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Author's contribution to the studies (** denotes a high contribution, *** a leading role)

	I	II	III	IV
Original idea	**	**	***	***
Study design	**	***	***	***
Data collection	***	***	***	***
Analysis and interpretation	***	***	***	***
Manuscript writing	**	***	***	***

1. INTRODUCTION

Differences in body size are among the most evident manifestations of phenotypic diversity in animals. They can be observed at any taxonomic level, making body size a central parameter in ecology and evolution (Stern, 2001). Historically, biologists have long been interested in predicting patterns of body size variation based on life-history, evolution, geography, and environmental factors (e.g., Pincheira-Donoso et al., 2019; Kuntner & Coddington, 2020; Gergely & Tökölyi, 2023; Johnson et al., 2023). While no single pattern or mechanism fully explains body size diversity, its consistent correlations with physiological, behavioural, and life-history characteristics (Gouws et al., 2011) undoubtedly demonstrate that body size variation is central for understanding an organisms' evolutionary history, providing cues on how species adapt to environmental challenges through time and space.

Although differences in body size can sometimes be strikingly evident to human eyes, the quantitative representation of body size is not as straightforward as it may seem. This is because animals do not possess a single, fixed size but rather exhibit multiple size dimensions (Hayes & Shonkwiler, 2001). The size of a flying insect like butterflies or moths, for instance, can be expressed by multiple proxies, including fresh or dry mass (Choi, 2024), forewing length (García-Barros, 2015; Javoiš et al., 2019), wingspan (García-Barros, 2015; Seifert et al., 2023), body length (García-Barros, 2015), thorax width (Monalisa, 2023), abdomen length (García-Barros, 2015), wing area (García-Barros, 2015), wing scale size (Simonsen & Kristensen, 2003; Bálint et al., 2019), body volume (Monalisa, 2023), head width (García-Barros, 2015), or by structural size metrics (Hayes & Shonkwiler, 2001) derived from principal component analyses (De Souza et al., 2024). Likewise, several size metrics exist for non-flying arthropods, such as arachnids. Those include total body length (Kuntner & Coddington, 2009; Kuntner & Elgar, 2014; McLean et al., 2018; Kuntner & Coddington, 2020), carapace length (Kuntner et al., 2010; Kuntner & Coddington, 2020), the length of specific corporal segments (Fox et al., 2015; Kuntner & Coddington, 2020) or the use of weight measures as above (Kuntner et al., 2010; Kralj-Fišer et al., 2023). In both situations, the choice of the measurement method and character used to represent size depends on a combination of biological meaning of the metric, context at which the measurement is taken, and technicalities involved in measuring the chosen character.

Traditionally, ecologists working on invertebrates rely on weight or length measurements as proxies for body size. Weight (hereafter used interchangeably with the terms "mass" and "biomass") is generally the preferred metric when estimating complex biological parameters such as metabolic rates (Hudson et al., 2013), energy transfer across trophic levels (Barneche et al., 2021), and reproductive potential or investment (Warburg, 2011; Kuntner & Coddington, 2020) is the primary goal. In some ecological contexts, combining weight and length can be particularly informative. Examples include the calculation of condition indices

based on mass-to-length ratios, or residuals from mass-length regressions, although the validity of such indices has been questioned due to their statistical dependence on body size itself (Hayes & Shonkwiler, 2001). When working with weight measurements, a decision must be made between using live or dry weight. For invertebrates in general, live mass is often easier and quicker to measure, making it a practical non-destructive proxy for body size that can be obtained in field and applied to many ecological contexts (Eklöf et al., 2017). For example, live masses can be directly related to the living condition of the organism, providing immediate insights into its current physiological state (Dekanová et al., 2023), being also useful in the assessments of ecosystem quality and productivity (Eklöf et al., 2017).

Very often, however, ecologists and evolutionary biologists aim to describe the relationship between body size and other life-history traits, to quantify how other traits scale with body size at both inter- and intraspecific levels, which often requires the calculation of species-level body size estimates (e.g., species means). The covariation with body size is thus the phenomenon of interest, and the choice between dry or live mass can significantly influence the results. In this context, the use of live mass can be particularly problematic for listable reasons. First, live mass is highly variable due to water content, which fluctuates with environmental conditions and the organism's hydration state (Dekanová et al., 2023). Second, temporary changes in live mass can also result from the feeding status of the individual (Hayes & Shonkwiler, 2001), as commonly reported for predator arthropods such as arachnids (Moya-Laraño et al., 2008; Schmidt et al., 2012; Réveillion et al., 2022; Wu et al., 2023). Third, even in species with non-feeding adult, such as many lepidopterans, live mass is expected to vary with age while the overall body dimension (body length) remains fixed (Molleman et al., 2011, 2022). Fourth, specimen collection and preservation methods can substantially alter live mass, either underestimating or overestimating it depending on the technique used (Knapp, 2012; Dekanová et al., 2023). These sources of variation are not mutually exclusive, and accounting for their effects on live mass estimation when dealing with wild-caught specimens can be impractical. More importantly, the statistical noise they introduce often does not reflect true biological variation, making alternative measures of body size more appropriate.

Most of the limitations associated with using live mass can be mitigated by measuring dry mass instead. When measured properly (see below), dry mass offers a more stable and consistent alternative proxy for biomass and body size, as it removes variability introduced by water content (Dekanová et al., 2023; Eklöf et al., 2017). Additionally, dry mass is less affected by preservation methods, particularly when specimens are preserved using dry techniques, as is common for flying insects. This brings about the important advantage of enabling the quantification of biomass from historical specimen collections (Kinsella et al., 2020), making it possible to weigh specimens collected decades or even centuries ago. By excluding water-related variation, dry mass offers a more accurate representation of biologically active tissue and is thus a better proxy for energy content in studies of nutrient cycling (Eklöf et al., 2017; Weil et al., 2019).

Furthermore, it facilitates standardized comparisons across studies and taxa, enhancing the potential for meta-analyses and large-scale ecological syntheses (Reed et al., 2016; Gogina et al., 2022). When analysed jointly, live and dry masses enable the calculation of energy densities (kcal/unit dry weight, e.g., Lourenço-de-Moraes et al., 2025), which are widely used in bioenergetic models and in studies of optimal foraging, body condition, and energy budgets (James et al., 2012).

Nevertheless, use of dry mass does not resolve all of the issues associated with live mass, nor is it free from technical challenges. For example, age-related changes in tissue density or composition, as well as the nutritional status of the individual, are expected to introduce some variation in body weight, which can be undesirable, depending on the study context. More evident, however, is the fact that obtaining dry mass requires extensive handling to properly prepare specimens for measurement. While live mass can be quickly and easily obtained in the field, dry mass involves a more time-consuming process that may require specialised equipment in laboratory conditions. Furthermore, the drying procedure is itself (to some degree) destructive, and improperly handled dried specimens are at risk of partial or complete loss, which is of particular concern when working with rare museum specimens.

Fortunately, weight measurements are not the only means of representing body size. Alternatives include simple and intuitive metrics based on linear measurements, which are widely employed by biologists either to represent body size directly or to derive more complex proxies through natural and consistent morphometric scaling laws (e.g., Sohlström et al., 2018; Straus & Avilés, 2018; Kinsella et al., 2020; Mazón et al., 2020; Ruiz-Lupión et al., 2020; Weiss & Linde, 2022; Harianja et al., 2023; Yazdanian et al., 2023). For invertebrates, linear measurements such as total body length or the length of specific body parts (e.g., wing length or wingspan in flying insects, carapace length in arachnids) are non-destructive and widely used proxies for body size due to their simplicity and ease of acquisition, especially in species with relatively simple body plans (García-Barros, 2015). Unlike dry or live mass, length-based metrics like total body length are less affected by an organism's hydration state or feeding status and are less sensitive to size changes induced by aging, since body growth in arthropods ceases once they reach adulthood (Chown & Gaston, 2010). This also applies to most measurements taken from sclerotised body parts such as the head and thorax in insects, and the carapace in arachnids (McArthur et al., 2018; McLean et al., 2018; Réveillion et al., 2022). Not surprisingly, most length metrics show strong correlations with both dry and live mass (Lovich & Gibbons, 1992; Kuntner & Coddington, 2020). The relationship between body mass and length often follows a power law, in which mass is proportional to length raised to an exponent b, commonly expressed as mass $\propto$ length^3 (Caruso & Migliorini, 2009). This pattern is grounded in Euclidean geometry, where volume (and by extension, mass: volume $\propto$ length^3 $\propto$ mass) scales with the cube of linear dimensions (Caruso & Migliorini, 2009; Kuntner & Coddington, 2020; Ruiz-Lupión et al., 2020). This principle is intimately connected to the concept of allometry,

which, in simple terms, describes the scaling of a trait relative to overall body size (Huxley, 1932; Pélabon et al., 2014; Voje et al., 2014; Pélabon et al., 2018).

Allometric relationships are commonly described by a power law function of the form $Y = AX^b$, where *Y* represents trait size, *A* is a constant estimated from the data, *X* is body size, and *b* is the exponent that describes the growth of *Y* relative to *X* (Huxley, 1932; Voje et al., 2014). When analysed on a log-log scale, the relationship becomes linear (but see Venditti et al., 2024) in the form $\log(Y) = \log(A) + b \times \log(X)$, with *A* as the intercept and *b* as the slope, the latter representing the scaling of trait size relative to overall body size (Huxley, 1932; Pélabon et al., 2018). The allometric slope *b* is of particular interest as it tells how much change in the trait size is expected to occur per unit change in body size. Based on that information, the allometric slopes can be categorized into isometric ($b = 1$, trait size increases proportionately to body size), negative ($b < 1$, trait size increases slower than body size), or positive ($b > 1$, trait size increases faster than body size) (Bonduriansky, 2007; Shingleton, 2010; Ruiz-Lupión et al., 2020). While this example refers to a specific case of allometric scaling in a hypothetical morphological trait, the concept of allometry is much broader. In fact, allometric relationships are found across a wide range of physiological, behavioural, ecological, and life-history traits (West et al., 1997; Frank, 2009; Voje et al., 2014; Han et al., 2015; Glazier, 2024). Moreover, the characterization of allometric relationships is not limited to individuals of the same sex (Abouheif & Fairbairn, 1997; Fairbairn, 1997), age (Cheverud, 1982; Pélabon et al., 2013; Glazier, 2024), or even species (Abouheif & Fairbairn, 1997; Klecka & Boukal, 2013). Specifically, allometric analyses can target different levels of biological organization: a single individual across developmental stages (ontogenetic allometry), multiple individuals at the same life stage within a population or species (static allometry), or comparisons across species (evolutionary allometry) (Shingleton, 2010; Pélabon et al., 2014; Sherratt et al., 2022). While a full discussion of how these forms of allometry relate to one another is beyond the scope of this text (reviewed by Cheverud, 1982; Pélabon et al., 2013), it is important to note that morphological evolution in taxa with a shared Bauplan (e.g., insects or arachnids) is mostly driven by modifications in static allometry, as much of the observed morphological variation arises from shifts in the relative proportions of body parts rather than changes in absolute size (Shingleton, 2010). Altogether, the definition of allometric relationships facilitates the identification of trait optima relative to body size and the assessment of developmental (genetic) correlations in comparative frameworks (Lande, 1979; Pélabon et al., 2014; Voje et al., 2014; Pélabon et al., 2018; Venditti et al., 2024). Moreover, simple and accurate models for estimating complex proxies for body size from simpler trait measurements can be obtained from allometric relationships (Knight et al., 2022; Sherratt et al., 2022).

Since the late 1960s, numerous equations based on allometric principles have been proposed to predict invertebrate body size from linear measurements. A meta-analysis by Ruiz-Lupión et al. (2020) compiled 283 predictive equations for soil arthropods, the majority of which ($n = 215$) were derived from interspecific data (evolutionary allometry). A closer examination of their supplementary

material highlights the marked underrepresentation of certain arthropod groups, notably Lepidoptera and Scorpiones. While this pattern may be partly due to the stringency of the data inclusion criteria employed by Ruiz-Lupión et al. (2020), it also reflects a broader lack of attention to these taxa in studies developing predictive models for body size. In lepidopterans, most predictive models have been developed using datasets that include a limited number of species that are often distantly related – e.g., a few species from different families (e.g., Rogers et al., 1977; Sample et al., 1993; Hódar, 1996, 1997). This is problematic because the limited number of lepidopteran species used in these models certainly underrepresents the clade's morphological diversity, thereby restricting the applicability of such models (Kinsella et al., 2020). Recent efforts improved both the taxonomic and geographic representativeness of predictive body size models for Lepidoptera (e.g., García-Barros, 2015; Sohlström et al., 2018). While valuable, especially in proposing equations based on more inclusive datasets and in exploring the predictive value of linear traits beyond body length, these contributions share at least two persistent shortcomings. The first is the fact that they rely on imprecise input data for body size due to the absence of a fixed ontogenetic reference point at which body size is measured, as discussed above. The second is the general absence of a rigorous phylogenetic comparative framework – one that accounts for the non-independence of species-level data and enables the detection of phylogenetic patterns in allometric relationships (Blomberg et al., 2003). This approach could allow researchers to infer potential macroevolutionary constraints on trait size (Knight et al., 2022; Sherratt et al., 2022; Voje et al., 2022). Unfortunately, these limitations are not unique to studies on lepidopterans.

Very few predictive methods have been developed for estimating body size in arachnids, and the limited research that exists tends to focus on specific groups, mainly spiders and harvestmen (e.g., Höfer & Ott, 2009; Penell et al., 2018; Straus & Avilés, 2018). This is concerning, given the critical ecological roles arachnids play across nearly all terrestrial ecosystems. As primarily generalist predators, they occupy diverse trophic niches and feed on a wide variety of prey, contributing to the regulation of arthropod and insect populations (de Hart et al., 2017; Tourinho & Lo-Man-Hung, 2021; Lyubechanskii et al., 2023). Their predatory role is key to maintaining food web stability and controlling pest populations. For a perspective, a 2017 study estimated that the global spider community alone kills between 400 and 800 million metric tonnes (fresh weight) of prey annually, with insects and collembolans making up over 90% of this diet (Nyffeler & Birkhofer, 2017). Arachnids are also highly abundant: spider densities can reach 1,000 individuals per square metre, while in some ecosystems, scorpion biomass may exceed that of vertebrates (Polis & Yamashita, 1991; Gefen et al., 2009). Moreover, their sensitivity to habitat disturbance and microclimatic changes make them effective bioindicators, with important applications in environmental monitoring and management (Tourinho & Lo-Man-Hung, 2021; Elliott et al., 2024). While the reasons for the underrepresentation of arachnids in body size prediction studies remain speculative, the development of taxon-

specific methods is clearly overdue and would significantly advance ecological and entomological research.

Recent advances in molecular systematics have enabled the reconstruction of taxonomically comprehensive phylogenetic trees for invertebrate groups, including robust family-level phylogenies for geometrid moths and buthid scorpions (e.g., Murillo-Ramos et al., 2019; Štundlová et al., 2022; Ghanavi et al., 2024; Õunap et al., 2025). When combined with a systematically compiled and taxonomically broad trait dataset, it becomes possible to estimate reliable parameters for predicting body size from simpler linear measurements while accounting for evolutionary dependencies among species. Such practices are valuable in their own right, also providing foundation for further comparative research on body size evolution and its ecological associations with environmental conditions and life-history traits in these organisms.

This thesis summarises the results of four phylogenetic comparative studies that present analytical approaches for predicting body size metrics in two species-rich groups of invertebrates and demonstrate how such predictions can be applied in macroevolutionary contexts. The goals were to employ phylogenetic comparative methods to derive parameters that can be used to generate reliable estimates of body size for two distinct arthropod groups: moths of the family Geometridae and scorpions of the family Buthidae, as well as to apply these estimates to investigate ecological and evolutionary processes underlying body size variation in these taxa. The Studies I and III address the challenges of deriving labour-intensive body size metrics in geometrid moths (I) and buthid scorpions (III). The second and fourth studies provide empirical examples of how predicted body size metrics can be effectively used to address macroevolutionary questions, using moth (II) and scorpion (IV) datasets as case studies. In Study II, phylogenetic comparative methods were applied to examine the relationships between body size and various life-history traits in geometrids, followed by reconstructions of the evolutionary pathways that may have led to these associations. Study IV focuses on patterns of sexual size dimorphism (SSD) in Neotropical buthid scorpions, employing models of continuous trait evolution to infer the tempo and mode of body size evolution in males and females. In addition, the study offers a comparative assessment of evolutionary allometry across 10 morphometric traits in both sexes.

2. MATERIAL AND METHODS

2.1. Study taxa

Geometridae Leach, 1815, is a megadiverse family of moths comprising approximately 24,000 described species distributed across a wide range of habitats (Murillo-Ramos et al., 2019; Yoshimatsu et al., 2020). Geometrids have been widely used in ecological research, both in field and laboratory settings (e.g., Javoiš et al., 2019; Holm et al., 2022; Seifert et al., 2023; Tammaru & Teder, 2025), and their ecology and life history are relatively well documented in some regions (Mikkola et al., 1985; Skou, 1986; Mikkola et al., 1989; Hausmann, 2019). The larvae of geometrid moths feed on a variety of plants, including shrubs, trees, and ferns (Teder, 2020; Zielonka et al., 2022). The remarkable taxonomic diversity found within Geometridae often translates into an equally diverse set of functional roles displayed by these insects. While some geometrids exhibit high host specificity, feeding exclusively on one plant species (Janse Van Rensburg et al., 2024), numerous species are generalist herbivores that feed on a wide range of plant species. This feeding behaviour can substantially impact plant community dynamics and forest structure (Summerville & Crist, 2008; De Smedt et al., 2019; Janse Van Rensburg et al., 2024). Moreover, many geometrid moths frequently visit flowers and carry pollen, contributing to the pollination of various plant species. It has been shown that geometrids are particularly important pollinators in urban gardens and natural ecosystems where they interact with a diversity of flowers (Wonderlin et al., 2019; Ribas-Marquès et al., 2022). Perhaps needless to say is the fact that geometrids serve as a vital food source for many vertebrate and invertebrate predators. Therefore, their abundance and diversity make them a relevant component of the food web (De Smedt et al., 2019; Summerville & Crist, 2008).

The other taxon studied in this thesis is the family Buthidae C. L. Koch, 1837, which is the most species-rich family of scorpions, currently with 1,284 valid species (Rein, 2025). Buthid scorpions are present in almost all terrestrial habitats but are particularly diverse and abundant in arid and semiarid regions (Stockmann & Ythier, 2010). Despite their nearly cosmopolitan distribution at the family level, they tend to exhibit geographically restricted distributions at the genus level. Notable examples include the genera *Ananteris* Thorell, 1891, *Centruroides* Marx, 1890, and *Tityus* C. L. Koch, 1836, all of which are confined to the Americas and contain numerous endemic species (Lourenço, 1993; Stockmann & Ythier, 2010). These three genera alone account for 34% of all described species within Buthidae (Rein, 2025). Buthid scorpions are solitary, nocturnal predators that typically feed on a wide range of invertebrates, including conspecifics (Stockmann & Ythier, 2010; Dionisio-da-Silva et al., 2024). The family exhibits high interspecific variation in body size, with species ranging from as small as 1.2 cm to as large as 15 cm in total length (Teruel, 2001; Viquez & Armas, 2005). Both intra- and interspecific variation in body size (and shape) plays a key role in explaining critical life history traits, including courtship behaviour, fecundity,

metabolic rates, sexual selection, intraguild predation, cannibalism, microhabitat stratification, and ecophysiological adaptations (Polis, 1990).

2.2. Trait data

Due to differences in body plan and data availability, distinct variables were used to represent body size in moths and scorpions. For geometrid moths, body size was expressed as dry body mass (DBM), whereas for scorpions, separate analyses employed two commonly used proxies for body size in the group: total length, measured from the anterior margin of the carapace to the tip of the telson with the metasoma extended, and carapace length, measured from the anterior to the posterior margin of the carapace (see Fig. 1 for details).

In the first study of geometrid moths (I), DBM was taken from freshly eclosed adults reared under laboratory conditions obtained in previous research (Javoiš et al., 2011; Holm et al., 2019) in order to avoid ontogenetic weight variation. The trait data and phylogeny were composed of 105 geometrid species from temperate (Estonia, n = 67 species) and tropical (Uganda, n = 38) habitats. Adults were weighed one day after eclosion to avoid including meconium weight it the measurements. For each species, an average of six males and six females were air-dried and weighed, and forewing lengths were measured on 1,299 individuals using callipers. Because additional morphological measurements were not possible on the same individuals, we collected linear traits from size-referenced photographs of 539 museum and wild specimens using ImageJ (Schneider et al., 2012). Five linear measurements were taken to be used as DBM predictors: forewing length, wingspan at the tips, maximum wingspan, body length, and abdomen width. A schematic representation describing these measurements is illustrated in Fig. 1a. To correct for size differences between lab- and wild-reared specimens, all image-based measurements were scaled using the ratio of forewing lengths from the two groups. Once the predictive models were established in Study I, DBM was predicted for the entire Northern European geometrid fauna (n = 372 species) from linear measurements of maximum wingspan and abdomen width whenever appropriate (i.e., only abdomen width was used in apterous species), for application in Study II. These linear measurements were extracted using ImageJ from 1,270 size-referenced images (ranging from 1 to 6 specimens per sex per species) sourced from the Geometridae Mundi (https://www.zsm.mwn.de) and Lepiforum (https://lepiforum.org/) databases.

The study with predicted DBM in geometrids (II) used life-history data (i.e., overwintering stage, host-plant growth form, dietary specialisation, voltinism, and diel activity) compiled by Teder (2020) across the species' European ranges. The variables were transformed into binary whenever required for statistical analyses. Larval overwintering was contrasted with other stages (adult, egg, or pupa) due to its unique ecological aspects (e.g., predation risk, mobility). Host-plant associations were divided into tree feeders (strict or facultative feeders on trees and shrubs) and herb feeders (primarily herbivorous species plus two lichen

feeders). Dietary specialisation was dichotomised by grouping polyphagous species as generalists, and monophagous and oligophagous species as specialists, to capture ecological differences in host-search effort. Voltinism (univoltine or multivoltine) and diel activity (diurnal or nocturnal) were already binary variables in their original forms.

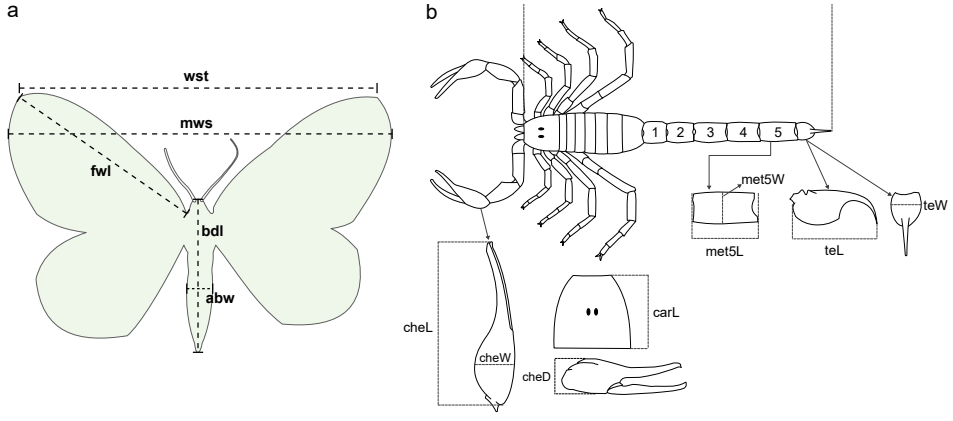

Figure 1. Linear measurements taken from (a) geometrid moths and (b) buthid scorpions. In moths, the predictive ability of wingspan at wing tips (wst), maximum wingspan (mws), forewing length (fwl), body length (bdl), and abdomen width (abw) for dry body mass at maturation was assessed in males and females of 105 geometrid species from tropical (n = 38) and temperate (n = 67) habitats. For buthid scorpions (195 species), two body size metrics were used: total length (toL) and carapace length (carL). These were predicted from chela length (cheL) and width (cheW), telson length (teL) and width (teW), and length and width of the fifth metasomal segment (met5L and met5W, respectively). The ability of carapace length to predict total length was also evaluated. Measurements of chela depth (cheD) and metasomal length (sum of the lengths of five metasomal segments) were collected a posteriori and included in the study of SSD in Neotropical buthids. (Adapted from Studies I and III).

For size predictions (III) and subsequent comparative analysis of SSD in scorpions (IV), meristic data on scorpion morphology, including body size, were compiled from the literature for 195 species, mostly taxonomic descriptions and systematic reviews of Buthidae. The set of traits analysed includes measurements of length (L), width (W), and depth (D) for the chela (cheL, cheW, cheD) and telson (teL, teW, teD), as well as the length and width of the mesosoma (mesL and mesW), the total length of the metasoma (metL), calculated as the sum of segments I–V, and the width of the fifth metasomal segment (met5W), which serves as a proxy for overall metasomal width. These traits are associated with key biological functions such as feeding, hunting, defence, and reproduction, and their respective allometric patterns are expected to covary, to some extent, with the functional roles they support (Prendini, 2001; Loria & Prendini, 2021; Coelho et al., 2022). A schematic representation of these measurements is illustrated in

Fig. 1b. The predictive value of carapace length (carL) for total length (toL) was also evaluated. Once the size predictive models were established (Study III), they were used to estimate missing body size (carL) data for a subset of species (n = 16) lacking this information in the original dataset, allowing their inclusion in the analysis of SSD in Study IV.

2.3. Phylogenetic trees

Study I uses the molecular phylogenetic tree provided by Holm et al. (2019) that includes both tropical and temperate geometrid species. This phylogenetic tree combines four subfamily-specific ultrametric trees based on eight genes fragments (6,543 bp in total) estimated by Bayesian inference into a single ultrametric tree with 373 terminals.

For studies II–IV, ultrametric phylogenies were obtained by estimating node ages using Bayesian inference, based on maximum likelihood tree topologies. Tree topologies were reconstructed using IQ-TREE2 (Minh et al., 2020) from sequence alignments comprising four genes (2,836 bp) for buthid scorpions (III–IV) and 11 genes (7,880 bp) for geometrid moths (II). DNA sequences were sourced primarily from GenBank and supplemented with newly generated data following taxon-specific protocols (e.g., Õunap et al., 2016; Wahlberg et al., 2016; Esposito et al., 2018). The maximum likelihood topologies were time-calibrated using fossil constraints and secondary calibrations from previous studies (Ojanguren-Affilastro et al., 2017; Esposito & Prendini, 2019), with branch lengths converted to units of time via Bayesian dating analyses in BEAST 1.10.4 (Suchard et al., 2018).

2.4. Data analysis

For each study, the phylogenies were pruned to retain only species present in the respective trait datasets. All continuous variables were log transformed prior analyses. Phylogenetic principal component analysis was used to provide a visual assessment of the correlations between body size metrics and their predictors in geometrid moths (I) and buthid scorpions (III). For both taxa, the ability of linear measurements in predicting target body size metrics was evaluated using phylogenetic generalised least square (PGLS) models. The procedure began by fitting simple regression models for each trait separately, and then choosing the trait (i.e., the model) that provided the best fit to the data. This trait was interpreted as the "best single predictor" of body size. Then, the best-fit simple predictor models were expanded into several multiple regression models by adding a secondary predictor (one at a time) to check whether increasing model complexity resulted in significant improvement in terms of prediction quality and model fit, which were assessed by Akaike information criterion (AIC) and root mean squared error (RMSE). Sexes were analysed separately where necessary to account for potential influences of SSD.

Relationships linking body size (DBM) with several other life-history traits in geometrids (II) were inferred using PGLS models in both simple and multiple regression configurations. These relationships were further investigated using the Bayesian threshold model (Felsenstein, 2012; Revell, 2014), applied to infer how transitions between states of a discrete variable evolving along the phylogeny correlated with body size. Pagel's test for correlated evolution between two binary characters (Pagel, 1994) was implemented to examine the sequence of trait evolution based on the associations revealed by the PGLS and threshold models. For example, if the PGLS analysis suggests that generalist species tend to be significantly larger than specialists, Pagel's test can be used to infer the likely evolutionary pathways that produced large-bodied generalist species. A limitation of the test is that it only accommodates binary traits. As a result, body size was discretised into two categories using the partition around medoids algorithm (Kaufman & Rousseeuw, 1990), which yielded two size classes: "small" (n = 173) and "large" (n = 199) species, with mean ± standard deviation body sizes of 5.35 ± 1.41 mg and 15.5 ± 1.59 mg, respectively.

SSD and sex-related differences in body parts between male and female buthid scorpions (IV) were examined using Bayesian phylogenetic mixed regression models implemented in the R package MCMCglmm (Hadfield, 2010). Carapace length was chosen to represent body size as this measure is presumably less prone to error than total length (McLean et al., 2018). Body size (carL) was always included as a covariate in the mixed models testing for sex differences in the size of body parts. The same class of models were employed to quantify male and female allometric slopes and at the same time, to test whether the slopes differed between sexes. A phylogenetic major axis regression was applied to test whether body size in Neotropical buthids conforms to the predictions of Rensch's rule by regressing $\log_{10}$ female size (response variable) onto $\log_{10}$ male size (independent variable). In this setting, Rensch's rule is supported if the slope of the major axis regression is significantly less than 1 (Abouheif & Fairbairn, 1997; Webb & Freckleton, 2007).

Lastly, continuous models of trait evolution implemented in the R package geiger (Pennell et al., 2014) were used to characterise the tempo and mode of body size evolution in male and female scorpions. To this end, three models were fitted separately for each sex. The first, the Brownian motion (BM) model, is defined by two parameters: θ, the ancestral trait value at the root of the phylogeny (also referred to as the phylogenetic mean), and σ^2, the rate parameter describing how fast trait values undergo random fluctuations over time. The BM model assumes trait evolution follows a random walk, with changes accumulating directionless through time (Beaulieu et al., 2012; Cooper et al., 2016). The second model, the Ornstein-Uhlenbeck (OU) model, builds on the BM framework by introducing an additional parameter, α, which captures the strength of attraction toward a central tendency (θ), consistent with a stabilising selection process (Beaulieu et al., 2012). Like BM, the OU model also includes the evolutionary rate parameter σ^2. The selection strength α can be expressed more intuitively as the phylogenetic half-life ($t_{1/2} = \ln 2/\alpha$), representing the time it takes for a trait to

move halfway from its ancestral state to the selective optimum (Hansen et al., 2008), and the metric ρ, which quantifies the proportion of trait variance reduced by selection over a given time period, relative to the variance expected under pure drift (Cornuault, 2022). The best-fit models for each sex were used in bootstrap simulations to estimate 95% confidence intervals for the parameters θ and σ^2.

3. RESULTS

3.1. Morphometric predictors of body size in geometrids (Study I)

There was considerable interspecific variation in body size (DBM) across the 105 geometrid species, spanning nearly 25-fold in females and 23-fold in males. All morphometric traits showed positive correlations with body mass, although the strength of these correlations varied. Among them, maximum wingspan consistently appeared as the most reliable single predictor of DBM for both sexes. In males, the simple regression model with maximum wingspan as predictor differed from the second best-fit model (wingspan tips as predictor) by three AICc units. For females, wingspan tips was also the second-best single predictor of DBM, scoring 11 AICc units away from the best-fit model (maximum wingspan). In contrast, abdomen width exhibited the weakest association and lowest predictive power when used alone. It scored 82 and 37 AICc units away from the best-fit simple regression model in female and, respectively. Phylogenetic principal component analyses supported the interpretation of the first axis (PC1) representing an overall size gradient for geometrids, with all measurements loading negatively (Fig. 2). However, abdomen width was nearly orthogonal to the other traits, indicating that it captured additional variation beyond overall size (Fig. 2), likely reflecting aspects of body plan. In fact, models combining maximum wingspan (size descriptor) and abdomen width (body plan descriptor) explained more variation in DBM than any other multiple regression model, showing substantially improved fit (lower AICc values) and reduced prediction error. Perhaps surprisingly, interaction terms (e.g. sex, region, clade) had only minor effects on allometric slopes, further supporting the robustness and generality of the predictive relationships.

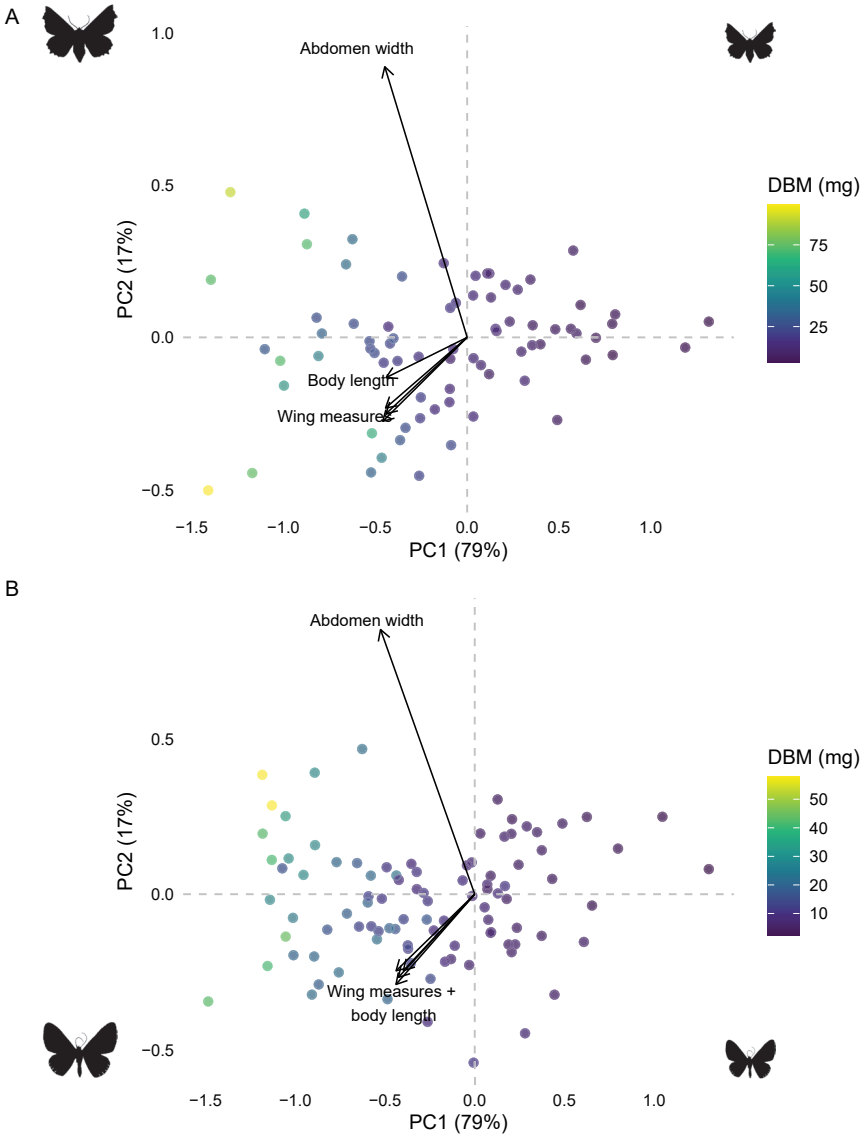

Figure 2. Ordination of geometrid moth species (n = 105 species) obtained via phylogenetic principal component analysis of five linear measurements in (A) female and (B) male specimens. Species (points) are coloured by their respective body sizes, expressed as dry body mass (DBM) at the maturation time. PC1 represents an overall size descriptor, with larger species scoring negatively. PC2 captures information on body plan, representing species with slender to stout abdomens. (Source: Study I).

3.2. Life-history correlates in geometrid body size (Study II)

Predicted DBM in Northern European geometrids was found to correlate significantly with the overwintering stage, dietary breadth, host-plant growth form, and diel activity (Fig. 3a-d). In the absence of covariates (i.e., in single predictor PGLS regression analyses) species overwintering as larvae were, on average, larger than those overwintering in other stages. Likewise, generalist feeders, tree-associated (i.e., tree feeders) species, and nocturnal moths tended to have larger body sizes than their respective counterparts. Multiple regression PGLS models, which included all traits as predictors, largely supported the findings from the bivariate analyses described above (Fig. 3a–d). Overwintering stage, dietary specialisation, and diel activity retained significant associations with body size in the full model. The effect of host-plant growth form was no longer significant in the presence of covariates (all other traits), suggesting that its association with body size may be confounded or mediated through other ecological factors. Voltinism showed no evidence of association with size in any model.

The analyses using the Bayesian threshold model broadly corroborated the results from the PGLS models. Body size showed a positive correlation with larval overwintering (mean $r = 0.25$), indicating that increases in body size are associated with transitions to overwintering in the larval stage. A negative correlation was found between body size and the liability for diurnal activity ($r = –0.44$), supporting the conclusion that nocturnality is associated with larger body size. The association between body size and host-plant growth form was also negative ($r = –0.19$), again suggesting that dietary shifts toward the herb-feeding state were associated with smaller sizes. Among the traits tested, only dietary specialisation showed a weaker signal in the threshold model than in the PGLS analysis: the 95% credible interval for the correlation coefficient slightly overlapped zero, although the posterior distribution still favoured a positive association. No correlation with voltinism was detected in either modelling framework.

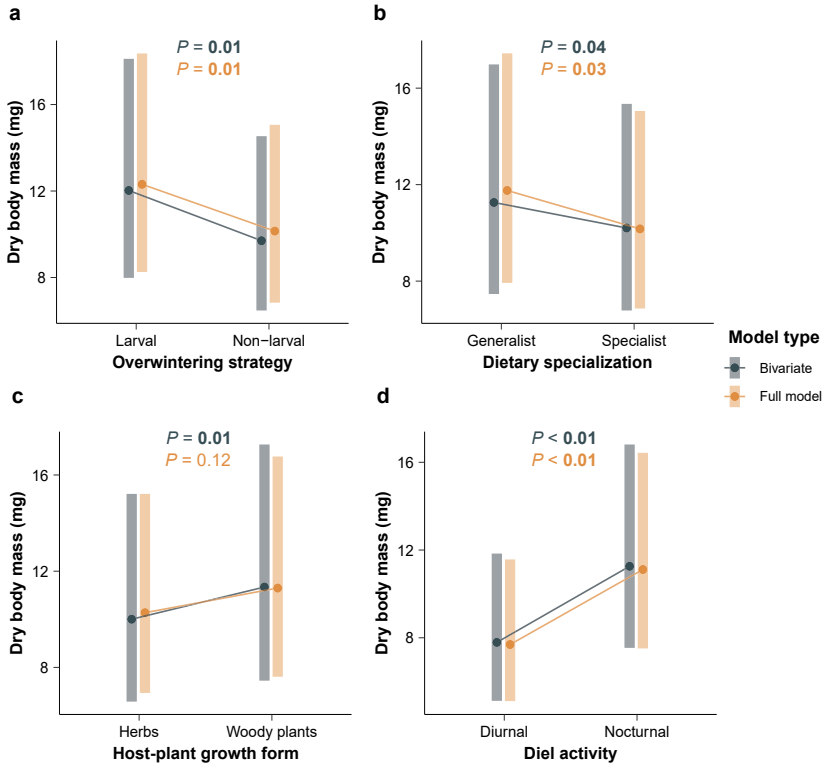

Figure 3. Relationship between predicted body size (dry body mass at maturation) and life-history traits in Northern European geometrid moths (n = 372 species) obtained through simple and multiple phylogenetic regression models. Point estimates are presented with their respective 95% confidence intervals (slabs). Overwintering stage (a), dietary specialisation (b), host-plant growth form (c), and diel activity (d) were consistently associated with body size in the studied species, with no qualitative differences between simple and multiple regression outcomes, except for the effect of host-plant growth form, which became non-significant in the multiple regression model (c). (Source: Study II).

Discrete character models were fitted to assess the sequence of trait evolution linking body size with its correlates identified from the PGLS and threshold model analyses. Results from these discrete models indicated that body size and several life-history traits had coevolved (Fig. 4a–c). Large species that overwinter in the larval stage derived mostly from small ancestors that already had the ability to overwinter in the larval stage (Fig. 4a), suggesting that larval overwintering strategy preceded increases in body size. The same analogy was supported for explaining the emergence of large generalist (Fig. 4b), and large woody plant feeder species (Fig. 4c). Their ancestors were most likely generalists, and woody plant feeders of small size, indicating that the ability to feed on a greater variety of plant items, and in woody plant foliage, may have preceded the evolution of larger sizes. These findings collectively suggest that changes in overwintering biology and feeding strategies may have facilitated evolutionary increases in body size, rather than being secondary consequences of shifts in body size.

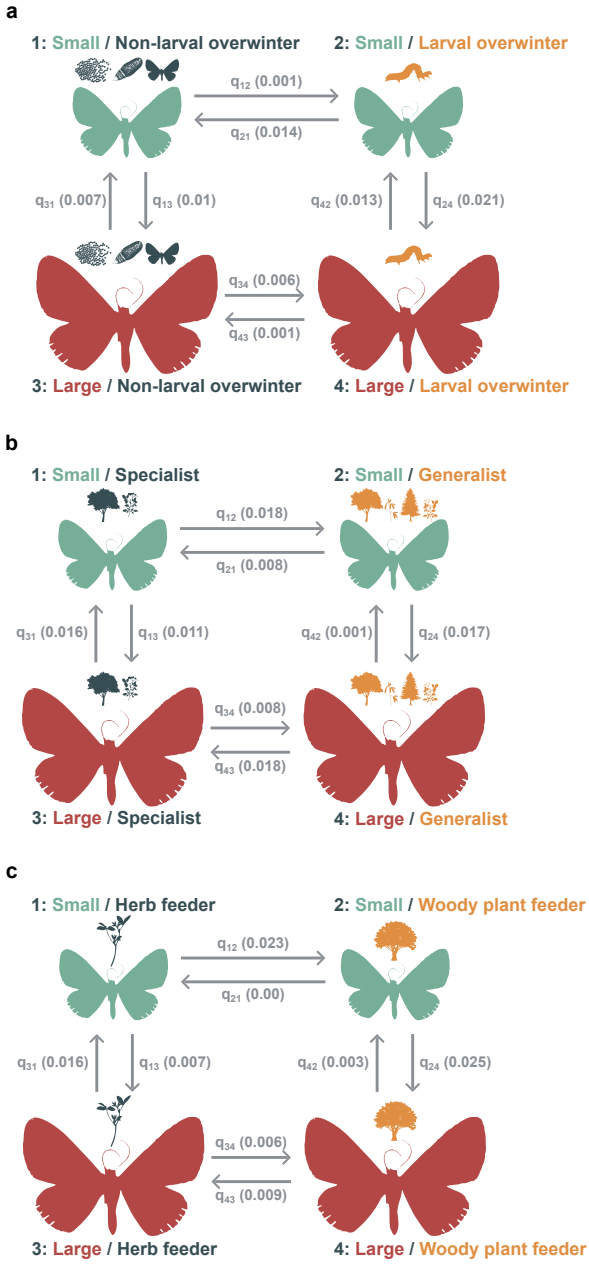

Figure 4. Evolutionary transitions in body size classes and life-history traits in Northern European geometrid moths. Arrows indicate the direction of each transition between pair of states of body size and overwintering stage (a), dietary specialisation (b), and host-plant growth form (c), which were both correlated with body size in the phylogenetic regression analyses (see Results). Large species that overwinter in the larval stage derived mostly from small ancestors that were already larval overwinterers. Similar analogy applies to explain the emergence of large generalist and large woody-plant feeder geometrids. (Source: Study II).

3.4. Morphometric predictors of body size in buthid scorpions (Study III)

In buthid scorpions, strong correlations were found among all linear measurements (carL, toL, cheL, cheW, met5L, met5W, teL, teW), and phylogenetic principal component analysis confirmed the presence of a dominant size axis (PC1) with all measurements loading negatively for both sexes (Fig. 5a–b). None of the variables were able to effectively capture information on overall body plan, although PC2 appeared to separate species based on aspect ratios of chela, metasoma and telson, with slender (rather than stout) structures loading negatively on PC2 for females (Fig. 5a), and positively for males (Fig. 5b).

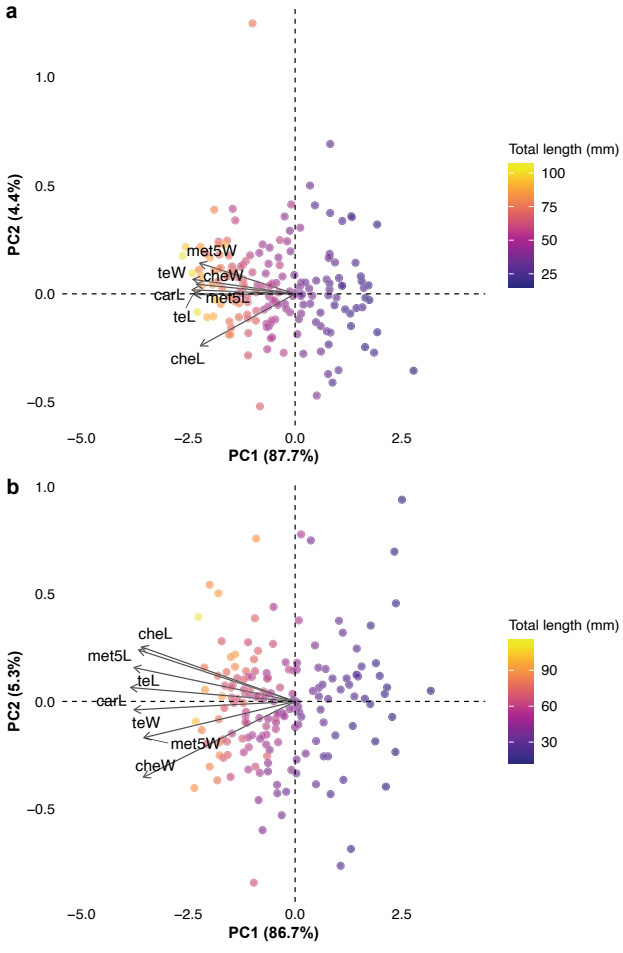

Figure 5. Phylogenetic principal component analysis on morphometric traits in (a) male and (b) female buthid scorpions (n = 195 species). The first axis (PC1) captured information on overall size, while the second axis (PC2) described variation in chela, metasoma, and telson aspect ratio, although none of the traits could effectively represent overall body plan in the studied species. See Figure 1 for trait abbreviations. (Source: Study III).

Overall, all predictor linear measurements proved useful in providing accurate predictions of body size, even when they were used alone: RMSE values remained below 13 mm for toL and 1.1 mm for carL. For toL, the most accurate single predictor was met5L, with average RMSE values below 7 mm across sexes. Carapace length was most precisely predicted by teL, with prediction errors generally below 1 mm. The addition of secondary predictors yielded only marginal improvements in prediction accuracy. Trait-size relationships held practically constant across both male and female datasets and were broadly applicable beyond the family Buthidae, as confirmed by additional predictions made on 30 non-buthid species, where RMSE values stayed below 7.5 mm for toL and 2.1 mm for carL.

3.5. Sexual size dimorphism and evolutionary allometry in Neotropical buthids (Study IV)

The pattern of SSD in Neotropical buthid scorpions is female-biased, although the size difference between sexes was succinct, with females being 8% larger than males. The posterior mean size-difference between sexes was estimated at 4.1 mm, with 95% credible intervals ranging from 2.7 to 6.7 mm. Despite females being the larger sex in absolute terms, males were larger than females for seven out of the ten traits when controlling for body size in the analysis (Fig. 6a). The only exceptions were telson length and mesosoma length, where no statistical differences were observed between sexes, and mesosoma width, with female mesosoma being on average 13% wider than that of males.

None of the traits showed statistically significant differences in allometric coefficients (slopes) between sexes (Fig. 6b). However, some differences in allometric patterns were observed. In males, chela length and chela depth exhibited positive allometry, whereas in females, these traits followed an isometric pattern (Fig. 6b). The phylogenetic major axis regression revealed that the relationship between female and male body size in the Neotropical buthids is consistent with Rensch's rule (intercept = 0.29, $\beta = 0.87$, $P = 0.001$).

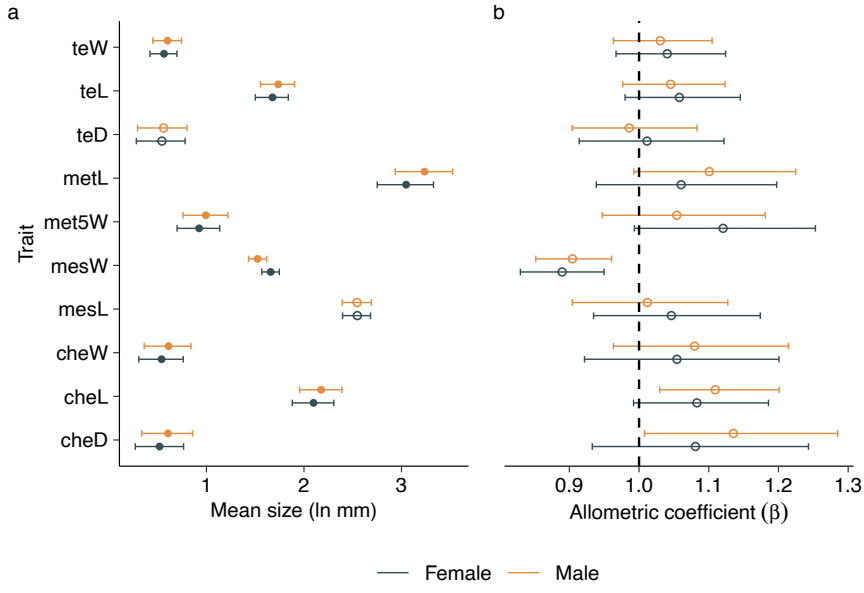

Figure 6. Trait size differences (a) and allometric slopes (b) of 10 morphometric traits measured in male and female Neotropical buthid scorpions inferred with Bayesian phylogenetic mixed regression models. Trait size differences were estimated accounting for body size. Mean estimates (points) are shown with their respective 95% credible intervals (whiskers). Solid points indicate statistically significant effects (pMCMC < 0.05). The vertical dashed line in panel (b) marks the isometric expectation for the allometric relationships. See Figure 1 for trait abbreviations. (Source: Study IV).

Regarding the tempo and mode of body size evolution, the BM model provided the best fit for the female data, although the OU model also received substantial support based on AIC weights (68 vs 32, respectively). In contrast, male body size evolution was better described by an OU process, with the BM model ranking second (AIC weights for OU and BM: 0.81 and 0.19, respectively). The estimated phylogenetic mean (θ) for body size did not differ between sexes (P = 0.87; Fig. 7a), but the rate at which body size evolves (σ^2) was nearly three times higher in males than in females (P = 0, Fig. 7b). The α parameter from the OU models indicated that the strength of selection on male body size was three times greater than that estimated for females (0.021 vs 0.007). As a result, male size is expected to reach its phenotypic optimum more rapidly than female size, as reflected in the phylogenetic half-lives. The time required for male size to shift halfway from the ancestral state to the phenotypic optimum was estimated at 33.2 million years, whereas the corresponding estimate for females was 105.3 million years. When expressed relative to the tree height (66 million years), these values correspond to 50% and 160% for male and female body size, respectively. Additionally, the proportion of trait variance reduced by selection (ρ) was twice as high for males (66%) as for females (33%).

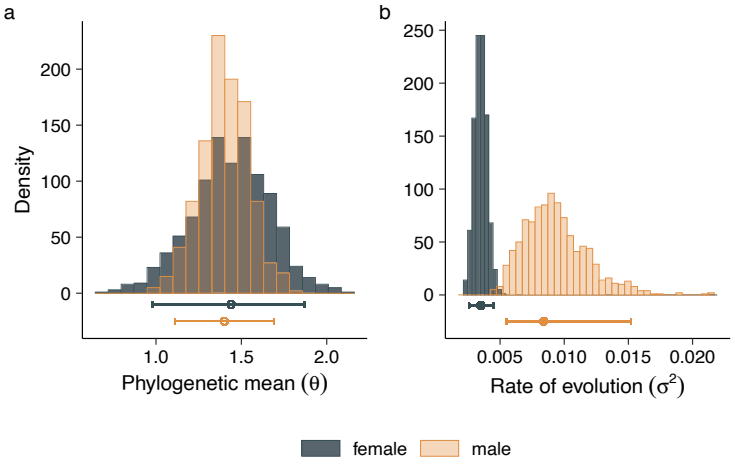

Figure 7. Phylogenetic mean (a) and rate of body size evolution (b) in male and female Neotropical buthid scorpions estimated under Ornstein-Uhlenbeck and Brownian motion processes for males and females, respectively. Distributions and 95% confidence intervals for parameter estimates were created by permuting the best-fit models for each sex 1000 times. Solid points denote statistically significant differences ($P < 0.05$) in Monte Carlo test. (Source: Study IV).

4. DISCUSSION

Predictive equations based on allometric relationships offer an effective and practical means of estimating time-consuming body size metrics using simpler morphological traits. Most existing models for insects and arachnids have been developed from taxonomically broad datasets (see Ruiz-Lupión et al., 2020) that may not adequately capture the morphological diversity within the focal groups. As a result, the accuracy of size estimation is often limited in the absence of taxon-specific models grounded in robust datasets (Sohlström et al., 2018). This limitation also hampers comparative research on species-rich clades, where reliable size imputation techniques are essential to improve data completeness. Although cross-taxon comparison is not the focus of this thesis, it could be convincingly demonstrated that body size metrics such as dry body mass (DBM) at maturation time in moths, and length-based measurements (total length and carapace length) in scorpions, can be accurately predicted from simple linear measurements of individual body structures, without requiring multiple predictors (i.e., no more than two) and complex model elements, such as interactions.

4.1. Body size prediction in geometrid moths (Study I)

DBM at maturation in moths can be reliably estimated using single linear measurements, particularly those taken from the forewings, such as wingspan and wing length. These findings were not unexpected, as wing size is closely associated with body weight in flying insects to maintain efficient flight performance (Shi et al., 2022; Darveau, 2024; Zhu et al., 2025). Among the studied wing measurements, maximum wingspan was the most accurate single predictor of DBM and is also one of the most used proxies for body size in Lepidoptera, widely adopted in large-scale faunistic inventories and catalogues (e.g., Skou, 1986; Hausmann, 2019; Murillo-Ramos et al., 2019). This allows DBM to be predicted from readily available wingspan data from the literature, significantly expanding the potential use of the proposed predictive methods. In fact, we showed that any of the three forewing measurements (maximum wingspan, wingspan at the tips, and forewing length) can be used to predict DBM with consistent accuracy. Among these, forewing length holds particular practical value, as it can be measured without requiring specimens to be mounted in the traditional way. This is especially beneficial when DBM needs to be estimated for large numbers of individuals, such as those obtained from mass trap collections in ecological studies.

The results also indicate that prediction accuracy improves slightly when maximum wingspan is combined with abdomen width. Geometrid moth species exhibit considerable variation not only in body size, but also in body plan. While many members of the family possess a butterfly-like morphology, with slender bodies and broad wings, others are more stout-bodied, resembling typical noctuids or even bombycoids. Given this diversity, it is reasonable to expect that combining a general measure of body size with a metric reflecting body plan would

enhance model performance. It could be observed in the phylogenetic principal component analysis of moth traits that species' body plans can be represented along a gradient from slender to stout forms, primarily captured by the second principal component, with abdomen width showing the highest loading on this axis. Thus, the contribution of abdomen width to improving model fit likely results from its capacity to represent overall body plan, offering additional, independent morphological information for estimating DBM. The particular property of abdomen width in representing overall body plan can be better understood by taking the ecological relevance of abdomen width into account. In our analysis, broader abdomens were typical of temperate species in the genera *Lycia* Hübner, 1825, *Biston* Leach, 1815, *Ennomos* Treitschke, 1825, and *Colotois* Hübner, 1823, which do not feed as adults and are therefore extreme capital breeders (Tammaru & Haukioja, 1996). This contrasts with most geometrids, which depend to varying degrees on adult feeding (Javoiš et al., 2011). In previous work, relative abdomen mass has been identified as a morphological indicator of a species' position along the continuum from income to capital breeding strategies (Davis et al., 2016), with abdomen width serving as a practical proxy for this trait. It remains unclear whether geometrid species with non-feeding adults are present in equatorial Africa (Holm et al., 2019). If such species were absent from our tropical subsample, this may explain the lack of extreme abdomen width values among Ugandan species.

4.2. Natural-history correlates of body size in Northern European geometrids (Study II)

Linear measurements of maximum wingspan and abdomen width were successfully converted into DBM for 372 geometrid species occurring in Northern Europe, representing the entire geometrid fauna of the region (Õunap et al., 2025). Overall, correlations between DBM and life-history traits were weak but statistically significant, mostly consistent with previous comparative findings (e.g., Teder, 2020; Seifert et al., 2022, 2023). Phylogenetic regressions and threshold model analysis consistently supported the association between large body size and overwintering in the larval stage. This finding aligns with earlier ecological studies linking body size to overwintering strategies in geometrids (e.g., Davis et al., 2013; Seifert et al., 2022, 2023) and other lepidopterans (Zeuss et al., 2017; but see García-Barros, 2000), suggesting a general pattern. As a novel contribution though, we found that this association is unlikely to result from an indirect effect mediated by a third variable, as evidenced by the absence of interactive effects. Furthermore, the model of correlated evolution supported the hypothesis that larval overwintering more commonly preceded the evolution of larger body size. This suggests that evolutionary transitions from non-larval to larval overwintering may have favoured the development of larger body sizes, rather than larger size driving the adoption of larval overwintering.

In explaining the tendency for larval overwinterers to be larger, it is important to consider that the state of the variable "overwintering stage" would have been undefined during a portion of the evolutionary history of the studied species. This is because some ancestors were undoubtedly tropical moths that did not undergo overwintering. It is reasonable to assume, however, that although tropical ancestors did not overwinter, they may have possessed an inherent predisposition to do so in one developmental stage rather than another. This idea is well captured by the concept of liability in the threshold model analyses (Felsenstein, 2012). Although identifying the exact biological mechanisms that determine overwintering stage lies beyond the capabilities of the threshold model, the results still indicate that these determinants coevolve, to some extent, with body size. Interestingly, previous studies have indicated that the larval stage is the most susceptible to predation (Cornell & Hawkins, 1995; Tanhuanpää et al., 2001; Remmel et al., 2011), implying that species would preferably avoid overwintering at this life stage. Indeed, the tendency of overwintering in a life stage other than the larval is confirmed by our study and other comparative analyses on geometrids (Seifert et al., 2023), and in Lepidoptera, more broadly (Teder, 2020). The species that do overwinter as larvae must therefore gain a compensatory advantage. We suggest the principal benefit lies in the ability of overwintering larvae to immediately exploit the flush of fresh spring foliage upon resumption of activity. In many cases, this early-season foliage is known to be of higher nutritional quality (Feeny, 1970; Roslin & Salminen, 2009; Tikkanen & Lyytikäinen-Saarenmaa, 2002). Such benefits might counterbalance the mobility challenges of larval overwinterers in leaving the host plant in search of a suitable overwintering shelter and the requirement to return and recolonise the host plant in spring.

Another phenological studied trait is voltinism, which did not correlate with body size in the analysis of Northern European geometrids. Indeed, among European lepidopterans, links between body size and voltinism appear less consistent than those involving other phenological traits like overwintering stage (Teder, 2020; Seifert et al., 2023). Some studies report significant correlations (Teder, 2020; Seifert et al., 2023), while others do not (Seifert & Fiedler, 2024). The threshold models revealed no association even at the level of latent liabilities. While smaller size might seem advantageous for fitting several generations into the short northern summer (Zeuss et al., 2017; Teder, 2020), the rapid growth of lepidopteran larvae (Tammaru & Esperk, 2007) suggests that direct trade-offs between body size and voltinism have limited influence. Reported associations may instead be indirect. For instance, tree feeders, which are often large, tend to be univoltine due to their reliance on young foliage (Van Asch & Visser, 2007; Teder, 2020).

Across species, body size is generally negatively associated with dietary specialisation, as shown in geometrids (Davis et al., 2013; Seifert et al., 2022, 2023) and other insects (Brändle et al., 2000; but see García-Barros, 2000). Seifert et al. (2023) suggested that this relationship may depend on host-plant growth form. Our results confirmed a significant interaction between specialisation and host-

plant growth form, with generalists being larger than specialists only among tree feeders. This supports the idea that larger size in generalists may help them overcome woody plants' quantitative defences. The interaction also explains why host-plant growth form affected body size in simple but not in multiple phylogenetic regression models that included dietary specialisation. In line with Davis et al. (2013) and Seifert et al. (2023), we argue for special emphasis on interactive effects when examining ecological links between body size and diet breadth. Unfortunately, the threshold model and the Pagel's model of sequence trait evolution currently apply only to binary traits in bivariate settings. Despite this, our transition rate analyses favoured correlated over independent evolution for both body size and dietary specialisation, and for body size and host-plant growth form, suggesting that large generalists tended to evolve generalism before large size, and large tree feeders typically shifted to woody hosts before increasing in size.

We also found that larger body sizes were consistently linked to nocturnal activity in both phylogenetic regression and threshold model analyses. Diurnality in geometrid moths is rare and generally associated with smaller sizes, likely to reduce detectability (Tammaru et al., 2018). We agree with Tammaru et al. (2018) that large-bodied diurnal lepidopterans likely require effective antipredator defences to offset higher predation risk. Nonetheless, our results suggests that a direct causal connection between body size and diel activity in geometrids is difficult to establish, as no evidence was found for correlated evolution between these traits in the Pagel's model of sequence trait evolution. The contrast between these findings and earlier studies points to possible influences from unmeasured factors, such as predation pressure, which is difficult to assess in adult moths.

4.3. Body size prediction in buthid scorpions (Study III)

In the case of body size prediction in scorpions, the inclusion of an additional size predictor in a multiple regression setting is not strictly required to achieve reliable estimates. This holds true for both total length and carapace length, which are the two most widely used proxies for body size in scorpions (e.g., Outeda-Jorge et al., 2009; Seiter & Stockmann, 2017; Lira et al., 2021). This outcome likely reflects a strong size component shared across all linear measurements, with no single variable capturing substantial variation in body plan, as shown by the phylogenetic principal component analysis based on both male and female data. This limitation is not particularly problematic for buthid scorpions, as most species in this family exhibit a narrow-bodied morphology, with no pronounced variation in overall body plan (a few exceptions may apply for a small number of cave-dwelling species). In fact, while body size can vary greatly among species of the same family (11.9 to 119.1 mm in total length in the present study), differences in body plan among scorpions are generally more evident above the family level. For instance, species within Scorpionidae, Euscorpiidae, Scorpiopidae, and Chactidae display markedly different body plans compared to buthids, typically

characterised by stouter builds and proportionally shorter and robust appendages (Stockmann & Ythier, 2010).

Conveniently, the general absence of statistically significant interactions involving sex, indicates that the predictive models can be reasonably applied to both male and female scorpions. This is particularly advantageous in cases where morphological differences between the sexes are subtle, or when specimens are too damaged or incomplete to allow for reliable sex determination. Such situations are common across various fields, including palaeontology, where only partial remains may be preserved or accessible for measurement (e.g., Santiago-Blay et al., 2004; Riquelme et al., 2015; Lourenço, 2023), and studies of feeding ecology, where only fragments of specimens are often recovered (e.g., Sahley et al., 2015; Qashqaei et al., 2023; Nordberg et al., 2018). In addition, the predictive equations will prove useful for estimating body size in specimens stored in scientific collections, where conventional measurements can be difficult to obtain without risking damage to the specimen.

The single predictor phylogenetic regression models showed that carapace length is an effective predictor and a suitable proxy for body size (i.e., total length). While this result may seem expected, given the widespread use of carapace length as an indicator of body size in scorpions (e.g., DeSouza et al., 2016; Seiter & Stockmann, 2017; Moreira et al., 2022; Giménez Carbonari et al., 2024), Study III represents the first empirical validation of its reliability for predicting/representing total length, supported by robust comparative data. With few exceptions (e.g., McLean et al., 2018), the use of carapace length as a proxy for body size has rarely been justified in methodological terms. From a technical standpoint, carapace length offers several practical advantages over total length, the most evident being its ease of measurement. Ideally, however, such advantages should be supported by empirical validation, which is now provided in Study III.

In terms of predictive ability, the simple phylogenetic regression models identified met5L as the best single predictor of total length. Met5L offers particular advantages for measurement, as it typically does not require full extension of the metasoma or manipulation of other body parts. Additionally, metasomal segments are highly sclerotised in scorpions, making them less susceptible to breakage than more fragile structures such as the aculeus. It is not uncommon to find reports of specimens with broken aculeus tip (e.g., Armas, 1999; Teruel & Rein, 2010; Teruel & Kovařík, 2014), which depending on the size of the scorpion, may compromise the quality of the size predictions, especially in smaller species (e.g., species in the genus *Microtityus* Kjellesvig-Waering, 1966 or *Ananteris* Thorell, 1891). Fortunately, all other predictors also performed reasonably well in estimating both total length and carapace length. Thus, the general recommendation is to use telson length for size prediction only when the aculeus is fully intact.

4.4. Sexual size dimorphism and evolutionary allometry in Neotropical buthids (Study IV)

In the studied species, SSD was female-biased, with females being 8% larger than males, on average. This pattern matches previous intraspecific findings (Giménez Carbonari et al., 2024). Mesosoma length and width were the only traits where males did not significantly surpass females when controlling for body size. Females had significantly wider mesosomas, implying greater mesosomal areas assuming a basic length × width estimate. This may partly reflect selection acting on pre- and post-embryonic aspects of scorpion reproduction. Pre-embryonically, a larger mesosoma could house more reserves in the hepatopancreas, an organ accounting for around 40% of body mass and directly involved in oogenesis and vitellogenesis (Warburg, 2011). Post-embryonically, broader mesosomas may offer increased surface area for carrying scorpionlings, potentially supporting larger broods in number or size. However, this interpretation remains to be tested, as mesosomal area in scorpions has yet to be precisely quantified anatomically.

The observed female-biased SSD aligns with the reasoning that reproductive advantages linked to larger body size may favour selection for larger females in scorpions (reviewed by Giménez Carbonari et al., 2024). In Neotropical buthids, SSD follows Rensch's rule, being more pronounced in smaller species and nearly absent in larger ones. This suggests that stronger selection on female fecundity (i.e., larger sizes are selected for), or reduced male size due to selective pressures, may underlie SSD, particularly in smaller species (see below). Proximate causes of SSD could include sex-specific differences in mortality, energy intake, and energy use related to maintenance, reproductive organs, or behaviour (Mollet et al., 2023). Unfortunately, there are no comparative studies exploring these mechanisms in scorpions, leaving their relative roles unclear. However, insights can still be drawn from experimental data on species within Study IV. In *Tityus neibae* Armas, 1999, for example, males can mature by the fourth instar under weekly feeding, while females do not (Seiter et al., 2020), suggesting that males may prioritise early maturity at the cost of body size, potentially to reduce predation risk. Females, by contrast, attain larger sizes, likely enhancing reproductive output (Seiter et al., 2020). Similar patterns have been reported in *Tityus pusillus* Pocock, 1893, where earlier male maturation at a smaller size is believed to be an adaptive response to compensate increased exposure to predators due to their greater foraging activity (Albuquerque & Lira, 2016; Lira et al., 2018). These findings point to strategic growth trade-offs between development time, body size, and mortality risk (Tuni & Berger-Tal, 2012; Albuquerque & Lira, 2016). Comparable mechanisms have been proposed for spiders, where females may grow larger by extending development either through additional instars (Higgins & Goodnight, 2010, 2011; Kuntner et al., 2012; Agnarsson et al., 2024) or by lengthening each instar (Higgins & Goodnight, 2011). They may also assimilate energy more efficiently and exhibit lower activity levels than males (Chelini et al., 2019). It is worth mentioning, however, that such observations come from spiders with extreme female-biased SSD, which is clearly not the case

in buthid scorpions. Furthermore, while longer development often leads to larger size in invertebrates (recently reviewed by Tammaru & Teder, 2025), this is not a fixed rule in Neotropical buthids. For instance, in *Ananteris mauryi* Lourenço, 1982, males mature slightly later than females, yet females still achieve larger adult sizes on average (Lira et al., 2021).

As briefly mentioned, an alternative explanation for female-biased SSD in Neotropical buthids may lie in male size reduction rather than female size increase. This is consistent with the "Ghiselin-Reiss small-male hypothesis", which posits that smaller males are likely to evolve when reproductive success is largely determined by scramble competition for access to females (Blanckenhorn et al., 1995). Under such conditions, males are expected to prioritise reproductive investment over somatic growth, potentially resulting in reduced survival and a corresponding relaxation of male-male competition (Blanckenhorn et al., 1995; Mollet et al., 2023). In other arachnids, smaller male size has been linked to greater reproductive success in mating systems characterised by scramble competition, where rapid mate location is key (Danielson-François et al., 2012; Jordan et al., 2014). Under this scenario, SSD in Neotropical buthids may result from divergent sex-specific roles, with males selected for speed and mobility, and females for enhanced reproductive output and parental care, as hypothesised in intraspecific studies (Carlson et al., 2014; Miller et al., 2016). The SSD pattern observed here, consistent with Rensch's rule, indicates that male size reduction is more evident in smaller species, also meaning that males of larger species must benefit from increased absolute size. This last aspect likely reflects the influence of pre-copulatory sexual selection, such as male-male competition and territoriality, reported in larger species (Tang, 2023), including in Neotropical buthids (Wyman et al., 2025), but presumably less relevant in smaller-bodied ones. Nonetheless, the subtle yet significant size differences in Neotropical buthids remain difficult to attribute to a single cause. As in other arthropods (e.g., Higgins & Goodnight, 2011; Quiñones-Lebrón et al., 2021; Agnarsson et al., 2024), intersexual genetic correlations and the energetic and ecological costs of achieving and maintaining larger body sizes in both sexes (Blanckenhorn, 2000; Blanckenhorn et al., 2007; Chelini et al., 2019; Higgins & Goodnight, 2011) are likely to constrain SSD evolution.

The models of continuous trait evolution revealed substantial sex-specific differences in both the rate and mode of body size evolution among Neotropical buthids. Male body size evolved approximately three times faster than female size, with an OU model best fitting the male data and a BM model fitting the female data. These results support the reasoning that each sex is subject to different selective pressures of unequal intensity. Although intuitive, such evolutionary processes have not previously been quantified for body size in scorpions. The BM model for females suggests body size evolution is better explained by stochastic processes, lacking a clear directional pull toward an adaptive size optimum. However, this should not be interpreted as an absence of constraint, as the low evolutionary rate (σ^2) points to limited evolvability. Moreover, statistical support for an OU model was not absent, suggesting potential weak stabilising

selection. A similar caveat applies to males, though the stronger support for the OU model indicates stabilising selection toward an optimal size (estimated at 4.06 mm carapace length). Additionally, the higher evolutionary rate in males reflects a faster exploration of trait space, yet this is not unconstrained. The absolute strength of selection (α) was three times greater in males than females (using an OU model for both sexes for illustrative purposes). This is further supported by the shorter phylogenetic half-life and greater reduction in trait variance (ρ) for male size, pointing to strong selective pressures, likely sexual selection. While both sexes show evidence of evolutionary constraint, the mode and intensity of selection differ, with male size shaped by stronger and more directed forces. These findings provide a valuable starting point for future comparative studies of body size evolution in scorpions and other arthropods.

Perhaps surprisingly, the analysis of allometric scaling revealed no sex-specific differences in slopes, though certain traits displayed distinct patterns between sexes. Chela length and depth showed positive allometry in males but were isometric in females. In line with previous intraspecific studies (Giménez Carbonari et al., 2024), this is expected given the role of these traits in mating. Scorpion courtship involves the male grasping the female with his chelae and performing coordinated movements to initiate copulation (Foerster et al., 2021; Simone & van der Meijden, 2021), a process that can last minutes to hours depending on female resistance. In species with female-biased SSD, this requires considerable pinch force from males. Indeed, chela depth is strongly correlated with pinch force in size-corrected analyses (van der Meijden et al., 2010). The positive allometry in male chela depth suggests that males of smaller species may exert disproportionately higher pinch force relative to their size, consistent with the greater SSD seen in these species. Positive allometry in male chela length was also observed, although this may reflect selection for greater closing speed rather than force, as previously proposed (van der Meijden et al., 2010). If so, this adaptation would again be most evident in smaller-bodied species, which exhibit stronger SSD. In any case, further studies are needed to assess the link between male pinch force (and chela morphology) and SSD using comparative data. As phylogenetic hypotheses and comparative datasets continue to accumulate (Štundlová et al., 2022; Santibáñez-López et al., 2023), and with the development of increasingly sophisticated phylogenetic comparative methods, future analyses will be better equipped to explain the evolutionary processes responsible for the emergence and maintenance of female-biased SSD in scorpions.

5. CONCLUSIONS

The predictive equations developed in Studies I and III, and presented in this thesis, offer ecologists practical tools for estimating body size in two invertebrate groups: the diverse moth family Geometridae (I) and the species-rich scorpion family Buthidae (III). These methods allow accurate size estimation for both taxa without the need for complex computations or multiple predictor variables. Their potential applications range from biomass estimation in ecological studies to reliable size inference from incomplete palaeontological records. The equations can also be used as taxon-specific imputation methods for enhancing data completeness in comparative analyses. This last application is demonstrated in the two case studies summarised in this thesis, where predicted size values were used to explore different ecological and evolutionary aspects of body size variation in moths (II) and scorpions (IV). Specifically, dry body mass predictions enabled a detailed examination of life-history correlates in Northern European geometrid moths, offering new insights into how body size is evolutionarily linked with traits related to larval host specialisation and phenology. Similarly, the imputation of carapace length using the predictive methods developed for scorpions enabled the development of the most taxonomically comprehensive analysis to date of SSD and evolutionary allometry in the group, conducted within an explicitly phylogenetic framework. The methodological framework, phylogenetic reconstructions, and comparative datasets developed as part of this thesis are valuable resources that will likely stimulate future research on body size evolution, a field of growing interest within evolutionary biology that still lacks a more inclusive perspective on invertebrate taxa.

SUMMARY

Body size is a fundamental aspect of animal form and function, shaped by evolutionary history and ecological adaptations. However, measuring body size across taxa remains challenging due to the diversity of morphological proxies and the multiple sources of variation associated with size metrics. For invertebrates, body size is typically represented by either mass (live or dry) or linear measurements, such as total body length or the dimensions of particular body parts. Mass-based measures are especially useful when studying processes that scale directly with biomass, such as metabolic rates, trophic energy transfer, or reproductive investment. However, mass measurements, particularly those taken from live specimens, are vulnerable to short-term fluctuations in water content, feeding status, and age-related changes, as well as artefacts introduced by collection and preservation methods. Dry mass reduces much of this variability and can even be measured from museum material, making it more consistent than live mass in some contexts. Length-based metrics, on the other hand, offer a widely applicable alternative. They are non-destructive, unaffected by temporary physiological changes such as hydration state, and tend to remain stable after growth ceases in adulthood.

Many length measurements correlate strongly with both live and dry mass and follow predictable allometric scaling relationships. Allometry, in its broadest sense, describes how one trait changes in relation to overall body size. It can be studied at the intraspecific level (ontogenetic or static allometry) or at the interspecific level (evolutionary allometry, which is the focus of this thesis). The slope of an allometric relationship indicates whether a trait scales proportionately, more rapidly, or more slowly than body size. Together with the intercept, it forms the basis of predictive models used to estimate one trait from another. In a phylogenetic context, such models provide a powerful means of generating body size estimates for large datasets, enabling the acquisition of indirect but accurate measures of body size that would otherwise be impractical to obtain. Moreover, predictive models based on allometric relations are the best (and perhaps the only) way to impute missing data on body size when direct measurements are not possible, such as with museum specimens or fossil records.

Despite the long history of allometric studies, predictive models for many invertebrate groups remain scarce. In Lepidoptera, most existing models rely on small species samples and non-phylogenetic statistical methods. A comparable situation occurs in arachnids, where research is largely concentrated on spiders and harvestmen, with virtually no studies addressing scorpions, despite their ecological significance as abundant generalist predators. To help filling this gap, this thesis builds on recent advances in the field of invertebrate phylogenetics to address methodological and evolutionary questions concerning body size estimation and its applications in macroevolutionary research focused on insects and arachnids. Four phylogenetic comparative studies are presented using two ecologically distinct and species-rich groups, geometrid moths and buthid scorpions.

Studies I and III develop predictive equations for estimating body size metrics from simple linear measurements in geometrid moths (I) and buthid scorpions (III) while accounting for phylogenetic relatedness. Studies II and IV apply these predictions to investigate ecological and evolutionary correlates of body size, focusing on life-history traits in Northern European geometrid moths (II) and patterns of sexual size dimorphism in Neotropical buthid scorpions (IV).

Phylogenetic principal component analyses supported the interpretation of the first axis as representing an overall size descriptor in geometrid moths. However, abdomen width, however, was nearly orthogonal to the first axis, indicating that it captured variation beyond overall size, likely reflecting aspects of body plan. In fact, models combining maximum wingspan (size descriptor) and abdomen width (body plan descriptor) accounted for more variation in DBM than any other multiple regression model. In Northern European geometrids, predicted body size was significantly associated with larval overwintering strategies, nocturnal activity of the adults, and generalist feeding habits of the larvae. Discrete trait models further indicated that shifts in overwintering and feeding strategies preceded increases in size.

In buthid scorpions, most morphometric traits served as reliable predictors of body size, but the phylogenetic principal component analysis indicated limited ability of the studied traits in providing information on body plan. All linear measurements reliably predicted both total length and carapace length in male and female buthids and performed well even in non-buthid scorpions. Carapace length was strongly correlated with total length, but despite that, total length was best predicted by the length of metasomal segment V, whereas telson length provided the most accurate predictions of carapace length in the simple regression analyses. Increasing model complexity by adding multiple predictors had negligible effects on prediction accuracy and was therefore unnecessary.

In the study of sexual size dimorphism in scorpions, Neotropical buthids exhibited female-biased size dimorphism, although males possessed relatively larger structures after accounting for body size. Male traits such as chela length and depth scaled with positive allometry, contrasting with the isometric patterns observed in females. Patterns of body size evolution differed between sexes: female size followed a Brownian motion model, while male size fit an Ornstein-Uhlenbeck process, suggesting stabilising selection and more rapid evolution (towards trait optima) in males. Together, these studies demonstrate the value of phylogenetically informed allometric models for estimating body size and addressing evolutionary questions in morphologically diverse invertebrates. The methodological approach, phylogenetic reconstructions, and comparative datasets generated during this thesis constitute valuable resources that will likely stimulate further research on body size evolution, an area of growing interest in evolutionary biology that still lacks a sufficiently inclusive perspective on invertebrate taxa.

SUMMARY IN ESTONIAN

Kehasuuruse fülogeneetilis-võrdlevad uurimused putukatel ja ämblikulaadsetel: ennustustest rakendusteni

Kehasuurus on loomade fundamentaalne, kõiki eluavaldusi mõjutav parameeter. Liigiomane kehasuurus sõltub evolutsioonilisest ajaloost, kuid on aldis muutuma ka vastusena kaasaegsetele valikusurvetele. Kehasuuruse uurimise eelduseks on oskus kehasuurust mõõta. Isendi suuruse kvantifitseerimine eri taksonite lõikes on siiski jätkuvalt keerukas, seda tulenevalt nii kehasuuruse mõõtudena kasutatavate morfoloogiliste parameetrite mitmekesisusest kui ka nende parameetrite sageli suurest varieeruvusest, millel on omakorda mitmeid erinevaid põhjusi. Selgrootutel väljendatakse kehasuurust tavaliselt kas massina (elus- või kuivmass) või erinevate lineaarmõõtude abil, näiteks keha kogupikkus või teatud kehaosade mõõtmed. Massipõhised suuruse mõõdud on eriti asjakohased selliste protsesside uurimisel, mis on kehamassiga otseselt seotud; sellisteks on näiteks ainevahetuse kiirus, troofiline energiaülekanne või reproduktiivne investeering. Kehamass, eriti elusmass, on paraku sõltuv organismi füsioloogilisest seisundist kuna reageerib näiteks muutustele looma veesisalduses ja toitumuses ning sageli korreleerub ka isendi vanusega; samuti on mass tundlik erinevatest kogumis- ja säilitamismeetoditest tulenevatele artefaktidele. Kuivmassi kasutamine elusmassi asemel võimaldab vältida suurt osa sellist tüüpi probleemidest ning seda saab mõõta isegi muuseumieksemplaridel, mis muudab kuivmassi teatud kontekstides elusmassist usaldusväärsemaks kehasuuruse mõõduks. Pikkusel põhinevad kehasuuruse mõõdud pakuvad massipõhistele mõõtudele laialdaselt rakendatavat alternatiivi: nende määramine on sageli mitteinvasiivne, need ei sõltu lühiajalistest muutustest isendi füsioloogias (nt hüdratatsiooniseisundist) ning nende väärtused püsivad sageli stabiilsena pärast kasvu lõppemist täiskasvanueas. Paljud pikkusmõõdud korreleeruvad tugevalt nii elus- kui kuivmassiga ning alluvad allomeetrilistele seaduspäradele, mis võimaldab erinevaid kehasuuruse mõõte vastastikku teisendada.

Allomeetria kirjeldab selle sõna kõige üldisemas tähenduses seda, kuidas mingi meetrilise tunnuse väärtus muutub seoses keha üldise suuruse muutumisega. Allomeetriat saab uurida liigisiseselt (ontogeneetiline ehk staatiline allomeetria) või liikide vahel (evolutsiooniline allomeetria, mis on käesoleva väitekirja keskseks teemaks). Allomeetrilise seose tõus näitab, kas tunnuse väärtus skaleerub keha suurusega võrdeliselt või muutub sellest kiiremini või aeglasemalt. Koos vabaliikmega moodustab allomeetrilise võrrandi tõus aluse ennustusmudelitele, mille abil saab ühe tunnuse alusel teise tunnuse väärtust hinnata. Fülogeneetilises kontekstis pakuvad sellised mudelid võimsa vahendi kehasuuruse analüüsimiseks suuremahuliste andmestike põhjal. Need võimaldavad saada oma olemuselt kaudseid, kuid siiski piisavalt täpseid kehasuuruse (eelkõige massi) mõõte, mille vahetu määramine oleks ebapraktiline. Veelgi enam – allomeetrilistel seostel põhinevad ennustusmudelid on parim (ja tihti ainus) võimalus

saada võrreldavaid andmeid olukordades, kus massi otsene määramine pole üldse võimalik, näiteks muuseumimaterjali või fossiilide puhul.

Hoolimata allomeetriaga seotud uurimuste pikast ajaloost on paljude selgrootute rühmade jaoks asjaomaseid ennustusmudeleid endiselt vähe. Liblikaliste puhul põhineb enamik olemasolevaid mudeleid väikestel valimitel ja fülogeneesi mitte arvestavatel statistilistel meetoditel. Sarnane on olukord ka ämblikulaadsete puhul, kus uurimused on keskendunud valdavalt ämblikele ja koibikutele. Skorpionid on seni jäänud väärilise tähelepanuta, seda hoolimata nende ökoloogilisest tähtsusest arvukate generalistkiskjatena.

Käesolev väitekiri käsitleb metodoloogilisi ja evolutsioonilisi küsimusi, mis on seotud kehasuuruse hindamise ja kehasuuruse hinnangute rakendamisega makroevolutsioonilises uurimistöös. Töö hõlmab nelja fülogeneetilis-võrdlevat uurimust, milles mudeltaksonitena kasutatakse kahte morfoloogiliselt ja ökoloogiliselt erinevat liigirikast lülijalgsete rühma – liblikaliste hulgast vaksiklasi ja skorpionide sugukonda *Buthidae*. Töö tugineb värskeimatele edusammudele uuritavate rühmade fülogeneesi rekonstrueerimisel.

Uurimustes I ja III töötati välja liikide fülogeneetilist sugulust arvestavad ennustusvõrrandid kehamassi hindamiseks isendite lineaarmõõtmete alusel, vastavalt vaksiklaste ja skorpionide jaoks. Uurimustes II ja IV rakendati selliseid ennustusi kehasuuruse ökoloogiliste ja evolutsiooniliste seoste uurimiseks, keskendudes elukäigutunnustele Põhja-Euroopa vaksiklastel (II) ning kehasuuruse soolise dimorfismi mustritele Neotroopika skorpionidel (IV). Analüüsi esimese sammuna uuriti võimalusi kombineerida erinevaid kehasuuruse mõõtusid rakendades fülogeneesi arvestavat peakomponentanalüüsi. Leitud peakomponentidest esimene on vaksiklaste puhul tõlgendatav kehasuuruse mõõduna. Tagakeha laius osutus esimesega teljega peaaegu ortogonaalseks muutujaks ja on kasutatav kui kehaehituse tüübi iseloomustaja. Mudelid, mis kombineerisid tiibade siruulatust ja tagakeha laiust selgitasidki suuremat osa kehamassi varieeruvusest kui ükski alternatiivne mitmese regressiooni mudel. Järgnenud fülogeneetilis-võrdlev analüüs näitas, et ennustatud kehasuurus on seoses talvituva arengujärguga, valmikute ööpäevase aktiivsuse ja röövikute toiduspetsialisatsiooni astmega. Analüüsist ilmnes lisaks, et talvitumis- ja toitumisstrateegiate muutused eelnesid evolutsioonilisele muutusele suurema kehasuuruse suunas.

Skorpionide sugukonnas *Buthidae* osutus enamik morfomeetrilisi tunnuseid kehasuuruse usaldusväärseteks ennustajateks, kuid erinevalt vaksiklastest ei ilmnenud kehaehituse erinevusi hästi kirjeldavat üksikmuutujat või peakomponenti. Kõik lineaarmõõtmed ennustasid usaldusväärselt nii kogupikkust kui ka peakilbi pikkust nii isastel kui emastel skorpionidel. Peakilbi pikkus korreleerus tugevalt kogupikkusega, ent kogupikkust ennustas siiski kõige täpsemalt metasoma V lüli pikkus, samas kui telsoni pikkus osutus parimaks peakilbi pikkuse ennustajaks. Mudelite keerukuse suurendamine avaldas ennustustäpsusele vaid tühist mõju ning mitme sõltumatu muutujaga mudelite kasutamine osutus seetõttu ebavajalikuks.

Ennustusvõrrandid osutusid üldistatavateks üle sugude ja rakendatavateks ka väljaspool sugukonda *Buthidae*. Leidis kinnitust, et Neotroopika skorpionidel on

emased isastest suuremad, kuid mitmete üksikmõõtude osas osutusid isased emastest suurematekspeale üldise kehasuuruse mõju statistilist eemaldamist. Isastel ilmutasid sellised tunnused nagu chela pikkus ja sügavus positiivset allomeetrilist seost kehasuurusega, mis erines emastel täheldatud isomeetriast. Kehasuuruse evolutsiooni mustrid erinesid sugude lõikes: emaste suurus allus Browni liikumise mudelile, samas kui isaste suurus oli kooskõlas Ornsteini-Uhlenbecki protsessiga, mis viitab stabiliseerivale valikule ja kiiremale evolutsioonile optimumi suunas isastel.

Kokku võetuna näitavad väitekirja osauurimused fülogeneetilist teavet arvestavate allomeetriliste mudelite sobivust kehasuuruse hindamisel ja evolutsioonilise küsimuste käsitlemisel morfoloogiliselt mitmekesiste selgrootute puhul. Väitekirjaprojekti käigus välja arendatud metodoloogiline lähenemine, fülogeneetilised rekonstruktsioonid ja võrdlevad andmestikud on ressursid, mis usutavasti aitavad oluliselt kaasa edasisele uurimistööle kehasuuruse evolutsiooni vallas – evolutsioonilise ökoloogia ühes keskses uurimissuunas, millel on jätkuvalt palju võita erinevate selgrootute loomade taksonite senisest laiemast kaasamisest.

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PUBLICATIONS

CURRICULUM VITAE

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Education:

2020–…..	University of Tartu, Zoology and Hydrobiology, PhD
2018–2020	Universidade Federal de Pernambuco, Genetics, M.Sc.
2010–2015	Universidade Federal Rural de Pernambuco, Biological Sciences, B.Sc.

Courses & Workshops

2025	Computational Molecular Evolution, Hellenic Centre for Marine Research, Crete, Greece. Instructors: Alexandros Stamatakis, Ben Redelings, Bruce Rannalla, Mike May, Maria Anisimova, Ziheng Yang, Adam Leache.
2024	BayesTraits Workshop, University of Reading, Reading, UK. Instructor: Joanna Baker.
2023	Evolutionary Analysis of Morphology, Okinawa Institute of Science and Technology, Okinawa, Japan. Instructors: Liam J. Revell, Luke J. Harmon, Michael E. Alfaro, Evan P. Economo, Anjali Goswami, Emma Sherratt, Peter Wainwright.
2022	RevBayes Workshop, University of Oslo, Oslo, Norway. Instructors: Sebastian Höhna, Rachel C. M. Warnock.

Teaching activities

LTOM.01.002 Data Analysis in Community Ecology (3 ECTS), University of Tartu, Lecturer in charge: Meelis Pärtel, Carlos P. Carmona

Conference presentations

2025	Congress of the European Society for Evolutionary Biology (ESEB 2025), Barcelona, Spain. Poster: Co-evolutionary dynamics of dietary breadth and body size in moths.
2025	EMBO Practical Course Computational Molecular Evolution, Crete, Greece. Poster: Evolutionary transitions in dietary breadth and their relationships with body size in geometrid moths.

2022 XXII European Congress of Lepidopterology, Laulasmaa, Estonia. Poster: You do not need a scale to weigh a Geometridae moth: applying allometric relationships to predict dry body weight at maturation stage.

Research interests: Phylogenetic comparative methods, evolutionary ecology, trait evolution, arachnids, insects.

Scientific publications

Brito-Almeida, T. R., **Foerster, S. Í. A.**, Lima, J. R., Da Silva, M. A., Moura, G. J. B., & Lira, A. F. A. (2025). Free pasture of exotic goats reduces diversity and negatively affects body condition in scorpions (Arachnida: Scorpiones) assemblage from Brazilian seasonal dry tropical forest. *Ecology and Evolution*, *15*(1), e70804.

Costa, J. M. R., **Foerster, S. Í. A.**, Pessoa, V. B., Tizo-Pedroso, E., Moura, G. J. B., & Lira, A. F. A. (2025). Biotic interactions rather than habitat complexity predict the occurrence of bark-dwelling social pseudoscorpions in urban environments. *Biologia*. https://doi.org/10.1007/s11756-025-01985-6

Fetnassi, N., **Foerster, S. Í. A.**, Õunap, E., Ghamizi, M., & Tammaru, T. (2025). Complementary roles of agricultural and natural habitats in supporting moth diversity in semi-arid landscapes of Morocco. *European Journal of Entomology*, *122*, 173–183. https://doi.org/10.14411/eje.2025.022

Foerster, S. Í. A. (2025). Body size prediction in scorpions: A phylogenetic comparative examination of linear measurements of individual body parts. *PeerJ*, *13*, e18621. https://doi.org/10.7717/peerj.18621

Ude, K., **Foerster, S. Í. A.**, Fetnassi, N., & Tammaru, T. (2025). Forest clear-cuts support diverse moth fauna but lack common grassland species. *Journal of Applied Ecology*, 1365–2664.70063. https://doi.org/10.1111/1365-2664.70063

Dionisio-da-Silva, W., **Foerster, S. Í. A.**, Gallão, J. E., & Lira, A. F. A. (2024). What's for dinner? Prey consumption by Neotropical scorpions across contrasting environments. *The Journal of Arachnology*, *52*(1). https://doi.org/10.1636/JoA-S-22-060

Foerster, S. Í. A., Clarke, J. T., Õunap, E., Teder, T., & Tammaru, T. (2024). A comparative study of body size evolution in moths: Evidence of correlated evolution with feeding and phenology-related traits. *Journal of Evolutionary Biology*, *37*(8), 891–904. https://doi.org/10.1093/jeb/voae072

Foerster, S. Í. A., Javoiš, J., Holm, S., & Tammaru, T. (2024). Predicting insect body masses based on linear measurements: A phylogenetic case study on geometrid moths. *Biological Journal of the Linnean Society*, *141*(1), 71–86. https://doi.org/10.1093/biolinnean/blad069

Lira, A. F. A., Moura, G. J. B., & **Foerster, S. Í. A.** (2024). Scorpion assemblages in threatened Brazilian forests: The role of environmental factors in explaining beta-diversity patterns. *Insect Conservation and Diversity*, *17*(1), 128–138. https://doi.org/10.1111/icad.12699

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Cunha, H. P., Santos, A. B., **Foerster, S. Í. A.**, Moura, G. J. B., & Lira, A. F. A. (2022). Can contrasting habitats influence predatory behavior in tropical forest scorpions? *Acta Ethologica*, *25*(2), 107–113. https://doi.org/10.1007/s10211-022-00390-5

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ELULOOKIRJELDUS

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Haridustee

2020–…..	Tartu Ülikool, zooloogia ja hüdrobioloogia, doktoriõpe
2018–2020	Universidade Federal de Pernambuco, geneetika, magistriõpe
2010–2015	Universidade Federal Rural de Pernambuco, bioloogia, bakalaureuseõpe

Läbitud erialased kursused

2025	Computational Molecular Evolution, Hellenic Centre for Marine Research, Crete, Greece. Juhendajad: Alexandros Stamatakis, Ben Redelings, Bruce Rannalla, Mike May, Maria Anisimova, Ziheng Yang, Adam Leache.
2024	BayesTraits Workshop, University of Reading, Reading, UK. Juhendaja Joanna Baker.
2023	Evolutionary Analysis of Morphology, Okinawa Institute of Science and Technology, Okinawa, Japan. Juhendajad: Liam J. Revell, Luke J. Harmon, Michael E. Alfaro, Evan P. Economo, Anjali Goswami, Emma Sherratt, Peter Wainwright.
2022	RevBayes Workshop, University of Oslo, Oslo, Norway. Juhendajad: Sebastian Höhna, Rachel C. M. Warnock.

Õppeülesannete täitmine

LTOM.01.002 Ökoloogiliste koosluste andmeanalüüs (3 EAP), Tartu Ülikool, vastutavad õppejõud Meelis Pärtel ja Carlos P. Carmona

Konverentsiettekanded

2025	Congress of the European Society for Evolutionary Biology (ESEB 2025), Barcelona, Spain. Poster: Co-evolutionary dynamics of dietary breadth and body size in moths.

2025	EMBO Practical Course Computational Molecular Evolution, Crete, Greece. Poster: Evolutionary transitions in dietary breadth and their relationships with body size in geometrid moths.
2022	XXII European Congress of Lepidopterology, Laulasmaa, Estonia. Poster: You do not need a scale to weigh a Geometridae moth: applying allometric relationships to predict dry body weight at maturation stage.

Peamised uurimisvaldkonnad: fülogeneetilised võrdlevad meetodid, evolutsiooniline ökoloogia, tunnuste evolutsioon, ämblikulaadsed, putukad

Teaduspublikatsioonid

Brito-Almeida, T. R., **Foerster, S. Í. A.**, Lima, J. R., Da Silva, M. A., Moura, G. J. B., & Lira, A. F. A. (2025). Free pasture of exotic goats reduces diversity and negatively affects body condition in scorpions (Arachnida: Scorpiones) assemblage from Brazilian seasonal dry tropical forest. *Ecology and Evolution*, *15*(1), e70804.

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