Sexual selection drives maladaptive learning under climate warming

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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 climate crisis is not the worst human-induced rapid environmental change (HIREC hereafter), but it is the best documented for its negative effects on biodiversity (IPBES, 2019; IPCC & Press, 2014). Climate warming is expected to lead to a global extinction rate of 15% by 2100 (Cahill et al., 2013; Urban, 2015). This predicted extinction rate should be taken with caution, however, because estimation models do not incorporate key biological responses of species (Urban, 2015). One such biological response is learning ability, where animals can modify their behaviour in response to changes in the environment (Candolin & Wong, 2012a). Learning has emerged as a major response of species to HIREC, as was shown both theoretically (Botero et al., 2015) and empirically (Brown, 2013; Dukas, 2017; Sih et al., 2011, 2016; Snell-Rood et al., 2018; West-Eberhard, 2005). It is also now acknowledged that most organisms can modify their behaviours through learning (Morand-Ferron et al., 2016; Verzijden et al., 2012), including short-lived, non-social, and small-brained animals (Morand-Ferron et al., 2016; Nieberding & Holveck, 2018). 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 (Ozawa & Johansen, 2018; Rodrigues et al., 2010; Tedjakumala & Giurfa, 2013), or biased learning toward the easiest cues to learn (Westerman et al., 2012). Learned behavioural responses of organisms may thus produce widely different predictions about species responses to HIREC compared to innate behaviours. Second, most documented cases of learning in response to HIREC have recently shown that learned behaviours are actually maladaptive (Greggor et al., 2019). Maladaptation occurs whenever a "strategy" in a population becomes prevalent while it decreases the fitness of individuals (Crespi, 2000; Nesse, 2005). Learning may, therefore, accentuate the extinction risk of species, rather than alleviate it (as is usually assumed (Thorpe,

1963)), leading to so-called evolutionary traps (i.e., adaptive traits become maladaptive; Robertson et al., 2013; Schlaepfer et al., 2002).

While most work on climate warming documents (mal)adaptation under natural selection, 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 (Cahill et al., 2013). Sexual selection is an important biotic force of evolution (West-Eberhard, 2014) that is affected by climate warming as well (Candolin & Heuschele, 2008; Candolin & Wong, 2012b; Grazer & Martin, 2012b). 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 (Servedio & Boughman, 2017). Sexual selection may thus act against natural selection, increasing the risk of population extinction (Kokko & Brooks, 2003; Martínez-Ruiz & Knell, 2017; Tanaka, 1996).

Sexual interactions are strongly affected by learning (in vertebrates: Verzijden et al., 2012, and insects: Dion et al., 2019), but whether and how animal responses to the climate crisis are mitigated by learned sexual behaviours remains virtually unexplored (Barrett et al., 2019; Greggor et al., 2019). We used an ectothermic insect as a model, the African butterfly *Bicyclus anynana* (Butler 1879; Nymphalidae), which has been studied in-depth for sexual selection (San Martin et al., 2011), and whose sexual interactions are affected by learning. Indeed, exposure of females to males with modified artificial wing ornamentation influenced mate preferences (Westerman et al., 2012). Many insects, such as *B. anynana*, display strong developmental plasticity to cope with seasonally varying climatic conditions typical of the tropical zone: a wet season form adapted to the wet, warmer season favourable to reproduction, and a dry season form adapted to the cooler, stressful season with limited food resources and strongest selection for reproduction and survival. *B. anynana* thus provides morphological evidence of adaptation

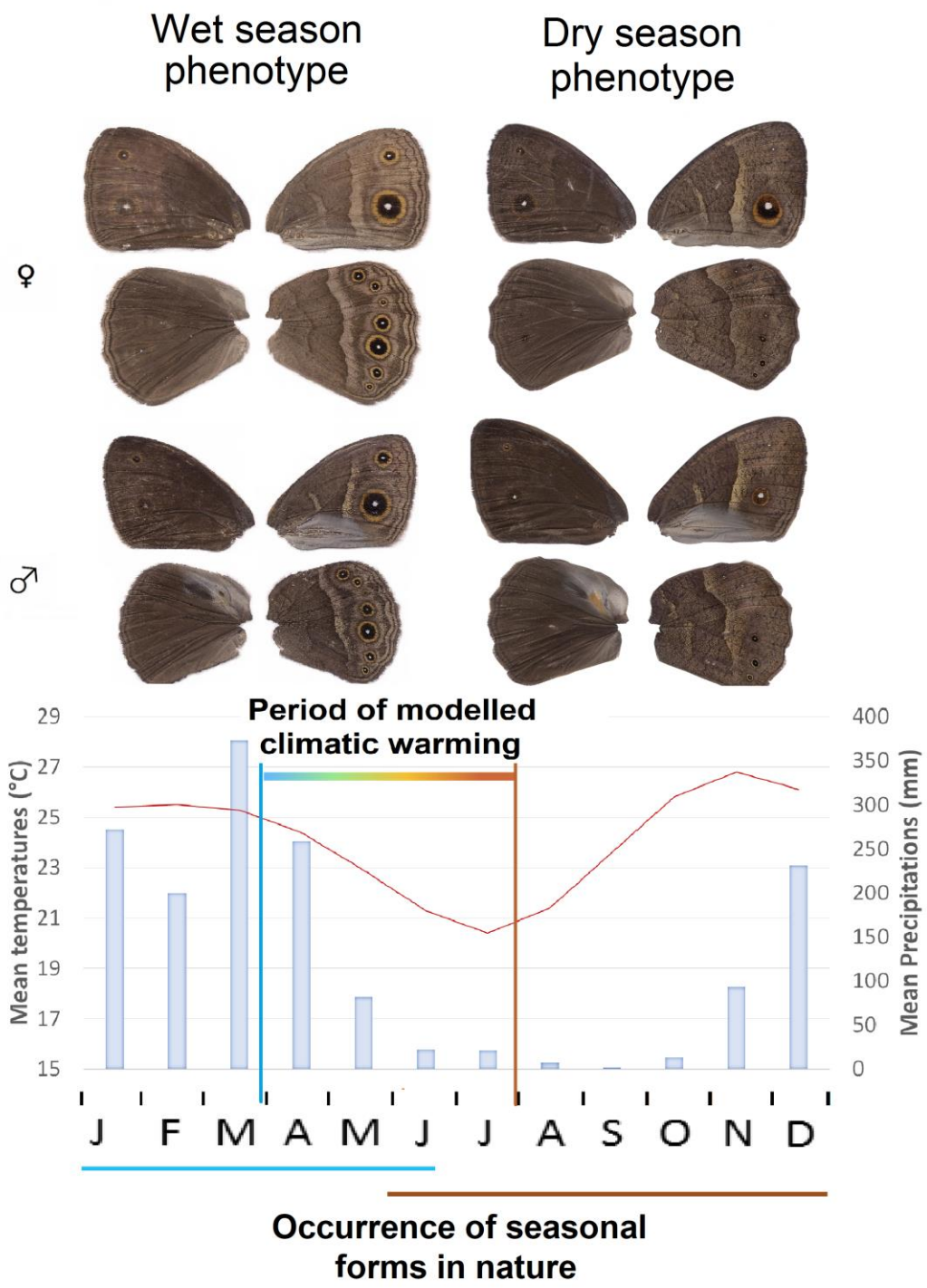


Fig. 1. Morphological differences of males and females between wet and dry season phenotypes and their temporal distribution across seasons in Malawi (Brakefield & Reitsma, 1991), in relation with monthly average values of precipitation (blue bars) and temperature (red curve) in the field (data available at (World-Bank-Group, 2019). The 120-day period of the climatic warming we modelled (Julian day 88 to 192, as in Fig. 2) is depicted.

to changing, seasonal climates that is easy to track (Muller et al., 2019). We focused here on the transition from the wet to the dry season when both seasonal forms co-occur with an intermediate seasonal form whose presence can be abundant, but is transient in the wild (Brakefield et al., 2007; Brakefield & Reitsma, 1991; Prudic et al., 2011; Shapiro, 1976; Windig et al., 1994). Under current climatic conditions, wet and intermediate seasonal forms are progressively replaced by a single generation of dry season individuals that cope with harsher environmental conditions until the next wet season (Fig. 1; Fig. S1).

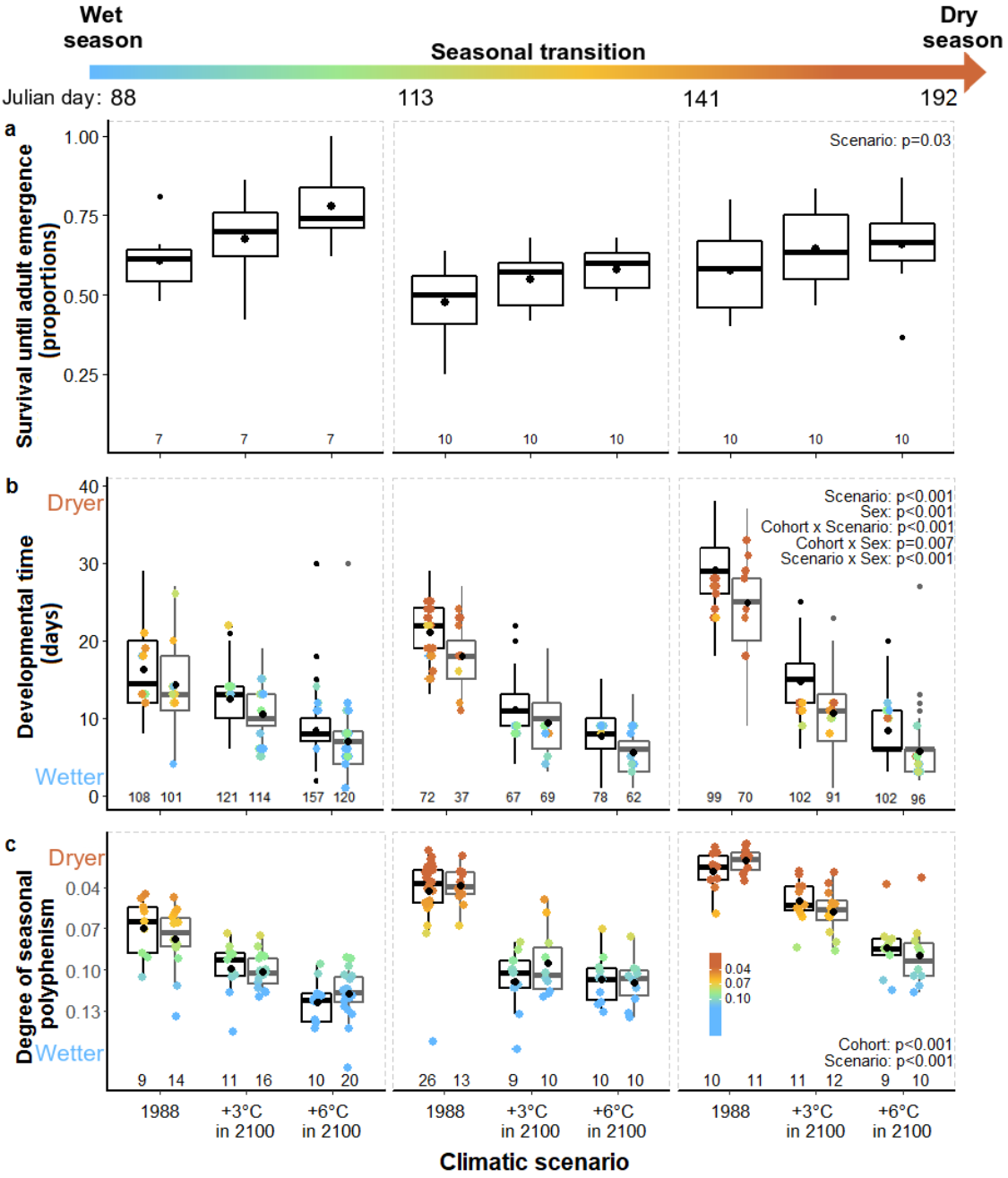
Here, we modelled the seasonal transition as it will occur in 2100 in the native population of our African butterfly, located in Malawi. Given that the production of phenotypes strongly depends on developmental temperature (Kooi & Brakefield, 1999), we expected that climate warming would lead to the production of wet season individuals at the beginning of the dry season due to the overall increase in temperature (prediction 1). To test how climate-induced changes in seasonal phenotypes affect sexual selection, we then quantified naive and learned mate preferences of females after exposure to males of the different seasonal forms. We expected naive females to prefer dry season males, because previous studies have shown that mating with dry season males increased female life expectancy and egg number compared to mating with wet season males (Prudic et al., 2011) (prediction 2). We further expected that social exposure to different male seasonal phenotypes will change mate preference of experienced compared to naive females (prediction 3). We also determined the effects of mating with different male seasonal forms on female survival and fertility as a proxy for reproductive fitness. We expected learning through social exposure to improve fitness and fertility of females mated with dry season males (prediction 4). Our results revealed that social learning of females about the availability of males with different adaptive values to warmer and colder climates produces learned sexual preferences that become maladaptive under climate warming.

Results

Climate warming produces 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 (Brakefield et al., 2009) by implementing hour-to-hour modelled changes in temperature and humidity 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, we found 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. S2).

We 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 expected for ectothermic species (Colinet et al., 2015). 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 and humidity decrease 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



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142 **Fig. 2.** Climate warming during the wet to dry seasonal transition increases the proportion of
143 surviving larvae until adult emergence (a), reduces developmental time (day 1 = first emerged
144 butterfly per cohort; b), and produces wet season butterflies at the onset of the dry season (c)
145 (Table S1). Data are presented from left to right using three cohorts of larvae whose
146 development cover the entire seasonal transition (cohort 1: from the 88th day of the year to the
147 112th, cohort 2 from the 113th to the 140th day and cohort 3 from the 141st to the 192th day). For
148 (b-c), colours indicate whether the individuals display the dry (brown), intermediate (yellow
149 and green), or wet (blue) season forms, based on the relative eyespot area of females (black)
150 and males (grey)(as in Muller et al., 2019). Mean values are indicated (black dot inside each
151 boxplot) and samples sizes (below each boxplot) are numbers of replicates in (a) and individuals
152 in (b-c).

153 seasonal transition. This wet seasonal form is typical for individuals developing at the beginning
154 of the seasonal transition under 1988 climatic conditions, confirming our first prediction (Fig.
155 2c). As the changes in humidity, the length of the seasonal transition, and the amplitude in
156 temperature during the seasonal transition are similar between past and future climatic scenarios
157 (Fig. S2), the appearance of the wet season form at the onset of the dry season in 2100 can be
158 attributed to an increase in absolute temperature.

159 The question is how maladaptive the altered appearance of seasonal forms is. Seasonal
160 polyphenism in *B. anynana* entails multiple morphological, physiological, behavioural, and life
161 history traits improving survival in the corresponding wet or dry season (Brakefield et al., 2007;
162 Pijpe et al., 2008), and the adaptive benefits of the dry season form in the dry season have
163 clearly been demonstrated (Prudic et al., 2014; Simpson et al., 2011). Increased temperature at
164 the onset of the dry season could further reduce vegetation cover, which will make the wet
165 season phenotype even more conspicuous and maladapted to the dry season environment
166 compared to the dry season phenotype (Prudic et al., 2014). In addition, the dry season form
167 has a lifespan two to three times longer than that of the wet season form, both in the lab (Pijpe
168 et al., 2007) and in the field (Brakefield & Reitsma, 1991), meaning that wet season individuals
169 are less likely to survive throughout the dry season. In the wild, adults with mismatched wing
170 patterns with respect to the season are rare in Malawi (e.g., only 8% of field caught individuals
171 in Malawi belonged to the intermediate seasonal form across all seasons between 1988 and
172 1991 (Windig et al., 1994)). Currently, the dry season in Malawi lasts 6 to 7 months, and
173 although rainfall patterns and the length of the dry season are not expected to change after
174 climate warming based on our simulations, emergence of wet season phenotypes that live
175 shorter at the onset of the dry season are expected to increase the extinction risk of the
176 population during the dry season.

177

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

180 Female lifespan and reproductive output depend on the seasonal form of her mating partner
181 (Prudic et al., 2011). We focused on mate preference of wet season females, because this is the
182 choosiest female seasonal form (Prudic et al., 2011) and wet season individuals prevail at the
183 onset of the dry season under the 2100 climatic scenarios. We quantified naive (innate) female
184 sexual preference for the different seasonal phenotypes that co-occur during the seasonal
185 transition. Naive females preferred to mate with dry season males over intermediate or wet
186 season males (Fig. 3a; Table S2): the mating proportions of dry season males were significantly
187 higher, while the mating proportions of intermediate and wet season males were lower than
188 expected based on phenotype-specific male courtship rate.

189 Innate preference for dry season males is adaptive, because females that mated with a
190 dry season male increased their life expectancy by ~65% and laid between ~30 to ~240% more
191 eggs compared to females mated with a wet season male, in line with our second prediction.
192 Despite the sexual benefits of mating with dry season males, the innate preference for dry season
193 males may, however, become maladaptive by 2100, because dry season males will become rare
194 after climate warming, meaning that females will have to mate with wet season males, which
195 we know reduces reproductive fitness. Mating with wet instead of dry season males may thus
196 drastically reduce the proportion of females and developing eggs surviving the harsh, dry season
197 until the next wet season, increasing the extinction risk of *B. anynana* populations.

198

199 ***Exposure to both seasonal male forms leads to maladaptive learned mate preferences***

200 Short-term exposure to males with artificial eyespot numbers is known to modify female mating
201 preferences in *B. anynana* (Westerman et al., 2012). We thus hypothesized that changes in the

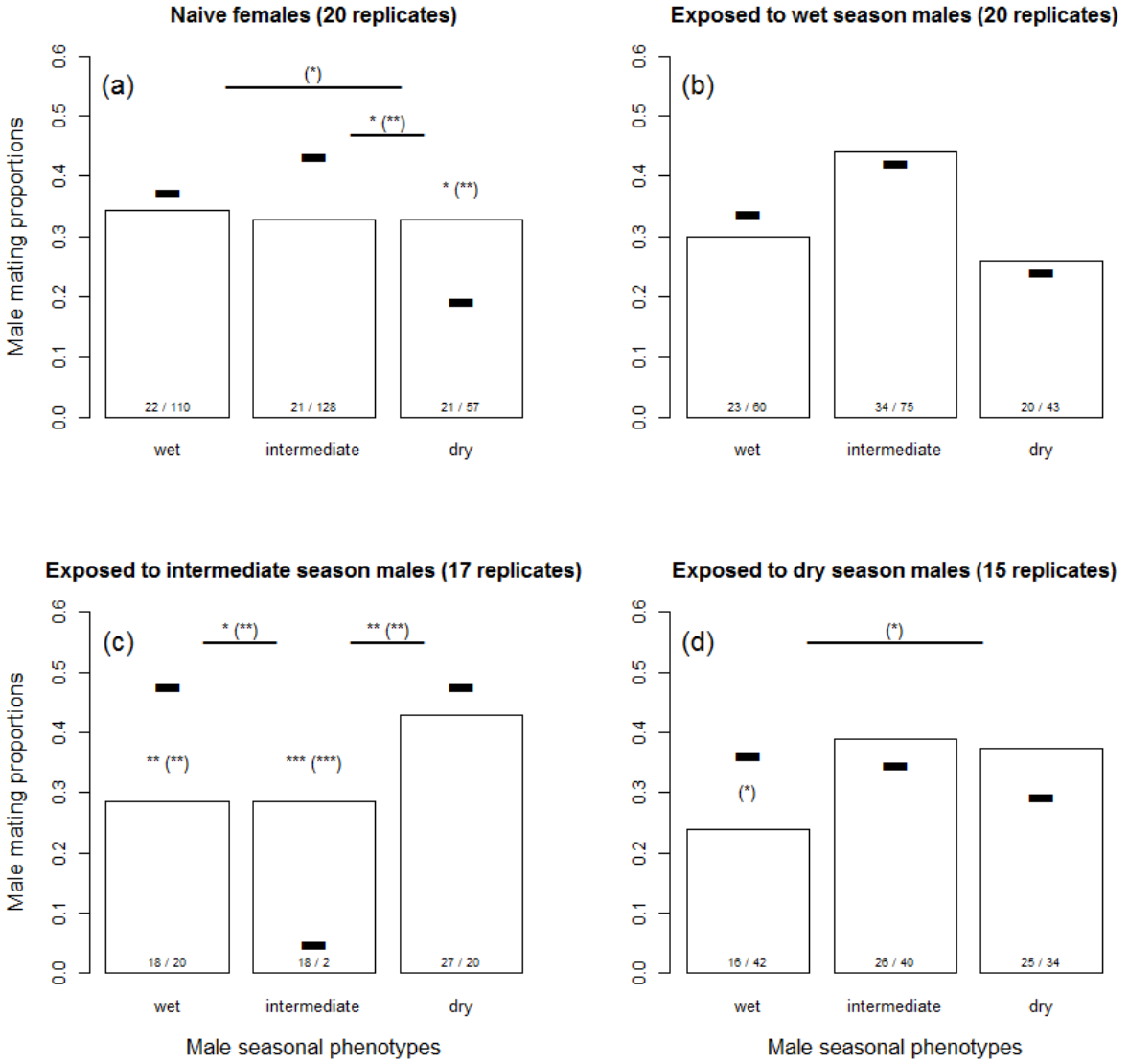


Fig. 3. Male mating success depends on the seasonal form (wet, intermediate or dry) and whether females are naive (a) or have been previously exposed to wet (b), intermediate (c) or dry season males (d). Adjusted Holm-Bonferroni *P*-values (and uncorrected *P*-values in brackets) indicate significant 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; Supplementary Table S4). Samples sizes inside each bar are numbers of male matings/courtships.

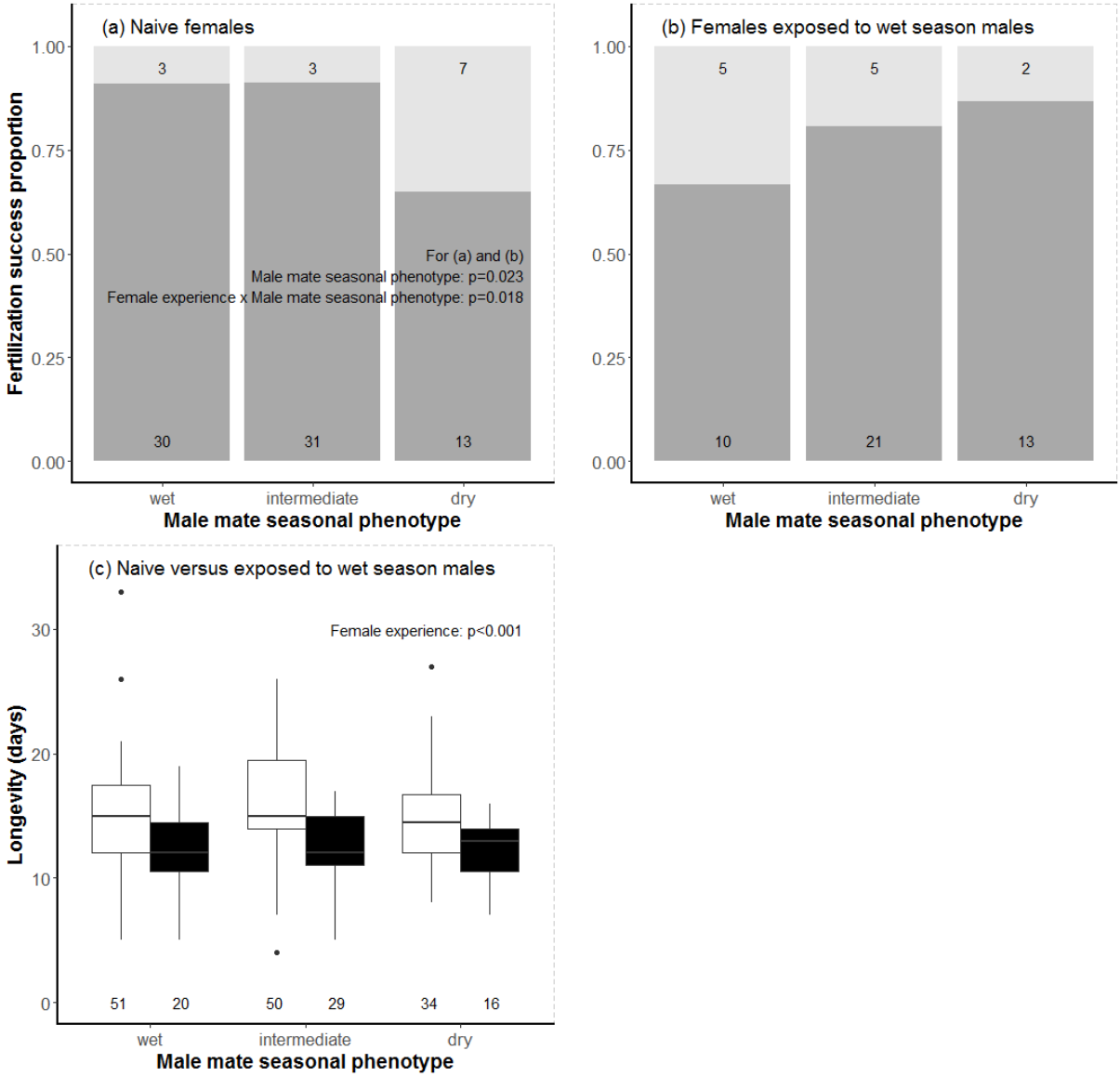
seasonal phenotype of males, which includes variation in eyespot size, modifies the innate mate preference through learning, as in many other insects (Dion et al., 2019). To test this, we exposed virgin, wet season females for a 3-hour period (as in Westerman et al., 2012) to wet

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 (Brakefield & Reitsma, 1991); Fig. 3c). 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 surprisingly 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.

Learning of sexual preference affects female fitness

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 fourth prediction, experienced females had reduced longevity (Fig. 4c), suggesting that social learning generates some costs (Barrett et al., 2019). 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

241 **Figure 4**



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243 **Fig. 4.** Both the proportion of wet season females whose eggs were fertilized (a-b; in dark grey)
244 and female longevity (c) differ depending on whether the females are naive (a) or have been
245 exposed previously to wet season males (b). Naive and experienced females are depicted by
246 white or black boxplots, respectively in (c). Fertilization success, but not longevity, also
247 depends on the seasonal form (wet, intermediate, dry) of males. Sample sizes are given inside
248 each bar or below each boxplot.
249

250 males depends on local environmental conditions, for which variation is known to affect the
251 expression of sexual preference in *B. anynana* and in many other sexually reproducing species
252 (e.g., choice or no-choice mating experiments, density, sex ratio (Holveck et al., 2015; Miller
253 & Svensson, 2014; Nieberding & Holveck, 2018)). 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 (Prudic et al., 2011)).

Discussion

We have provided a first example of a learned sexual interaction that produces maladaptation under climate warming (Barrett et al., 2019; Greggor et al., 2019). 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 become 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 (Candolin & Vlieger, 2013; Huey Raymond et al., 2012), 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 (Prokuda & Roff, 2014). As social learning is costly (in general, Mery & Kawecki, 2005; here, we find potential survival costs for *B. anynana*), and has a genetic basis (Barrett et al., 2019), maladaptive learned sexual preference could be counter-selected (Lotem, 1993).

There is significant gene flow among *B. anynana* populations across its distribution range (Bacquet et al., 2016; de Jong et al., 2011), 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; Phillips & McIntyre, 2000). Yet, there is little genetic variation for seasonal polyphenism between geographically distant populations (de Jong et al., 2010). More southern populations develop into the wet season form at lower temperatures than the Malawi population (de Jong et al., 2010); 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 (de Jong et al., 2010; Roskam & Brakefield, 1999). *B. anynana* populations from the Northern hemisphere may use rainfall, and not temperature, as a cue for predicting the onset of the dry season (Roskam & Brakefield, 1999). 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.

304 However, local adaptation by genetic evolution may be very limited for the Malawi population
305 of *B. anynana* because most mutations are non-adaptive (Brakefield et al., 2009), and because
306 there is little genotypic variation for several aspects of seasonal polyphenism, both regarding
307 the development of wing patterns in response to temperature (Wijngaarden et al., 2002) and
308 other life history traits forming the wet or dry season phenotypes, such as starvation resistance
309 and resting metabolic rate (Oostra et al., 2018).

310 The broader relevance of our results rests on two pillars. First, while learning is usually
311 assumed to improve immediate adaptation to environmental variation (within the lifetime of an
312 organism), the fitness effects of learning remain rarely assessed (Candolin & Wong, 2012b;
313 Dion et al., 2019; Morand-Ferron et al., 2016; Nieberding et al., 2018). Here, we discovered
314 that learning reverses both mate preference and its effects on longevity and reproductive fitness.
315 Our results thus reveal that using behavioural data from naive individuals to predict sexual
316 responses of animals may lead to erroneous conclusions. Whether learning increases or limits
317 adaptation to sexual selection under climate warming remains largely undocumented so far (but
318 see Botero et al., 2009 who found that more complex, learned male bird songs were present in
319 more unpredictable and unfavourable climatic environments). Maladaptive or suboptimal
320 learning was, however, previously found for foraging (Avarguès-Weber et al., 2018) and two
321 recent reviews document that learning in response to HIREC is maladaptive for a large number
322 of environmental threats and behaviours (Barrett et al., 2019; Greggor et al., 2019). We suggest
323 that maladaptive learning in sexual interactions under HIREC may occur in many species, as
324 most animals studied to date modify their sexual behaviours through learning (Dion et al., 2019;
325 Verzijden et al., 2012), which could lead to evolutionary traps (Robertson et al., 2013).

326 Second, our results highlight the importance of sexual selection as a strong evolutionary
327 force to include for quantifying species responses to HIREC, such as climate warming
328 (Candolin, 2019; Candolin & Heuschele, 2008). 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 (Musolin & Saulich, 2012; Parmesan, 2006; Thackeray et al., 2016). However, the effects of anthropogenic environmental changes on sexual selection matter as well, because sexual selection may increase the extinction risk of populations (Holland, 2002; Martínez-Ruiz & Knell, 2017; Parrett & Knell, 2018; Plesnar-Bielak et al., 2012). It is indeed increasingly acknowledged that human activities disturb important aspects of sexual selection (e.g., eutrophication and turbidity including algal blooms (Seehausen et al., 1997), urban noise (Montague et al., 2013), selective harvest in hunting (Knell & Martínez-Ruiz, 2017). This is expected as sexual selection has a strong environmental component (Ingleby et al., 2010; Parrett & Knell, 2018). Regarding the climate crisis, sexual selection is altered through the availability of sexual partners (Twiss et al., 2007) with potential effects on the proportion of extra-pair mating opportunities (Bichet et al., 2016), relative fitness of mono- versus polyandrous females (Grazer & Martin, 2012a), assortative mating (Santos et al., 2018), sexual conflict (García-Roa et al., 2019), secondary sexual traits (Evans & Gustafsson, 2017), and mate preferences (Candolin, 2019; Fuxjäger et al., 2019). 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 that represent most of the animal biomass and species diversity on Earth (Bar-On et al., 2018) and generally show strong phenotypic plasticity to cope with alternating seasons (Simpson et al., 2011). Furthermore, tropical biomes both contain most biodiversity and are most threatened by climate warming (Deutsch et al.,

2008; Hoffmann et al., 2013; Lister & Garcia, 2018; Sunday et al., 2011). 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 (Crespi, 2000; Robertson et al., 2013). 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 (Bell, 2013; Bradshaw & McNeilly, 1991). 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 (Brakefield et al., 2009). Between 400 and 600 butterflies per generation were used to maintain high levels of heterozygosity and polymorphism (Van't Hof et al., 2005) 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* (Brakefield et al., 2009). 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 regime and a high relative humidity (70 ± 5%) representing the wet season in the field (Brakefield et al., 2009), 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),

because the developmental temperature experienced during this time window determines the expression of adult polyphenism (Bear & Monteiro, 2013; Brakefield & Reitsma, 1991; Kooi & Brakefield, 1999; Oostra et al., 2011). 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. S2). 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 (Taylor et al., 2012). 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. S2). 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)(IPCC & Press, 2014), 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. S2). Pupae were collected and placed in 1-dm³ circular plastic boxes, after which butterflies were frozen at -80°C. We then evaluated the effects of global warming 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; Muller et al., 2019; 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 (Brakefield et al., 2007; Brakefield & Reitsma, 1991; Muller et al., 2019; Oostra et al., 2011; Prudic et al., 2011). 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 (Wedell, 2010), *(ii)* differ among seasonal forms (Bear & Monteiro, 2013), and *(iii)* predict male mating success (Holveck et al., 2015; Nieberding & Holveck, 2017, 2018). 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 (Holveck et al., 2015; Nieberding & Holveck, 2017, 2018). 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 (Heuskin et al., 2014; Nieberding et al., 2008, 2012). We used 3-

454 6-day-old virgin females as females readily mate at this age in the laboratory (Brakefield et al.,
455 2009; Nieberding et al., 2008, 2012). These ages also match the general age of females in
456 behavioural experiments with this species (Holveck et al., 2015; Nieberding & Holveck, 2017).
457 We first introduced the males into the experimental area and left them to adapt and interact with
458 one another for 1 hour, after which females were added. Experimental cages (120 x 59 x 60 cm)
459 containing two maize plants to increase perching and hiding opportunities were used, and moist
460 cotton with banana slices provided. This cage size, a density below the recommended threshold
461 of 0.1 individual/dm^3 for *B. anynana*, and a sex ratio of 3 males for 1 female within the species-
462 specific range creates semi-natural conditions and allows the full expression of courtship
463 display by males (including flight), and of female mate choice that allows rejection of a male
464 by flying away from an unwanted male (Holveck et al., 2015; Nieberding & Holveck, 2017,
465 2018). Each replicate was observed for 10 min every 30 min, with total observation duration of
466 30 min per replicate. Direct behavioural observations for these 10 min were encoded using the
467 software The Observer 5.0 (Noldus Information Technology, Wageningen, The Netherlands)
468 and when a male started courting a female, we followed this courtship until it ended before
469 focusing on another male. Throughout each experiment, we noted the identity of mates of all
470 formed couples.
471
472 ***Fitness of wet season females mated with different male seasonal forms***
473 To test the fitness consequences of social learning in females, we measured fertilization success
474 of eggs laid by either naive or experienced wet season females mated with males of different
475 seasonal forms, as well as female longevity (details in Supplementary Methods). After
476 experiments were finished, both naive and experienced females were singly placed in a 1-dm^3
477 plastic box with wet cotton as water supply and a maize leaf to oviposit (Brakefield et al., 2009).
478 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 (RStudio 2016). 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 (Bates et al., 2015) 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 (Elston et al., 2001; Holveck et al., 2015), 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 (Millot, 2009). We also performed Fisher's Exact tests when the expected frequencies were below 5.

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Competing interests

The authors declare no competing financial interests.

Data availability

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

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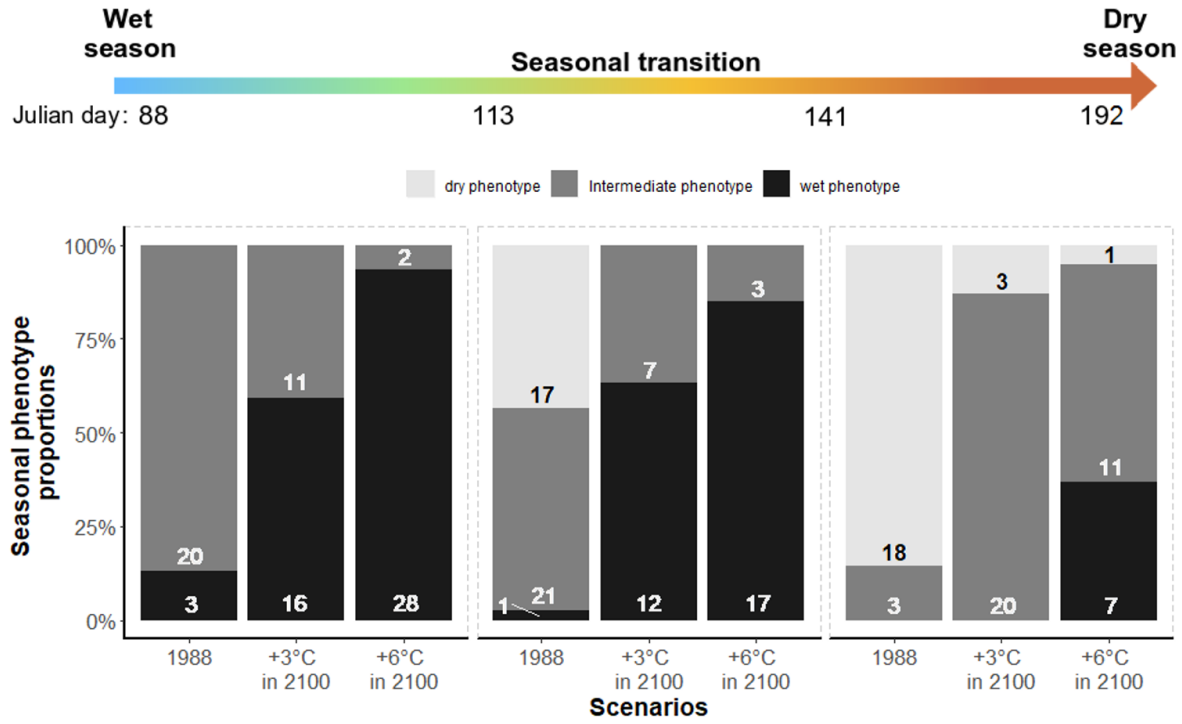
841 **Supplementary Figures**



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843 ***Fig. S1.*** Proportions of male seasonal forms (dry, intermediate, wet) under the three different
844 climatic scenarios for cohort 1, 2 and 3 (each in 1 graph) for the entire duration of the seasonal
845 transition from the wet to the dry season.

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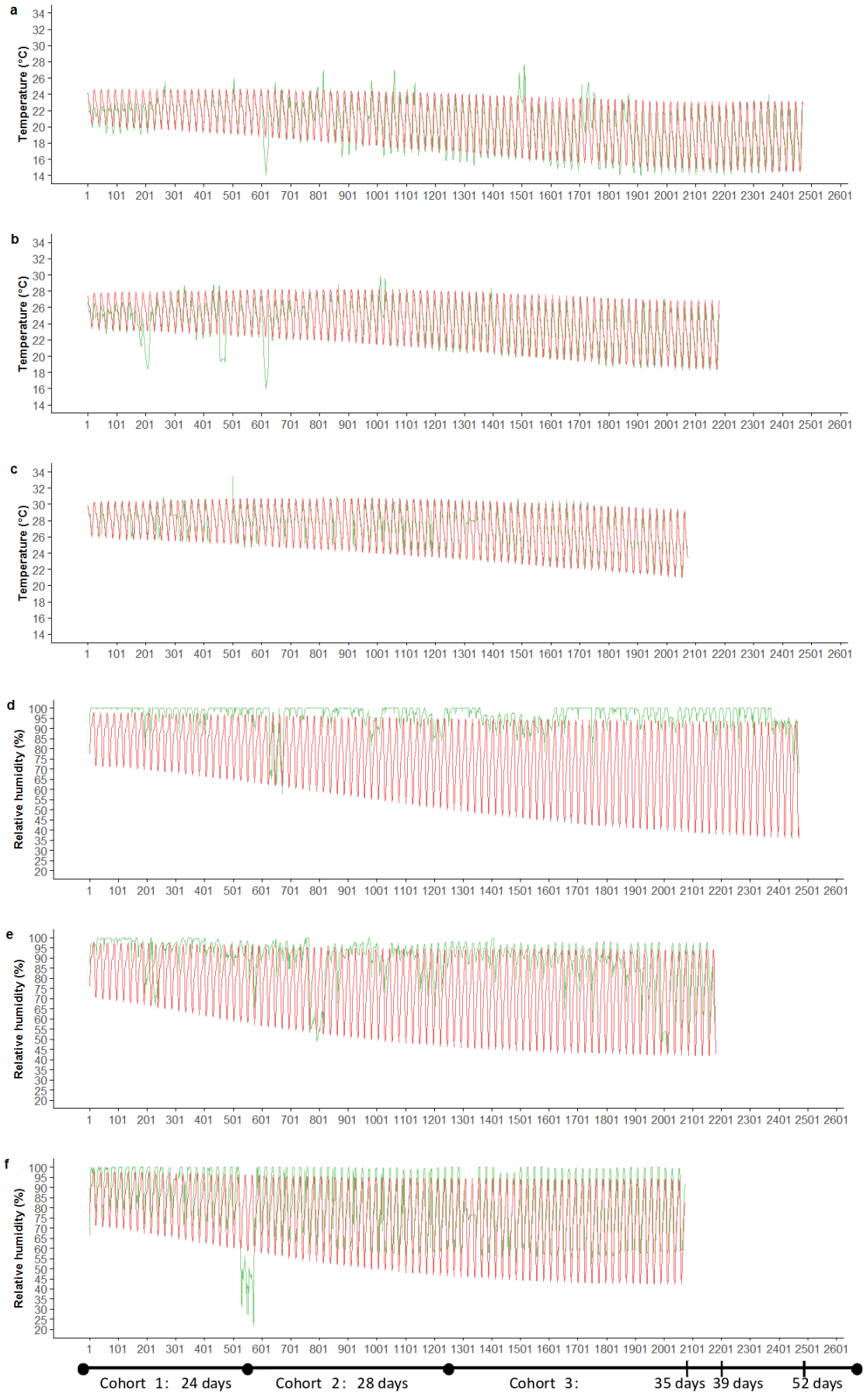

Fig. S2. Experimental and theoretical temperature and relative humidity throughout the seasonal transition. We registered the experimental temperature (°C; a-c) and relative humidity (%; d-f) with sensors (HOBO U23-001) in the incubators (green) and compared them to theoretical climatic conditions (red) 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 developmental time compared 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

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

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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	Chi^2	df	*P*	Chi^2	df	*P*	Chi^2	df	*P*	Chi^2	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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