Sexual selection drives maladaptive learning under climate warming

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Keywords: Seasonal polyphenism; global warming; simulations; social exposure; fitness

Abstract

Current predictions for the effects of the climate crisis on biodiversity loss have so far ignored the effects of learning ability and sexual selection. Using the African butterfly *Bicyclus anynana*, which shows strong phenotypic plasticity in response to temperature, we show that learning produces a maladaptive mate preference under climate warming. We modelled climate warming and found that as temperature becomes an unreliable cue at the onset of the dry season, adult butterflies displayed the wet season rather than the dry season form. Female learning further suppressed their innate, adaptive sexual preference for dry season males. Instead, females learned to prefer a phenotype transiently present during the seasonal transition. Female fertility and longevity were also affected by learning, reducing female fitness following climate warming. Our results emphasize the importance of sexual selection, learning, and their fitness consequences for understanding (mal)adaptation of natural populations to climate warming.

Introduction

The current climate crisis is the best documented human-induced rapid environmental change for its negative effects on biodiversity [1,2]. Climate warming is indeed expected to lead to a global extinction rate of 15% by 2100 [3,4]. This predicted extinction rate should be taken with caution, however, because estimation models do not incorporate key biological responses of species [4]. One such biological response is learning ability, where animals can modify their behaviour in response to changes in the environment [5]. Learning has emerged as a major response of species to human-induced rapid environmental change, as was shown both theoretically [6] and empirically [7–12]. Learned behaviours for species responses to climate change are important for two reasons: First, learning can significantly change (innately expressed) behaviours, such as aversive and reversal learning in response to danger or fear [13–15], or biased learning toward the easiest cues to learn [16]. Learned behavioural responses of organisms may thus produce widely different predictions about species responses to human-induced rapid environmental change compared to innate behaviours. Second, most documented cases of learning in response to human-induced rapid environmental change have recently shown that learned behaviours are actually maladaptive [17]. Maladaptation occurs whenever a "strategy" in a population becomes prevalent while it decreases the fitness of individuals [18,19]. Learning may, therefore, accentuate the extinction risk of species, rather than alleviate it (as is usually assumed [20]), leading to so-called evolutionary traps (i.e., adaptive traits become maladaptive [21,22]).

Most work on climate warming documents (mal)adaptation under natural selection; yet another key biological mechanism to consider for improving the forecasting of species extinction rates is sexual selection. Over 50% of recorded climate change impacts are not due to direct effects of increased temperature, but to biotic interactions [3]. Sexual selection is an important biotic force of evolution [23] that is also affected by climate warming [24–26]. Sexual

selection is further important to consider, because it can reduce local adaptation due to the cost of sexual ornaments (handicap hypothesis) and sexual conflict [27]. Sexual selection may thus act against natural selection, increasing the risk of population extinction [28–30], but see [31].

Sexual interactions are strongly affected by learning (in vertebrates: [32], and insects: [33]), but whether and how animal responses to the climate crisis are mitigated by learned sexual behaviours remains virtually unexplored [17,34]. We used an ectothermic insect as a model, the African butterfly *Bicyclus anynana* (Butler 1879; Nymphalidae), which has become one of the best-known examples of developmental plasticity in response to temperature. During the wet season, which lasts about ~5 months, temperature and precipitation are high (Fig. 1), leading to lush, green vegetation and an abundance of resources [35–38]. High temperatures (> 23ºC; [35]) lead to the development of a typical wet season male butterfly morph that is characterized by conspicuous eyespots to avoid predation [39–41]. Several successive generations of wet season butterflies appear during the wet season. During the seasonal transition, from wet to dry, temperature and precipitation are lower (between ~19ºC and 23ºC; [35]), leading to a higher frequency and development of an intermediate male phenotype. During the dry season, precipitation is at a low, leading to reduced vegetation cover and a harsher, more stressful environment. A low temperature (<19ºC; [35]) leads to development of the typical dry season male form, which is dull with reduced eyespots (Fig. 1). Only one generation spans the entire dry season, which lasts about 7 months. Wet, intermediate, and dry season wing patterns are determined primarily by larval rearing temperature, not genetic differences or humidity [35]. Both wet and dry season forms are adapted to the conditions of their respective seasons: wet season individuals favour reproduction, while dry season individuals have adapted to cope with limited food availability, while increasing longevity [36]. Mating and mate preference have been studied predominantly in the wet season phenotype, where males show extensive courtship activity and females choose a mate based on visual and

chemical cues [42]. Previous work showed that females prefer mating with the dry season male phenotype when offered a choice, increasing fitness (egg numbers) [43]. It was proposed that male *B. anynana* may transfer a nuptial gift during mating [43], leading to an increase in fitness, but so far no empirical evidence has supported this claim [44]. Another study further revealed that a previous exposure to a male with a more eyespots increases female preference for these artificially enhanced ornaments [45]. *B. anynana* thus provides morphological evidence of adaptation to changing, seasonal climates that is easy to track [46], while mate preferences are under strong selection, particularly in changing environments.

Here, we modelled the seasonal transition as it will occur in 2100 in the native population of our African butterfly, located in Malawi. We made three predictions with regard to the occurrence of seasonal phenotypes, as well as mate choice preferences of naïve and experienced females, and their fitness effects: Prediction 1: Climate warming will lead to the production of wet season individuals at the beginning of the dry season due to the overall increase in temperature. Prediction 2: Naïve females prefer dry season males and mating with dry season forms increases fitness. Prediction 3: Social exposure to different male seasonal phenotypes changes mate preference of experienced females away from the dry season form, decreasing fitness. Our results revealed that an increase in temperature will alter the appearance of seasonal forms, reducing mating opportunities of females with the most adaptive and preferred seasonal form (dry season). We further showed that social learning of females about the availability of males produces learned sexual preferences (for intermediate season males) that become maladaptive under climate warming (i.e., reducing fitness).

Results

Climate warming leads to a maladaptive increase in wet season forms at the onset of the dry season

We mimicked the entire wet to dry seasonal transition (120 days) as it occurs in Malawi (Fig. 1; [47]) by implementing hour-to-hour modelled changes in temperature and monthly changes in photoperiod. Three climatic scenarios were applied to butterfly development: *1)* climatic conditions reported for 1988 ("reference" scenario); *2)* the expected climate in 2100, with a 3°C temperature increase; and *3)* the expected climate in 2100, with a 6°C temperature increase. Overall, climatic modelling showed that the alternation of wet and dry seasons was maintained in 2100, with a wet season of 5 to 6 months. Under the warmest scenario, however, the average temperature of both seasons increased by a quantity comparable to the amplitude of the seasonal cycle (6°C, as was found for all examined models). Consequently, the higher temperatures typical of the wet season in 1988 will be common during the dry season in 2100 (Fig. S1). We then reared three successive cohorts of *B. anynana* larvae under these climatic conditions until adult emergence. Comparing the 1988 data to the +6°C climatic scenario, climate warming increased survival by 21% (Fig. 2a; Table S1), and reduced development time by half at the beginning of the seasonal transition (15.4 to 7.8 days), and by 74% (27.4 to 7.2 days) at the end (Fig. 2b; Table S1). An increase in survival and reduced development time are indeed generally expected for ectothermic species [48]. Regarding seasonal phenotypes, we found that climate warming increased the expression of the wet season phenotype throughout the seasonal transition (Fig. 2c). Although butterflies displayed an increasingly dry season phenotype throughout the seasonal transition under the current scenario (which can be expected as temperature decreases during the seasonal transition; Fig. 2c), development under the +3°C and +6°C climatic scenarios produced a wet season phenotype at the end of the seasonal transition.

This wet seasonal form is typical for individuals developing at the beginning of the seasonal transition under the climatic conditions of 1988, confirming our first prediction (Fig. 2c).

Innate sexual preference for increasingly rare dry season males can increase population extinction risk during the dry season

Female lifespan and reproductive output depend on the seasonal form of her mating partner [43]. We focused on mate preference of wet season females, because this is the choosiest female seasonal form [43] and wet season individuals prevail at the onset of the dry season under the 2100 climatic scenarios. We quantified naive (innate) female sexual preference under semi-natural conditions, where an equal proportion of the three male phenotypes that co-occur during the seasonal transition competed for access to females through female choice [37]. Naive females preferred to mate with dry season males over intermediate or wet season males (Fig. 3a; Table S2): the mating proportions of dry season males were significantly higher, while the mating proportions of intermediate and wet season males were lower than expected based on phenotype-specific male courtship rates. Fitness consequences in terms of longevity and fertility were pronounced: females that mated with a dry season male increased their life expectancy by ~65% and laid between ~30 to ~240% more eggs compared to females mated with a wet season male, showing that innate preference for dry season males is adaptive (Fig. 4), in line with our second prediction. Despite the sexual benefits of mating with dry season males, the innate preference for dry season males may, however, become maladaptive by 2100, because dry season males will become rare after climate warming, meaning that females will have to mate with wet season males, which we know reduces reproductive fitness. Mating with wet instead of dry season males may thus drastically reduce the proportion of females and developing eggs surviving the harsh, dry season until the next wet season, increasing the extinction risk of *B. anynana* populations.

Exposure to both seasonal male forms leads to maladaptive learned mate preferences that affect female fitness

Short-term exposure to males with artificial eyespot numbers is known to modify female mating preferences in *B. anynana* [16]. We thus predicted that changes in the seasonal phenotype of males, which includes variation in eyespot size, modifies the innate mate preference through learning [33]. To test this, we exposed virgin, wet season females for a 3-hour period (as in [49]) to wet season males (the predominant form based on the 2100 scenarios; Fig. 3b), dry season males (the predominant form at the onset of the dry season based on past climatic conditions in Malawi; Fig. 3d), or intermediate seasonal phenotypes (found primarily during the seasonal transition in Malawi [37]; Fig. 3c). During pre-exposure, females had access to all phenotypic traits of males (i.e., olfactory, visual, and auditory), except for direct contact or mating. Overall, exposure of virgin wet season females to males of different seasonal forms induced a long-term (3 to 6 days) suppression of innate female preferences for dry season males (Fig. 3; Table S2), meaning that long-term memory formation was involved. In addition, pre-exposure to different male seasonal forms increased female mate preference towards intermediate season males, compared to naive females (Fig. 3; Table S2). Indeed, mating proportions of intermediate season males either matched (Fig. 3b, d) or exceeded (Fig. 3c) the expected mating rate based on courtship activity, as compared to their lower than expected mating numbers with naive females (Fig. 3a). The preference of wet season females for intermediate season males was highest when wet season females were exposed to intermediate season males (Fig. 3c; Table S2), in line with our third prediction.

We assessed the (mal)adaptive value of learning on mating preference by quantifying two fitness parameters of naive and experienced wet season females: longevity and fertilization success. In line with our third prediction, experienced females had reduced longevity (Fig. 4c),

suggesting that social learning generates some costs [34]. In addition, the proportion of successfully fertilized eggs of naive females decreased when they mated with dry rather than with intermediate or wet season males (Fig. 4a). This contradicts the work of Prudic *et al.* (2011), suggesting that the fitness benefits of naive females mated with different types of males depends on local environmental conditions, for which variation is known to affect the expression of sexual preference in *B. anynana* and in many other sexually reproducing species (e.g., choice or no-choice mating experiments, density, sex ratio [50–52]). In contrast, experienced females displayed the highest proportion of fertilization success after mating with dry season males (Fig. 4b; Table S1).

Social exposure of females to males of different seasonal phenotypes is likely adaptive by shifting learned mate preference towards available males under natural, past, climatic conditions. By 2100, social exposure of females to males of the wet season form will reduce their life expectancy (by 40%) and reproductive fitness (by at least 25%), adding to the negative effects on population survival chances throughout the dry season. Moreover, when females will be surrounded by wet season males at the onset of the dry season in 2100, social exposure will reduce their fertility by 23% compared to exposure and mating with dry season males, which is maladaptive. Reduced fertility adds up to the loss of the other direct benefits that females gain when mating with dry season males (increased life expectancy and oviposition rate [43]).

Discussion

We have provided a first example of a learned sexual interaction that produces maladaptation under climate warming [17,34]. As environmental cues become unreliable, in the case of *B. anynana* through temperature values that no longer predict the onset of the dry season, several maladaptive responses became apparent: *i)* production of the wet season form; *ii)* suppression of naive mate preference for dry season males after exposure to wet or intermediate season

males; and *iii)* reduced longevity and fertilization success by experienced females mating with wet season males. This leads to an increased risk that long-term maintenance of the population is disrupted in the wild. While it remains difficult to predict the fate of *B. anynana* populations in Malawi based on available information [53,54], our experimental results are relevant and important to consider for predicting responses in nature. In the field, most virgin females likely get socially exposed to potential mates during the few days of sexual maturation following adult emergence, because this species is protandrous (i.e., males emerge before females), which we show induces a form of sexual imprinting. Maladaptation can be suppressed over evolutionary time by genetic evolution and gene flow. Notably, genetic adaptation can occur by selection on female mate preference, provided that there is genetic variance for innate and/or learned mate preference [55]. As social learning is costly (in general, [56]; here, we find potential survival costs for *B. anynana*), and has a genetic basis [34], maladaptive learned sexual preference could be counter-selected [57].

There is significant gene flow among *B. anynana* populations across its distribution range [58,59], thus more adapted populations from other parts of the distribution range may also replace the local Malawi population. The alternation and duration of the dry and wet seasons differs extensively with latitude across the distribution range of *B. anynana* (e.g., variation in seasons documented in Uganda; [60]). Yet, there is little genetic variation for seasonal polyphenism between geographically distant populations [61]. More southern populations develop into the wet season form at lower temperatures than the Malawi population [61]; hence southern immigrant butterflies would increase maladaptation to the Malawi climate by 2100. The patterns of temperature-rainfall correlation vary strongly throughout the large geographical range of *B. anynana*, and different regions are expected to pose different selection pressures on the species' plastic responses to temperature [61,62]. *B. anynana* populations from the Northern hemisphere may use rainfall, and not temperature, as a cue for predicting the onset

of the dry season [62]. Replacement of southern populations, such as Malawi, by northern populations could lead to the emergence of the dry season form at the onset of the dry season despite the increase in temperature. However, local adaptation by genetic evolution may be very limited for the Malawi population of *B. anynana*, because most mutations are non-adaptive [47], and because there is little genotypic variation for several seasonal polyphenic traits, both regarding the development of wing patterns in response to temperature [63] and other life history traits forming the wet or dry season phenotypes, such as starvation resistance and resting metabolic rate [64].

The broader relevance of our results rests on two pillars. First, while learning is usually assumed to improve immediate adaptation to environmental variation (within the lifetime of an organism), the fitness effects of learning remain rarely assessed [25,33,65,66]. Here, we discovered that learning reverses both mate preference and its effects on longevity and reproductive fitness. Our results thus reveal that using behavioural data from naive individuals to predict sexual responses of animals may lead to erroneous conclusions. Whether learning increases or limits adaptation to sexual selection under climate warming remains largely undocumented so far (but see [67] who found that more complex, learned, male bird songs were present in more unpredictable and unfavourable climatic environments). Maladaptive or suboptimal learning was, however, previously found for foraging [68] and two recent reviews document that learning in response to human-induced rapid environmental change is maladaptive for a large number of environmental threats and behaviours [17,34]. We suggest that maladaptive learning in sexual interactions under human-induced rapid environmental change may occur in many species, as most animals studied to date modify their sexual behaviours through learning [32,33], which could lead to evolutionary traps [21]. Second, our results highlight the importance of sexual selection as a strong evolutionary force to include for quantifying species responses to human-induced rapid environmental change, such as climate

warming [24,69]. The effect of natural selection on species responses to the climate crisis has received considerable interest. Studies have shown that at the intraspecific level, climate warming leads to adaptive plastic and genetic changes in key phenotypic traits, including dispersal capacity and other morphological, physiological, behavioural, and life-history traits associated to phenology [70–72]. However, the effects of anthropogenic environmental changes on sexual selection matter as well, because sexual selection may increase the extinction risk of populations [30,73–75]. It is indeed increasingly acknowledged that human activities disturb important aspects of sexual selection (e.g., eutrophication and turbidity including algal blooms [76], urban noise [77], selective harvest in hunting [78]). This can be expected, as sexual selection has a strong environmental component [75,79]. Regarding the climate crisis, sexual selection is altered through the availability of sexual partners [80] with potential effects on the proportion of extra-pair mating opportunities [81], relative fitness of mono- versus polyandrous females [82], assortative mating [83], sexual conflict [84], secondary sexual traits [85], and mate preferences [69,86]. Our results suggest that the effect of global warming on *B. anynana* may lead to rapid extinction of populations within a single or a few dry seasons, due to cascading effects of learned sexual interactions and fitness of reproducing females at the onset of the dry, harsh, tropical season.

Our case study using the tropical butterfly *B. anynana* may be representative of a more general pattern, because butterflies are arthropods, which represent most of the animal biomass and species diversity on Earth [87], and generally show strong phenotypic plasticity to cope with alternating seasons [88]. Furthermore, tropical biomes both contain most biodiversity and are most threatened by climate warming [89–92]. Understanding how maladaptations arise is increasingly important as humans rapidly transform the Earth into an environment where maladaptation is expected to become prevalent for most species [19,21]. Our results suggest that global warming can have additive effects reducing, more than has been considered so far,

the long-term survival probabilities of various taxa once learning and sexual selection are included as important biological mechanisms of species responses [93,94]. Our results thus advocate for integrating sexual selection, learning, and their fitness consequences to better understand (mal)adaptation to climate warming.

Methods

Insect rearing

Experiments were performed with a laboratory population of *Bicyclus anynana* that was originally established from 80 gravid females collected in Malawi in 1988 [47]. Between 400 and 600 butterflies per generation were used to maintain high levels of heterozygosity and polymorphism [95] to avoid loss of genetic diversity in the lab population. Larvae were fed with maize, *Zea mays*, and adults with moist, organic banana, *Musa acuminate* [47]. Insects were reared, kept, and tested in a large climate-controlled room (5.8 x 5.7 m and 2.27 m high) under a standard temperature regime (27 ± 1°C; SD), a 12:12h light:dark and a high relative humidity (70 ± 5%) representing the wet season in the field [47], except when explicitly mentioned otherwise. For experiments, eggs were repeatedly collected from the stock population as described below. Eggs of all thermal treatments were first reared in the standard rearing environment at 27°C. Larvae were then placed in groups for the different thermal treatments from the 4th larval instar until the second half of their pupal stage (in sleeves; n = 25-50/sleeve), because the developmental temperature experienced during this time window determines the expression of adult polyphenism [37,40,96,97]. Newly emerged adults were sexed and individually marked on the ventral forewing with an indelible felt-tip pen. Groups of the same sex, seasonal form, and age of at most 10 males or 20 females were placed in cylindrical netted cages (diameter of 30 cm, height of 38 cm), except when stated otherwise. All experiments with adult butterflies were performed at a temperature of 27°C, unless mentioned otherwise.

Climate warming and proportions of seasonal forms

To test if climate warming leads to the production of wet season individuals at the beginning of the dry season, we modelled past and future natural, hourly, circadian cycles of both temperature and relative humidity for 104 consecutive days representing the transition from the wet to the dry season in Malawi (from March 30th to July 12th; Fig. S1). We modelled three climatic scenarios: the past climate in 1988, and two future scenarios, i.e., RCP4.5 and RCP8.5 (with a 3°C and 6°C increase in the region of interest, respectively). The photoperiod followed the light decrease throughout the seasonal transition with a 15-min monthly step. We encoded the three modelled climatic scenarios in three separate incubators. Given the difficulty of obtaining reliable, in-situ meteorological data, we constructed an idealized, smooth seasonal cycle of temperature and relative humidity by averaging 10 years of meteorological data during 1979-1989 [data from the Modern-Era Retrospective analysis for Research and Applications (MERRA), at latitude 12S and longitude 34E (Global-Modeling-and-Assimilation-Office-(GMAO)]. We then considered climate modulations available from the CMIP5 database at the same location [99]. Specifically, we computed the seasonal cycle of temperature anomalies (period 2080-2099 *versus* 1970-1990) of three models (CCSM4, HadGEM2-ES, and IPSL-CM5A-MR; at the time these data were downloaded, the HadGEM2-ES historical data were available until 1984 only), and added them to the reference scenario. Simulations of relative and specific humidity tend to be less reliable; hence a different approach was needed. We considered that the important explanatory factor for our experiment is the duration and timing of the wet, rainy season. Consequently, we measured the simulated change in timing and duration of the wet season between 1970-1990 and 2080-2099, and expressed these changes as anomalies of relative humidity, based on the reference values of humidity throughout the dry and wet seasons in the reference seasonal cycle obtained from the MERRA dataset (Fig. S1).

We retained the HadGEM2-ES model, because its climate sensitivity is intermediate and considers two future climatic scenarios, i.e., RCP4.5 (about 3°C increase in the region of interest) and RCP8.5 (6°C increase)[1], in addition to reference climatology for 1979-1989.

To cover the entire seasonal transition, we reared three cohorts of butterflies: 24 days in cohort 1, 28 days in cohort 2, and 35 to 50 days in cohort 3 (Fig. 1). Pupae were collected and placed in 1-dm³ plastic boxes, after which butterflies were frozen at -80°C. We then evaluated the effects of increasing temperature on survival until adult emergence (proportion of surviving individuals between the start of the thermal treatment and the first day of emergence), developmental time (day 1 = first emerged butterfly per cohort), and adult polyphenism using the relative area of the fifth eyespot on the right ventral hindwing (i.e., hv5; [46]; Fig. 2).

Mating success of different male seasonal forms with naive and experienced females

To test how the seasonal phenotype of males during the seasonal transition affects sexual selection, we produced the wet (temperature of 27°C), intermediate (23°C), and dry (17°C) seasonal forms [37,43,46,97,100]. We obtained naive wet season females by placing all wet season pupae individually in closed plastic cylindrical containers (diameter 3.5 cm, height 7 cm, 60 ml) and adding a piece of white paper sheet to prevent visual, olfactory, gustatory and acoustic contact with other individuals. We obtained experienced wet season females by exposing freshly emerged females to 8-16-day-old males of one seasonal form in a flight cage (10 to 15 males per cage of 60 x 60 x 60 cm) during 3 hours. Males within the same age range were used for all exposures during experiments to more accurately mimic natural conditions. Experienced females were kept separately in their container with a custom-modified, wire mesh cap (7 x 7 mm), allowing them to see, smell and touch the flying males above them, but preventing any mating or visual and gustative contacts with the other females exposed at the same time (maximum 30 females spaced 5 cm apart). The males used for exposure were

different than those used for subsequent mating experiments. All females were fed with a slice of banana in their individual container.

We used male courtship activity as theoretical mating proportions because *B. anynana* females, as in many insects, do not engage in mating activities unless a male initiates courtship. In addition, male courtship activity is known to *(i)* reduce butterfly survival [101], *(ii)* differ among seasonal forms [96], and *(iii)* predict male mating success [51,52,102]. We ran four mating experiments: one with naive wet season females (20 replicates) and three with experienced wet season females, either exposed the day of their emergence to wet (20 replicates), intermediate (17 replicates), or dry season males (15 replicates). For each replicate 15 virgin males (i.e., 5 selected randomly from each of the three thermal treatments), 8 to 11 days of age, were left to compete in the presence of 5 virgin, wet season females, 3 to 6 days of age, in semi-natural conditions [51,52,102]. Eight to 11-day-old virgin males were used, because all three components of the male sex pheromone are present at significant levels at this age [103–105]. We used 3-6-day-old virgin females as females readily mate at this age in the laboratory [47,104,105]. These ages also match the general age of females in behavioural experiments with this species [51,102]. We first introduced the males into the experimental area and left them to adapt and interact with one another for 1 hour, after which females were added. Experimental cages (120 x 59 x 60 cm) containing two maize plants to increase perching and hiding opportunities were used, and moist cotton with banana slices provided. This cage size, a density below the recommended threshold of 0.1 individual/dm^3 for *B. anynana*, and a sex ratio of 3 males for 1 female within the species-specific range creates semi-natural conditions and allows the full expression of courtship display by males (including flight), and of female mate choice that allows rejection of a male by flying away from an unwanted male [51,52,102]. Each replicate was observed for 10 min every 30 min, with total observation duration of 30 min per replicate. Direct behavioural observations for these 10 min were encoded using the software

The Observer 5.0 (Noldus Information Technology, Wageningen, The Netherlands) and when a male started courting a female, we followed this courtship until it ended before focusing on another male. Throughout each experiment, we noted the identity of mates of all formed couples.

Fitness of wet season females mated with different male seasonal forms

To test the fitness consequences of social learning in females, we measured fertilization success of eggs laid by either naive or experienced wet season females mated with males of different seasonal forms, as well as female longevity. After experiments were finished, both naive and experienced females were placed singly in a 1-dm^3 plastic box with wet cotton as water supply and a maize leaf to oviposit [47]. Part of the females obtained from the mating success experiments (i.e., all 57 naive females, and 9 females exposed to wet season males) also received banana slices *ad libitum*. Every three days, we replaced leaves and checked egg fertilization success, as well as female longevity (i.e., number of days between butterfly emergence and death).

Statistical analyses

We performed all statistics with RStudio 1.0.143 [106]. First, we analysed the effect of the climatic scenarios in interaction with cohort on the *survival until adult emergence* using generalized linear mixed models GLMM (lme4 package in R [107] with a binomial distribution (logit link function) and bobyqa optimizer. The number of successfully emerged butterflies and the number of experimental larvae not surviving to adulthood were bound together with the "cbind" function. Random factors were cohort identity nested in scenario identity, i.e., scenario(cohort). We added the interaction with sex (categorical variable) to analyse fixed effects on *developmental time* and the *relative area of adult polyphenic hv5 eyespot pupils* (with

a Box-Cox transformation to achieve normality) using GLMM with a Poisson distribution, a bobyqa optimizer and an observation-level random effect to capture overdispersion [51,108], and with a normal distribution, respectively. Random and nested factors were scenario(cohort(sleeve)).

We analysed the effect of male thermal treatment (17, 23, or 27°C) and female experience (naive or exposed to wet season males) on *female fitness and survival* as follows: *(i)* we analysed the effects of male thermal treatment in interaction with female experience on *fertilization success* (binary). We added the age at mating of both sexes and the thermal treatment duration (i.e., proportion of time that the female pupae spent in thermal treatment relatively to the entire pupation stage) as fixed factors. We used a GLMM with a binomial distribution, a bobyqa optimizer and an observation-level random effect to capture overdispersion. Feeding status after mating was starved for all females; *(ii)* we ran a similar GLMM on *female longevity* with a Poisson distribution, in adding female feeding status after mating in interaction with male thermal treatment and whether or not females could choose among males of the different thermal treatments as fixed factors, and experimenter(experiment(replicate)) as random factors. In all these analyses, we rescaled and centred the continuous explanatory variables on the mean, thus generating standardized z-scores, to evaluate the relative effects of variables measured on different scales and to lessen the correlation between the interactions and their component variables.

In the analyses of mating success experiments, we first tested for homogeneity among replicates per experiment using a Pearson's Chi-squared test (with simulated *P*-value based on 1^{e+06} replicates to obtain a correct approximation; all $P > 0.05$) before performing analyses on the pooled data set. Second, we tested differences in *mating probabilities* among males of different seasonal phenotypes in comparing the observed counts to the theoretical counts of mating of the three male thermal treatments per experiment using Pearson's Chi-squared tests

of goodness-of-fit. Third, we searched for the male phenotype(s) responsible for these differences in comparing the observed counts to the theoretical counts of mating *(i)* for each of the three male thermal treatments per experiment and *(ii)* in paired comparisons between male phenotypes per experiment, applying Pearson's Chi-squared tests and reporting *P*-values with and without Holm-Bonferroni correction for multiple comparisons [109]. We also performed Fisher's Exact tests when the expected frequencies were below 5.

Acknowledgements

We would like to thank Hans van Dyck for sharing his insect rearing facilities, Christophe Pels for his help with the rearing of insects, as well as Philippe Vernon, Franjo Weissing, Magdalena Kozielska, and Georges Lognay for careful and insightful comments on previous versions of this manuscript. This research was supported by a "FRIA" PhD grant to DM and a "Chargée de Recherches" postdoctoral grant to MJH provided by the National Fund for Scientific Research (FNRS) of Belgium. This work was further funded through UCLouvain and the Fédération Wallonie-Bruxelles (Grant ARC 17/22-086) to CN. This is publication BRC350 of the Biodiversity Research Centre.

Competing interests

The authors declare no competing financial interests.

Data availability

All data described in this paper is available at https://visserlab.be

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Figures

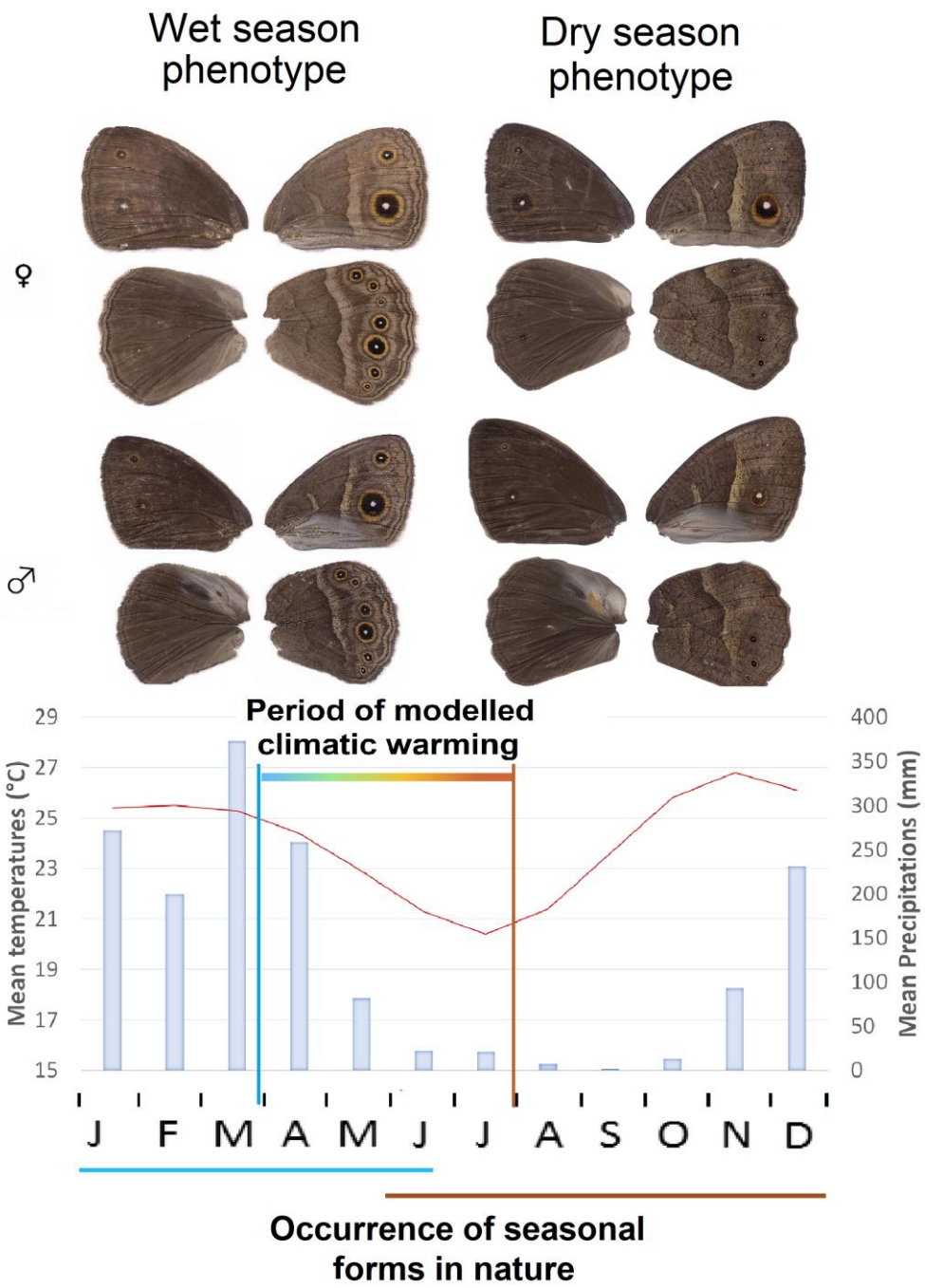

Fig. 1. Morphological differences of males and females between wet and dry season phenotypes and their temporal distribution across seasons in Malawi [37], in relation with monthly average values of precipitation (blue bars) and temperature (red curve) in the field (data available at [110]. The 120-day period of the climatic warming we modelled (Julian day 88 to 192, as in Fig. 2) is depicted.

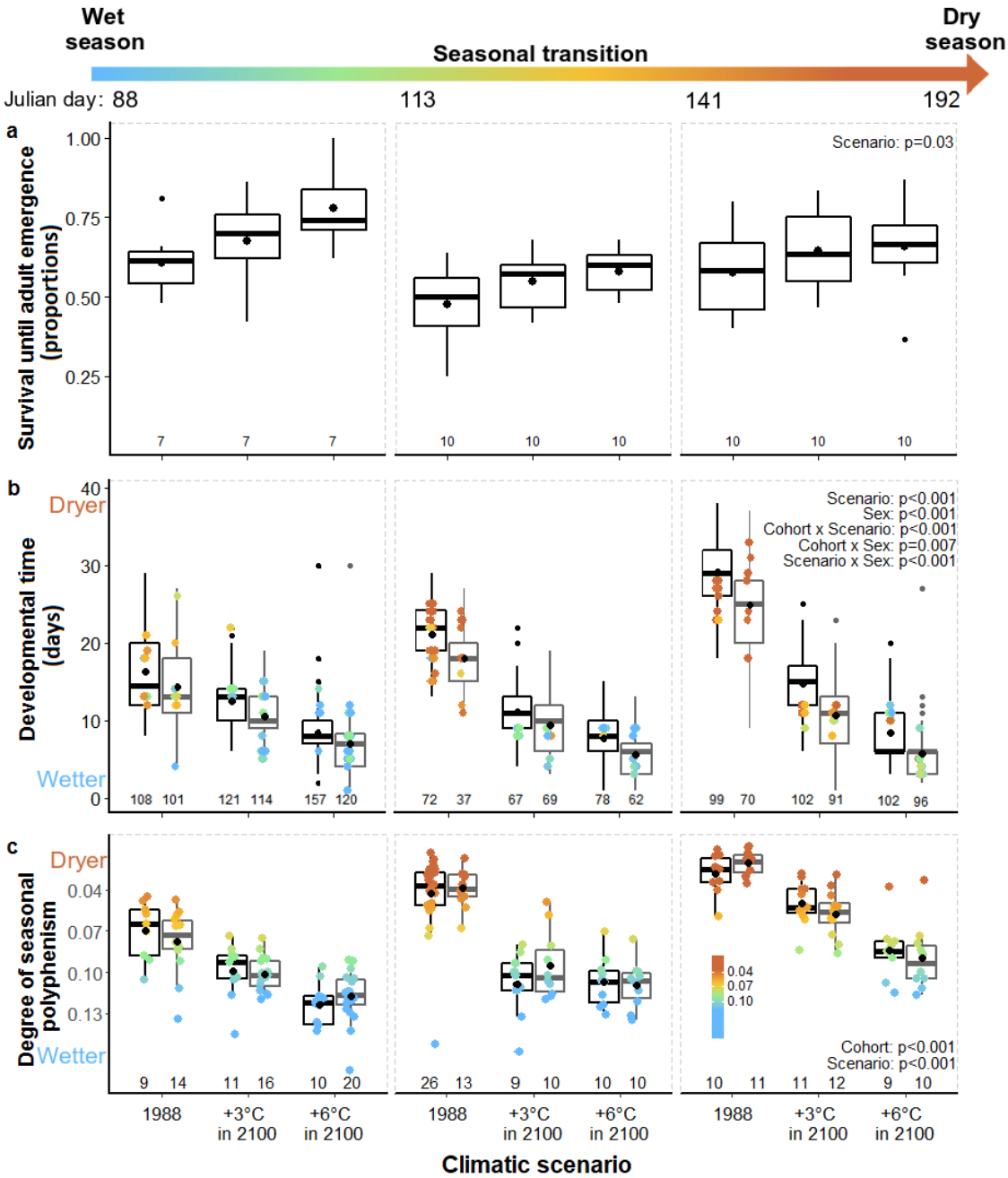

Fig. 2. Climate warming during the wet to dry seasonal transition increases the proportion of surviving larvae until adult emergence (a), reduces developmental time (day 1 = first emerged butterfly per cohort; b), and produces wet season butterflies at the onset of the dry season (c) (Table S1). Data are presented from left to right using three cohorts of larvae whose development cover the entire seasonal transition (cohort 1: from the 88th day of the year to the 112th, cohort 2 from the 113th to the 140th day and cohort 3 from the 141st to the 192th day). For (b-c), colours indicate whether the individuals display the dry (brown), intermediate (yellow and green), or wet (blue) season forms, based on the relative eyespot area of females (black) and males (grey) (as in [46]). Mean values are indicated (black dot inside each boxplot) and samples sizes (below each boxplot) are numbers of sleeves (n = 25-50 larvae/sleeve) in (a) and individuals in (b-c).

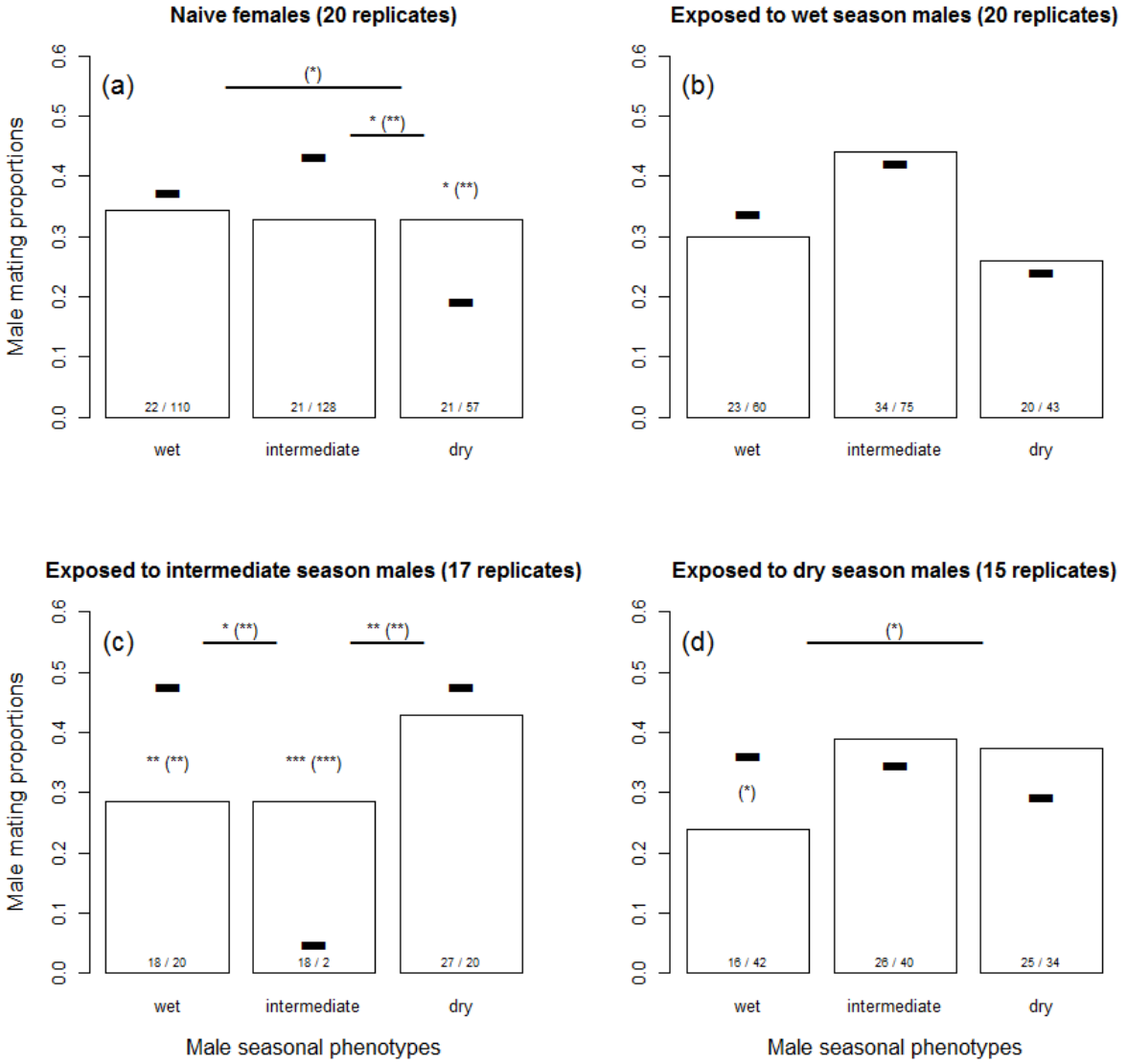

Fig. 3. Male mating success depends on the seasonal form (wet, intermediate or dry) and whether females are naive (a) or have been previously exposed to wet (b), intermediate (c) or dry season males (d). Adjusted Holm-Bonferroni *P*-values (and uncorrected *P*-values in brackets) indicate significant differences (*<0.5, **<0.01, ***<0.001) between observed (bars) and theoretical (dashes) mating proportions, after adjustment for courtship activity, for each male phenotype and in paired comparisons between phenotypes (reported for each bar and comparison; Table S2). Samples sizes inside each bar are numbers of male matings/courtships.

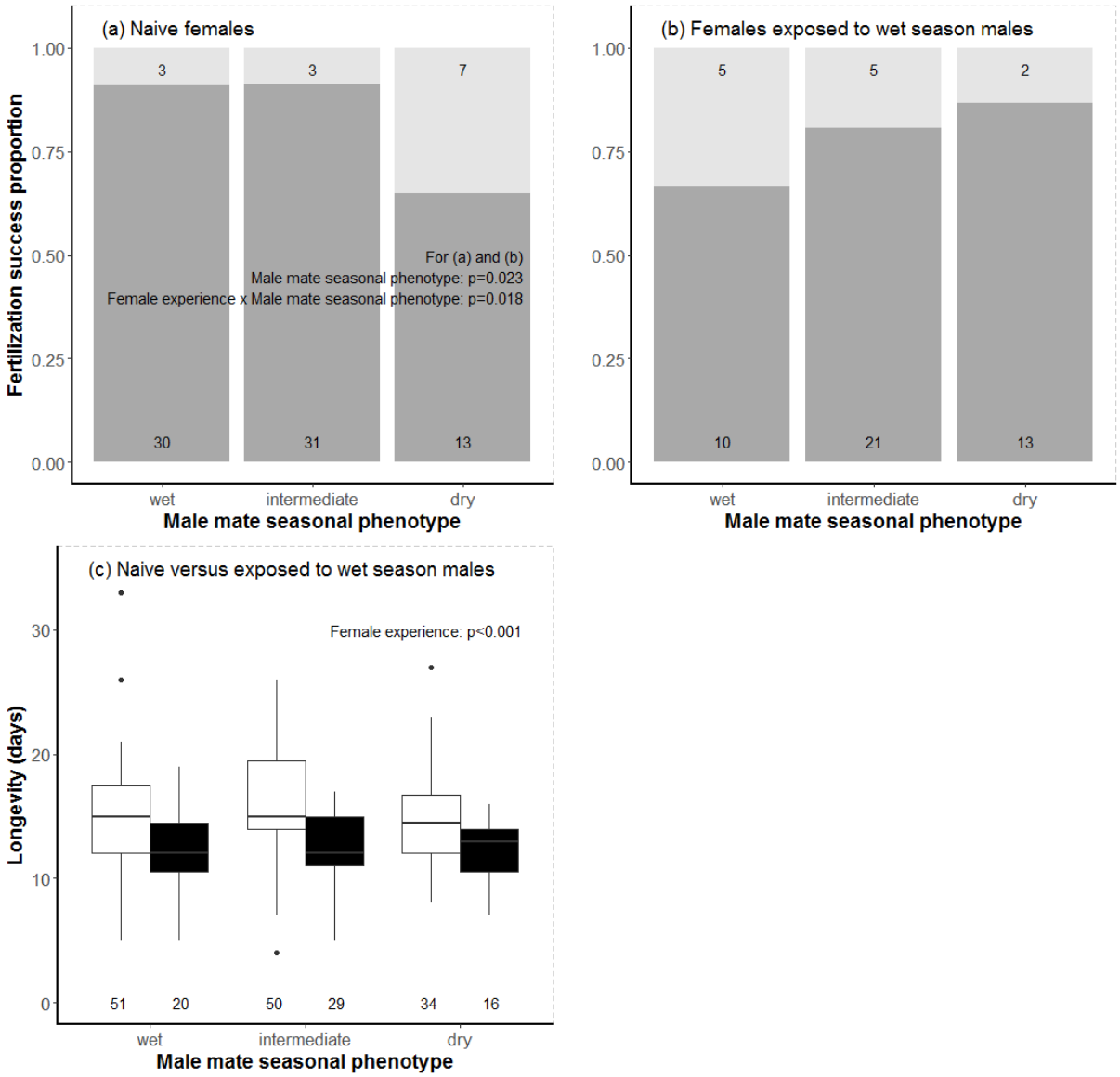

Fig. 4. The proportion of wet season females whose eggs were fertilized (in dark grey) differ depending on whether the females are naive (a) or have been exposed previously to wet season males (b). The same was found for longevity, where naive and experienced females are depicted by white or black boxplots, respectively (c). Fertilization success, but not longevity, also depends on the seasonal form (wet, intermediate, dry) of males. Sample sizes are given inside each bar or below each boxplot.

Supplementary Figures

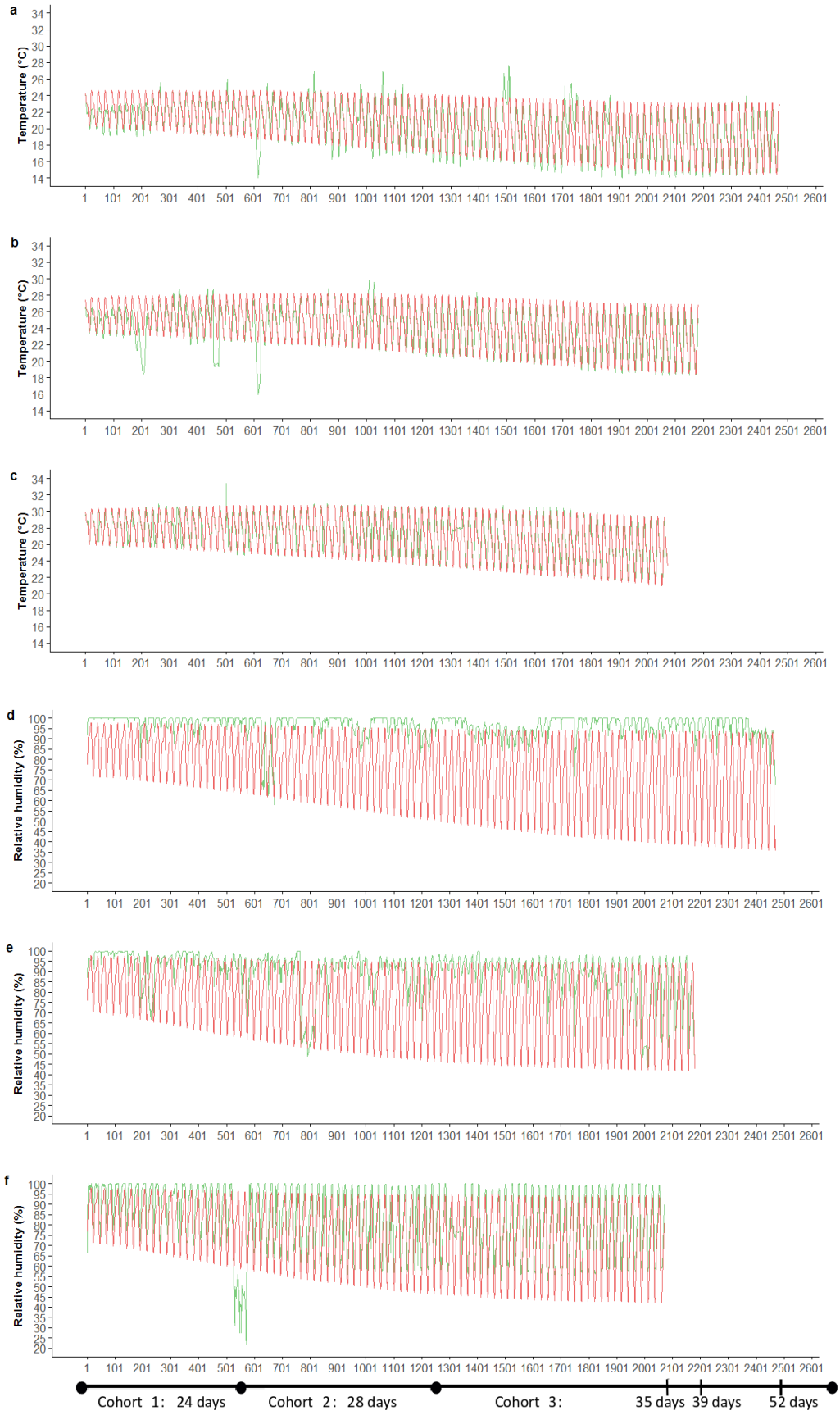

Fig. S1. Experimental and theoretical temperature and relative humidity throughout the seasonal transition. We registered the experimental temperature (°C; a-c) and relative humidity (%; d-f) with sensors (HOBO U23-001) in the incubators (green) and compared them to theoretical climatic conditions (red) per hour throughout the whole transition from the wet to the dry season, which started at the 88th day of the year. We modelled three climatic scenarios: the past reference climate from 1988 (a and d), the predicted RCP4.5 climate of +3°C on average in 2100 (b and e) and the predicted RCP8.5 climate of +6°C on average in 2100 in Malawi (c and f).

Table S1. Model-averaged standardized coefficients following conditional average of the set of supported candidate models for each response variable. For each conditional average of supported candidate models ($\Delta_i < 2$), we provide the relative importance of explanatory variables ($P \leq 0.05$ in bold). Of note, sexes differ in their developmental response to climate warming (Fig. 2b): males emerged earlier than females; female development time decreased faster with warming (scenario-by-sex interaction) and increased faster throughout the seasonal transition (cohort-by-sex interaction) compared to males. These sex differences become smallest under the warmer scenario and at the beginning of the seasonal transition.

Response	Explanatory	Estimate	SE	Adjusted SE	*z* value	*P* value	w_+
Survival until adult emergence[a]	Intercept	0	0	0	NA	NA	0.70
	Scenario	0.026	0.012	0.012	2.2	**0.03**	0.49
Developmental time[b]	Intercept	0	0	0	NA	NA	0.94
	Cohort	-0.008	0.006	0.006	1.5	0.15	0.94
	Scenario	-0.046	0.005	0.005	8.4	**< 0.001**	0.94
	Sex	-0.015	0.001	0.001	13.8	**< 0.001**	0.94
	Cohort x Scenario	0.019	0.006	0.006	3.4	**< 0.001**	0.94
	Cohort x Sex	0.004	0.002	0.002	2.7	**0.007**	0.94
	Scenario x Sex	-0.006	0.001	0.001	3.9	**< 0.001**	0.94
	Cohort x Scenario x Sex	0.002	0.001	0.001	1.6	0.11	0.54
Relative area of adult polyphenic hv5 eyespot pupils[a]	Intercept	0	0	0	NA	NA	0.61
	Cohort	0.470	0.075	0.075	6.2	**< 0.001**	0.61
	Scenario	0.662	0.078	0.079	8.4	**< 0.001**	0.61
	Cohort x Scenario	-0.095	0.071	0.071	1.3	0.18	0.27
Fertilization success[a]	Intercept	0	0	0	NA	NA	0.35
	Female experience	-0.139	0.913	0.921	0.2	0.9	0.35
	Female age at mating	1.861	0.977	0.986	1.9	0.059	0.35
	Male mate thermal treatment	2.111	0.918	0.925	2.3	**0.023**	0.35
	Female experience x Male mate thermal treatment	-2.151	0.900	0.907	2.4	**0.018**	0.35
	Thermal treatment duration	-0.616	0.985	0.993	0.6	0.5	0.10

Female longevity[a]	Intercept	0	0	0	NA	NA	0.27
	Female experience	-0.025	0.006	0.006	3.9	**<0.001**	0.27
	Mate choice allowed	-0.006	0.006	0.006	1.0	0.3	0.14
	Female feeding status after mating	-0.005	0.005	0.005	0.9	0.3	0.14
	Male mate age at mating	-0.005	0.006	0.006	0.8	0.4	0.14
	Male mate thermal treatment	0.002	0.005	0.005	0.5	0.6	0.13

Δ_i = difference in AIC[b] (or AICc[a]) of model *i* with the best candidate model (i.e., the model with the smallest AIC[b] or AICc[a]). SE = Conditional standard errors; Adjusted SE = Adjusted standard error estimator with improved coverage. w_+ = sum of the normalized Akaike weights across all candidate models (Δ_i <2) in which the variable occurred. NA = not applicable.

Table S2. Analyses of male mating proportions adjusted by courtship activity as a function of male seasonal phenotype in the experiments with naive or experienced wet season females. Using Chi-squared tests for given probabilities, we first tested for differences in mating probabilities among males of different seasonal phenotypes; second, we searched for the male phenotype(s) responsible for these differences by comparing the observed and theoretical mating proportions for each of the three male phenotypes and in paired comparisons between male phenotypes, by computing *P*-values with and without (in brackets) Holm-Bonferroni correction for multiple comparisons. $P \leq 0.05$ are in bold.

			Naive females (20 replicates; Fig. 3a)			Females exposed to wet males (20 replicates; Fig. 3b)			Females exposed to intermediate males (17 replicates; Fig. 3c)			Females exposed to dry males (15 replicates; Fig. 3d)		
Tests		Comparisons	Chi²	df	*P*	Chi²	df	*P*	Chi²	df	*P*	Chi²	df	*P*
Comparison of mating probabilities between male phenotypes		wet *vs.* intermediate *vs.* dry males	7.8	2	**0.02**	0.5	2	0.8	80	2	**<0.001**[a]	4.6	2	0.098
Searching for the phenotype(s) responsible for differences in mating probabilities	Per male phenotype	wet males (*vs.*intermediate and dry males)	0.2	1	0.6 (0.6)	0.5	1	1.0 (0.5)	9.2	1	**0.005 (0.002)**	4.4	1	0.11 **(0.036)**
		intermediate males (*vs.*wet and dry males)	2.9	1	0.2 (0.088)	0.1	1	1.0 (0.7)	78.8	1	**<0.001 (<0.001)**[b]	0.6	1	0.5 (0.5)
		dry males (*vs.*wet and intermediate males)	7.5	1	**0.019 (0.006)**	0.1	1	1.0 (0.7)	0.6	1	0.4 (0.4)	2.1	1	0.3 (0.15)
	In paired comparisons	wet *vs.* intermediate males	0.4	1	0.5 (0.5)	0.4	1	1.0 (0.5)	73	1	**<0.001 (<0.001)**[c]	2.9	1	0.2 (0.09)
		wet *vs.* dry males	4.1	1	0.084 **(0.042)**	0.4	1	1.0 (0.5)	1.8	1	0.2 (0.2)	4.4	1	0.11 **(0.037)**
		intermediate *vs.* dry males	7.3	1	**0.021 (0.007)**	0.01	1	0.9 (0.9)	52	1	**<0.001 (<0.001)**[d]	0.2	1	0.7 (0.7)

Wet = wet season males (27°C). Intermediate = intermediate season males (23°C). Dry = dry season males (17°C). When expected frequencies were below 5, we also report the *P*-value of Fisher's exact test: [a]$P = 0.042$, [b]$P < 0.001$ (<0.001), [c]$P = 0.014$ (0.007), [d]$P = 0.008$ (0.003).

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