

SILLE HOLM

Comparative ecology of geometrid moths:
in search of contrasts between
a temperate and a tropical forest



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LIST OF ORIGINAL PAPERS

- I. **Holm, S.**, Davis, R.B., Javoiš, J., Õunap, E., Kaasik, A., Molleman, F., and Tammaru, T. (2016). A comparative perspective on longevity: the effect of body size dominates over ecology in moths. *Journal of Evolutionary Biology*, 29: 2422–2435.
- II. **Holm, S.**, Javoiš, J., Õunap, E., Davis, R.B., Kaasik, A., Molleman, F., Tasane, T., and Tammaru, T. (2018). Reproductive behaviour indicates specificity in resource use: phylogenetic examples from temperate and tropical insects. *Oikos*, 127: 1113–1124.
- III. **Holm, S.**, Javoiš, J., Molleman, F., Davis, R.B., Õunap, E., Roininen, H., and Tammaru, T. (2019). No indication of high host-plant specificity in Afrotropical geometrid moths. *Journal of Insect Science*, 19: 1–16.
- IV. **Holm, S.**, Javoiš, J., Kaasik, A., Õunap, E., Davis, R. B., Molleman, F., Roininen, H., and Tammaru, T. (2019). Size-related life-history traits in geometrid moths: a comparison of a temperate and a tropical community. *Ecological Entomology*, 44: 711–716.
- V. **Holm, S.**, Kaasik, A., Javoiš, J., Molleman, F., and Tammaru, T. Longevity in the tropics: a comparative example from geometrid moths. Manuscript.

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The participation of the author in preparing the listed publications (* denotes a moderate contribution, ** a high contribution, *** the leading role).

	I	II	III	IV	V
Original idea	*	*	***	*	*
Study design	**	**	***	**	**
Data collection	***	***	***	***	***
Data analyses	***	**	***	**	**
Manuscript preparation	***	***	***	**	***

1. INTRODUCTION

Understanding the variation in life-history strategies (i.e. the ways in which organisms acquire and expend resources throughout their life (Bonnet et al. 1998)) lies at the core of modern evolutionary ecology. How and why life-history traits vary across species are frequently asked questions (reviewed in e.g. Morrison and Hero 2003 (amphibians), Robinson et al. 2010 (birds), Kuzawa and Bragg 2012 (genus *Homo*)). However, the picture is still fragmentary because most groups of organisms have remained unexplored due to a lack of comparable data. Data are especially scant for the highly vulnerable tropical regions, where the species themselves and interactions between them are still largely unknown (Basset et al. 2012, Scheffers et al. 2012).

The vast majority of the world's (tropical) insect fauna remains unexplored in terms of species ecology and life-histories. When comparing the ecological traits of tropical and temperate insects, evolutionary ecologists have placed the main focus on latitudinal gradient in host-plant specialisation (reviewed in, e.g. Lewinsohn and Roslin 2008, Forister et al. 2015). Lepidoptera are generally believed to show an increase in specificity (i.e. decrease in larval diet breadth) towards the tropics (Dyer et al. 2007, Forister et al. 2015). As is frequently suggested, this may primarily be because tropical plants rely more heavily on qualitative defences, such as species-specific alkaloids, tannins, proteins, peptides, isoflavones, triterpenoids and latex. Several studies have shown more toxic substances and/or higher concentrations of these chemicals in tropical plants (reviewed in Schemske et al. 2009, Becerra 2015). Therefore, simultaneous adaptation to a high number of host species must be complicated for a herbivore when defences vary among plant species (Ehrlich and Raven 1964, Becerra 2015). However, other considerations lead to prediction of species being less specialised in the tropical region. For example, the diverse vegetation in the tropics increases the challenge of finding particular plant species, which should select for low host specificity. The challenge of finding suitable plants holds especially true when adults are short-lived or have little control over their dispersal (Dixon et al. 1987). Through larval polyphagy, short-lived adult females could cope with the challenge of locating suitable host-plants for the larvae from a myriad of species (Carey 2001, Prinzing 2003, Jervis et al. 2007a).

The challenge of finding the host plant becomes particularly severe for females carrying a high load of eggs in their abdomens (Jervis et al. 2005, Wagner and Liebherr 1992, Zera and Denno 1997). This allows us make further predictions about ecological differences between temperate and tropical insects, concerning not only their specificity but also breeding strategy and longevity. Carrying a high load of resources for reproduction is characteristic of capital breeding species, i.e. for species, whose reproductive success depends primarily on the resources acquired in the larval stage (the capital) (Tammaru and Haukioja 1996, Snäll et al. 2007, Javoiš et al. 2011, Davis et al. 2016). Thus, the capital breeding strategy may be expected to prevail in the temperate habitats

rather than in the tropics, where high mobility is required. Typical capital breeders are short lived as adults, and rather non-selective regarding oviposition substrates (Price 1994, Jervis et al. 2005). Consistently, a high degree of larval polyphagy has indeed been found in capital breeding moths (Davis et al. 2016). Complementarily, income breeders, i.e. species heavily relying on adult feeding in reproduction, may be expected to prevail in the tropics. This is because income breeding allows high mobility (facilitated by lower relative abdomen mass) and longer adult lifespans (Tammaru and Haukioja 1996, Snäll et al. 2007, Javoiš et al. 2011, Davis et al. 2016). Mobile and long-living adults should cope well among the diverse tropical vegetation. Furthermore, adult foraging itself, as well as the correlated longer lifespans should be facilitated by the stable supply of adult food in weakly seasonal tropical environments (nectaring plants, fruits Chapman et al. 1999). Also, the positive correlation between extrinsic mortality risk and body size in caterpillars (Rommel et al. 2011), and high predation on caterpillars in the tropical region (Roslin et al. 2017) may contribute to adult foraging being favoured over larval foraging in the tropics.

Differences in plant defences and predation pressure between temperate and tropical habitats allows predictions concerning body size and egg size of the species. In temperate habitats where plants rely more on quantitative (e.g. leaf toughness) rather than qualitative defences (e.g. secondary metabolites), larger body size of a herbivore should gain higher importance (Lindström et al. 1994, Novotny and Wilson 1997, Reavey 1999). Thus, newly hatched caterpillars both need to be larger in the temperate region and also have the opportunity for this because of lower predation. These selective pressures allow us to also expect larger egg sizes in temperate compared to the tropical habitats.

Due to their species richness, abundance and diversity, insects appear to be a promising candidate as a target taxon for large-scale comparative studies, and can help us to organise and improve our understanding of living nature across a diverse range of contexts. However, the tremendous effort needed to collect data for multi-species comparative analyses still poses a great obstacle. As a result, attempts to compare life-history traits among tropical and temperate insect communities have so far remained scarce (see, however, Garcia-Barros 2000, Gerard et al. 2018). Furthermore, the results remain conflicting with respect to host-plant specificity at different latitudes (Beaver 1979, Fiedler 1995, Dyer et al. 2007, Forister et al. 2015, Hardy et al. 2015). Relying on just observational data is clearly insufficient, and we need more systematic approaches when describing the ecologies of insects across biomes. Moreover, if the traits in focus themselves are hard to observe, establishing and thereafter using easy-to-record proxies of ecological traits may allow us to obtain comparable data much more rapidly. This work cannot wait: describing ecological interactions of tropical insects is an urgent task due to the current rapid destruction of their native ecosystems.

Furthermore, for several decades, researchers have been aware of the need of considering phylogenetic relatedness when analysing among-trait relationships at the level of among-species comparison (Felsenstein 1985). The progress in

the technology of molecular-phylogenetic analyses has finally enabled the application of the theory. Though, for insects, it is mostly still on the responsibility of the comparative ecologist to construct the phylogenetic tree underlying the analyses.

The major aim of the current thesis is to compare – in the conceptual framework outlined above – ecological and life-history traits of moth species from the family Geometridae from two forest ecosystems at different latitudes. Original data were collected on life-history traits for about 250 species of geometrid moths from a temperate and a tropical region. Original phylogenetic reconstructions were derived to conduct phylogenetically informed analyses. The following hypotheses on host-plant specificity, longevity and breeding strategy were tested:

1) Host-plant specificity (II, III, IV)

- the caterpillars of tropical species were expected to show higher host specificity, i.e. to utilise a lower number of plant species as hosts than the temperate species (III).
- Differences in host plant use in different regions were expected to lead to corresponding differences in size-related life-history traits (adult body mass, body composition and egg size) of herbivorous insects (IV).
- Differences in host plant use were expected to be reflected in adult behaviour, which, in turn, should facilitate using behavioural traits as predictors of ecological interactions. In particular, in the absence of a suitable host, adult females of the geometrid species of higher host-plant specificity were expected to wait longer before commencing oviposition (Fitt 1986, Friedrich 1986, Tammaru et al. 1995, Tammaru and Javoiš 2000). A broad generalist should not have evolved the ability to considerably delay oviposition in response to (a lack of) environmental stimuli. This is because, in nature, a generalist has high odds that it will encounter a suitable host plant quickly, without extensive searching, or can even ‘hope’ that its offspring will find a suitable host plant by themselves (Schäpers et al. 2016). In contrast, a specialist should be adapted to invest substantial amounts of time into locating a suitable plant to ensure survival of its progeny, and to abstain from ovipositing until such a substrate is found. Therefore, it can be expected that a long waiting time under laboratory conditions should correspond to careful host-location behaviour in nature. In accordance with the waiting time, the probability of laying any eggs on an unfavourable substrate was expected to decrease with an increase in host-plant specificity. Thus, it was tested whether oviposition latency and incidence of oviposition in host-deprived moths could serve as index of host specificity of the species (II).

2) Assuming an increase in specificity towards the tropics, tropical adult moths (vs those of temperate zone) can be expected to allocate more time for locating suitable hosts in nature, and this was expected to manifest in prolonged pre-oviposition waiting time and low incidence of oviposition in host-deprived moths in the lab (II).

3) Longevity (I, V)

- Two general approaches explaining the among-species variation in longevity were compared based on our sample of temperate species. First, the physiological explanation views longevity as a side effect of body size. Larger organisms generally have a slower metabolism (Kleiber's law: e.g. McMahon, 1973) and thus experience slower physiological time (the rate of living theory: Lindstedt and Calder 1981). According to the physiological explanation, larger moths can be expected to live longer (I, V). Second, the ecological explanation proposes that longevity has evolved in straightforward accordance with extrinsic mortality (Medawar 1952, Williams 1957). For insects, we may expect a positive rather than a negative correlation between extrinsic mortality risk and body size (Rommel et al. 2011, Penney et al. 2012, Tufto et al. 2012, Tsurui et al. 2013, Smith et al. 2014). Thus, with the ecological explanation (vs the physiological explanation), larger moths can be expected to have shorter adult longevity (I, V).
- The stable supply of adult food in the tropics (Chapman et al. 1999) and the challenge of locating suitable hosts by adults was expected to select for an increase in adult longevity of tropical species, compared to the temperate species (V).

4) Breeding strategy (IV)

- It was expected that income (as opposed to capital) breeding strategy (i.e. usage of adult-derived nutrients for reproduction (Tammeru and Haukioja 1996, Snäll et al. 2007, Javoiš et al. 2011, Davis et al. 2016)) is more prevalent in the tropics than in temperate habitats because of the stable supply of adult food and the need for higher mobility. As said above, income breeding strategy allows to be better flyers because of a lower load of resources in the body (IV)

2. MATERIALS AND METHODS

2.1 Study system

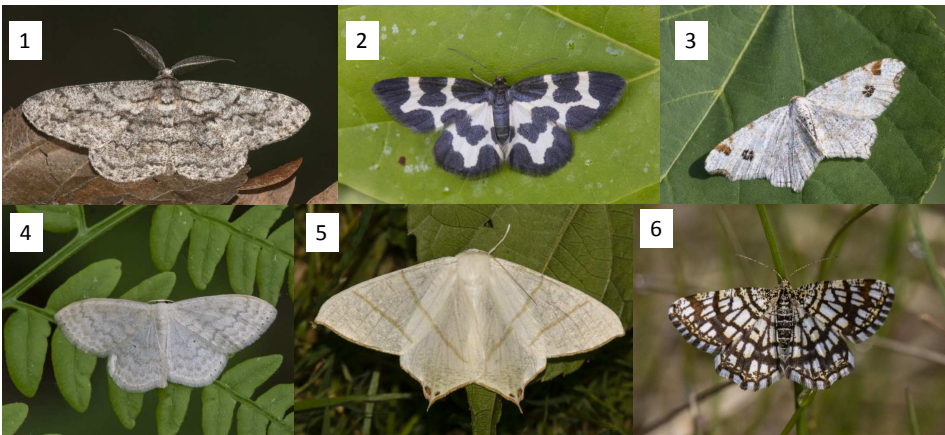
Data were collected in the years 2010 to 2013 in two contrasting geographical locations. The temperate region was represented by the surroundings of Tartu (58°N, 27°E) in Estonia, Northern Europe, and the tropical region by Kibale National Park (01°N, 30°E) in Uganda, East Africa. Estonia is characterised by low-elevation hemiboreal forest, whereas Kibale National Park is a fragment of submontane equatorial woodland (Figure 1). There is a marked difference in plant diversity between the two regions: while 87 native tree and shrub species have been recorded for Estonia (Leemet and Karoles 1995), as much as 90% of the forest coverage is dominated by *Pinus sylvestris*, *Picea abies*, *Betula* spp. and *Alnus* spp. Kibale National Park is a diverse forest with 216 of more than 440 tree species recorded for Uganda (Howard 1991). Because of its position on the equator, Uganda has a warm tropical climate with two rainy seasons. The mean annual temperature in Kibale is 19.2°C (Climate-Data.org, en.climate-data.org), while in Estonia there is a pronounced half-a-year winter season, when most insects are inactive, and the mean summer temperature of the period when most studied moth species are active (May to August) is 14.6°C (Estonian Weather Service, www.ilmateenistus.ee).

A sample of geometrid moths (Lepidoptera: Geometridae) from both local species assemblages was used in the current study (Figure 2, Figure 3). Geometridae is a species-rich family with a worldwide distribution, and approximately 24 000 described species (Nieukerken et al. 2011). Species richness and the (relatively well-described) ecological diversity of geometrid moths makes this family a promising target group for large-scale comparative analyses (Javoiš et al. 2011, 2019, Davis et al. 2012, 2013, 2016, Brehm et al. 2019). From a technical perspective, an additional advantage is that geometrid moths are easy to handle in the laboratory.

Traits related to species' host-plant specificity, longevity and breeding strategy were measured (Figure 4) and included in a phylogenetically informed analyses.



Figure 1. Examples of the habitats of the locations compared: forest in Uganda (on the left) and forest in Estonia (on the right).



1) *Hypomecis roboraria* (Ennominae); 2) *Lomaspilis opis* (Ennominae); 3) *Macaria notata* (Ennominae); 4) *Scopula floslactata* (Sterrhinae); 5) *Ourapteryx sambucaria* (Ennominae); 6) *Chiasmia clathrata* (Ennominae). Photos by Ain Piir.

Figure 2. Examples of some common geometrid moths from Estonia.



1) *Oedicertra gerydaria* (Ennominae); 2) *Pingasa commutata* (Geometrinae); 3) *Metallopora catori* (Ennominae); 4) *Cyclophora diplosticta* (Sterrhinae); 5) *Epigynopteryx* sp. SH05 (Ennominae); 6) *Cleora subcincta* (Ennominae). Photos by Sille Holm.

Figure 3. Examples of some common geometrid moths from Kibale National Park in Uganda.

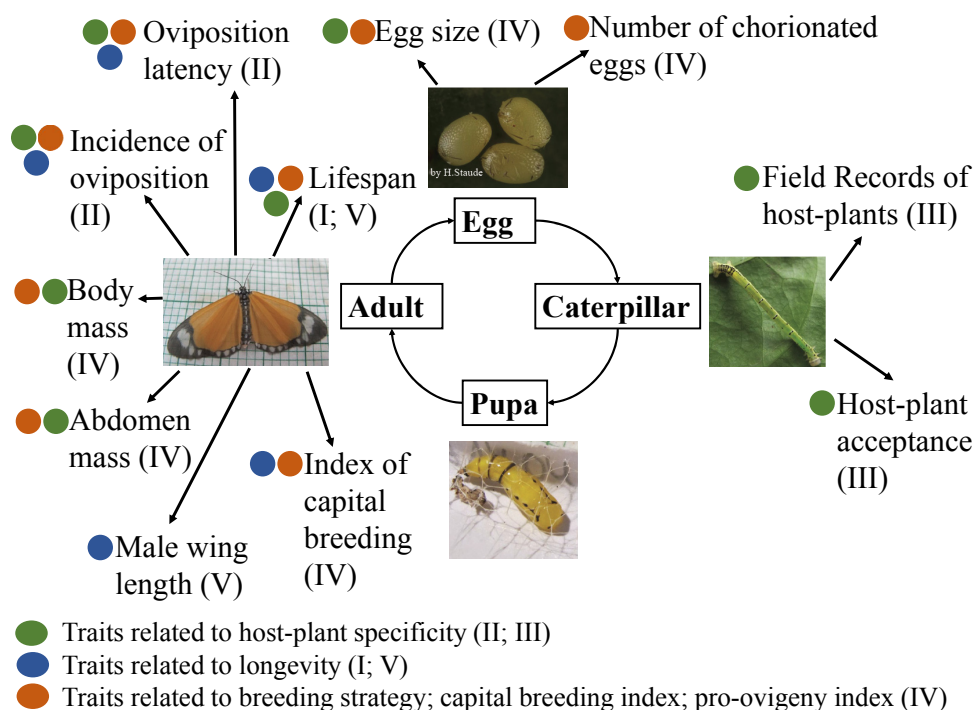


Figure 4. Life cycle of a geometrid moth and the ecological and life-history traits measured from different life stages that were used to investigate host-plant specificity, longevity and breeding strategy of geometrid moths in this theses. The Roman numbers in the brackets indicate the number of the article in which the trait was investigated.

2.2 Phylogeny

In order to carry out phylogenetically informed analysis on the ecological and life-history traits measured, the phylogenetic relationships of the species from a tropical and a temperate region needed to be determined. Phylogenetic information for the Geometridae is accumulating rapidly (e.g. Snäll et al. 2007, Wahlberg et al. 2010, Sihvonen et al. 2011, Öunap et al. 2016, Murillo-Ramos et al. 2019), but Afrotropical species have not been covered well. During the course of the studies presented in this thesis, three separate phylogenetic trees were constructed (I, II, III) according to accumulation of the molecular data. The largest phylogeny (III) comprised 373 species (original sequences obtained for 252 spp.); it was constructed using 6543 base pairs from eight markers (COI, EF1-alpha, WGL, GAPDH, RpS5, IDH, MDH, CAD) that have repeatedly been used for phylogenetic inference in geometrid moths (Wahlberg et al. 2010, Sihvonen et al. 2011). Sequences were aligned using CLUSTALW (Thompson et al. 1994) in BIOEDIT 7.2.5 (Hall 1999) and analysed using BEAST 1.8.1. (Drummond et al. 2012). The tree was pruned according to the species sample of each particular study (see Figure 5 as an example).

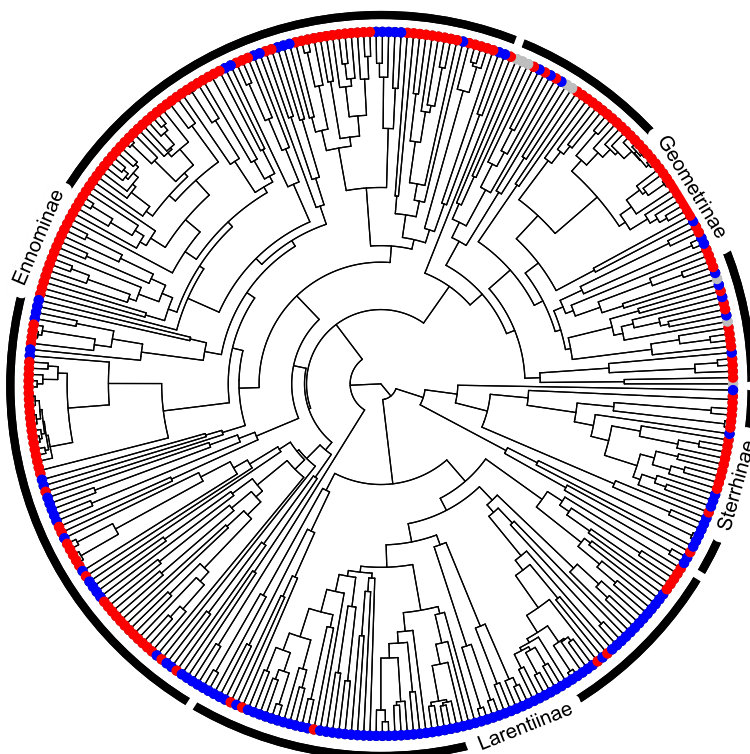


Figure 5. The phylogeny used in Holm et al. 2018 (II). The colouration of each tip represents of the species' native country (blue = Estonia (temperate); red = Uganda (tropical); grey= other regions). Species from other regions were included in order to avoid problems related to long-branch-attraction (LBA).

2.3 Study design

2.3.1 Lifespan (I, V), oviposition latency, incidence of oviposition (II)

Adult lifespan and oviposition latency of around 200 species of geometrid moths was recorded in laboratory conditions. Moths were collected as adults, using light trapping for nocturnal species and netting for diurnal species (I, II, V). In Estonia the data were collected from spring to autumn in the years 2010–2012. In Uganda the data were collected in the years 2011–2013. The temperate region specimens were identified on arrival at the laboratory; tropical specimens were brought *post hoc* to Estonia to be identified; specimens are stored at the facilities of the Department of Zoology at the University of Tartu. Identification of tropical species, based on wing patterns or genitalia dissections, were cross-checked with their COI barcodes (for about 1300 Ugandan specimens original COI barcodes were created). However, many Ugandan moths could not be reliably associated with any known species and were thus assigned biospecies names (e.g. *Biston* sp. SH01) for the analysis.

Samples were collected non-selectively, disregarding the physical condition of each individual. Collected moths were immediately placed individually in 50 ml or 100 ml transparent vials, depending on the individual's size. In the vials, the moths were provided with food in the form of tissue paper immersed in 10% sugar solution, the paper was fixed in place by hanging it between the vial and the lid. Each vial also contained a roughly 4×1 cm piece of plastic mesh as an oviposition substrate, but no plant material. Sugar solution was offered to all species, including those known not to feed as adults, to ensure an identical environment for all species. The tissue paper was re-moistened with water daily, and sugar solution was added a week after capture. In the temperate region, the moths in vials were kept in thermoregulated rearing chamber; two different temperature treatments – cool (15 °C) and warm (23 °C) – were applied to test the robustness of resulting patterns. Due to the lack of equipment in the tropics, the moths were kept in the vials at ambient temperature, and the temperature of the laboratory was recorded hourly. The average temperature an individual experienced over lifetime in the tropical sample was 21.5 °C (maximum 24.3 °C, minimum 19.4 °C).

Residual lifespans (i.e. the remaining lifespan of each moth after it had been brought to the lab) were measured by daily checking the survival status (I, V). In the analyses of the temperate sample (I), four species traits were tested for associations with lifespan: 1) male wing span, 2) flight period, 3) larval diet breadth, 4) abdomen/body mass ratio of females. Data were collected in the following ways: 1) Male wing span data were obtained from Mikkola et al. (1985, 1989), and used as an index of body size. 2) Flight period (i.e. reproductive season within the year) was, following Davis et al. (2016), expressed as the number of daylight hours at the peak of the flying season (data from Mikkola et al. 1985, 1989; Tartu Observatory, <https://to.ee>). 3) Larval diet breadth was quantified as the number of host plant genera (Seppänen 1970, Crafer 2005).

4) Abdomen/body mass ratio of freshly eclosed adult females served as an index of the degree of capital breeding, and was calculated as: cube root abdomen dry weight / cube root whole body dry weight (see Javoiš et al. 2011, Davis et al. 2012, 2013). To estimate the strength of phylogenetic signal in geometrid moth lifespan, Pagel's λ was calculated (Pagel 1999) using the *caper* package for the R statistical environment (R Development Core Team 2012). To study the relationship between body size and longevity in the tropical species (V), wing lengths (mm) were measured from pristine collection specimens.

Oviposition latency (i.e. waiting time before oviposition in days) and incidence of oviposition of each individual was recorded by checking the vials daily for eggs laid; this was done at approximately the same time every day. To test whether these measures could serve as indices of host specificity, larval diet data of the temperate species were obtained from the handbook by Mikkola et al. (1985, 1989) (II).

To test for lifespan associations with body size (male wing span), flight period, larval diet breadth, and abdomen/body mass, data were analysed by using a phylogenetic restricted maximum likelihood (REML) method. Measurement error in the estimation of the model parameters was incorporated based on the work of Ives et al. (2007) (I). To test for oviposition latency association with larval diet breadth (II) and lifespan association with body size in the tropics (V), the data were analysed by Bayesian inference implemented in the R package *rstan* (Stan Development Team 2016) for fitting the phylogenetic generalised linear models (GLM) to individual-level data. The latter property of the analysis is particularly important for the current studies as the species-specific samples differed considerably in size, and proper weighting of those was crucial.

2.3.2 Host-plant acceptance and taking field records of host plants (III)

Host-plant specificity of forest geometrid moths in equatorial Africa was investigated by using host-plant acceptance trials with neonate larvae, complemented by our original host-plant records from the field site. In the host-plant acceptance trials, the feeding performance of the larvae on the most abundant tree species in the forest was tested. To obtain caterpillars for the acceptance trials, adult female geometrid moths were collected non-selectively by light trapping (years 2011–2013) and allowed to oviposit in plastic vials. Eggs were allowed to hatch in the same vial where laid. On the day of hatching, the caterpillars of each brood (= offspring of an individual female) were divided between vials with cut leaves from 15 common tree species, representing a wide array of plant families. After 48 hours, the response of the larvae to the plant was recorded (0 – not accepted, 1 – accepted). Original host-plant records were obtained by visually searching for caterpillars from the forest, and rearing the caterpillars to the adult stage on the same plant species they were found from.

To compare acceptance rates between tropical and temperate regions, host-plant acceptance trials with six hemiboreal species belonging to the temperate

sister groups of the studied Ugandan species were carried out. These trials followed the same protocol as described above for the tropical region. To provide a selection of host-plant species comparable to that used in the tropics, the 15 most widely distributed and common forest tree species in the hemiboreal region (using Estonia as the reference location) were chosen. For the rest of temperate species (N = 34) included in the comparison, literature-based data on diet breadth were retrieved from Seppänen (1970) and Mikkola et al. (1985, 1989) (see details of the rationale in III).

To study the differences in acceptance rate between regions (temperate vs tropical) in a phylogenetic context, a phylogenetic ANOVA was conducted, using the function *phylANOVA* in the package *phytools* (Revell 2012) for the R statistical environment (R Development Core Team 2012).

2.3.3 Life-history traits related to breeding strategy and host-plant specificity (IV)

Species-specific values of morphometric indices associated with the degree of capital breeding and specificity were measured, and compared among the two regions. To record these values, adult specimens of geometrid moths were obtained by *ex ovo* rearing of the offspring of the females collected at light, complemented by moth specimens originating from wild-collected larvae. The adults were euthanised on the second day following their eclosion from pupae. The moths were air dried and weighed thereafter. Abdomens were then removed and weighed separately. Chorionated eggs in the abdomens of the females were counted and measured. The traits analysed were 1) dry mass of the adults, 2) relative abdomen mass (dry mass of the abdomen divided by the dry mass of the entire body), 3) index of egg size (i.e. calculated volume assuming cylindrical shape), and 4) index of pro-ovigeny, calculated as [index of egg size \times number of chorionated eggs / abdomen dry mass] (Davis et al. 2016).

It was assumed that larger adult body mass is linked to higher mobility. The relative abdomen size of females at adult eclosion indicates to what extent the eggs are formed from the capital derived at the larval stage, so that females with relatively larger abdomens represent the more capital breeding species (Javoiš et al 2011). The index of pro-ovigeny characterises the relative volume of eggs in the abdomen of a freshly eclosed female (Javoiš et al. 2011). This variable is expected to be lower in the more income breeding species (Jervis et al. 2005). Egg size is a trait putatively associated with the ability to overcome defence mechanisms of the host plants.

To test for differences in the described traits between the temperate and the tropical region, the data were analysed by using Bayesian inference implemented in the R package *rstan* (Stan Development Team 2016).

3. RESULTS

Life-history traits for a total of about 250 geometrid moth species from a temperate and a tropical community were measured. Data were analysed in a phylogenetic comparative framework to study variation in indices of host-plant specificity, longevity and breeding strategy, with an emphasis on the comparison between tropical and temperate regions. The results are presented as follows, and summarised in Table 1.

3.1 Host-plant specificity (II, III, IV)

In the host-plant acceptance trials (III) performed in the tropical region, the larval diet breadth of 62 geometrid moth species was scored. A positive result ('acceptance') was obtained for 141 out of 868 moth species \times plant species combinations (16%). Experimental data of the host-specificity patterns of 34 closely related temperate species were compared. Similarly to the temperate region, there were broadly polyphagous tropical species in several clades of Geometridae, utilising hosts belonging to different plant families. No significant effect of region on host-plant specificity was detected.

To answer the question whether oviposition latency (the waiting time before commencing oviposition in captivity) can serve as an index of host-plant specificity, we tested if this index correlates with known larval diet breadth across species (II). Indeed, oviposition latency of temperate species was found to be associated with larval diet breadth: the females of more specialised species waited longer before laying eggs on the unsuitable substrate provided. An analogous trait, incidence of oviposition (the probability to lay any eggs on an unsuitable substrate) showed broadly the same pattern, which adds to robustness of the results.

To study if oviposition latency and incidence of oviposition depend on geographic location (II) a sample of 997 individuals (699 from Estonia and 298 from Uganda) of 165 species (83 in Estonia, and 82 in Uganda) was obtained. The analysis revealed no credible effect of location on latency nor on incidence of oviposition. On average, Estonian moths waited slightly longer than Ugandan moths before commencing oviposition, but there was no credible effect of region (average latency 3.2 and 2.7 days, respectively).

To study if morphometric traits differ between locations (potentially, in part because of differences in plant defences – see Introduction), data for 935 individuals representing 71 species (484 females, belonging to 60 spp.) from the tropical region and 967 individuals representing 72 species (473 females, belonging to 60 spp.) from the temperate region were used (IV). Ugandan moths were found to be larger than Estonian ones, the difference in adult mass being 1.43 times in terms of dry adult weight (calculated from the location averages of species averages), and statistically credible. Absolute size of the eggs did not

differ between the habitats being compared. Nevertheless, a credible effect of region was found on egg size when maternal body sizes were accounted for: tropical females were found to have relatively smaller eggs.

3.2 Longevity (I, V)

To test the two conceptual approaches explaining the variation in longevity (I), the post-capture lifespan for 2472 individuals (728 females, 1744 males) from 98 temperate geometrid moth species was measured. The overall mean length of time a moth lived for in the laboratory was 7.0 days (maximum 28 days, median 6 days). For females, mean lifespan was 9.6 days in the cool treatment (median 9 days) and 5.2 days in the warm treatment (median 5 days), and for males, 8.6 days (median 8 days) and 5.3 days (median 4 days), respectively. The among-species differences in lifespan of wild-caught individuals remained limited, and there was no indication of phylogenetic signal in this trait. In the phylogenetic comparison, larger species (estimated by male wing span) showed significantly longer adult lifespans. The largest moths (*Hypomecis roboraria*, 49 mm wing span) lived 3 times – or 6 days – longer, on average, than the smallest ones (*Eupithecia pusillata* and *Hydrelia flammeolaria*, 18 mm). Lifespan did not correlate with adult flight phenology and larval diet breadth. Longer adult lifespan was associated with lower abdomen/body mass ratio in females, thus presumably with an income breeding strategy.

To study if lifespan is longer in the tropics (potentially because of the stable supply of adult food in the tropics and the challenge of locating suitable hosts) (V) the post-capture lifespan for 734 individuals (358 females, 376 males) from 110 geometrid moth species was measured. The mean lifespan in the laboratory was 5.1 days (maximum 17.0 days (*Cleora subcincta*), median 5.0 days). In the phylogenetic comparison, larger species (estimated by wing length) showed longer adult lifespans, and the effect of body size was found to be statistically credible, similarly as in the temperate region. The largest moths (*Colocleora* sp. nr *potaenia*, 34 mm wing length, average lifespan 7.1 days) lived 1.8 times – or 3.2 days – longer on average than the smallest ones (*Scopula* sp. SH01, 9 mm, average lifespan 3.9 days).

In a quantitative comparison, the lifespans were found to be rather similar between the compared locations; the species-specific median lifespan was 6 days for the tropical region and 6.8 days for the temperate region. Also, at broadly similar temperature ranges, sex-specific lifespans showed similar values. Consistently, the dependence of lifespan on body size was quantitatively similar in the two regions.

3.3 Breeding strategy (IV)

To test whether the tropical moths use more income breeding strategy than temperate moths, data for 484 females belonging to 60 spp. from the tropical region and 473 females belonging to 60 spp. from the temperate region were collected. The traits analysed in the context of breeding strategy were a) relative abdomen mass (abdomen/body mass ratio in females) and b) index of pro-ovigeny, which characterise the relative volume of eggs in the abdomen at female eclosion. Ugandan moths had lower relative abdomen masses (0.50 vs 0.54); despite the limited magnitude of the difference, this was found to be statistically credible. However, the difference in relative abdomen mass was not paralleled by a difference in the index of pro-ovigeny.

Table 1. Summarised results of comparative analyses of life-history traits of a sample of tropical and temperate region geometrid moths.

	Temperate region	Tropical region	Conclusions over regions
Host-plant specificity (II, III, IV, V)			
Original field records on host plants	–	25 new host-plant records for larvae of 14 moth species	A substantial share of polyphagous species are present in the tropics (similarly as among the temperate species)
Host-plant acceptance trials	19% of the plants were accepted	15% of the plants were accepted	Larval diet breadth was similar (no significant effect of region)
Oviposition latency	Oviposition latency was longer for more specialised species	–	
	Average latency was 3.2 days	Average latency was 2.7 days	Similar oviposition latency (no credible effect of location), suggests similar host-plant specificity
Egg size	The temperate females had relatively larger eggs	The tropical females had relatively smaller eggs	Difference in egg sizes when body size was accounted for (statistically credible)
Body mass	Temperate species were smaller	Tropical species were larger	Body mass differences (statistically credible) suggest that tropical species may be more mobile

Table 1 (continued). Summarised results of comparative analyses of life-history traits of a sample of tropical and temperate region geometrid moths.

	Temperate region	Tropical region	Conclusions over regions
Longevity (I, V)			
Lifespan	Mean lifespan at 23°C was 5.2 days for females; 5.3 days for males; Mean lifespan at 15°C was 9.6 days for females; 8.6 days for males	Mean lifespan at 21.5°C was 4.4 days for females; 5.8 days for males	Lifespans were broadly similar
Male wing span/length	Larger species showed longer lifespans	Larger species showed longer lifespans	Larger species lived longer (statistically credible)
Relative abdomen mass	More capital breeding females showed shorter lifespans	–	
Flight period	No correlation was found between lifespan and flight period	–	
Larval diet breadth	No correlation was found between lifespan and larval diet breadth	–	
Breeding strategy (IV)			
Relative abdomen mass	Dry abdomen to body mass ratio was 0.54	Dry abdomen to body mass ratio was 0.50	Ugandan moths had lower relative abdomen masses (statistically credible)
Index of pro-ovigeny	Index of pro-ovigeny was 0.32	Index of pro-ovigeny was 0.31	Egg producing strategy was similar (no credible effect of region), no support for different breeding strategies was found

4. DISCUSSION

For a sample of geometrid moths from a temperate and a tropical forest ecosystem at different latitudes, ecological and life-history traits were compared by collecting respective data experimentally. The data were analysed in phylogenetically informed analyses using original phylogenetic reconstructions. As has been shown previously, and corroborated by the current study, the species richness and (well-described) ecological diversity of geometrid moths make this family a promising target group for large-scale comparative analyses (Davis et al. 2012, 2013, 2016, Heidrich et al. 2018, Javoiš et al. 2019).

The present study advanced the methods of obtaining comparable data on among-species differences. In particular, oviposition latency (= waiting time before oviposition) and lower incidence of oviposition when deprived of hosts were found to be associated with narrower diet breadth in the temperate region. A long latent period recorded in captivity should correspond to the long time that females are prepared to spend looking for suitable hosts in nature. In generalists, as opposed to specialists, natural selection appears to have favoured less careful and less time-consuming host-searching behaviour, which is reflected in the behaviour of captive moths. Incidence of oviposition (the probability to lay any eggs on an unfavourable substrate) showed broadly the same pattern, which adds to robustness of the conclusions. These results provided support for the use of oviposition latency and incidence of oviposition as indirect measures to compare host-plant specificity between different moth assemblages.

The latency and the probability to oviposit were similar in the temperate and tropical communities. This corroborates the finding of our study on caterpillars of the similarity of host-plant acceptance rates in these regions. The evidence thus suggests that the degree of host specialisation may not be so different between tropical and temperate geometrids. This is rather unexpected, considering recent global-scale comparisons on Lepidoptera that generally report an increase in specificity towards the tropics (Dyer et al. 2007, Forister et al. 2015, but see also Morris et al. 2014). It might be that the diverse vegetation in the tropics is a substantial obstacle for the females of geometrids when they locate suitable host plants. This may have led to lower host-plant specificity in these insects than expected. It is possible that the Geometridae – being relatively weak fliers – therefore represent a taxon that does not follow the frequently proposed latitudinal trend (see Hardy et al. 2015 for similar examples). In support of this possibility, a relatively high rate of polyphagy in Neotropical Geometridae has been suggested by Brehm (2002, 2003). However, the diversity of the tropical habitats of Earth cautions against generalising the results of the present study to a broad comparison across biomes.

Based on our study of size-related traits, it seems that the different defence mechanisms of host plants in different regions (more quantitative in the temperate region vs. more qualitative in the tropical region) may have, indeed, led to some differences in life-histories of herbivorous insects. In particular, tropical females

had relatively smaller eggs when maternal body size was accounted for. This is consistent with the expectation that neonate larvae need to be larger in temperate habitats in which plants rely on quantitative rather than qualitative defences (Nakasuji 1987, Schemske et al. 2009). The larger body mass in the tropical moths is consistent with the hypothesis of stronger selection on adult mobility. Such a selection should primarily act in the direction of increasing the mass of thoraces, including wings and flying muscles (Berwaerts et al. 2002). Being more mobile probably allows the tropical moths to better find suitable hosts among the highly diverse vegetation of the tropics and may increase their chance of escaping intensive predation. There are, however, reasons why the among-regions size-difference should be interpreted with some caution. In particular, strong overrepresentation of the Larentiinae in the temperate region, combined with the small size of these moths, strongly contributed to this pattern. In addition, sampling of the moths may be involuntarily size-selective, and differently so in different environments. Moreover, Brehm et al. (2019) showed that altitudinal differences may cause body sizes to vary considerably at relatively small geographical scales. Despite the statistically credible among-region differences in life-history traits, our overall inference still points towards the differences in respective traits being relatively low between the two regions compared, and these differences should therefore have just a limited ecological relevance.

Consistently, residual lifespans of wild-caught individuals were found to be weakly influenced by ecological factors. Addressing the ecological explanations for longevity in temperate moths, we failed to detect the predicted effects of the degree of host specialisation and phenology. The limited variation of lifespans is unlikely to be explained by phylogenetic constraints, since no indication of phylogenetic signal was found in this trait. In temperate species, longer adult lifespan was associated with a lower abdomen-to-body mass ratio in females, thus presumably with species using a more income breeding strategy (i.e. where adult-derived nutrients are more important in reproduction). Although it was predicted that lifespans may be longer in the tropics than in temperate habitats (because of the stable supply of adult food and the time needed to locate suitable hostplants in the dense and diverse forest), we found no evidence in support of major differences. It can be hypothesised that high predation pressure (Roslin et al. 2017) balances resource and climate stability in the tropics. Unfortunately, estimates of adult mortality rates in the field are scarce for flying insects (see, however, Sang and Teder 2011, Tiitsaar et al. 2013), and are lacking for the tropical region completely. Nevertheless, even though we are not able to estimate the relative role of the negative and positive selective pressures on lifespan in the tropics and contrast these with those in the temperate region, it appears highly unlikely that these would exactly cancel each other out.

A clear positive correlation was found between body size (estimated as wing length) and lifespan in both regions. Ecologically based arguments would have allowed us to expect the opposite. Indeed, larger geometrids should be attacked by predators more frequently, because larger insects are both easier to notice

(Mänd et al. 2007), and also present greater motivation for predators as larger food items (Mänd et al. 2007, Hossie et al 2015). However, the results of the present study suggest that ecological selective pressures apparently do not dominate over physiological ones as evolutionary determinants of species longevity. Indeed, the positive size–longevity relationship is consistent with the physiological explanations of longevity, providing further evidence that insects are no exception to the general metabolism-to-size negative allometry (Chown et al. 2007, Ehnes et al. 2011).

Although it was predicted that income breeding (Tammaru and Haukioja 1996, Snäll et al. 2007, Javoiš et al. 2011, Davis et al. 2016) may be more prevalent in the tropics than in temperate habitats, the patterns found were inconclusive and do not provide clear evidence in support of major differences. Tropical moths had slightly lower relative abdomen masses. Low female abdomen mass is a trait associated with an income (rather than capital) breeding strategy (Javoiš et al. 2011, Davis et al. 2016). However, the difference in relative abdomen mass was not paralleled by another index of income breeding: the index of pro-ovigeny, which characterises the relative volume of eggs in the abdomen at female eclosion (Davis et al. 2016). This suggests that the between-region difference in relative abdomen mass results rather from selection of higher mobility (large thoraces) in tropical moths and not from different breeding strategies.

As perhaps is always the case in ecology, the question is not if there are detectable differences between communities, but whether the differences are large enough to be ecologically meaningful. Quite opposite to expectations, the world the moths experience and the factors that shape their life histories may not be so different between the tropical and temperate zones after all. However, naturally, in order to make large-scale generalisations, a comparison of just two locations is not sufficient and a much broader sample of sites is needed to confirm any systematic differences or similarities between biological communities across latitudes. I would still suggest that this does not discount the value of the present contribution, because such location-specific and taxon-specific studies constitute the primary input when addressing general patterns. Moreover, the information accumulated on particular species in the course of collecting data for such comparisons is highly valuable in the light of rapid destruction of their native ecosystems.

SUMMARY

Describing and understanding variation in the ways in which organisms acquire and expend resources throughout their life is at the core of evolutionary ecology. Large-scale comparative studies are hindered by a lack of species-specific data. In contrast to their enormous diversity, data are especially scant for (tropical) insects.

Like various other insects, Lepidoptera are believed to show an increase in host specificity toward the tropics. This is primarily because of an increase in the species-specific qualitative defences of plants at lower latitudes, which makes simultaneous adaptation to several host-plant species complicated. However, dense and diverse vegetation and high predation risk may act as an obstacle when a female is trying to locate a particular host-plant species. Such obstacles may create strong selection towards higher mobility and longer adult lifespans in the tropics, while at higher latitudes such pressures might be weaker. This may lead to an opposite latitudinal pattern in specificity. The abundance of adult food in the tropics may facilitate longer lifespans and higher mobility than in the temperate zone, and may also increase the importance of adult-derived nutrients in reproduction (via income breeding as opposed to capital breeding strategy).

The major aim of the current thesis was to compare ecological and life-history traits of moths of species from the family Geometridae from two forest ecosystems at different latitudes (Estonia and Uganda). For about 250 temperate and tropical region geometrid species, data on life-history traits related to host-plant specificity, longevity and breeding strategy were compared in phylogenetically informed analyses relying on originally derived phylogenies.

The suitability of 15 common tree species as host plants were tested in host-plant acceptance trials with newly hatched caterpillars and the larval diet breadth of tropical and temperate species was compared. Similarly to the temperate region, there were broadly polyphagous tropical species in several clades of Geometridae, utilising hosts belonging to different plant families. No significant effect of region on host-plant specificity was detected.

It was found that oviposition latency and incidence of oviposition in captivity with no host plant present can be used as an estimate of host-plant specificity; the females of more specialised species waited longer before laying eggs on the unsuitable substrate provided, and more often did not lay any eggs. This provides support for the use of oviposition latency and incidence of oviposition in captivity as indirect measures of host specificity. When using these two indices to compare the host-plant specificity between temperate and tropical regions, analyses revealed no significant effect of location on latency or incidence of oviposition. This may be seen as another piece of evidence suggesting that host-plant specificity is similar in both regions.

When comparing size-related morphological traits, tropical species were found to be larger as adults than temperate ones. There appears to be selection for large thoraxes (wings and flying muscles), which increase mobility in the

dense and diverse tropical vegetation. Also, tropical females have relatively smaller eggs when maternal body size was accounted for. This is consistent with the expectation that neonate larvae need to be larger in temperate habitats as here plants rely on quantitative (e.g. leaf toughness) rather than qualitative defences.

Residual lifespans of wild-caught adult moths were found to be similar for both regions. It was predicted that the stable supply of adult food in the tropics might facilitate longer lifespans and also adult foraging for the resources. Furthermore, the time needed to locate suitable hosts in the dense vegetation should increase adult longevity in tropical species. However, this was not the case. Also, contrary to expectation, income breeding strategy was not found to be more prevalent in the tropics than in the temperate habitat, despite the putative abundance of adult resources. In the study of the temperate region, host-plant specialisation and phenology showed no association with lifespan. Neither could the limited inter-species variation in lifespan be explained by phylogenetic constraints, since no indication of phylogenetic signal was found in this trait. In temperate species, longer adult lifespan was associated with lower abdomen/body mass ratio, thus presumably with an income breeding strategy. Larger species (estimated by wing length) were shown to have longer lifespans, both in temperate and tropical region.

The results of the thesis suggest that the differences in the studied traits are rather low between the two regions and may not be ecologically relevant. Quite opposite to expectations, the world the moths experience and the factors that shape their life histories may not be so different for the tropical and temperate zone after all.

SUMMARY IN ESTONIAN

Vaksiklaste ökoloogia võrdlevad uuringud parasvöötme ja troopilises metsas

Evolutsioonilise ökoloogia tuumikteema on liikide ressursikasutuse kirjeldamine ning selle varieerumise tagamaade uurimine. Liigipõhiste ökoloogiliste andmete vähesus piirab laiaulatuslike võrdlevate uuringute läbiviimist. Putukate mitmekesisus on erakordselt suur, kuid (troopiliste) liikide kohta käivad andmed napid.

Laialdast kinnitust on leidnud hüpotees, et liblikaliste röövikud on toidutaimede osas kitsamalt spetsialiseerunud madalamatel kui kõrgematel laiuskraadidel. Arvatakse, et troopiliste taimede efektiivsed kvalitatiivsed kaitsemehhanismid (eelkõige erinevad mürgised ühendid) muudavad mitmele toidutaimele samaaegse spetsialiseerumise herbivooride jaoks keeruliseks, mille tõttu on troopilistel putukatel kitsas toidutaimede spekter. Samas on teiselt poolt põhjust arvata, et troopilise metsa tihe ja mitmekesine taimkate, kus valitseb lisaks ka kõrge kiskluse oht, on emasele liblikale suureks takistuseks röövikute toidutaimede otsingul. See annab alust arvata, et troopilises metsas võib olla soositud just vähesem spetsialiseerumine toidutaimedele.

Tihe taimkate on eriti suureks takistuseks nendele emastele liblikatele, kes kannavad enda tagakehas suurt munalasti (varusigijad) ja kelle lennuvõime on seeläbi kesisem. Lisaks on varusigijatele iseloomulikuks lühike eluiga. Samas aga võib valmikutoit võimaldada taimkatte omapäradest ja kisklusest tulenevate takistuste ületamist. Seda seeläbi, et kui valmikutoit on stabiilselt kättesaadav, siis võib olla soositud hoopis tulusigimine. Tulusigimine on selline paljunemisstrateegia, mille puhul on paljunemisedukus sõltuv valmiku elu jooksul hangitud ressurssidest ning mune toodetakse juurde kogu elu jooksul. Sellised emased liblikad ei pea enda tagakehas rasket munalasti kaasas kandma. Kergem tagakeha parandab lennuvõimet ja lihtsustab tihedas taimkattes navigeerimist. Stabiilselt kättesaadav valmikutoit võib võimaldada ka eluea pikenemist.

Töö peamiseks eesmärgiks oli võrrelda parasvöötme (Eesti) ja troopika (Uganda) metsaökosüsteemist pärit vaksiklaste (*Geometridae*) ökoloogia ja elukäiguga seotud tunnuseid. Andmeid koguti ligi 250 vaksikuliigi toidutaimekasutuse, eluea ja paljunemisstrateegiaga seotud tunnuste kohta. Uuritud liikidele koostati originaalandmetel põhinev fülogeneesipuu. Andmeanalüüsis kasutati liikidevahelist sugulust arvesse võtvaid meetodeid.

Troopiliste vaksiklaste toidutaimede spektri laiust uuriti katsega, mille käigus selgitati 15 sagedase puuliigi sobivust vastkoorunud röövikute toiduks. Tulemusi võrreldi parasvöötme pärit lähisugulaste toidutaimede kasutusega. Sarnaselt parasvöötmele leidis ka troopikas vaksikuliike, kes olid võimelised toituma mitmest sugukonnast pärit taimeliikidest. See lubab arvata, et troopika ja parasvöötme vaksikuliikide spetsialiseerumine toidutaimedele võib olla pigem sarnane.

Uuriti, kas ja kui kiiresti hakkab emane liblikas munema keskkonnas, kus puudub liigi röövikutele sobilik toidutaim. Leiti, et munema hakkamise tõenäosus ja munemiseelne ooteaeg korreleeruvad liigi toidutaimede spektri lausega: need vaksikuliigid, kelle järglased toituvad väiksemast arvust taimeliikidest, viivitasid munema hakkamisega pikemalt. Seega on munemiseelne ooteaeg kasutatav toidutaimede spektri kaudse mõõduna. Kuna troopiliste vaksiklaste toidutaimede ja toidutaimedele spetsialiseerumise kohta on andmeid väga vähe, siis kasutati eelkirjeldatud meetodit, et uurida, kas ja millisel määral erineb toidutaimede spektri laius parasvöötmes ja troopikas elavatel vaksiklastel. Leiti, et ooteaeg ja munema hakkamise tõenäosus olid troopilistel ja parasvöötme vaksiklastel sarnased, mis kinnitab järeldust, et toidutaimede spektri laius on mõlemas piirkonnas sarnane.

Morfoloogiliste tunnuste võrdluse käigus leiti, et troopiliste liikide kehamass on suurem kui parasvöötme liikidel. Massierinevused tulenevad just rindmike suurematest massidest, mis omakorda viitab paremale lennuvõimele, mis aitab navigeerida troopika tihedas ja mitmekesises taimkattes. Samuti leiti, et kui võtta arvesse emaslooma keha suurus, siis munevad troopilised liigid suhteliselt väiksemaid mune. See on kooskõlas hüpoteesiga, et parasvöötmes peavad vastkoorunud röövikud olema suuremad kui troopikas, et tulla toime toidutaimede kvantitatiivsete kaitsemehhanismidega (näiteks lehe sitkus).

Parasvöötme ja troopika vaksikuliikide valmikute keskmine eluiga osutus sarnaseks. Kinnitust ei leidnud hüpotees, et stabiilselt saada olev valmikutoit ning taimkatte struktuurist tingitud raskused toidutaimede leidmisel on viinud pikema eluea evolutsioneerumisele troopilistel liikidel. Hoolimata valmikutoidu stabiilsimatest ressurssidest, ei olnud tulusigimine troopikas enam levinud kui parasvöötmes. Parasvöötmes ei mõjutanud eluiga oluliselt sellised ökoloogilised tegurid nagu liigi lennuaja fenoloogia ja toidutaimede spektri laius. Küll aga elavad kauem nende liikide isendid, kelle emaste tagakeha massi ja kogu keha massi suhe on madalam. Selline madalam suhe on omane tulusigijatele. Nii parasvöötmes kui ka troopikas leiti suuremad liigid elavat kauem kui väiksemad.

Töö tulemuste põhjal võib järeldada, et toidutaimakasutus, eluiga ja paljunemisstrateegia on troopika ja parasvöötme uuritud piirkonna vaksiklastel pigem sarnased ning leitud erinevustel on vaid piiratud ökoloogiline tähtsus. Näib, et maailm, mida liigid kogevad, ja tegurid, mis kujundavad nende elukäiku, ei pruugigi parasvöötmes ja troopikas olla nii erinevad, nagu enamasti arvatakse. Uurimaks, kui levinud on see sarnasus, tuleb suurendada uuritavate piirkondade arvu.

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- April Karkulahti, Master's Degree, 2016, (sup) Heikki Roininen, Anu Valtonen and Sille Holm. (Host plant specialization of lepidopteran larvae (*Erebidae* and *Geometridae*) in an Afrotropical rainforest (Perhostoukkien (*Erebidae* ja *Geometridae*) erikoistuminen ravintokasveille Ugandan trooppisessa sade-metsässä). University of Eastern Finland, Department of Biology.

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