Sexual selection drives maladaptive learning under climate warming

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24   *Abstract*

25   Current predictions for the effects of the climate crisis on biodiversity loss have so far ignored

26   the effects of learning ability and sexual selection. Using the African butterfly *Bicyclus*

27   *anynana*, which shows strong phenotypic plasticity in response to temperature, we show that

28   learning produces a maladaptive mate preference under climate warming. We modelled climate

29   warming and found that as temperature becomes an unreliable cue at the onset of the dry season,

30   adult butterflies displayed the wet season rather than the dry season form. Female learning

31   further suppressed their innate, adaptive sexual preference for dry season males. Instead,

32   females learned to prefer a phenotype transiently present during the seasonal transition. Female

33   fertility and longevity were also affected by learning, reducing female fitness following climate

34   warming. Our results emphasize the importance of sexual selection, learning, and their fitness

35   consequences for understanding (mal)adaptation of natural populations to climate warming.

36 **Introduction**

37 The climate crisis is not the worst human-induced rapid environmental change (HIREC

38 hereafter), but it is the best documented for its negative effects on biodiversity (IPBES, 2019;

39 IPCC & Press, 2014). Climate warming is expected to lead to a global extinction rate of 15%

40 by 2100 (Cahill et al., 2013; Urban, 2015). This predicted extinction rate should be taken with

41 caution, however, because estimation models do not incorporate key biological responses of

42 species (Urban, 2015). One such biological response is learning ability, where animals can

43 modify their behaviour in response to changes in the environment (Candolin & Wong, 2012a).

44 Learning has emerged as a major response of species to HIREC, as was shown both theoretically

45 (Botero et al., 2015) and empirically (Brown, 2013; Dukas, 2017; Sih et al., 2011, 2016; Snell-

46 Rood et al., 2018; West-Eberhard, 2005). It is also now acknowledged that most organisms can

47 modify their behaviours through learning (Morand-Ferron et al., 2016; Verzijden et al., 2012),

48 including short-lived, non-social, and small-brained animals (Morand-Ferron et al., 2016;

49 Nieberding & Holveck, 2018). Learned behaviours for species responses to climate change are

50 important for two reasons: First, learning can significantly change (innately expressed)

51 behaviours, such as aversive and reversal learning in response to danger or fear (Ozawa &

52 Johansen, 2018; Rodrigues et al., 2010; Tedjakumala & Giurfa, 2013), or biased learning toward

53 the easiest cues to learn (Westerman et al., 2012). Learned behavioural responses of organisms

54 may thus produce widely different predictions about species responses to HIREC compared to

55 innate behaviours. Second, most documented cases of learning in response to HIREC have

56 recently shown that learned behaviours are actually maladaptive (Greggor et al., 2019).

57 Maladaptation occurs whenever a "strategy" in a population becomes prevalent while it

58 decreases the fitness of individuals (Crespi, 2000; Nesse, 2005). Learning may, therefore,

59 accentuate the extinction risk of species, rather than alleviate it (as is usually assumed (Thorpe,

60   1963)), leading to so-called evolutionary traps (i.e., adaptive traits become maladaptive;

61   Robertson et al., 2013; Schlaepfer et al., 2002).

62   While most work on climate warming documents (mal)adaptation under natural

63   selection, another key biological mechanism to consider for improving the forecasting of

64   species extinction rates is sexual selection. Over 50% of recorded climate change impacts are

65   not due to direct effects of increased temperature, but to biotic interactions (Cahill et al., 2013).

66   Sexual selection is an important biotic force of evolution (West-Eberhard, 2014) that is affected

67   by climate warming as well (Candolin & Heuschele, 2008; Candolin & Wong, 2012b; Grazer

68   & Martin, 2012b). Sexual selection is further important to consider, because it can reduce local

69   adaptation due to the cost of sexual ornaments (handicap hypothesis) and sexual conflict

70   (Servedio & Boughman, 2017). Sexual selection may thus act against natural selection,

71   increasing the risk of population extinction (Kokko & Brooks, 2003; Martínez-Ruiz & Knell,

72   2017; Tanaka, 1996).

73   Sexual interactions are strongly affected by learning (in vertebrates: Verzijden et al.,

74   2012, and insects: Dion et al., 2019), but whether and how animal responses to the climate crisis

75   are mitigated by learned sexual behaviours remains virtually unexplored (Barrett et al., 2019;

76   Greggor et al., 2019). We used an ectothermic insect as a model, the African butterfly *Bicyclus*

77   *anynana* (Butler 1879; Nymphalidae), which has been studied in-depth for sexual selection (San

78   Martin et al., 2011), and whose sexual interactions are affected by learning. Indeed, exposure

79   of females to males with modified artificial wing ornamentation influenced mate preferences

80   (Westerman et al., 2012). Many insects, such as *B. anynana*, display strong developmental

81   plasticity to cope with seasonally varying climatic conditions typical of the tropical zone: a wet

82   season form adapted to the wet, warmer season favourable to reproduction, and a dry season

83   form adapted to the cooler, stressful season with limited food resources and strongest selection

84   for reproduction and survival. *B. anynana* thus provides morphological evidence of adaptation
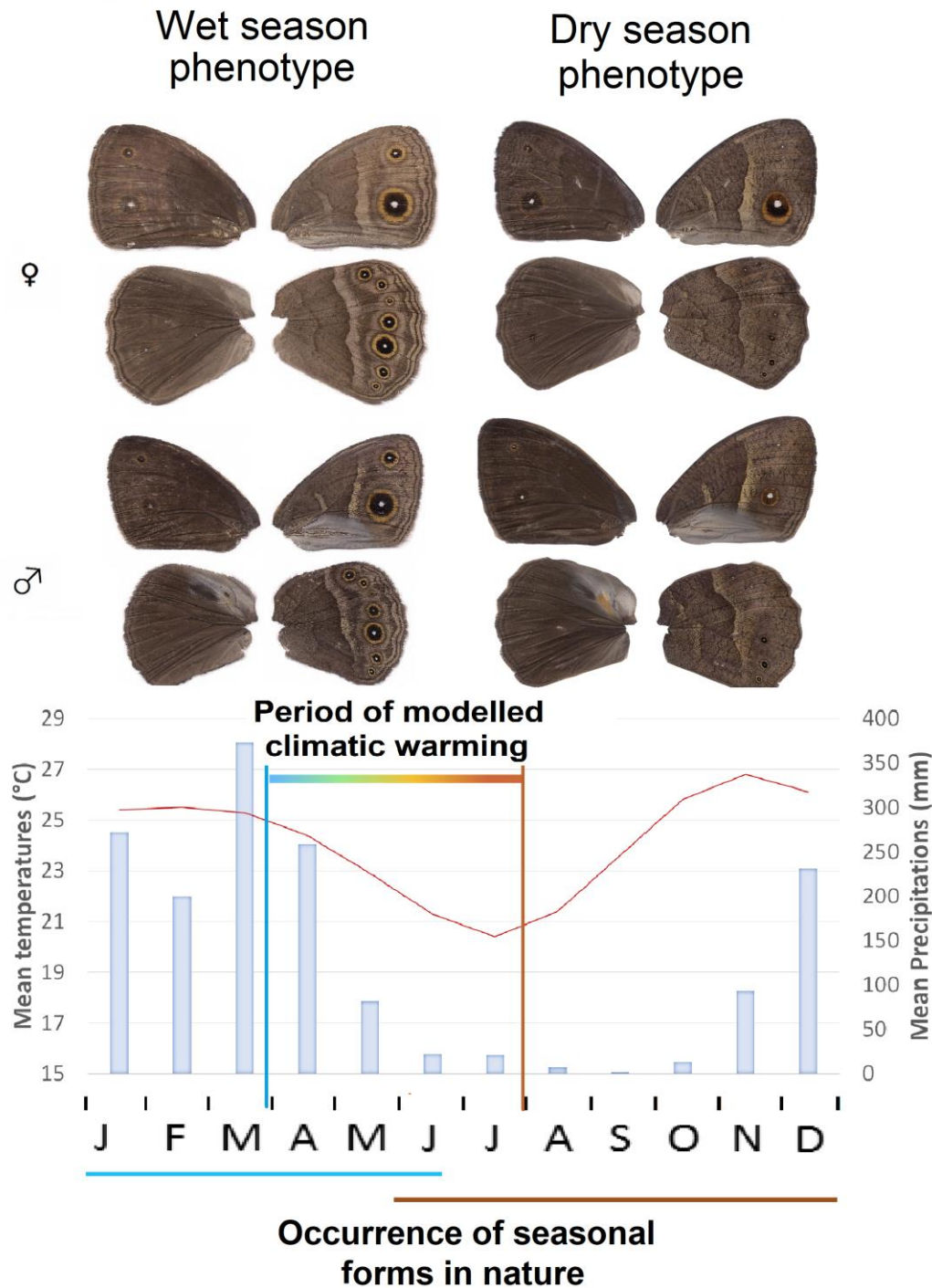
Fig. 1. Morphological differences of males and females between wet and dry season phenotypes and their temporal distribution across seasons in Malawi (Brakefield & Reitsma, 1991), in relation with monthly average values of precipitation (blue bars) and temperature (red curve) in the field (data available 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.

91 to changing, seasonal climates that is easy to track (Muller et al., 2019). We focused here on

92 the transition from the wet to the dry season when both seasonal forms co-occur with an

93 intermediate seasonal form whose presence can be abundant, but is transient in the wild

94 (Brakefield et al., 2007; Brakefield & Reitsma, 1991; Prudic et al., 2011; Shapiro, 1976; Windig

95 et al., 1994). Under current climatic conditions, wet and intermediate seasonal forms are

96 progressively replaced by a single generation of dry season individuals that cope with harsher

97 environmental conditions until the next wet season (Fig. 1; Fig. S1).

98   Here, we modelled the seasonal transition as it will occur in 2100 in the native

99 population of our African butterfly, located in Malawi. Given that the production of phenotypes

100 strongly depends on developmental temperature (Kooi & Brakefield, 1999), we expected that

101 climate warming would lead to the production of wet season individuals at the beginning of the

102 dry season due to the overall increase in temperature (prediction 1). To test how climate-induced

103 changes in seasonal phenotypes affect sexual selection, we then quantified naive and learned

104 mate preferences of females after exposure to males of the different seasonal forms. We

105 expected naive females to prefer dry season males, because previous studies have shown that

106 mating with dry season males increased female life expectancy and egg number compared to

107 mating with wet season males (Prudic et al., 2011) (prediction 2). We further expected that

108 social exposure to different male seasonal phenotypes will change mate preference of

109 experienced compared to naive females (prediction 3). We also determined the effects of mating

110 with different male seasonal forms on female survival and fertility as a proxy for reproductive

111 fitness. We expected learning through social exposure to improve fitness and fertility of females

112 mated with dry season males (prediction 4). Our results revealed that social learning of females

113 about the availability of males with different adaptive values to warmer and colder climates

114 produces learned sexual preferences that become maladaptive under climate warming.

115

116   **Results**

117   *Climate warming produces a maladaptive increase in wet season forms at the onset of the dry*

118   *season*

119   We mimicked the entire wet to dry seasonal transition (120 days) as it occurs in Malawi

120   (Brakefield et al., 2009) by implementing hour-to-hour modelled changes in temperature and

121   humidity and monthly changes in photoperiod. Three climatic scenarios were applied to

122   butterfly development: *1)* climatic conditions reported for 1988 ("reference" scenario); *2)* the

123   expected climate in 2100, with a 3°C temperature increase; and *3)* the expected climate in 2100,

124   with a 6°C temperature increase. Overall, we found that the alternation of wet and dry seasons

125   was maintained in 2100, with a wet season of 5 to 6 months. Under the warmest scenario,

126   however, the average temperature of both seasons increased by a quantity comparable to the

127   amplitude of the seasonal cycle (6°C, as was found for all examined models). Consequently,

128   the higher temperatures typical of the wet season in 1988 will be common during the dry season

129   in 2100 (Fig. S2).

130   We reared three successive cohorts of *B. anynana* larvae under these climatic conditions

131   until adult emergence. Comparing the 1988 data to the +6°C climatic scenario, climate warming

132   increased survival by 21% (Fig. 2a; Table S1), and reduced development time by half at the

133   beginning of the seasonal transition (15.4 to 7.8 days), and by 74% (27.4 to 7.2 days) at the end

134   (Fig. 2b; Table S1). An increase in survival and reduced development time are indeed expected

135   for ectothermic species (Colinet et al., 2015). Regarding seasonal phenotypes, we found that

136   climate warming increased the expression of the wet season phenotype throughout the seasonal

137   transition (Fig. 2c). Although butterflies displayed an increasingly dry season phenotype

138   throughout the seasonal transition under the current scenario (which can be expected as

139   temperature and humidity decrease during the seasonal transition; Fig. 2c), development under

140   the +3°C and +6°C climatic scenarios produced a wet season phenotype at the end of the

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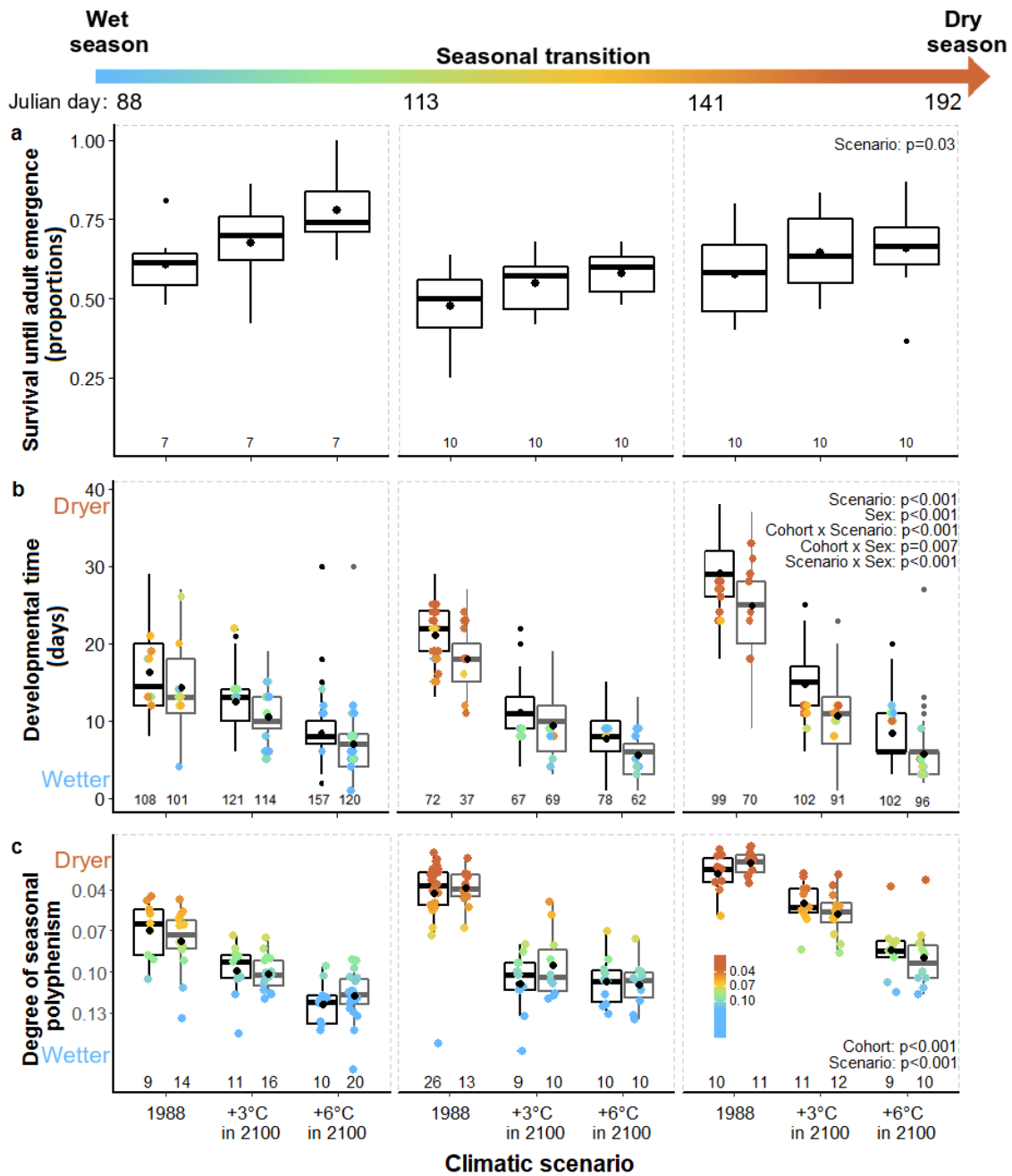
Fig. 2. Climate warming during the wet to dry seasonal transition increases the proportion of surviving larvae until adult emergence (a), reduces developmental time (day 1 = first emerged butterfly per cohort; b), and produces wet season butterflies at the onset of the dry season (c) (Table S1). Data 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 Muller et al., 2019). Mean values are indicated (black dot inside each boxplot) and samples sizes (below each boxplot) are numbers of replicates in (a) and individuals 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
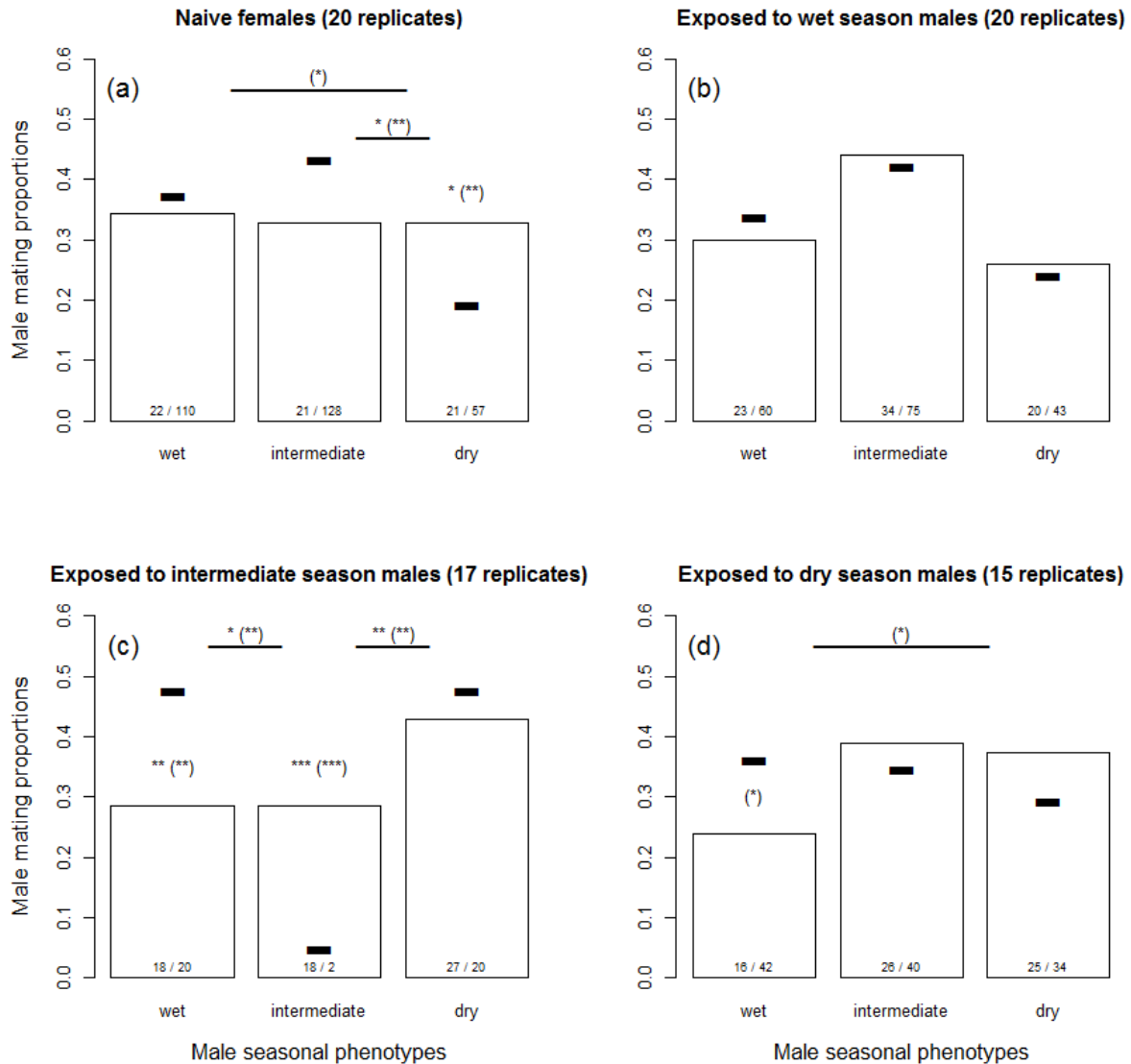
Fig. 3. Male mating success depends on the seasonal form (wet, intermediate or dry) and whether females are naive (a) or have been previously exposed to wet (b), intermediate (c) or dry season males (d). Adjusted Holm-Bonferroni *P*-values (and uncorrected *P*-values in brackets) indicate significant 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

216   season males (the predominant form based on the 2100 scenarios; Fig. 3b), dry season males

217   (the predominant form at the onset of the dry season based on past climatic conditions in

218   Malawi; Fig. 3d), or intermediate seasonal phenotypes (found primarily during the seasonal

219   transition in Malawi (Brakefield & Reitsma, 1991); Fig. 3c). Females had access to all

220   phenotypic traits of males (i.e., olfactory, visual, and auditory), except for direct contact or

221   mating. Overall, exposure of virgin wet season females to males of different seasonal forms

222   induced a long-term (3 to 6 days) suppression of innate female preferences for dry season males

223   (Fig. 3; Table S2), meaning that long-term memory formation was involved. In addition, pre-

224   exposure to different male seasonal forms surprisingly increased female mate preference

225   towards intermediate season males, compared to naive females (Fig. 3; Table S2). Indeed,

226   mating proportions of intermediate season males either matched (Fig. 3b, d) or exceeded (Fig.

227   3c) the expected mating rate based on courtship activity, as compared to their lower than

228   expected mating numbers with naive females (Fig. 3a). The preference of wet season females

229   for intermediate season males was highest when wet season females were exposed to

230   intermediate season males (Fig. 3c; Table S2), in line with our third prediction.

231

232   ***Learning of sexual preference affects female fitness***

233   We assessed the (mal)adaptive value of learning on mating preference by quantifying two

234   fitness parameters of naive and experienced wet season females: longevity and fertilization

235   success. In line with our fourth prediction, experienced females had reduced longevity (Fig. 4c),

236   suggesting that social learning generates some costs (Barrett et al., 2019). In addition, the

237   proportion of successfully fertilized eggs of naive females decreased when they mated with dry

238   rather than with intermediate or wet season males (Fig. 4a). This contradicts the work of Prudic

239   *et al.* (2011), suggesting that the fitness benefits of naive females mated with different types of

240

241 **Figure 4**
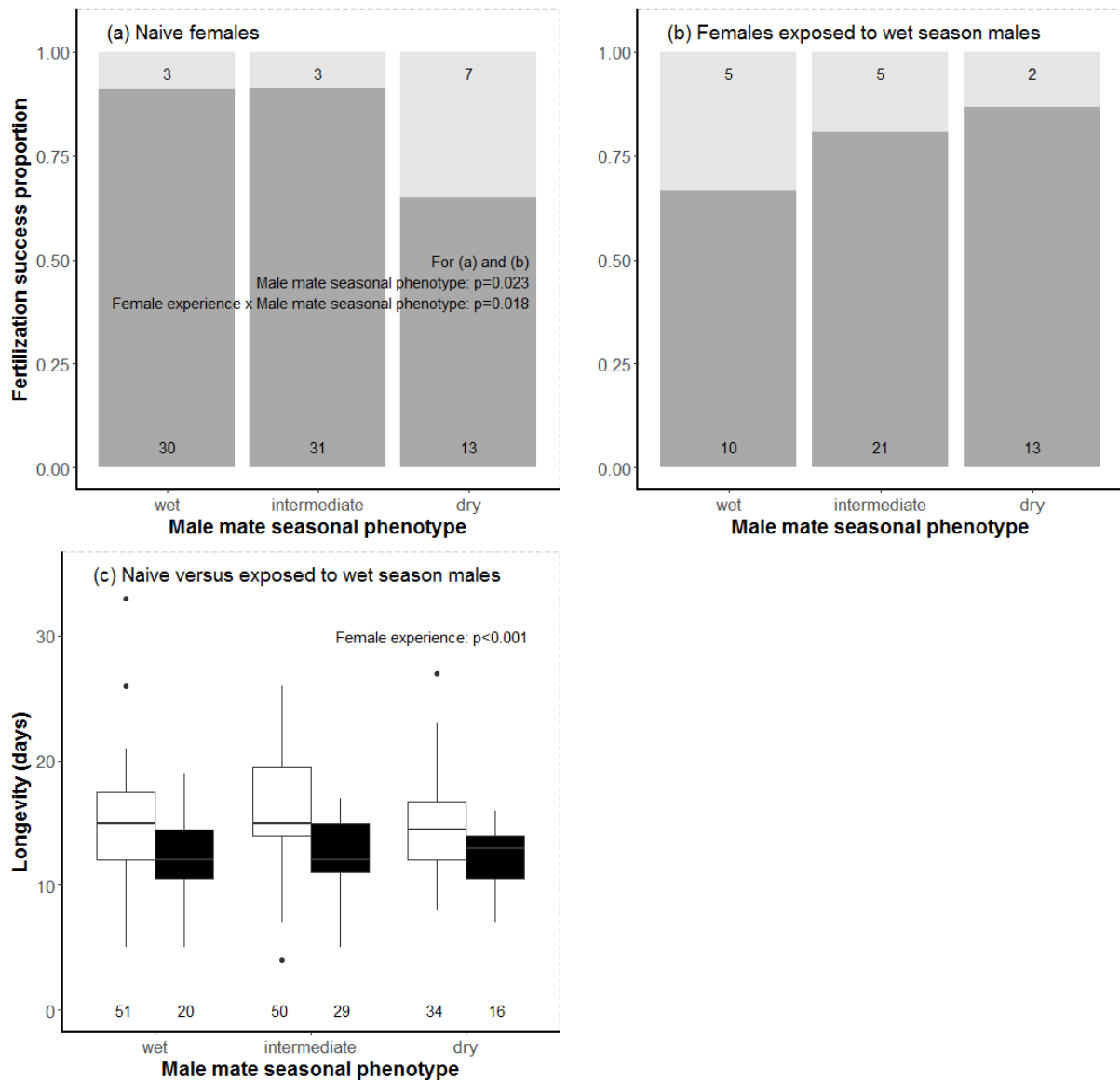
242

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

254 the highest proportion of fertilization success after mating with dry season males (Fig. 4b; Table

255 S1).

256   Social exposure of females to males of different seasonal phenotypes is likely adaptive

257 by shifting learned mate preference towards available males under natural, past, climatic

258 conditions. By 2100, social exposure of females to males of the wet season form will reduce

259 their life expectancy (by 40%) and reproductive fitness (by at least 25%), adding to the negative

260 effects on population survival chances throughout the dry season. Moreover, when females will

261 be surrounded by wet season males at the onset of the dry season in 2100, social exposure will

262 reduce their fertility by 23% compared to exposure and mating with dry season males, which is

263 maladaptive. Reduced fertility adds up to the loss of the other direct benefits that females gain

264 when mating with dry season males (increased life expectancy and oviposition rate (Prudic et

265 al., 2011)).

266

267 **Discussion**

268 We have provided a first example of a learned sexual interaction that produces maladaptation

269 under climate warming (Barrett et al., 2019; Greggor et al., 2019). As environmental cues

270 become unreliable, in the case of *B. anynana* through temperature values that no longer predict

271 the onset of the dry season, several maladaptive responses become apparent: *i)* production of

272 the wet season form; *ii)* suppression of naive mate preference for dry season males after

273 exposure to wet or intermediate season males; and *iii)* reduced longevity and fertilization

274 success by experienced females mating with wet season males. This leads to an increased risk

275 that long-term maintenance of the population is disrupted in the wild. While it remains difficult

276 to predict the fate of *B. anynana* populations in Malawi based on available information

277 (Candolin & Vlieger, 2013; Huey Raymond et al., 2012), our experimental results are relevant

278 and important to consider for predicting responses in nature. In the field, most virgin females

279　likely get socially exposed to potential mates during the few days of sexual maturation

280　following adult emergence, because this species is protandrous (i.e., males emerge before

281　females), which we show induces a form of sexual imprinting. Maladaptation can be suppressed

282　over evolutionary time by genetic evolution and gene flow. Notably, genetic adaptation can

283　occur by selection on female mate preference, provided that there is genetic variance for innate

284　and/or learned mate preference (Prokuda & Roff, 2014). As social learning is costly (in general,

285　Mery & Kawecki, 2005; here, we find potential survival costs for *B. anynana*), and has a genetic

286　basis (Barrett et al., 2019), maladaptive learned sexual preference could be counter-selected

287　(Lotem, 1993).

288　　　There is significant gene flow among *B. anynana* populations across its distribution

289　range (Bacquet et al., 2016; de Jong et al., 2011), thus more adapted populations from other

290　parts of the distribution range may also replace the local Malawi population. The alternation

291　and duration of the dry and wet seasons differs extensively with latitude across the distribution

292　range of *B. anynana* (e.g., variation in seasons documented in Uganda; Phillips & McIntyre,

293　2000). Yet, there is little genetic variation for seasonal polyphenism between geographically

294　distant populations (de Jong et al., 2010). More southern populations develop into the wet

295　season form at lower temperatures than the Malawi population (de Jong et al., 2010); hence

296　southern immigrant butterflies would increase maladaptation to the Malawi climate by 2100.

297　The patterns of temperature-rainfall correlation vary strongly throughout the large geographical

298　range of *B. anynana*, and different regions are expected to pose different selection pressures on

299　the species' plastic responses to temperature (de Jong et al., 2010; Roskam & Brakefield, 1999).

300　*B. anynana* populations from the Northern hemisphere may use rainfall, and not temperature,

301　as a cue for predicting the onset of the dry season (Roskam & Brakefield, 1999). Replacement

302　of southern populations, such as Malawi, by northern populations could lead to the emergence

303　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

329   responses to the climate crisis has received considerable interest. Studies have shown that at the

330   intraspecific level, climate warming leads to adaptive plastic and genetic changes in key

331   phenotypic traits, including dispersal capacity and other morphological, physiological,

332   behavioural, and life-history traits associated to phenology (Musolin & Saulich, 2012;

333   Parmesan, 2006; Thackeray et al., 2016). However, the effects of anthropogenic environmental

334   changes on sexual selection matter as well, because sexual selection may increase the extinction

335   risk of populations (Holland, 2002; Martínez-Ruiz & Knell, 2017; Parrett & Knell, 2018;

336   Plesnar-Bielak et al., 2012). It is indeed increasingly acknowledged that human activities

337   disturb important aspects of sexual selection (e.g., eutrophication and turbidity including algal

338   blooms (Seehausen et al., 1997), urban noise (Montague et al., 2013), selective harvest in

339   hunting (Knell & Martínez-Ruiz, 2017). This is expected as sexual selection has a strong

340   environmental component (Ingleby et al., 2010; Parrett & Knell, 2018). Regarding the climate

341   crisis, sexual selection is altered through the availability of sexual partners (Twiss et al., 2007)

342   with potential effects on the proportion of extra-pair mating opportunities (Bichet et al., 2016),

343   relative fitness of mono- versus polyandrous females (Grazer & Martin, 2012a), assortative

344   mating (Santos et al., 2018), sexual conflict (García-Roa et al., 2019), secondary sexual traits

345   (Evans & Gustafsson, 2017), and mate preferences (Candolin, 2019; Fuxjäger et al., 2019). Our

346   results suggest that the effect of global warming on *B. anynana* may lead to rapid extinction of

347   populations within a single or a few dry seasons, due to cascading effects of learned sexual

348   interactions and fitness of reproducing females at the onset of the dry, harsh, tropical season.

349   Our case study using the tropical butterfly *B. anynana* may be representative of a more

350   general pattern, because butterflies are arthropods that represent most of the animal biomass

351   and species diversity on Earth (Bar-On et al., 2018) and generally show strong phenotypic

352   plasticity to cope with alternating seasons (Simpson et al., 2011). Furthermore, tropical biomes

353   both contain most biodiversity and are most threatened by climate warming (Deutsch et al.,

354   2008; Hoffmann et al., 2013; Lister & Garcia, 2018; Sunday et al., 2011). Understanding how

355   maladaptations arise is increasingly important as humans rapidly transform the Earth into an

356   environment where maladaptation is expected to become prevalent for most species (Crespi,

357   2000; Robertson et al., 2013). Our results suggest that global warming can have additive effects

358   reducing, more than has been considered so far, the long-term survival probabilities of various

359   taxa once learning and sexual selection are included as important biological mechanisms of

360   species responses (Bell, 2013; Bradshaw & McNeilly, 1991). Our results thus advocate for

361   integrating sexual selection, learning and their fitness consequences to better understand

362   (mal)adaptation to climate warming.

363

364   **Methods**

365   *Insect rearing*

366   Experiments were performed with a laboratory population of *Bicyclus anynana* that was

367   originally established from 80 gravid females collected in Malawi in 1988 (Brakefield et al.,

368   2009). Between 400 and 600 butterflies per generation were used to maintain high levels of

369   heterozygosity and polymorphism (Van't Hof et al., 2005) to avoid loss of genetic diversity in

370   the lab population. Larvae were fed with maize, *Zea mays*, and adults with moist, organic

371   banana, *Musa acuminate* (Brakefield et al., 2009). Insects were reared, kept, and tested in a

372   large climate-controlled room (5.8 x 5.7 m and 2.27 m high) under a standard temperature

373   regime (27 ± 1°C; SD), a 12:12h light:dark regime and a high relative humidity (70 ± 5%)

374   representing the wet season in the field (Brakefield et al., 2009), except when explicitly

375   mentioned otherwise. For experiments, eggs were repeatedly collected from the stock

376   population as described below. Eggs of all thermal treatments were first reared in the standard

377   rearing environment at 27°C. Larvae were then placed in groups for the different thermal

378   treatments from the 4th larval instar until the second half of their pupal stage (in sleeves),

379 because the developmental temperature experienced during this time window determines the

380 expression of adult polyphenism (Bear & Monteiro, 2013; Brakefield & Reitsma, 1991; Kooi

381 & Brakefield, 1999; Oostra et al., 2011). Newly emerged adults were sexed and individually

382 marked on the ventral forewing with an indelible felt-tip pen. Groups of the same sex, seasonal

383 form, and age of at most 10 males or 20 females were placed in cylindrical netted cages

384 (diameter of 30 cm, height of 38 cm), except when stated otherwise. All experiments with adult

385 butterflies were performed at a temperature of 27°C, unless mentioned otherwise.

386

387 *Climate warming and proportions of seasonal forms*

388 To test if climate warming leads to the production of wet season individuals at the beginning of

389 the dry season, we modelled past and future natural, hourly, circadian cycles of both

390 temperature and relative humidity for 104 consecutive days representing the transition from the

391 wet to the dry season in Malawi (from March 30th to July 12th; Fig. S2). We modelled three

392 climatic scenarios: the past climate in 1988, and two future scenarios, i.e., RCP4.5 and RCP8.5

393 (with a 3°C and 6°C increase in the region of interest, respectively). The photoperiod followed

394 the light decrease throughout the seasonal transition with a 15-min monthly step. We encoded

395 the three modelled climatic scenarios in three separate incubators. Given the difficulty of

396 obtaining reliable, in-situ meteorological data, we constructed an idealized, smooth seasonal

397 cycle of temperature and relative humidity by averaging 10 years of meteorological data during

398 1979-1989 [data from the Modern-Era Retrospective analysis for Research and Applications

399 (MERRA), at latitude 12S and longitude 34E (Global-Modeling-and-Assimilation-Office-

400 (GMAO)]. We then considered climate modulations available from the CMIP5 database at the

401 same location (Taylor et al., 2012). Specifically, we computed the seasonal cycle of temperature

402 anomalies (period 2080-2099 *versus* 1970-1990) of three models (CCSM4, HadGEM2-ES, and

403 IPSL-CM5A-MR; at the time these data were downloaded, the HadGEM2-ES historical data

404   were available until 1984 only), and added them to the reference scenario. Simulations of

405   relative and specific humidity tend to be less reliable; hence a different approach was needed.

406   We considered that the important explanatory factor for our experiment is the duration and

407   timing of the wet, rainy season. Consequently, we measured the simulated change in timing and

408   duration of the wet season between 1970-1990 and 2080-2099, and expressed these changes as

409   anomalies of relative humidity, based on the reference values of humidity throughout the dry

410   and wet seasons in the reference seasonal cycle obtained from the MERRA dataset (Fig. S2).

411   We retained the HadGEM2-ES model, because its climate sensitivity is intermediate and

412   considers two future climatic scenarios, i.e., RCP4.5 (about 3°C increase in the region of

413   interest) and RCP8.5 (6°C increase)(IPCC & Press, 2014), in addition to reference climatology

414   for 1979-1989.

415   To cover the entire seasonal transition, we reared three cohorts of butterflies: 24 days in

416   cohort 1, 28 days in cohort 2, and 35 to 50 days in cohort 3 (Fig. S2). Pupae were collected and

417   placed in 1-dm³ circular plastic boxes, after which butterflies were frozen at -80°C. We then

418   evaluated the effects of global warming on survival until adult emergence (proportion of

419   surviving individuals between the start of the thermal treatment and the first day of emergence),

420   developmental time (day 1 = first emerged butterfly per cohort), and adult polyphenism using

421   the relative area of the fifth eyespot on the right ventral hindwing (i.e., hv5; Muller et al., 2019;

422   Fig. 2).

423

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

425   To test how the seasonal phenotype of males during the seasonal transition affects sexual

426   selection, we produced the wet (temperature of 27°C), intermediate (23°C), and dry (17°C)

427   seasonal forms (Brakefield et al., 2007; Brakefield & Reitsma, 1991; Muller et al., 2019; Oostra

428   et al., 2011; Prudic et al., 2011). We obtained naive wet season females by placing all wet

429   season pupae individually in closed plastic cylindrical containers (diameter 3.5 cm, height 7

430   cm, 60 ml) and adding a piece of white paper sheet to prevent visual, olfactory, gustatory and

431   acoustic contact with other individuals. We obtained experienced wet season females by

432   exposing freshly emerged females to 8-16-day-old males of one seasonal form in a flight cage

433   (10 to 15 males per cage of 60 x 60 x 60 cm) during 3 hours. Males within the same age range

434   were used for all exposures during experiments to more accurately mimic natural conditions.

435   Experienced females were kept separately in their container with a custom-modified, wire mesh

436   cap (7 x 7 mm), allowing them to see, smell and touch the flying males above them, but

437   preventing any mating or visual and gustative contacts with the other females exposed at the

438   same time (maximum 30 females spaced 5 cm apart). The males used for exposure were

439   different than those used for subsequent mating experiments. All females were fed with a slice

440   of banana in their individual container.

441   We used male courtship activity as theoretical mating proportions because *B. anynana*

442   females, as in many insects, do not engage in mating activities unless a male initiates courtship.

443   In addition, male courtship activity is known to *(i)* reduce butterfly survival (Wedell, 2010), *(ii)*

444   differ among seasonal forms (Bear & Monteiro, 2013), and *(iii)* predict male mating success

445   (Holveck et al., 2015; Nieberding & Holveck, 2017, 2018). We ran four mating experiments:

446   one with naive wet season females (20 replicates) and three with experienced wet season

447   females, either exposed the day of their emergence to wet (20 replicates), intermediate (17

448   replicates), or dry season males (15 replicates). For each replicate 15 virgin males (i.e., 5

449   selected randomly from each of the three thermal treatments), 8 to 11 days of age, were left to

450   compete in the presence of 5 virgin, wet season females, 3 to 6 days of age, in semi-natural

451   conditions (Holveck et al., 2015; Nieberding & Holveck, 2017, 2018). Eight to 11-day-old

452   virgin males were used, because all three components of the male sex pheromone are present at

453   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-dm³

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,

479   and 9 females exposed to wet season males) also received banana slices *ad libitum*. Every three

480   days, we replaced leaves and checked egg fertilization success, as well as female longevity (i.e.,

481   number of days between butterfly emergence and death).

482

483   ***Statistical analyses***

484   We performed all statistics with RStudio 1.0.143 (RStudio 2016). First, we analysed the effect

485   of the climatic scenarios in interaction with cohort on the *survival until adult emergence* using

486   generalized linear mixed models GLMM (lme4 package in R (Bates et al., 2015) with a

487   binomial distribution (logit link function) and bobyqa optimizer. The number of successfully

488   emerged butterflies and the number of experimental larvae not surviving to adulthood were

489   bound together with the "cbind" function. Random factors were cohort identity nested in

490   scenario identity, i.e., scenario(cohort). We added the interaction with sex (categorical variable)

491   to analyse fixed effects on *developmental time* and the *relative area of adult polyphenic hv5*

492   *eyespot pupils* (with a Box-Cox transformation to achieve normality) using GLMM with a

493   Poisson distribution, a bobyqa optimizer and an observation-level random effect to capture

494   overdispersion (Elston et al., 2001; Holveck et al., 2015), and with a normal distribution,

495   respectively. Random and nested factors were scenario(cohort(sleeve)).

496   We analysed the effect of male thermal treatment (17, 23, or 27°C) and female

497   experience (naive or exposed to wet season males) on *female fitness and survival* as follows: *(i)*

498   we analysed the effects of male thermal treatment in interaction with female experience on

499   *fertilization success* (binary). We added the age at mating of both sexes and the thermal

500   treatment duration (i.e., proportion of time that the female pupae spent in thermal treatment

501   relatively to the entire pupation stage) as fixed factors. We used a GLMM with a binomial

502   distribution, a bobyqa optimizer and an observation-level random effect to capture

503   overdispersion. Feeding status after mating was starved for all females; *(ii)* we ran a similar

504   GLMM on *female longevity* with a Poisson distribution, in adding female feeding status after

505   mating in interaction with male thermal treatment and whether or not females could choose

506   among males of the different thermal treatments as fixed factors, and

507   experimenter(experiment(replicate)) as random factors. In all these analyses, we rescaled and

508   centred the continuous explanatory variables on the mean, thus generating standardized z-

509   scores, to evaluate the relative effects of variables measured on different scales and to lessen

510   the correlation between the interactions and their component variables.

511   In the analyses of mating success experiments, we first tested for homogeneity among

512   replicates per experiment using a Pearson's Chi-squared test (with simulated *P*-value based on

513   1^{e+06} replicates to obtain a correct approximation; all $P > 0.05$) before performing analyses on

514   the pooled data set. Second, we tested differences in *mating probabilities* among males of

515   different seasonal phenotypes in comparing the observed counts to the theoretical counts of

516   mating of the three male thermal treatments per experiment using Pearson's Chi-squared tests

517   of goodness-of-fit. Third, we searched for the male phenotype(s) responsible for these

518   differences in comparing the observed counts to the theoretical counts of mating *(i)* for each of

519   the three male thermal treatments per experiment and *(ii)* in paired comparisons between male

520   phenotypes per experiment, applying Pearson's Chi-squared tests and reporting *P*-values with

521   and without Holm-Bonferroni correction for multiple comparisons (Millot, 2009). We also

522   performed Fisher's Exact tests when the expected frequencies were below 5.

523

532

Competing interests

534   The authors declare no competing financial interests.

535

Data availability

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

538

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841 **Supplementary Figures**
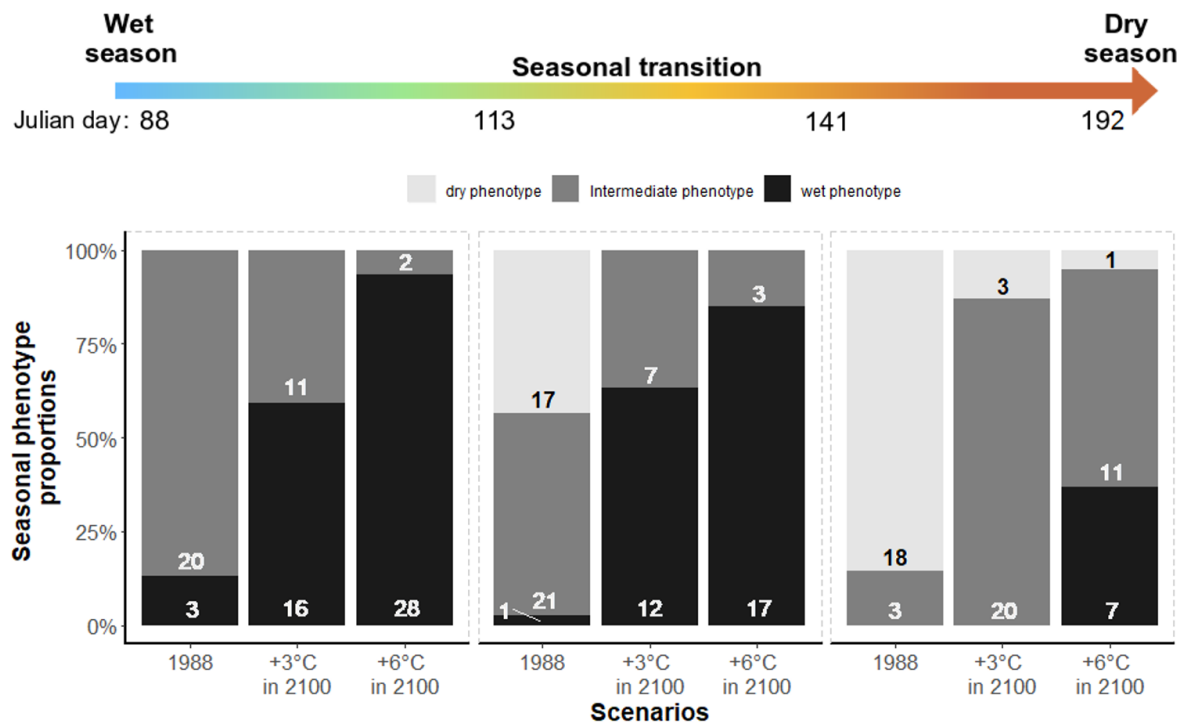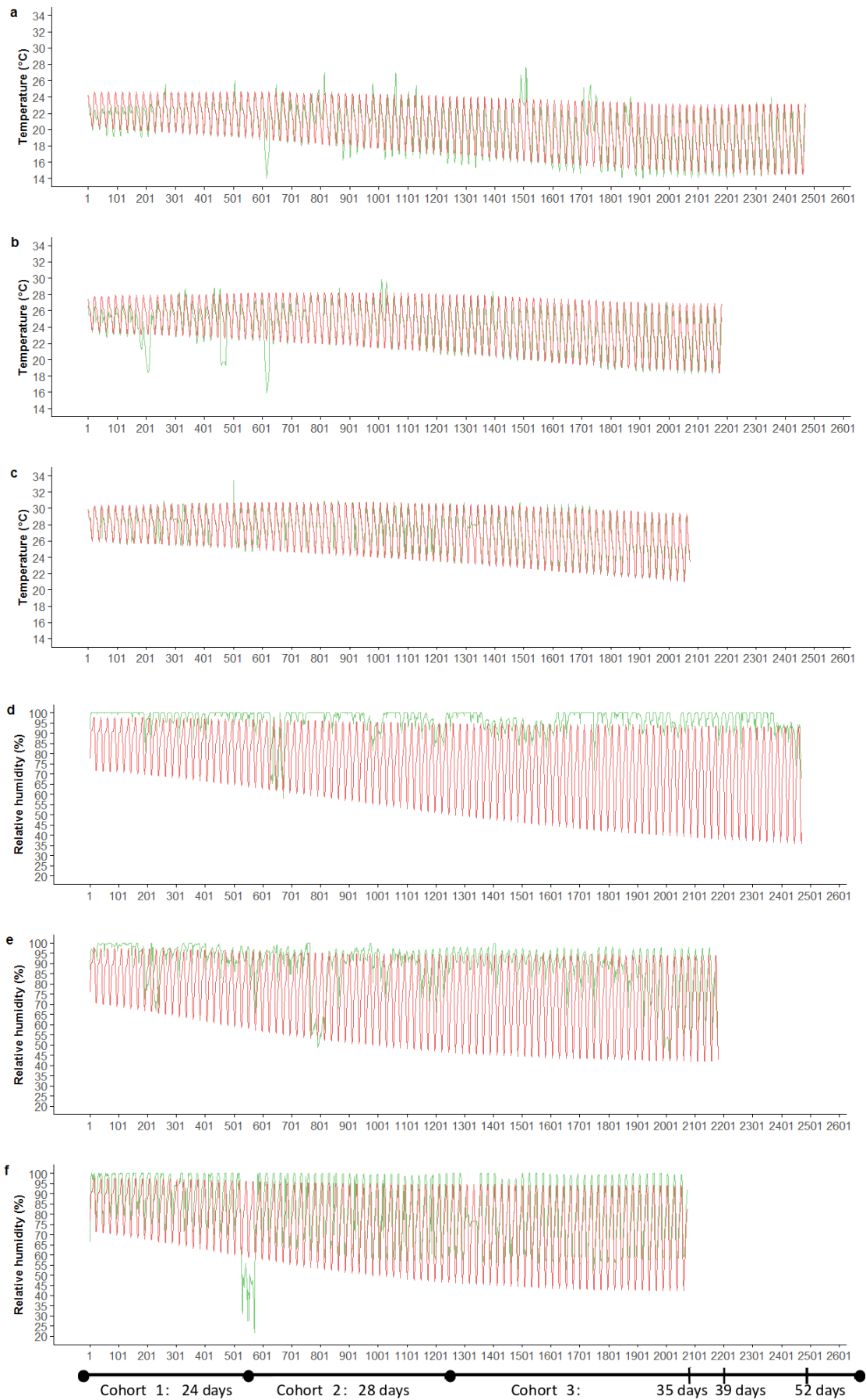

842

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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849   ***Fig. S2.*** Experimental and theoretical temperature and relative humidity throughout the
850   seasonal transition. We registered the experimental temperature (°C; a-c) and relative humidity
851   (%; d-f) with sensors (HOBO U23-001) in the incubators (green) and compared them to
852   theoretical climatic conditions (red) per hour throughout the whole transition from the wet to
853   the dry season, which started at the 88th day of the year. We modelled three climatic scenarios:
854   the past reference climate from 1988 (a and d), the predicted RCP4.5 climate of +3°C on average
855   in 2100 (b and e) and the predicted RCP8.5 climate of +6°C on average in 2100 in Malawi (c
856   and f).

857

858 ***Table S1.*** Model-averaged standardized coefficients following conditional average of the set of
859 supported candidate models for each response variable. For each conditional average of
860 supported candidate models ($\Delta_i < 2$), we provide the relative importance of explanatory
861 variables ($P \leq 0.05$ in bold). Of note, sexes differ in their developmental response to climate
862 warming (Fig. 2b): males emerged earlier than females; female developmental time compared
863 decreased faster with warming (scenario-by-sex interaction) and increased faster throughout the
864 seasonal transition (cohort-by-sex interaction) compared to males. These sex differences
865 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.

870

Tests	Comparisons	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)		
		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)

876 Wet, wet season males (27°C). Intermediate, intermediate season males (23°C). Dry, dry season males (17°C). When expected frequencies were
877 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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