LETTER

Seasonal environments drive convergent evolution of a faster pace-of-life in tropical butterflies

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Abstract

New ecological niches that may arise due to climate change can trigger diversification, but their colonisation often requires adaptations in a suite of life-history traits. We test this hypothesis in species-rich Mycalesina butterflies that have undergone parallel radiations in Africa, Asia, and Madagascar. First, our ancestral state reconstruction of habitat preference, using *c.* 85% of extant species, revealed that early forest-linked lineages began to invade seasonal savannahs during the late Miocene-Pliocene. Second, rearing replicate pairs of forest and savannah species from the African and Malagasy radiation in a common garden experiment, and utilising published data from the Asian radiation, demonstrated that savannah species consistently develop faster, have smaller bodies, higher fecundity with an earlier investment in reproduction, and reduced longevity, compared to forest species across all three radiations. We argue that time-constraints for reproduction favoured the evolution of a faster pace-of-life in savannah species that facilitated their persistence in seasonal habitats.

Keywords

Habitat templet, life-history, Miocene, parallel radiations, *r/K* strategy, savannahs, seasonality, time-constraints, trade-offs.

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INTRODUCTION

Signatures of historical climate change driving diversification in plants and animals are ubiquitous (e.g. Davis *et al.* 2005; Peña & Wahlberg 2008; Near *et al.* 2012). Major climate-induced changes in ecosystem structure can result in the emergence of novel niches with subsequent colonisations promoting adaptive diversification (e.g. MacFadden & Hulbert 1988; Couzens & Prideaux 2018). The origin of tropical savannahs is a dramatic example of climate-driven biome evolution (Cerling *et al.* 1997; Osborne 2008; Edwards *et al.* 2010), and the global expansion of these grass-dominated ecosystems during early-middle Miocene (24–11 Mya) had a major impact on diversification and ecological speciation in both invertebrates and vertebrates, especially in grazing taxa (e.g. MacFadden & Hulbert 1988; Aduse-Poku *et al.* 2009; Couzens & Prideaux 2018, Kergoat *et al.* 2018). In addition to changes in vegetation structure, this large-scale forest-to-grassland transition was also associated with dramatic changes in habitat seasonality (Osborne 2008). Closed-canopy forests can buffer extreme seasonal differences (for example in temperature or humidity; Montejo-Kovacevich *et al.* 2020) but savannah biomes typically demonstrate strong temporal fluctuations in climatic conditions. Therefore, vital resources for growth and reproduction, such as grasses for the larvae of phytophagous insects, can be sustained in shaded forests throughout the year (Moore 1986; Braby 1995; Halali *et al.*

2020). In contrast, the availability of these resources is typically limited to a single season (i.e. the wet season) in seasonal savannahs (Knapp & Smith 2001).

Given these opposing habitat characteristics, the colonisation of newly formed open savannahs from ancestral dense canopy forests is predicted to be difficult. Species with long life cycles may overcome some of the challenges of living in open savannahs by migrating with the seasonal rhythms and synchronising the production of young with the peaks in resource abundance (Sinclair *et al.*, 2000; Wittemyer *et al.* 2007). Species with shorter life cycles, such as insects, are often unable to track the favourable conditions and thus must evolve strategies to cope with the environmental heterogeneity of alternating seasons. An adaptive mechanism to avoid extreme environmental conditions is to become physiologically inactive during the dry season (seasonal dormancy; Tauber *et al.* 1986). Adaptive changes in a suite of life-history traits may also facilitate population persistence in environments with a more sharply defined reproductive season (Varpe 2017). Theory predicts that habitats that are heterogeneous in time and/or space, and thus more fluctuating in resource abundance, favour the evolution of a faster pace-of-life (Pianka 1970; Southwood 1977; Southwood 1988). Such 'fast' life-history strategies may include high growth rates and fecundity with reduced longevity and allow organisms to rapidly increase population size when opportunities for reproduction are available. In contrast, selection in less seasonal

habitats is thought to favour 'slow' (low growth rates and fecundity with increased longevity) life-history strategies (Southwood 1977).

The origin of tropical savannahs provides a unique opportunity to study how organismal life-histories have evolved in response to changes in temporal heterogeneity (e.g. Brennan & Keogh 2018), and here we use Mycalesina butterflies to address this question. This subtribe of tropical butterflies is distributed across the Old-World Tropics and comprises 10 genera (*c.* 320–330 species) that have undergone three geographically parallel radiations; one each on the African mainland, on Madagascar, and in Asia (Aduse-Poku et al. 2015, Fig. 1a). Some species of the Asian radiation extend into the sub-tropical regions of north-eastern Australia and others reach as far as Korea and Japan (see Aduse-Poku et al. 2015). These tropical butterflies feed mainly on grasses as larvae, and the majority of the species are found in dense rainforest habitats or forest margins (van Bergen et al. 2016). However, some Mycalesina butterflies inhabit more open grasslands and savannah woodlands where they are faced with the challenge of alternating seasons (Brakefield 2010). Long-term data from Malawi has revealed that savannah species only reproduce during the wet season (*c.* five months) and may fit in two or possibly more generations before undergoing reproductive diapause to cope with the lack of larval host plants in the dry season (Halali et al. 2020). The main survival strategy of these butterflies during this period is to remain inactive and cryptic, probably to conserve energy and avoid detection by predators (Brakefield & Reitsma 1991; van Bergen & Beldade 2019). In contrast, Mycalesina species occurring in less seasonal forest habitats remain active and reproduce throughout the year, suggesting that time-constraints for reproduction are stronger for savannah species (Braby 1995; Halali et al. 2020).

Focusing on a subset of species from the main African radiation (the genus *Bicyclus*), we recently demonstrated that several independent open-habitat lineages arose during the late Miocene and Pliocene (Halali et al. 2020), and these habitat shifts were likely associated to the expansion of seasonal grasslands during Miocene (Osborne 2008; Edwards et al. 2010; van Bergen et al. 2016). Here we broaden the ancestral habitat reconstruction, with near-complete taxa sampling across all geographically independent radiations, to describe patterns of habitat specialisation across the entire subtribe of Mycalesina butterflies. We hypothesise that the worldwide expansion of grass-dominated ecosystems also triggered the evolution of open habitat specialists in Asia and on Madagascar, and that transitions occurred in a similar time period.

From a macroevolutionary perspective, these repeated transitions from relatively aseasonal tropical forests into highly seasonal savannah habitats may have required adaptive changes in a suite of life-history traits. We predict that environmental factors that impede continuous breeding selected for relatively fast life-history strategies in savannah species. To test this hypothesis, we collect life-history data from a common garden experiment in the laboratory from replicate pairs of forest and savannah species, representing both the African and Malagasy radiation. The availability of data collected previously for three Australasian species (i.e. from the Asian radiation; see Braby & Jones 1994; Braby & Jones 1995; Braby 2002) allowed us to conduct a comparative analysis across all major radiations within Mycalesina butterflies.

Taken together, our results show that Mycalesina butterflies have independently colonised savannahs during the late Miocene and Pliocene in a stepwise fashion using forest margins and fringes as stepping-stone habitats. Furthermore, the common garden experiments reveal that savannah and forest species have evolved faster and slower life-history strategies respectively. We argue that the evolution of faster pace-of-life in savannah species is driven by strong time-constraints for breeding in open habitats, and that such life-history strategies contributed to population persistence in seasonal environments.

MATERIAL AND METHODS

Ancestral state reconstruction of habitat preference

The evolutionary history of Mycalesina butterflies was reconstructed by classifying the habitat preference for 287 species covering over 85% of all extant taxa and representing all three parallel radiations. Using the available literature, communications with local experts, and our own extensive field experience, species presence was scored in three categories; forest habitats (A), forest-fringes (B) and open or savannah habitats (C). Forest species are restricted to rainforests or habitats with extensive canopy cover. Forest-fringe species are those found in the outskirts of closed-canopy forests or fragmented forests, but never extending into savannahs. Finally, savannah specialists were quantified as species mainly occurring in open grasslands or woodlands where vegetation is dominated by grasses with few interspersed trees. Many species were assigned to two habitat classes (i.e. habitat class A+B or B+C; N = 98), and a small number of generalist species were assigned to all three habitats (habitat class A+B+C; N = 32). Allowing species to occupy multiple habitats, rather than being fixed to discrete categories, provides a continuum with an increasing degree of seasonality: A < A+B < B < B+C < C.

A recent phylogeny from Brattström et al. (2020) was used to reconstruct the ancestral states (see Supplementary Information for details on phylogenetic reconstruction). The evolution of habitat preference was modelled using *fitpolyMk* function in *phytools* ver. 0.7.47 (Revell 2012) which can handle polymorphic states. Since this function can only handle a maximum of two polymorphic states, species that can be found in three habitats (i.e. A+B+C) were dropped, leaving a total of 255 species. We fitted four ordered and four unordered models to the data (i.e. an equal-rates model, a symmetric model, an all-rates-different model, and a transient model, for each model type). The unordered models allow all possible transitions between habitat types, while the ordered models only allow transitions along the habitat continuum. Model performances were assessed using the Akaike Information Criteria (AIC) score and an ancestral state reconstruction was conducted for the best fitting model using Bayesian stochastic mapping (Bollback 2006) implemented in *phytools* using *make.simmap* function. We simulated 1000 character states on the Maximum Clade Credibility tree and summarised the
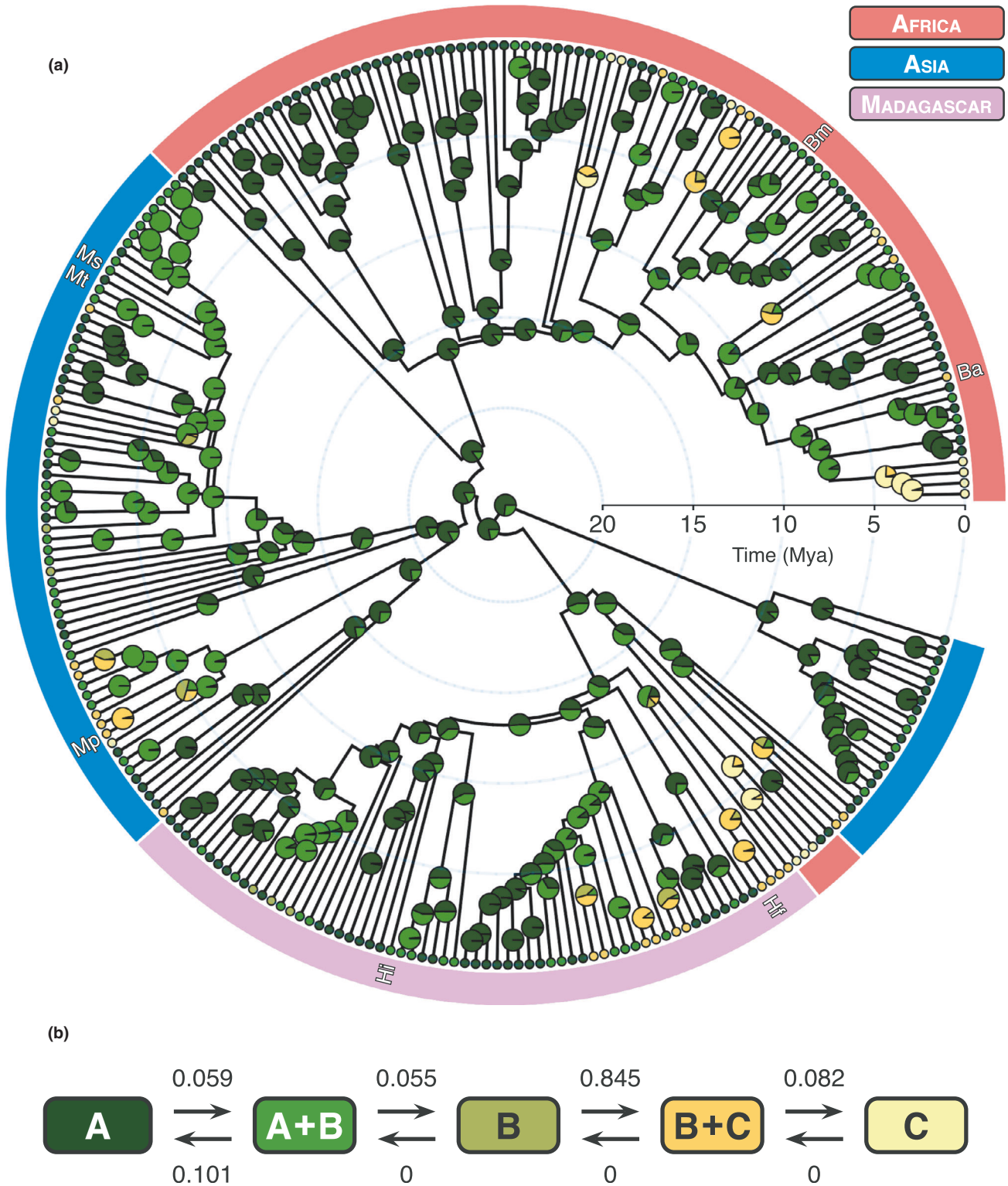
Figure 1 (a) Ancestral state reconstruction for habitat preference in Mycalesina butterflies and (b) the pathway depicting the evolution of habitat specialisation with arrows showing transition rates. Letters in the pathway represent habitats categories as follows; A = forests, B = forest-fringes, C = savannahs. Colours in the phylogeny match habitat categories in the evolutionary pathway. Abbreviations marked on the tips of the phylogeny highlight species for which life-history traits were quantified in the common garden experiment (African and Malagasy radiation) and the species from the Asian radiation for which life-history data was available from previously published studies (Ba = *Bicyclus anynana*, Bm = *Bicyclus martius*, Hf = *Heteropsis fraterna*, Hi = *Heteropsis iboina*, Mp = *Mycalesis perseus*, Ms = *Mydosama sirius*, Mt = *Mydosama terminus*).

states at each node to indicate the probability of a particular state to be ancestral. This analysis was complemented with a dispersal-extinction-cladogenesis (DEC) model that is used mainly to estimate historical biogeography (Ree & Smith 2008). We used the package *BioGeoBears* ver. 1.1.2 (Matzke 2018) and included all 287 species as this method does not constrain the number of polymorphic states. Our habitat preference classifications were coded as biogeographic zones in the analysis. We fitted two models: (1) 'unconstrained' model where species with any combination of habitats are allowed to be represented at nodes; (2) 'constrained' model where species from non-existent category (A+C) were not allowed to represent at nodes. The best fitting model was chosen based on the AIC score.

Common garden rearing

Laboratory populations of replicate pairs of forest and savannah species from the African (*Bicyclus spp.*) and the Malagasy (*Heteropsis spp.*) radiations were used to explore the role of seasonality in shaping the evolution of life-history strategies. Species inhabiting the stable African forests were represented by a laboratory population of *Bicyclus martius* (Fabricius, 1793) that was established in 2018 from gravid females collected in Bonkro, Ghana. This species is strongly linked to intact rainforests in West Africa but can also be found in fairly open clearings and forest margins as long as some canopy cover remains (habitat class A+B; see Larsen 2005; Oostra et al. 2014a). Species inhabiting the more seasonal habitats on the African mainland were represented by a population of *Bicyclus anynana* (Butler, 1879) from Nkhata Bay in Malawi (Brakefield et al. 2009). This extensively studied species is widely distributed across open woodland and savannah habitats in East Africa and never extends into forests with complete canopy cover (habitat class B+C; Larsen 1991; Windig et al. 1994). The Malagasy radiation was represented by *Heteropsis iboina* (Ward, 1870) (forest; class A+B) and *H. fraterna* (Butler, 1868) (savannah; class B+C). The laboratory stock of *H. iboina* was established in 2013 from gravid females collected in Andasibe-Mantadia NP in Madagascar (van Bergen et al. 2017), while *H. fraterna* was established in 2018 from females collected in Ranomafana NP (Madagascar). All laboratory stocks were maintained at 25 °C and 70% relative humidity (RH) under a 12:12 h L:D photoperiod resembling wet season conditions in the field. Young maize plants (*Zea mays*) were host plants for *B. anynana*, wheat plants (*Triticum aestivum*) for *H. fraterna*, and running mountain grass (*Oplismenus compositus*) for *B. martius* and *H. iboina*. *Oplismenus spp.* are natural hosts for many Mycalesina butterflies, and all stock populations demonstrate high performance on *Oplismenus* grasses (e.g. Kooi 1992; Oostra et al. 2014a; Nokelainen et al. 2016).

Measuring life-history traits

Eggs were collected from each laboratory population at 24-h intervals (between 9.30 to 10.30 h), from small *Oplismenus* plants and then transferred to petri dishes lined with a filter paper and kept in climate-controlled chambers (Sanyo/

Panasonic MLR-350H) at 25 °C and 70% RH under a 12:12 h L:D photoperiod. The eggs of each species were photographed using a Leica DFC495 camera coupled to a Leica M125 stereoscope, and the cross-sectional area of each egg measured from the resulting images in ImageJ (Schneider et al. 2012) using a customised macro. Area of eggs measured in this way are highly correlated with egg weight (e.g. Gibbs et al. 2010). The egg development time was estimated as the number of days between laying date and hatching date.

Upon hatching, three cohorts of 60 newly hatched larvae (N = 180) for each species were randomly allocated to large rearing cages (35 × 46 × 60 cm). Larval host plants (*Oplismenus* grass) were watered daily and replaced when necessary to ensure *ad libitum* feeding and the position of the cages within the climate-controlled chambers was changed daily. Larval development time was the number of days from egg hatching to pupation; pupal development time, the number of days from pupation until adult eclosion; and total development time, the sum of larval and pupal development times. All pupae were weighed to the nearest 0.1 mg (Mettler AE163) within 24 h of pupation. Larval growth rates were calculated by dividing the natural log of the pupal weight by the larval development time (see Gotthard et al. 1994). After eclosion, two to four day old virgin females (except two females which were one day old) were allowed to mate with virgin males to determine daily variation in fecundity and to compute individual fecundity curves. For *B. anynana*, *H. iboina* and *H. fraterna*, we were able to select 15 mating pairs in the first trial. For *B. martius*, we could not obtain any mating pairs in the first trial, and we only observed a single mating after multiple trials. Therefore, males and females of this species were kept in a single cage for approximately 15 days, after which eight females were randomly selected for measuring fecundity. After copulation, individual females were kept in cylindrical plastic pots (11.5 × 13.5 cm) and provided with a cutting of *Oplismenus* grass kept in water for oviposition. The number of eggs laid by the females was assessed every 24-h for 15 consecutive days. The females of *B. martius* were dissected after the monitoring period to confirm their mating status. Four non-mated females and one where spermatophore presence/absence could not be established were excluded from the data set yielding a total sample size of four for this species including the female for which mating was observed. Female longevity was measured as the percentage of females that were alive after the 15-day fecundity assessment period. For *B. martius* we included both non-mated and mated females (N = 9). All females were fed on slices of moist banana throughout the experiment.

Statistical analyses

Generalised linear models (GLM) were used to examine the effects of habitat class, genus, sex and their interactions, on a suite of life-history traits. Habitat class was a categorical variable (forest or savannah), and genus (*Bicyclus* or *Heteropsis*) was included to account for phylogenetic relatedness between the species. Sex was excluded from the models for egg size and egg development time since this variable cannot be established at this life stage. Data on development times (egg, larval, pupal and total) were analysed using GLMs with a

Poisson distribution and a log link function. GLMs with a Gaussian distribution were used to fit the data for egg size, pupal weight and growth rate. Post hoc pairwise comparisons (Tukey's HSD; $\alpha = 0.05$) were carried out using *emmeans* R package (Lenth 2020).

Individual fecundity curves were estimated using a generalised linear mixed model with a negative binomial distribution, as implemented in the R package *glmmTMB* (Brooks et al. 2017). In addition to habitat class and genus, the number of days (centred) and all interactive terms were included as fixed effects. Pupal weight, centred within each species, was added as a covariate. Finally, since the raw data suggested that the fecundity curves had non-linear distribution, we included a quadratic term for the number of days in the model. We initially fitted full models, allowing interactions between all predictors, and the minimum adequate model was found by AIC guided backward elimination. All statistical analyses were performed in R ver. 3.6.1 (R core team 2019).

RESULTS

Ancestral state reconstruction for habitat preference

An ordered all-rates-different model provided the best fit for the habitat preference data (see Table S1 in Supporting Information). This model suggested that the lineages that gave rise to three geographically independent radiations were forest specialists and that more open habitats were colonised repeatedly during the late Miocene and Pliocene (8-3 Mya; Fig. 1a). The transition matrix of the best-fit-model suggests that forest fringe habitats represent a stepping-stone towards adaptation to strictly open environments (Fig. 1b). In other words, the invasion of woodland and savannah habitats was preceded by adaptation to semi-shaded habitats. Moreover, parameter estimates suggest that back-transitions, that is transitions from open to forest, are unlikely (Fig. 1b). Furthermore, using the DEC model, the constrained model (AIC = 868.32) had a better fit than the unconstrained model (AIC = 953.95) and the ancestral state reconstruction generally confirmed the observed pattern that forest species were ancestral for all the three radiations and have repeatedly colonised savannahs during the late Miocene and Pliocene (Figure S1).

Egg size and development

We found that forest species laid larger eggs and that their offspring took longer to complete embryogenesis (habitat, $P < 0.001$ for both egg size and egg development time; Fig. 2). The effect of habitat-use was larger in the species representing the African radiation than in those representing the Malagasy radiation (habitat:genus, $P < 0.05$ for both traits; see Table S2 & S4). The results from our study are in line with the habitat-dependent patterns observed for the Australasian species from the Asian radiation (Braby & Jones 1994; Braby & Jones 1995). Here, compared to savannah species *Mycalesis perseus* (Fabricius, 1775), the two forest specialists *Mydosoma sirius* (Fabricius, 1775) and *Mydosama terminus* (Fabricius, 1775) laid larger eggs that took longer to develop (data from Braby & Jones (1994) are presented in

Fig. 2; see Supporting Information for details). Note that all three species were placed in the genus *Mycalesis* at the time of the original publication.

### Development times and growth rates

Compared to savannah species, forest species had longer larval, pupal and total development times (habitat, $P < 0.001$ for all traits; Fig. 3a; figures for larval and pupal development time in Fig. S2a & S2b). Differences in developmental times between habitat specialists were larger in the species representing the African radiation (habitat:genus, $P < 0.002$ for all traits; see Table S5–S7). Forest species had lower individual growth rates (habitat, $P < 0.001$) and a larger body mass (habitat, $P < 0.001$) than savannah species (Fig. 3b & 3c; Table S8 & S9). All species were sexually dimorphic for body size (all pairwise comparisons, $P < 0.001$) with female pupae weighing on average 22% more than males, except for *B. martius* where males were slightly heavier than females. These results complement the data on the Australian Mycalesina butterflies from the Asian radiation where two forest species had longer total development times, lower growth rates and larger body sizes than the savannah specialist (data from Braby & Jones (1994) are presented in Fig. S4).

Fecundity curves and longevity

In both the African and Malagasy radiations, the forest species had lower fecundity and laid eggs more uniformly across their lifespan than the savannah species (habitat, $P < 0.001$; Fig. 4; Table S10). The magnitude of these differences appeared to be slightly higher in the African than in the Malagasy radiation. For example, the African savannah species (*B. anynana*) had higher fecundity and a more pronounced early investment than the savannah species from the Malagasy radiation (*H. fraterna*) (Fig. 4). In contrast, the fecundity curves of both forest species were closely similar. After 15 days of fecundity measurements, 55% females of forest species and 6% of savannah species survived in the African radiation (Fig. 4). Similarly, 46% and 20% of forest and savannah species survived in the Malagasy radiation, respectively (Fig. 4). Note that the females from the forest species from Africa, *B. martius*, were kept in communal cages for 15 days prior to fecundity assessments (see Methods). The high proportion of females still alive after the assessment suggests that this species is potentially extremely long-lived. Similarly, in the Australian species, the savannah species had higher fecundity and a prominent early peak in fecundity compared to two forest species (data from Braby & Jones (1995) are presented in Fig. S5). Systematic data on longevity were not available for these species.

DISCUSSION

Adaptive radiations comprise the rapid differentiation of a single common ancestor into an array of species that inhabit a variety of environments and differ in the phenotypic traits used to exploit these ecological niches (Losos & Mahler 2010; Stroud & Losos 2016; Gillespie et al. 2020). The process
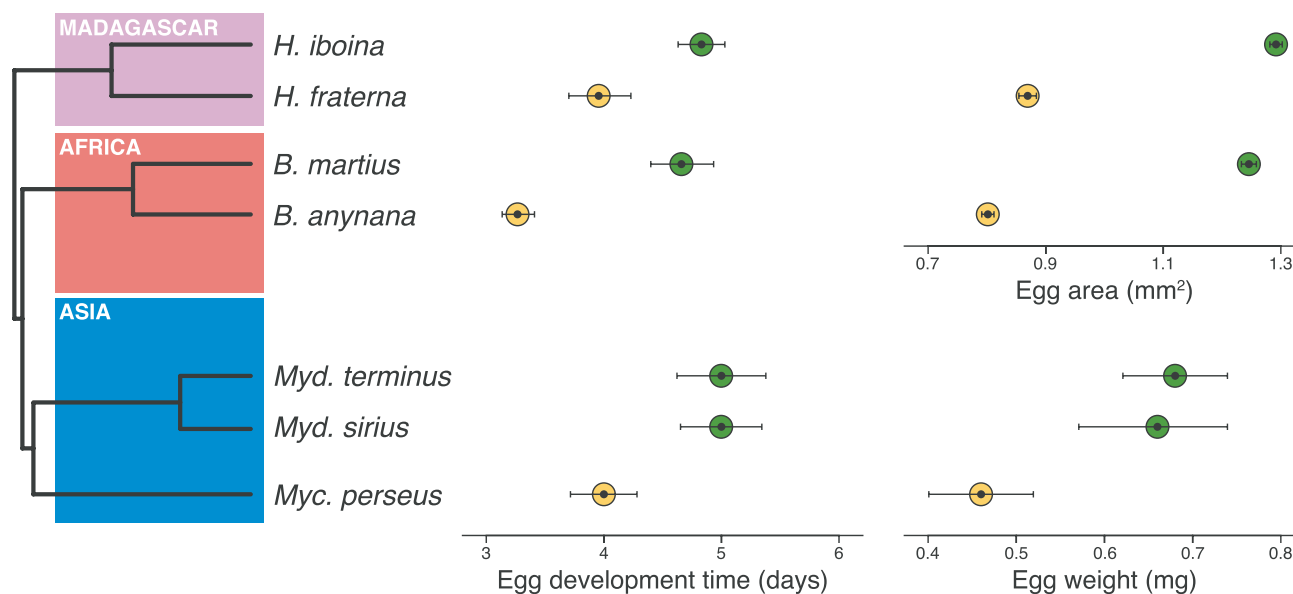
Figure 2 Phylogenetic relationships among the species included in the study which represent all three radiations, together with mean values and 95% confidence intervals for egg development time and egg size. Forest and savannah species are shown in green and yellow circles respectively. For the African and Malagasy radiation, savannah species had significantly reduced egg sizes and egg development times (see Results). The data on species from the Asian radiation were extracted from Braby & Jones (1994) (see Supporting Information) and error bars for the egg weights represent standard deviations.

includes both ecological diversification and speciation (Schluter 2000; Nosil 2012), and a striking feature of this phenomenon is that parallel radiations frequently produce convergent forms. For example, *Anolis* lizards have evolved closely similar series of ecomorphs and ecomorph-specific morphologies on numerous Caribbean islands (Losos et al. 1998; Mahler et al. 2013), benthic and limnetic ecotypes of stickleback fish have emerged repeatedly in postglacial lakes (Schluter & Nagel 1995; Rundle et al. 2000), and similar habitat-specific morphological features have evolved multiple times in cichlid fishes, both within and across lakes (Kocher et al. 1993, Muschick et al. 2012). Our results demonstrate that colonisation of open seasonal habitats occurred repeatedly in the three geographically parallel radiations of Mycalesina butterflies and that these transitions are associated with the convergent evolution of life-history strategies.

The global expansion of open woodland and savannah habitats during the Miocene is an important driver of ecological diversification in a variety of herbivorous taxa including both invertebrates (e.g. Zarlenga et al. 2006; Aduse-Poku et al. 2009; Kergoat et al. 2018) and vertebrates (e.g. MacFadden & Hulbert 1988; Couzens & Prideaux 2018; Fuchs et al. 2019). Our results suggest that this climate-driven biome shift also played a crucial role in the evolutionary history of Mycalesina butterflies (see also van Bergen et al. 2016; Halali et al. 2020). During Miocene, much of the trans-continental dense canopy forest was replaced by a mosaic of open woodland and savannah habitats (Jacobs et al. 1999; Jacobs 2004; Edwards et al. 2010), and this heterogeneous environment appears to have unlocked ecological opportunities for Mycalesina butterflies. Our ancestral state reconstruction for habitat preference suggests that colonisation of open habitats was preceded by adaptations to semi-shaded habitats, such as forest

clearings or margins. Such a 'stepping-stone' model of habitat preference evolution has been described for a variety of other taxa (e.g. Ruck et al. 2006, see examples in Donoghue & Edwards 2014), implying that direct transitions to more extreme habitats may be rare, and often require pre-adaptations or evolution of key traits which facilitate persistence in harsh environments (Donoghue & Edwards 2014).

Tropical forests and savannahs differ considerably in their degree of seasonality and the convergent evolution of life-history traits within this adaptive radiation of tropical insects is likely to be associated with the relative absence or presence of temporal heterogeneity. The habitat templet model (Southwood 1977; Southwood 1988) postulates that selection will favour slow strategies in species inhabiting stable habitats with continuous or prolonged breeding seasons, while fast strategies will occur in habitats with strong fluctuations in resource abundance where animals experience strong time-constraints for breeding. We have shown that savannah species of Mycalesina butterflies have consistently higher growth rates, which they achieve by decreasing adult body size and shortening the time needed to complete development. We hypothesise that these accelerated individual growth rates allowed savannah species to increase the number of generations they could fit into a single breeding season (Roff 1980; Abrams et al. 1996; Kivelä et al. 2009), which in turn improved their ability to persist in these novel and seasonal environments.

Despite strong temporal fluctuations, per capita resource availability is high during the wet season in open grassland habitats (Knapp & Smith 2001) and thus could relax density-dependent effects that may act in tropical forests where recruitment of individuals is continuous (Halali et al. 2020). The fast and slow life-history strategies observed in savannah and forest species respectively, could therefore parallel the
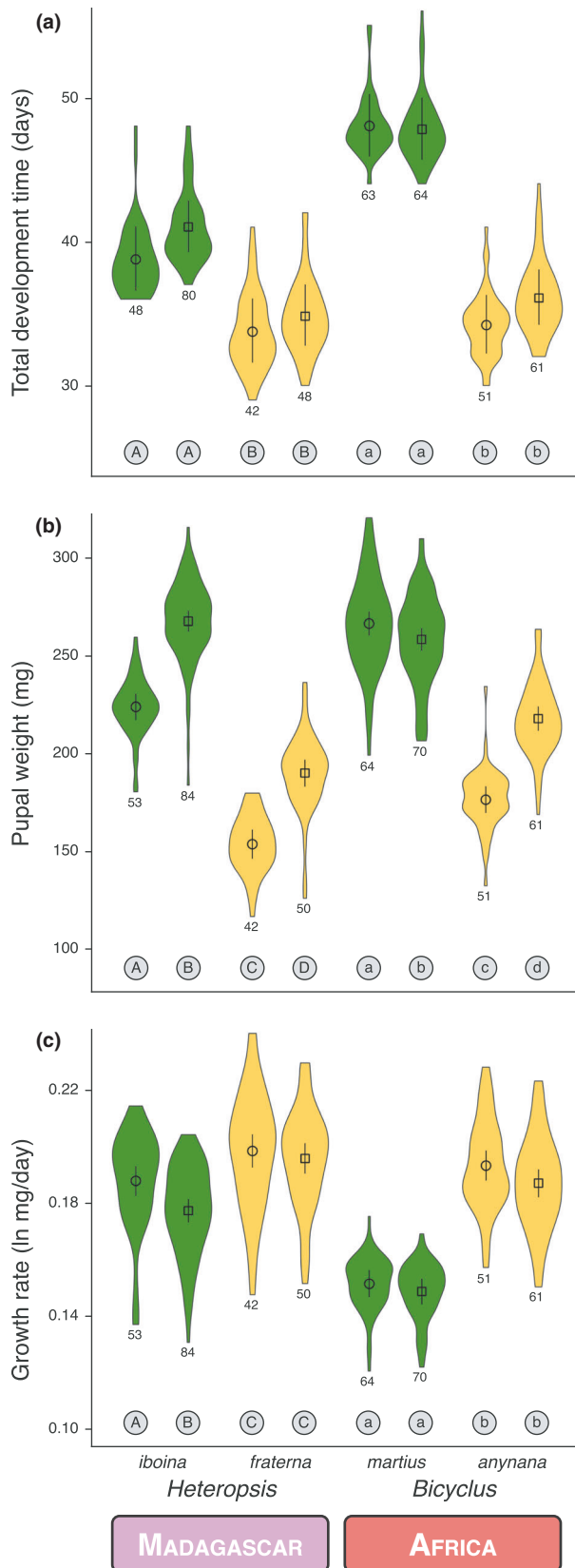
Figure 3 Violin plots with mean and 95% confidence intervals for the (a) total development time, (b) pupal weight and (c) growth rate for replicate pairs of forest and savannah species from the Malagasy and African radiation reared in the common garden experiment (green = forest species, yellow = savannah species). Sexes are denoted with different shapes (circles = males, squares = females) and significant differences between groups (Tukey's HSD, $P < 0.05$) are indicated by different letters, coding for each radiation independently. Number below each violin indicates the sample size. Data for these life-history traits for species from the Asian radiation are presented in Figure S4.

Reznick et al. 2002). High population densities and intense resource competition in tropical forests could favour the evolution of larger offspring with better competitive abilities. Since internal reserves for reproduction are limited (van Noordwijk & de Jong 1986), larger offspring sizes are typically associated with a decrease in fecundity, and vice versa (Smith & Fretwell 1974; Berrigan 1991). The colonisation of open grasslands by early lineages of Mycalesina butterflies could have resulted in relaxed density-dependent selection and facilitated a shift in position along the trade-off between offspring size and number. Our data reveal that forest species indeed produce relatively few eggs of high quality (i.e. greater egg area), while closely related savannah specialists produce more eggs that are much smaller in size. Similar habitat-dependent trade-offs between egg size and number were demonstrated in a comparative study of temperate forest and open habitat Satyrine butterfly species (Karlsson & Wiklund 2005). Note that egg size is generally positively correlated with female body size in insects (Berrigan 1991, García-Barros 2000) and that forest species are typically larger than savannah species (e.g. Braby 2002; see results). In our study, the differences in egg size and fecundity among habitat specialists remained significant after accounting for variation in body size (Table S3 & Fig. 4).

Time-constraints on reproduction may also have shaped patterns of reproductive effort across species. Theoretical studies predict that short-lived individuals with high early fecundity are favoured by selection in time-constrained environments compared to habitats where such constraints are absent or weak (Southwood 1977; Kivelä et al. 2009). Our fecundity estimates reveal that savannah species have higher reproductive effort early in their lifespan, while the distribution is more uniform in forest species. Furthermore, there is a trade-off between early reproductive effort and longevity (Miyatake 1997; Zera & Harshman 2001; Jervis et al. 2007), with larger bodied insects typically living longer and having higher fecundity (Honěk 1993; Nylin & Gotthard 1998; Holm et al. 2016). Indeed, we find that forest species are generally longer lived with larger body sizes than Mycalesina species from savannah habitats. Also, another forest species *Bicyclus sanaos* (Hewitson, 1866), a sister species of *B. martius*, has a significantly longer lifespan compared to the savannah species *B. anynana* (Oostra et al. 2014a). As a potential caveat we note that the fecundity of the African forest species *B. martius* was measured 15 days post-eclosion, and the females may have laid some eggs before the fecundity assessment. However, since this species is extremely long-lived (see Results and Oostra et al. 2014a) we are confident that our fecundity

dichotomy of *r*- and *K*-selected reproductive strategies (Pianka 1970; Gadgil & Solbrig 1972), which implies a combination of density-dependent and resource-driven selection (Boyce 1984;
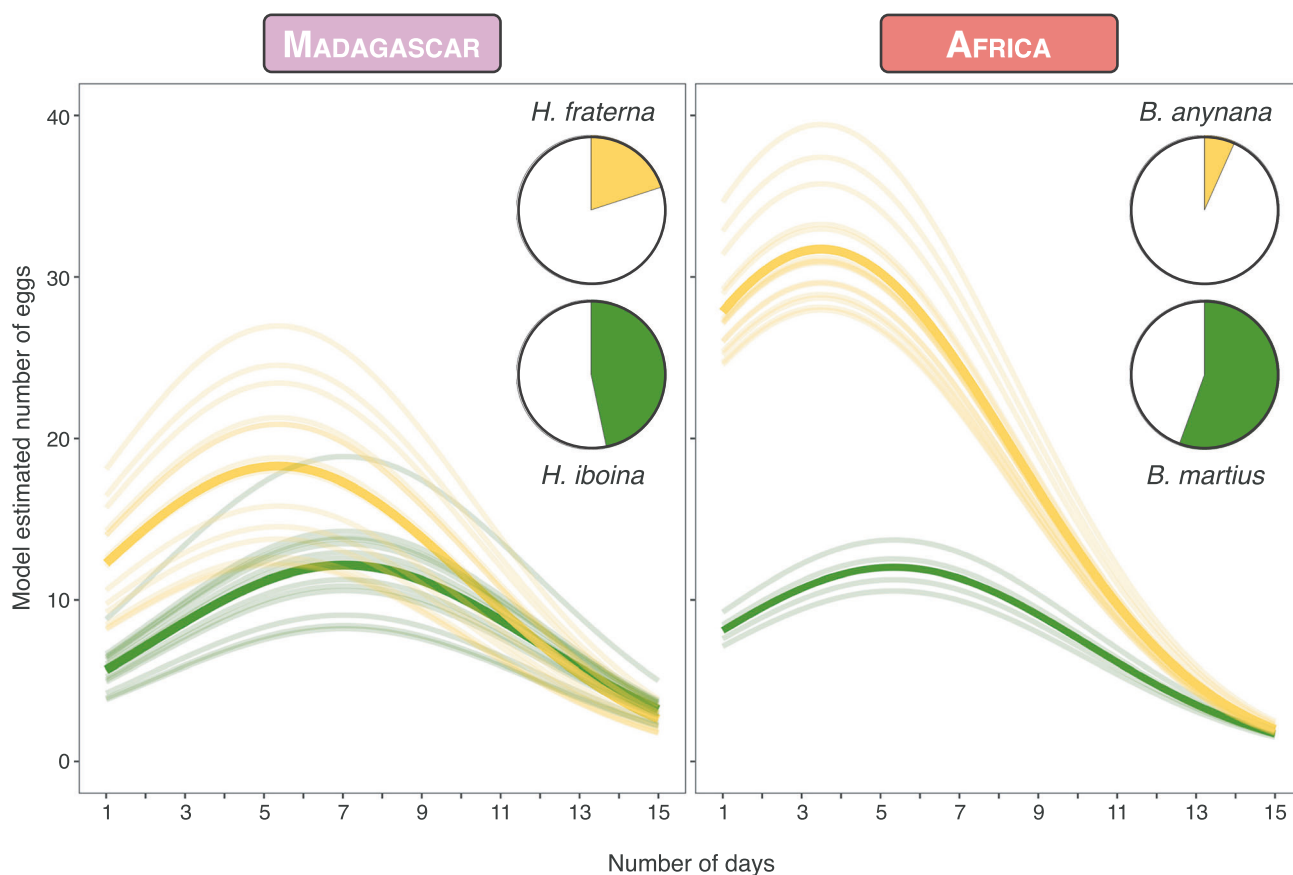
Figure 4 Fecundity curves for replicate pairs of forest and savannah species from the Malagasy and African radiation (green = forest species, yellow = savannah species). Thick and thin lines represent the model estimated average and individual fecundity curves respectively. In the inset, highlighted portions of pie charts show the percentage of surviving females after 15 days of fecundity assessment. Fecundity curves for species from the Asian radiation are presented in Figure S5.

measurement only represents a slight underestimate. In addition, the magnitude of the differences in all life-history traits between forest and savannah species from the African and Malagasy radiation were very similar to the differences observed in the Australian species where data were collected using wild-caught females (Braby & Jones 1994; Braby & Jones 1995). This suggests that the potential effects of relaxed (natural) selection and adaptation to laboratory conditions were minimal and did not substantially alter our results.

Variation in extrinsic mortality risk may play a role in the evolution of life-history traits across habitats. In seasonal environments, the availability of resources that are utilised by prey species is typically highly synchronised with the abundance of parasitoids and predator communities (Morais et al. 1999, Molleman et al. 2016). The wet season in open habitats may therefore represent a high predation risk environment where the production of many small eggs and investment in early reproduction is predicted to be advantageous (e.g. Reznick & Endler 1982; Reznick et al. 1990). Moreover faster larval growth rates may require longer or more frequent foraging bouts, which could increase the predation risk of savannah species (Johansson & Rowe 1999; Gotthard 2000). In contrast, the prolonged

development of forest species could potentially increase their exposure to natural enemies (Benrey & Denno 1997; Williams 1999). Overall, risks of enemy attacks in insects have been shown to be lower in closed-canopy forests compared to semi-open habitats such as forest clearings (Richards & Coley 2007). Future studies focussing on quantifying age-specific mortality (e.g. Reznick et al. 1996) are needed to improve our understanding on the role of extrinsic mortality on the evolution of life-history strategies in Mycalesina butterflies.

Ectotherms inhabiting seasonal environments often demonstrate developmental plasticity to cope with environmental heterogeneity (e.g. Beldade et al. 2011; Kivelä et al. 2013). This environmental regulation of development can result in a better match between adult phenotype and adult environment and typically involves the concerted response of a suite of traits to external conditions (Parsons & Robinson 2006; van Bergen et al. 2017). Mycalesina butterflies, particularly savannah species, demonstrate plasticity in morphological (e.g. Windig et al. 1994), physiological (e.g. Oostra et al. 2011), behavioural (e.g. van Bergen & Beldade 2019) and life-history traits (e.g. Oostra et al. 2014b). Individuals that fly during the wet season reproduce actively, have smaller body size and

shorter lifespan, while those emerging in the dry season undergo reproductive diapause, have larger body size and longer lifespan (Brakefield & Reitsma 1991, Halali et al. 2020). In this study we focussed on the life-history traits of reproductively active adults by rearing cohorts at temperatures that mirror the conditions of the wet season. The evolution of plasticity itself may also have played a crucial role in the colonisation of seasonal environments by Mycalesina butterflies and is the topic of future work.

The parallel nature of three independent and species-rich radiations of Mycalesina butterflies allowed us to extend our results beyond simple correlation between environment stability and associated life-history strategies. We show that even with considerable periods of independent evolution, r-selected Mycalesina butterflies have evolved repeatedly in seasonal savannahs, suggesting that the faster pace-of-life was required to be able to persist in these seasonal habitats (see Pianka 1970; Southwood 1977; Braby 2002). As recently found in parallel for the evolution of reproductive diapause (Halali et al. 2020), we argue that time-constraints on reproduction act as a strong selective agent in these open habitats and that trade-offs among life-history traits played a central role in the evolution of life-history strategies in these tropical butterflies.

AUTHOR CONTRIBUTIONS

SH, PMB and OB designed the study. SH carried out the experiment. EvB and OB collected data for habitat preference. CJB wrote a custom ImageJ macro. OB made figure illustrations. SH and EvB carried out analyses and wrote the manuscript with inputs from CJB, PMB and OB. All authors read and approved the final version of the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available from Figshare: https://doi.org/10.6084/m9.figshare.13001756.v1

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