A comparative study on insect longevity: tropical moths do not differ from their temperate relatives

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Abstract
Comparative studies on insects can significantly contribute to understanding the evolution of lifespan, as the trait can feasibly be measured in a high number of species. If the evolutionary determinants of longevity were mainly extrinsic (ecological), related species from different habitats should systematically differ in individual lifespans. We recorded adult longevities for 110 species of geometrid moths from a tropical community and paralleled the lifespans in this tropical assemblage with a temperate counterpart. Comparative analyses using an original phylogenetic reconstruction revealed that in the studied tropical assemblage, larger moth species tended to live longer, and that females had slightly shorter lifespans than males. Average adult lifespans in tropical geometrids, and the relationships of lifespan with other variables, were found to be highly similar to those reported for their temperate region relatives. The among-region similarity leads to the conclusion that intrinsic (physiological) determinants of longevity dominate over extrinsic (ecological) ones: the contrasting environments of tropical and temperate forests have hardly produced differences in moth longevities.

Keywords Ageing · Insect · Lepidoptera · Lifespan · Longevity · Phylogenetic comparative methods

Introduction

Longevity is certainly one of the most intensively studied life history traits. Quite understandably, research on human lifespan has received the most attention (Kirkwood 2005; Hulbert et al 2007; Aravinthan 2015; Beaulieu et al 2015; Ziegler et al 2015). Beyond that,
studies of ageing have largely been limited to just a few other model organisms (Ricklefs 2008; Austad 2010; Jones et al 2014). Focussing on a few profoundly known taxa is indispensable in studies on the mechanistic basis of the ageing process. In some contrast, the interpretation of ageing-related phenomena in the context of adaptive evolution requires comparing numerous different organisms which differ both with respect to longevity, and selective environment moulding the values of this trait. Comparative studies of longevity are now facilitated by the increasing availability of reliable phylogenetic reconstructions. Nevertheless, the potential of this direction of research appears to be clearly underused (Holmes and Kristan 2008; but see e.g. Minias and Podlaszczuk 2017; Wilkinson and Adams 2019).

Among-species differences in longevity may be viewed as caused by a combination of intrinsic or ‘physiological’ factors and extrinsic or ‘ecological’ factors. The ‘physiological explanation’ primarily views longevity as a side effect of body size. It is widely acknowledged that longevity is positively correlated with body size across species in vertebrate animals (Aristotle 350 BC; Prothero and Jürgens 1987; Healy et al 2014 and references therein; Scharf et al 2015; Stark and Meiri 2018). Among the proposed causal explanations to this pattern, the negative size-dependence of metabolic rate appears to be the most general one (McMahon 1973; Reich et al 2006).

According to the ‘ecological explanation’, longevity has primarily been shaped by the patterns of extrinsic mortality. Ageing arises in evolution through relaxed selection against harmful traits which are expressed in the phenotype at ages rarely reached in nature. This evolutionary process can be enhanced by positive effects of such traits on fitness attained earlier in life (Medawar 1952; Williams 1957; see also Kirkwood and Austad 2000; Reznick et al 2004; Chen and Maklakov 2012; Kimber and Chippindale 2013). Spatial and temporal distribution of the resources may have an additional role. In particular, organisms living under unpredictable conditions, e.g. species of harsh environments where the periods of favourable weather may be transient and the sources of food unstable, are to invest little resources in their own survival (Vinogradov 1998). Such animals are therefore expected to be shorter-lived (Peterson and Nilssen 1998) and to have a less durable physiological design. Contrary to that, species from more stable environments with more abundant adult food sources may evolve extended longevity because they are not limited by stored reserves (Dunlap-Pianka et al 1977; Carey 2001; Molleman et al 2009).

The extraordinary diversity of insects remains little used in phylogenetic comparative studies (Mayhew 2018), perhaps largely due to scarcity of comparable data. This also applies to studies on longevity. Indeed, gathering comparable data of insect lifespans under natural conditions for global multi-species analyses appears nearly impossible due to the typically small body size and high mobility of these animals (see also Zajitschek et al 2020). It is also nearly impossible to establish thriving populations of many insect species in the laboratory to measure lifespan in captivity. These problems can be mitigated by recording lifespans of wild-caught individuals in a controlled laboratory environment (Carey et al 2008; Holm et al 2016).

The few available comparative studies on insect longevity have had their main focus on the relationship between body size and adult lifespan. Such studies have thus primarily addressed the physiological explanation of longevity. Beck (2008) detected a weak positive effect of body size on adult longevity in rainforest butterflies, Holm et al (2016) reported that larger geometrid moths live longer, while others have failed to find an effect of body size in some other lepidopterans (Jervis et al 2007b), hymenopteran parasitoids (Blackburn 1991), and odonates (Sherratt et al 2011). Addressing the ecological determinants of longevity in insects appears to be rare (see, however, Jervis et al 2007b; Beck and Fiedler
In an earlier study, we failed to detect the predicted effects of ecological factors such as the degree of host-plant specialisation and phenology (Holm et al. 2016). However, the power of our analyses might have been low due to the limited variation in the values of the environmental parameters used as predictors (the study was restricted to species of the temperate forest zone). There should be a stronger potential for revealing the ecological effects when the geographical scope of the comparisons was extended, e.g. by including species from different climate zones. This would allow us to test directional hypotheses at the level of comparisons among biomes.

Tropical versus temperate habitats may select for different longevity for several reasons. Predation is the primary ecological factor suggested to shape longevity, and predation pressure on insects has been shown to increase towards lower latitudes (Roslin et al. 2017). However, other factors, such as stable supply of adult food (nectaring plants, fruits; Chapman et al. 1999) might facilitate the evolution of longer adult lifespans in the Lepidoptera of tropical regions (see e.g. Molleman et al. 2007). In addition, the patterns of specialisation in larval resource use may exert selective pressures on longevity—the adults may need long lives to be able to locate larval hosts which are scarce in the environment (Carey 2001; Prinzing 2003; Jervis et al. 2007a). Higher larval host-plant specificity in the tropics (compared to temperate areas) has been reported for Lepidoptera (Dyer et al. 2007; Forister et al. 2015; see, however, Holm et al. 2019b). Accordingly, in the tropics, we should expect stronger selection towards longer lifespans, imposed by the challenge of locating host plants among the diverse tropical vegetation.

In the present study, we measured post-capture adult lifespan for 110 species of tropical geometrid moths (Lepidoptera: Geometridae). Species richness, the rapidly accumulating phylogenetic information (Sihvonen et al. 2011, 2020; Murillo-Ramos et al. 2019, 2021) and feasibility of recording life-history traits in the laboratory makes this family of insects a promising target group for large-scale comparative analyses (Holm et al. 2016, 2018; Heidrich et al. 2018). We tested for the effects of body size and sex on lifespans of the moths, using wing wear and lab temperature as covariates. An original phylogenetic reconstruction (Holm et al. 2018, 2019b) was used to facilitate the comparative analysis. Further, we involved a comparable data set on longevity of temperate species (Holm et al. 2016) to test for among-region differences. The results are discussed in the light of the physiological and ecological explanations for species-specific values of lifespan.

Material and methods

Lifespan data

Residual (=post-capture) lifespans of 734 wild-caught adults (358 females, 376 males) representing 110 tropical rainforest geometrid moth species were measured under the close-to-ambient laboratory conditions at the Makerere University Biological Field Station in Kibale National Park (795 km², 900–1590 m a.s.l.) in Uganda, East Africa (01ºN, 30ºE). The study area represents species-rich, medium-altitude, moist, evergreen tropical primary forest (Struhsaker 1997). Moths were collected as adults by light trapping in the years 2011–2013. Sampling days (N = 141) were widely scattered over the study period to cover flight periods of different species. Samples were collected non-selectively, i.e. without regard to 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. The moths were kept in the vials in the laboratory at ambient temperature; temperature was recorded hourly. The average temperature an individual experienced over its lifetime was 21.5 °C (maximum 24.3 °C; minimum 19.4 °C). The moths were provided with food: 10% sugar solution offered on immersed tissue paper. Once per day, the tissue paper was moistened with water; sugar solution was added again in a week from the start of the experiment. Windows of the laboratory were covered with shades to darken the room. This was necessary to prevent escape flight towards the light and concurrent exhaustion which might have reduced lifespan. The survival status of each moth was recorded on a daily basis. The moths were identified based on external traits (coll. Herbulot at the Zoological Museum of Munich was consulted), genitalia dissection and/or DNA barcoding, see Holm et al. (2018) for further details. Any moths which failed to be reliably identified were considered conspecific if there was a less than 2% difference in barcode sequences. The specimens are stored at the facilities of the Department of Zoology, University of Tartu. Male forewing length, defined as the distance between basal tip and apex of the forewing, was measured from intact wild-caught specimens used in the experiments, supplemented by the collection of Ugandan geometrid moths at the University of Tartu. We could not obtain estimates of mean wing lengths for 46 species used in the experiments. This is because many individuals bore damaged wings by the end of their lives. For more than such 30 taxa, we were not able to reliably assign Latin binomials either, which prevented us from using external sources to fill in the gaps. Consequently, species with missing wing length data could not be included in the analyses involving the index of body size. However, 33 of such species were represented by just a single individual in our data. This implies that the effect of missing data was disproportionately low in our analyses which relied on weighing data points by sample sizes (see below). Temperature was included in the analyses as the mean temperature an individual experienced over its lifetime in the laboratory. Wing wear, a proxy of the moth’s age at capture (Javoiš and Tammaru 2004), was recorded as a binary trait (1: a pristine individual, 2: noticeable loss of scales). We further involved data on the longevity of temperate (Estonian) geometrids (43 species, 1281 individuals), obtained in an experiment with a similar design (described and analysed in Holm et al 2016). There was a methodological difference between the two data sets, however: the moths in Estonia were kept in thermoregulated chambers at two constant temperatures (15 °C and 23 °C), whereas this was not possible in Uganda.

Phylogenetic comparative analyses

The phylogenetic tree for subsequent comparative analyses was constructed on the basis of data extracted from GenBank (Wahlberg et al 2005, 2010; Snäll et al 2007; Viidalepp et al 2007; Wahlberg and Wheat 2008; Õunap et al 2008, 2011, 2016; Mutanen et al 2010; Strutzenberger et al 2010; Hausmann et al 2011; Sihvonen et al 2011; Holm et al 2016), which, with respect to the Ugandan species, was largely based on earlier work of the authors (Holm et al 2018, 2019a). The final data matrix comprised 373 taxa (of which 211 taxa represented the Ugandan fauna) and 6543 base pairs from eight markers: cytochrome oxidase subunit 1 (COI), elongation factor 1 alpha (EF-1a), wingless (wgl), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), ribosomal protein S5 (RpS5), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH) and carbamoyl
phosphate dehydrogenase (CAD). All sequences were aligned using ClustalW (Thompson et al 1994) in BIOEDIT 7.2.5 (Hall 1999).

The ultrametric tree required for subsequent statistical analysis was obtained in a two-step procedure (see Holm et al. 2018, and Appendix 5 for further details). First, four separate trees were created so that each of them had the focus on one of the principal subfamilies of Geometridae (Larentiinae, Sterrhinae, Geometrinae and Ennominae; see Appendices 6abcd). These time-calibrated ultrametric trees were constructed using BEAST 1.8.1 (Drummond et al 2012) on the CIPRES Science Gateway (Miller et al 2010) using calibration points taken from Wahlberg et al (2013). All these trees shared at least 22 taxa which facilitated combining them into a single 373-taxa ultrametric tree using the consensus.edges function from the R package phytools (Revell 2012). The constructed tree (Appendix 6) was then pruned for the purposes of statistical analyses based on the availability of longevity data (Appendix 1).

To identify the factors associated with species-specific values of adult lifespan in Ugandan Geometridae, we implemented trait-specific GLM models that accounted for phylogenetic autocorrelation. Body size, sex, wing wear, and temperature were the predictors considered in the analyses. As the number of individuals per species was highly variable, we chose a method of analysis which weighs data points (species, in our case) by sample sizes (individuals used in the experiment). Accordingly, we used analyses relying on Bayesian inference implemented in the R package rstan (Stan Development Team 2016; see Appendix 3 and Holm et al 2018, 2019a, for details). Due to the Bayesian framework, the impact of the predictors of longevity was assessed on the basis of examination of its credible interval (Table 1). The same statistical approach was applied in a further analysis in which longevity of tropical and temperate geometrids was compared. This analysis had to be limited to the subfamily Ennominae for the reason of reducing the sample to manageable size (the applied Bayesian analyses are extremely demanding in terms of computing time). Ennominae was chosen as the largest subfamily in the data set (65% of Ugandan species), and also as the only one in which both Ugandan and Estonian species are well represented (Appendix 2).

| Table 1 | Determinants of moth lifespan in the tropical region (Uganda, N = 654 individuals) based on a four-way phylogenetically informed GLM analysis relying on Bayesian inference (R package rstan) |
|---------|------------------------------------------------------------------------------------------|
| Model parameter | Estimate | 95% Credible interval |
| Intercept | 2.386 | (0.365; 3.815) |
| Temperature | −0.082 | (−0.116; −0.050) |
| Sex: Female | −0.250 | (−0.334; −0.169) |
| Wing wear: worn | −0.196 | (−0.307; −0.087) |
| Male wing length (mm) | 0.029 | (0.010; 0.049) |

The baseline for categorical model parameters are: a) sex: male; b) wing wear: pristine individuals; other categories are compared against the baseline categories. Estimates for 95% credible intervals of the posterior distribution of the difference which do not contain zero provide support for the model parameter: the effects of all the factors included in the model are supported.
Results and discussion

For a number of Ugandan geometrid moth species, post-capture lifespans were measured in the laboratory. Although the recorded residual lifespans do not directly represent the full potential of adult longevity, such values are still informative for comparative purposes (see Carey et al 2008 and Holm et al 2016 for discussion). The sample of 110 species included 3 species from the subfamily Larentiinae; 72 species from Ennominae; 10 species from Sterrhinae; 26 species from Geometrinae. While the maximum sample size per species was 153 individuals, for many species we had only a few specimens and there were 43 singletons. On average, the moths lived for 5.1 days (maximum was 17 days for a Cleora subcincta (Warren, 1901) female) in the laboratory. For females, mean lifespan was 4.4 days (median 4 days); for males, mean lifespan was 5.8 days (median 6 days). On average, individuals in a pristine condition lived 1.31 times longer than the individuals with worn wings. When the lifespans of worn individuals were adjusted for wing wear (multiplied by 1.31, the average ratio across the data set), the average lifespan calculated over species means was 5.9 days (median 6 days; maximum 13.1 days; minimum 2.0 days).

These values are very close to those recorded for temperate (Estonian) geometrid moths (average over species means 6.7 days, median 6.8 days; Holm et al 2016, see also Fig. 2). For the subfamily Ennominae, subjected to a formal analysis of the effect of region (Uganda vs. Estonia), the difference in lifespan was estimated to equal exactly zero (Table 2). In concert with the cross-region similarity of the mean values, we detected no species with extraordinary long lifespans among tropical geometrid moths, which is in contrast to the pattern in butterflies (Molleman et al 2007).

The among-region similarity is in disagreement with some a priori expectations. Undeniably, the tropical environment is climatically more stable and offers more steady availability of adult food (nectaring plants, fruits; Chapman et al 1999) in comparison with the temperate region. This stability could be seen as permissive for the evolution of long adult lifespans. It might be hypothesized that selection caused by high predation pressure in tropical environments (Roslin et al 2017) balances the positive impacts of resource and climate stability, leaving therefore the net outcome of adult lifespan similar to that in the temperate zone. Indeed, predator-mediated selective forces are expected to play a substantial role in Geometridae, as these moths typically lack chemical defences and/or mimicry, or the ability to outperform their predators in flight speed (see also Holm et al 2016 for further discussion). Such a high vulnerability is in contrast to the situation with many butterflies (Molleman et al 2019). This may partly—complementary to the adaptations to fruit feeding (Beck and Fiedler 2009; Molleman et al 2009)—explain the existence of long-living

Table 2  The effect of geographical location (Estonia vs Uganda, N=1935 individuals) on moth lifespan based on Bayesian inference (R package rstan) for a subset of the data, the subfamily Ennominae

| Model parameter                  | Estimate | 95% Credible interval |
|----------------------------------|----------|-----------------------|
| Intercept                        | 2.306    | (0.137; 3.563)        |
| Region: Uganda                   | 0.000    | (−0.113; 0.106)       |
| Temperature                      | −0.067   | (−0.073; −0.058)      |
| Sex: Female                      | −0.014   | (−0.079; 0.043)       |
| Wing wear: worn                  | −0.284   | (−0.343; −0.219)      |
| Male wing length (mm)            | 0.009    | (−0.006; 0.024)       |

See Table 1 for further details
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species among tropical representatives of this taxon (Molleman et al 2007), as opposed to the absence of those among studied geometrids. Estimates of adult mortality rates in the field are scarce for flying insects (see, however, Sang and Teder 2011; Tiitsaar et al 2013), and appear to be lacking for the tropical region completely, so that this hypothesis cannot be directly evaluated. However, the few warningly coloured diurnal geometrids in the Ugandan fauna (e.g. Cartaletis spp., not included in the present study) may offer a possibility to address this question via further comparative analyses.

Nevertheless, it appears rather unlikely that the putatively higher predation pressure in the tropics would exactly outweigh the stable availability of adult food there, and that this scenario applies for moths but not for butterflies. The similarity of adult lifespans of Estonian and Ugandan geometrids should thus rather be seen as a further piece of evidence of a limited role of ecological (vs. physiological) factors as determinants of species-specific longevities in insects (Holm et al 2016). Indeed, consistent with the ‘physiological hypothesis’, larger species in our tropical sample showed longer adult lifespans (Table 1; Fig. 1). 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). A twofold increase in a linear measure of body size approximately corresponded to 1.2-fold increase in lifespan (Fig. 1); not so much different from the 1.3-fold increase reported for temperate species (Holm et al 2016). It remains to be noted that no systematic difference in body sizes was found between Estonian and Ugandan geometrid moths (Holm et al 2019a), which implies that the size-dependence of lifespan does not directly interfere with the comparison of longevity among the regions.

Sex had a credible effect on lifespan, with females showing 1.3 times shorter lifespans on average than males (Table 1; Fig. 2). A sexual difference in lifespan is not unexpected, as the tasks which male and female insects have to accomplish during their lifetimes differ substantially (e.g. Tammaru et al 1996; Gotthard et al 2000; Hunt et al 2004). However, no sex difference was detected in the temperate data set (Holm et al 2016). Such an asymmetry might be related to the limited seasonality in Ugandan forests which results in overlapping generations of insects, in contrast to the strictly seasonal life cycles in the temperate climate. This could give the males more opportunities for multiple mating over

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**Fig. 1** Relationship between species-specific average lifespan and male wing length (mm). Each rectangle represents one species (N=64 species). The side lengths of the rectangles are proportional to the inverse of species-specific standard errors of respective variables. The indication of reliability is relative and should not be read against the scale on the axes. Non-phylogenetic linear regression line is added to visualise the results presented in Table 1.
an extended period of time (Tammaru et al. 1996). An among-region difference in selective pressures on female lifespan appears less likely, as Estonian and Ugandan moths do not differ in egg production strategies (capital vs. income breeding, Holm et al. 2019a), a major determinant of ecological traits in female moths (Davis et al. 2016).

On the other hand, the among-region similarity in female lifespan may be viewed as further support to the earlier conclusion that the degree of host-plant specialization in Geometridae is actually rather similar between the two studied regions (Holm et al. 2018, 2019b). Adult lifespan can be expected, and has been reported, to be negatively correlated with larval diet breadth (see Jervis et al. 2007b and references therein, but see also Beck and Fiedler 2009; Holm et al. 2016). The likely explanation is that higher degree of host specialization implies that the ovipositing female needs more time to find larval hosts. The challenge of locating the few suitable host-plant species from a dense and diverse vegetation should, if anything, lead to the evolution of prolonged female lifespans in the tropics. This was, however, not the case.

As expected, individuals that experienced higher average temperatures showed shorter adult lifespans (Table 1; Fig. 2). The effect of temperature was moderate, with roughly a 0.4-day decrease in lifespan per a 1-degree increase in average temperature experienced over the captive lifespan; the relationship was similar to that found in the temperate region (Fig. 2). It must be noted, however, that such quantitative between-region comparison should be treated with appropriate caution, because of methodological differences in measuring lifespans between the regions. Tropical moths were kept at ambient temperature (due to the lack of equipment in the tropics) whereas temperate species were housed in thermo-regulated climate chambers (Holm et al. 2016). Temperature was, however, accounted for in the comparative analyses to minimize temperature-caused differences. Even if this did not eliminate the potential bias caused by methodological differences completely, the qualitative conclusion appears straightforward: the tropical moths in our sample have rather similar adult lifespan patterns to their temperate relatives.

In summary, we found no evidence for extraordinary long lifespans in tropical geometrid moths. In particular, lifespans recorded for the tropical region were found not to differ considerably from those reported for the temperate region. A relationship between body
size and longevity—similar to the one for temperate moths—was confirmed at the among-species level. These observations provide evidence that physiological rather than ecological factors shape the evolution of longevity in geometrid moths. In a more general context, we believe that the present study adds to the examples of how comparative studies on species-rich taxa hold the potential to address questions on the evolution of senescence.

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Authors’ contributions FM, TT, JJ and SH conceived and planned the experiment. SH and FM carried out the experiment. SH and AK analysed the data. EÖ constructed the phylogeny. SH and TT led writing the paper with all other authors contributing.

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Availability of data and material (data transparency) All the data are available in Appendix 1, Appendix 2, Appendix 3, Appendix 4, Appendix 5, Appendix 6, Appendix 6a – 6d.

Code availability (software application or custom code) Not applicable.

Declaration

Conflicts of interest The authors have no conflict of interest to declare.

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