions are provided in brackets

	Geometridae	Ennominae	Larentiinae
Total number of species	1010	500	391
At least one male present	953 (0.94)	468 (0.94)	372 (0.95)
Two males present*	739 (0.78)	363 (0.77)	298 (0.80)
Three males present*	590 (0.58)	304 (0.65)	231 (0.62)

\* Proportions refer to the species numbers in which males were available for analysis.

**Table 2** Pearson correlation coefficients (a) between average wingspan and altitude (b) between the coefficient of variation of wingspan and altitude (c) between wingspan and extracted species scores from the *X*-axis of a correspondence analysis (see Appendix 1). Significant results remain so after sequential Bonferroni correction (Hochberg, 1988)

	Average wingspan vs. altitude ( $n = 22$ )	Coefficient of variation vs. altitude ( $n = 22$ )	Wingspan vs. CA scores (number of species in brackets)
Geometridae	-0.59**	0.38 n.s.	0.12*** ( $n = 1010$ )
Ennominae	0.24 n.s.	0.56**	-0.04 n.s. ( $n = 500$ )
Boarmiini	-0.46 n.s.	-0.37 n.s.	0.13 n.s. ( $n = 68$ )
Ourapterygini	-0.65***	0.27 n.s.	0.34** ( $n = 97$ )
Larentiinae	-0.24 n.s.	0.70***	0.10 n.s. ( $n = 391$ )
<i>Eois</i>	0.07 n.s.	0.27 n.s.	0.02 n.s. ( $n = 85$ )
<i>Eupithecia</i>	0.83***	0.83***	0.12 n.s. ( $n = 139$ )
<i>Psaliodes</i>	0.35 n.s.	0.45*	0.02 n.s. ( $n = 70$ )

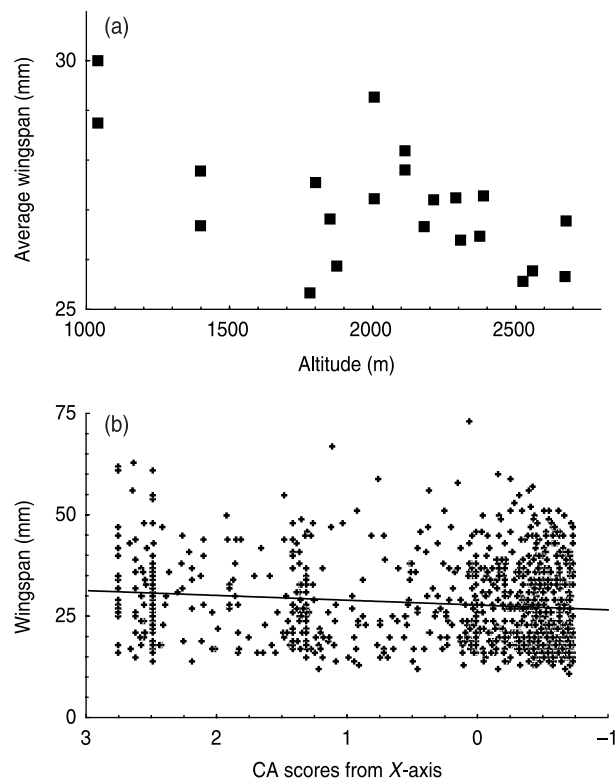
n.s. not significant, \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

typical feature of tropical arthropod samples and rare species should not be excluded from community studies (Novotny & Basset, 2000), we decided to include these species in the analysis. As a consequence, the wingspan data are based on a variable total number of one to three specimens per species. Measures based on single specimens were accepted because variability of wingspan within species was modest, and the overall effect on the results was expected to be low because of the high species numbers analysed. If two or three specimens were available, the arithmetic mean was calculated and used for subsequent analyses.

We chose two different approaches to analysing body size patterns along the elevational gradient, a more community-oriented approach, and a species-oriented approach. In the community-oriented approach, we plotted the mean wingspan of species of the ensembles of all 22 field sites against altitude (Fig. 1a). Ensembles contained between 134 and 292 species per site (Brehm *et al.*, 2003b). Variability of the data was measured as the relative coefficient of variation of wingspan across species per site. In an additional species-oriented approach, we plotted wingspan against the extracted scores of the first axis of a correspondence analysis (CA). The CA ordinating all 1010 nocturnal species occurring in the study area was illustrated by Brehm *et al.* (2003a), see Appendix 1. Brehm & Fiedler (2004) showed that the site scores of the *X*-axis were strongly negatively correlated with elevation ( $r = -0.94$ ,  $P < 0.001$ ). Therefore, we used the corresponding species scores of the *X*-axis as a measure for the species' preferred habitat elevation. The approximation algorithm of the CA oriented high altitude species to low *x*-scores and low altitude species to high *x*-scores. For clarity, the *X*-axis in Fig. 1(b) is shown inverted. Statistical analyses were performed using the software package Statistica (StatSoft, 1999).

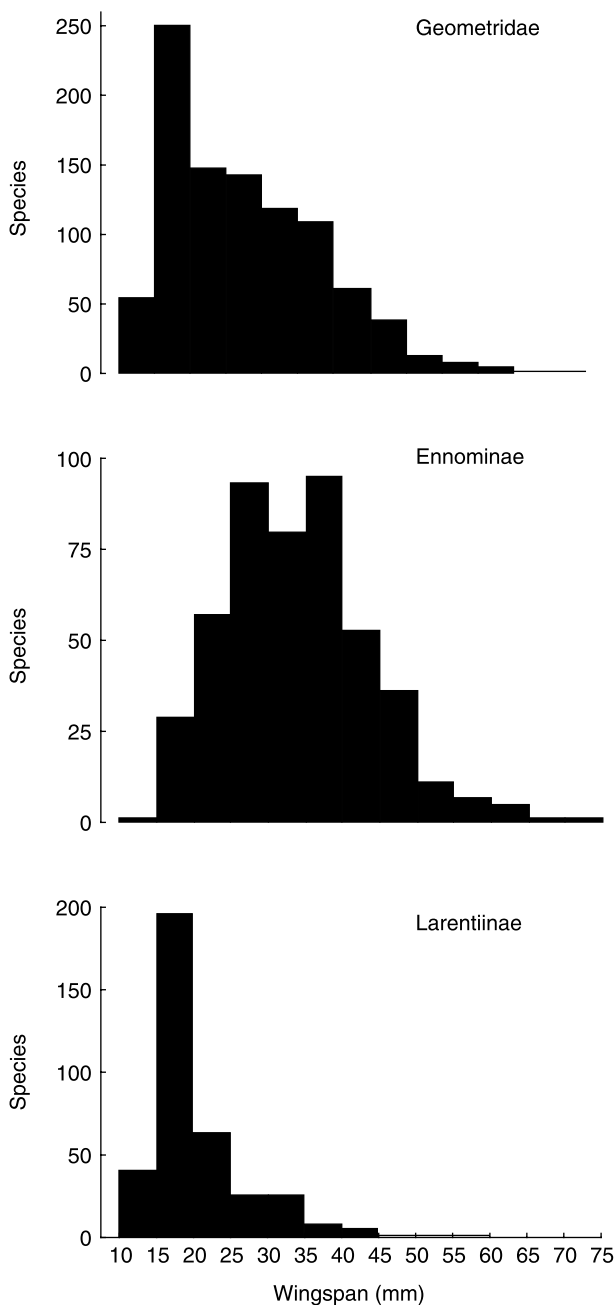
## RESULTS

Wingspan size for the Geometridae is right skewed due to the occurrence of the many small larentiine species (Fig. 2). Within the Larentiinae, the size distribution is also distinctly right skewed and small species of the category between 15 and 20 mm of wingspan dominate. This effect is mainly caused by the three most species-rich genera *Eois*, *Eupithecia* and *Psaliodes*. These genera



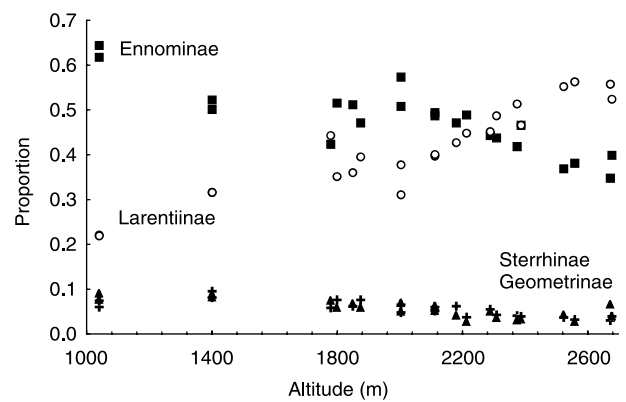
**Figure 1** (a) Average wingspan of all geometrid moths is negatively correlated with elevation ( $r = -0.59$ ,  $P < 0.005$ ). (b) Wingspan of all geometrid moths is weakly correlated with extracted species scores from the *X*-axis of a correspondence analysis ( $r = 0.12$ ,  $P < 0.001$ ). Note that the scale of the *X*-axis is inverted.

account for more than 70% of all species in the subfamily Larentiinae in the study area (Brehm & Fiedler, 2003), and comprise predominantly small species. On the contrary, wingspan sizes in Ennominae appear to be normally distributed. Ennomine species are significantly larger than larentiine species (Kolmogorov-Smirnov test,  $P < 0.001$ ; mean wingspan  $\pm$  SD: Ennominae  $34.4 \pm 9.7$  mm, Larentiinae  $21.2 \pm 6.9$  mm, Geometridae  $28.1 \pm 10.6$  mm, see also Fig. 2).



**Figure 2** Frequency distributions of wingspan sizes of the three largest taxa. Geometridae (skew:  $0.81 \pm 0.08$ , kurtosis:  $0.25 \pm 0.16$ ), Ennominae (skew:  $0.57 \pm 0.11$ , kurtosis:  $0.37 \pm 0.23$ ), and Larentiinae (skew:  $1.92 \pm 0.13$ , kurtosis:  $4.44 \pm 0.25$ ) in class intervals of 5 mm. Kolmogorov-Smirnov test for normal distribution: Geometridae  $d = 0.10$ ,  $P < 0.01$ , Ennominae  $d = 0.06$ , no significant deviation from normal distribution, Larentiinae  $d = 0.22$ ,  $P < 0.01$ .

In the community-oriented approach, correlations between altitude and wingspan sizes reveal no consistent pattern (Table 2). The correlation is significant in Geometridae and Ourapterygini, where a decrease of wingspan with increasing altitude is revealed (Fig. 1a). In contrast, wingspan increases significantly with



**Figure 3** Structural changes in the faunal composition of geometrid moths along the elevational gradient. While the subfamilies Ennominae (squares,  $r_s = -0.84$ ), Sterrhinae (triangles,  $r_s = -0.84$ ) and Geometrinae (crosses,  $r_s = -0.79$ ) decrease in the proportion of species numbers, the subfamily Larentiinae (circles,  $r_s = 0.92$ ) increases with increasing altitude. Proportional changes in all four subfamilies are highly significant ( $P < 0.001$ ).

altitude in the genus *Eupithecia*. No significant relationships can be found within each of the two large subfamilies and the remaining three taxa.

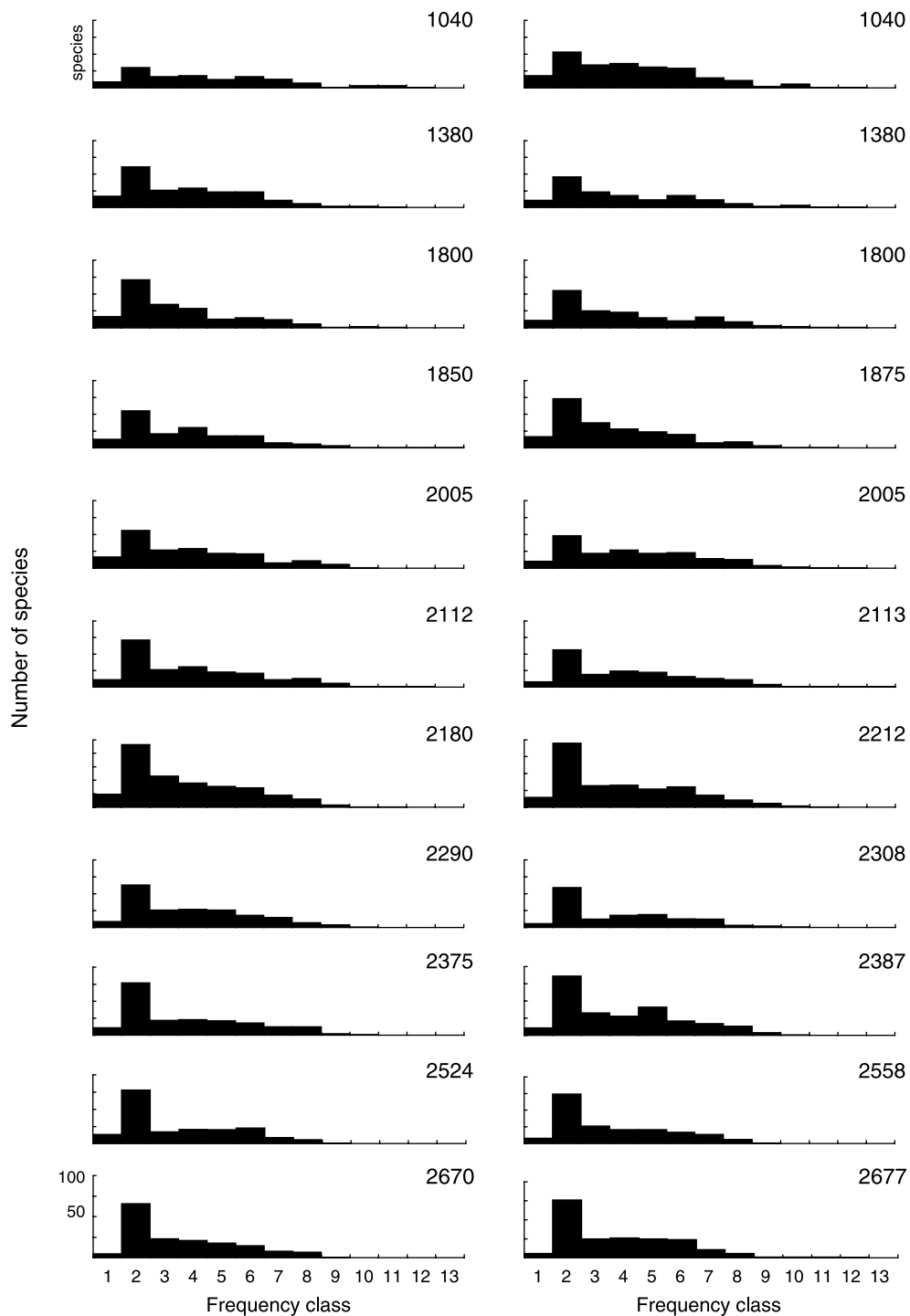
In the species-oriented approach, results are largely identical to the community-oriented approach (Table 2, Fig. 1b). In Geometridae, there is a significant increase of wingspan towards higher CA scores ( $r = 0.12$ ,  $P < 0.001$ ), which correspond to lower elevations. There is also a significant increase of wingspan in Ourapterygini (see Table 2), whereas no significant changes occur in the remaining six taxa, including *Eupithecia*.

The weak overall decrease of Geometridae in body size with increasing altitude was caused by changes in the structural composition of the family with smaller-sized Larentiinae replacing larger Ennominae at higher altitudes. Figure 3 shows this change in faunal composition. At the lowest elevations, species of Ennominae dominate the ensembles (proportion  $> 60\%$ ), while Larentiinae species are of minor importance (proportion  $< 25\%$ ). However, the latter subfamily becomes the dominant group at the highest elevations ( $> 50\%$  of the species).

Wingspan variability across sites tended to increase in all taxa examined except for the ennomine tribe Boarmiini. Figure 4 shows histograms of geometrid species for all 22 sites. The results are significant in the subfamilies Ennominae, Larentiinae and the genus *Eupithecia* (Table 2). Hence, while only inconsistent patterns of wingspan size can be found across the elevational gradient, in some taxa there is a higher variability of wingspan at higher elevations compared to lower altitudes.

## DISCUSSION

Among all taxa analysed, no or only weak support for Bergmann's rule was found. A highly significant increase of body size was shown for *Eupithecia*, but only by means of one of the two alternative methods applied. There was even an opposite trend in



**Figure 4** Frequency histograms of the wingspan of Geometridae at all 22 sites of the study area, arranged according to their elevational order. On the X-axis, frequency is shown in class intervals of 5 mm: 1: 5–10 mm, 2: 10–15 mm, 3: 15–20 mm, 4: 20–25 mm, 5: 25–30 mm, 6: 30–35 mm, 7: 35–40 mm, 8: 40–45 mm, 9: 45–50 mm, 10: 50–55 mm, 10: 55–60 mm, 11: 60–65 mm, 12: 65–70 mm, 13: 70–75 mm. The Y-axis shows the number of species.

Geometridae and Ourapterygini, while no significant changes occurred in the remaining taxa. The overall inconsistent trends show that mechanisms that explain generally larger body sizes at colder climates cannot apply to geometrid moths along the elevational gradient investigated. Despite fundamentally decreasing

ambient temperatures across the gradient ( $\Delta T$ : c. 10K), geometrid moths are not larger at higher elevations. Larger bodies have a more favourable ratio between surface and volume and can more effectively be insulated. This ratio is expected to play an important role for endothermic species such as mammals

and birds (Meiri & Dayan, 2003), but also for 'hot-blooded' insects such as hawk moths (Heinrich, 1993). However, geometrid moths tend to have relatively low thoracic temperatures during their flight (Utrio, 1995; Rydell & Lancaster, 2000), and do not require large bodies to maintain a certain flight temperature. The many small geometrid species at high elevations show that being small can be a successful strategy even in cool conditions, and notwithstanding that large-bodied insects might be better buffered against environmentally induced physiological stress (Wasserman & Mitter, 1978).

In Geometridae, an overall decrease in body size with increasing altitude was found. However, no significant changes occur in the two large subfamilies Ennominae and Larentiinae. These results suggest that the decrease in body size in geometrid moths might not be a 'true' pattern, but only a side effect of structural shifts in faunal composition. Phylogenetic relatedness could potentially generate a spurious relationship between body size and altitude, and is probably the dominant factor in this study. Larentiines appear to be well adapted to unfavourable weather conditions and might particularly benefit from low predation pressures at high altitudes as they are relatively weak fliers (Brehm & Fiedler, 2003). However, there is no evidence that larentiines are successful at high elevations *because* of their small body sizes. This is (1) because there is no overall significant change in body sizes within Larentiinae along the gradient, and (2) genera within this subfamily show no tendency towards smaller body sizes with rising altitude. On the contrary, in the community-oriented approach, species of the genus *Eupithecia* tended to be even larger at high elevations compared with lower altitudes.

The results show the importance of considering different taxonomic levels as body size trends can be contrasting between these levels. This is illustrated by the example *Eupithecia*. While the genus itself shows a highly significant increase in wingspan with increasing elevation using one of the two methodological approaches, no tendency can be detected in the corresponding subfamily Larentiinae. At the family level of Geometridae, an opposite trend even becomes apparent. Results might be biased if different taxonomic levels are not considered in the analysis of body size patterns. For example, Lindström *et al.* (1994) investigated the relationship between host plant specialism and body sizes of Finnish geometrid species. They concluded that host plant specialists were smaller than oligophagous or polyphagous species, and that small species were more frequently focused on herbs. We suspect that their result is biased because they did not consider phylogenetic relatedness of the taxa involved. In Europe, as shown for the Andes in our study, species of the subfamily Larentiinae appear to be smaller than species of Ennominae. Moreover, larentiines tend to be more specialized — many of them on herbaceous plants (e.g. Skou, 1986). This is particularly true for the genera that comprise many of the smallest and simultaneously most specialized species, i.e. *Eupithecia* and *Perizoma*.

It is perhaps surprising that three of the taxa analysed show a significant increase in the variability of their body size. The harsher environmental conditions (i.e. lower ambient temperatures and higher precipitation) appear not to restrict the body

sizes to a certain optimum range. Some selective forces such as predation pressure by bats and ants probably become smaller with increasing altitude (Brehm *et al.*, 2003b). It might be speculated whether, e.g. bat predation can have an effect with regard to the manoeuvrability of the moth species, including features of the body architecture. Species at high altitudes might be released to a certain extent from selective forces that apply at lower elevations, and subsequently exhibit a broader range of body sizes.

Our observations are in line with previous interspecific studies on Neotropical butterflies (Hawkins & DeVries, 1996) that body size relationships are mainly characterized by taxonomic idiosyncrasies. Further inter- and intra-specific studies on large-scale environmental gradients and on a broad range of insect taxa are required to show the existence of general trends in body size and the responsible mechanisms.

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## BIOSKETCHES

**Gunnar Brehm** is an ecologist focusing on biodiversity research of diverse moth communities in tropical rainforests. He is currently working in Ecuador and Costa Rica, and is also interested in host-plant relationships, in chemical ecology of moths and butterflies associated with pyrrolizidine alkaloids, and in conservation issues. He has a strong interest in insect systematics and taxonomy, in particular of Neotropical Geometridae.

**Konrad Fiedler** is an evolutionary biologist and ecologist. Besides the functional and evolutionary ecology of interspecific interactions (such as herbivory and mutualism), his research interests are concentrated on diversity patterns of rich arthropod communities along habitat gradients, and the processes and mechanisms which generate them.

**Appendix** Correspondence analysis of all 1010 species of geometrid moths of the study area. Note that many species scores are almost identical and therefore overlap. The *X*-axis reflects the elevational gradient (see Brehm *et al.*, 2003a). Scores of the *X*-axis were extracted for each species as a measure of its elevational distributional centre.

