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ORIGINAL PAPER

Different stress from parasites and mate choice in two female morphs of the blue-tailed damselfly

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Abstract

In Odonates, female colour polymorphism is common and implies the presence of two or more female types with different colours and behaviours. To explain this phenomenon, several hypotheses have been proposed that consider morph frequency, population density, the presence of parasites, and mating behaviour. We studied the blue-tailed damselfly *Ischnura elegans*, a species with a blue androchrome morph and two gynochrome morphs (the common green *infuscans*, and the rare orange *rufescens-obsoleta*). The size of adult males and females, the presence of parasites, and pairing behaviour between males and the three female morphs was assessed in field conditions throughout the reproductive season in NW Italy. Moreover, growth and emergence success of larvae produced by the different morphs was analyzed in standardized conditions. In the field, males showed a preference for the gynochrome *infuscans* females, despite a similar frequency of androchrome females. In test conditions, male preference for the *infuscans* females was also observed. Paired males and paired androchrome females were larger than unpaired individuals, while there were no differences in size between paired and unpaired *infuscans* females. Males and androchrome females were more parasitized than *infuscans* females. The survival and emergence success of larvae produced by androchrome females was higher than those of offspring produced by the *infuscans* females. Our results suggest that a higher survival of progeny at the larval stage could counterbalance the higher parasitism and the lower pairing success of andromorph adult females and highlight the importance of considering the whole life-cycle in polymorphism studies.

Keywords Female morphs · Parasites · Larval growth · Mate preference · Damselfly

Introduction

Polymorphism occurs when two or more morphs coexist in the same population (Burns 1956; Gray and McKinnon 2007). In dragonflies and damselflies, a particular kind of polymorphism, the female-limited colour polymorphism, is widespread (more than 100 species in the Holarctic region, Fincke et al. 2005). Usually, the coloration of the thorax

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and abdomen of a female morph resembles the male (androchrome female), while one or more morphs show a different coloration (gynochrome females). The polymorphism shows a strong genetic determination with the colour being controlled by a single autosomal locus with female-limited expression in different species studied so far (Johnson 1964, 1966; Cordero 1990; Andrés and Cordero 1999; Abbott and Svensson 2005; Sanmartín-Villar and Cordero-Rivera 2016).

To explain the maintenance of polymorphism in Odonates, several hypotheses were proposed. According to the "reproductive isolation" hypothesis (Johnson 1975) gynochrome females are more cryptic, but suffer a high harassment by males of different species (interspecific), while androchrome females are not sexually harassed but suffer a greater pressure by predators. Similarly, the "male mimicry" hypothesis (Robertson 1985) proposes that androchrome females could benefit from less intense intraspecific male harassment (unnecessary matings can be very costly), but suffer a higher predation risk due to having more showy colours. The "density-dependent" hypothesis proposed by Hinnekint (Hinnekint 1987) implies that androchrome females could benefit by a less intense male harassment at high male densities, but face greater mating failure than gynochromes at low densities. The existence of temporal cyclic variation in population density would permit the different morphs to achieve an evolutionary equilibrium.

Other hypotheses stress the behavioural component of this phenomenon and are often limited to a single or few species. According to the "learned mate recognition" hypothesis (Miller and Fincke 1999) male choice is influenced by female morph frequency, and males choose the commonest morph. The "female aggression" hypothesis (Sirot et al. 2003) underlines that androchrome females can limit harassments, because they are more aggressive toward males than gynochromes, while the "female receiver" hypothesis (Sirot and Brockmann 2001) highlights that androchrome aggressive females disrupt and interfere more with other females during oviposition, and another hypothesis by Van Noordwijk (1978) suggested that males might disrupt more the oviposition behaviour of gynochromes compared to androchromes. According to the "signal detection" hypothesis (Sherratt and Forbes 2001), frequency-dependent and frequency-independent factors combine to generate a balanced polymorphism, in which andromorphs are not only more similar to males, but are also encountered more by males. The "male harassment" hypothesis (Gosden and Svensson 2007) proposes that female morphs differ in their propensity to accept male mating attempts and in their degree of resistance towards mating attempts. Maintenance of polymorphism within a population is an evolutionary enigma, because a slight consistent advantage of one morph would be sufficient for selection to drive the other morphs to extinction (Brockmann 2001; Galicia-Mendoza et al. 2017).

Recently, two hypotheses emphasize the role of internal (physiological maturation) or external (parasites) conditions to maintain female morphs. According to the "sexual status signalling" hypothesis (Huang and Reinhard 2012) sexually immature females change their colour from androchrome to gynomorphic to signal sexual maturity and regulate reproduction. The "parasitism" hypothesis (Sánchez-Guillén et al. 2013b) considers an important role of parasites on morph fitness: androchrome females are more successful in evading male harassment, but pay a higher fecundity cost by being more parasitized than gynochromes.

Despite the plethora of hypotheses proposed to explain female polymorphism, its adaptive significance remains controversial. The fitness consequences maintaining female polymorphisms in natural populations are difficult to be adequately demonstrated (Fincke 1994; Wellenreuther et al. 2014), and different hypotheses are not always mutually exclusive.

Odonates, like other insect taxa, show two distinct life-history stages. During the course of ontogeny, they switch from being aquatic larvae to being terrestrial adults. Usually, research has examined the effect of behaviour and/or environmental conditions during the adult stage on mating success (Corbet 1980; Van Gossum et al. 2005), while less studies concerned the larval stage (Harvey and Corbet 1985). The trans generational effects of adult behaviour on the fitness of their progeny have been little studied (Thompson et al. 2011). Despite the wide occurrence of female polymorphism in Odonates, few studies have examined the growth and survival of the progeny generated by different female morphs (Abbott and Svensson 2005; Bots et al. 2010a; Bouton et al. 2011; Abbott 2013). Such studies are important, since fitness will ultimately depend upon selection that operates along successive generations (Stearns 1992).

In this study, we examined the Blue-tailed damselfly *Ischnura elegans,* a species where males are monomorphic while females occur in an androchrome and two gynochrome female morphs (*forma infuscans* and *forma rufescens-obsoleta*: (Parr 1999; Sánchez-Guillén et al. 2005). These morphs coexist in the same areas, and the frequency of each morph may vary among populations in the same season and among different seasons in the same population (Svensson and Abbott 2005; Hammers and Van Gossum 2008; Gosden and Svensson 2009). We collected biometrical data, sex ratio, morph frequency, mating success, and parasite burden for different morphs. We then tested the male preference for different morphs in controlled conditions through a binary test choice experiment. Finally, the fitness larval component for different female morphs was assessed by monitoring the hatching success, larval growth, and emergence success of the progeny produced by females.

Methods

Study areas

The studied populations were located at two artificial wetlands and one natural oxbow near the Po river (Alessandria, NW Italy). Lago Altafiore, Castellazzo Bormida AL (44.85785° N, 8.59319° E) is a 4.4 ha lake dedicated to sport fishing that was artificially created after gravel pit extraction activity. The basin has rather deep waters and steep banks, with fairly abundant aquatic vegetation in the first meter at the ground-water boundary and some *Phragmites* reed. Cava Allara, Sezzadio AL (44.78991° N, 8.55177° E) is a 15.3 ha lake artificially created after gravel pit extraction activity, with slightly inclined shores, shallow water, and some floating and submerged vegetation. *Phragmites* and *Typha* are widespread. Lanca di San Bernardo, Valenza AL (45.03701° N, 8.65516° E) has a surface of 2.8 ha and has lentic water with natural habitat coenosis characterized by abundant floating and submerged vegetation of different species. The vegetation is dominated by marsh plants, such as *Carex* spp., *Phragmites* spp., *Juncus* spp. and *Typha* spp., that are widespread along the shoreline.

Field census

Damselflies were captured with entomological nets and marked with a progressive number on the wing to avoid measuring the same individual twice. We never utilized observational data of individuals that were sight in the field but not captured. Sampling was carried out during the hours with maximum activity, i.e. between 11:00 and 15:00, throughout the reproductive season from May to September in 2013 and 2014. We always collected individuals found in the same environment, i.e. grassy vegetation placed in a strip about 3–10 m near the edge of the water body. Immediately after capture, a photo was taken with a digital camera with the animal positioned on a graph paper. The image was later analyzed with the ImageJ 1.48 software (Schneider et al. 2012) and total body length was measured to the nearest 0.1 mm. In the field, we recorded sex, morphotype of females, and the presence/absence of parasites. Odonates are commonly parasitized by the endoparasite gregarine Protozoa (Córdoba-Aguilar and Munguía-Steyer 2013; Gołab et al. 2013; Sánchez-Guillén et al. 2013b) and ectoparasite *Arrenurus* mites (Zawal 2006; Hassall et al. 2010). In this study, we only considered the ectoparasites because we could easily assess their presence when measuring adults (Forbes and Robb 2008), without killing the damselflies for endoparasite examination (Kaunisto et al. 2015). We did not collect any teneral individuals (when damselflies first emerge teneral individuals are duller in colour and their wings are translucent). Moreover, we did not include in statistical analysis the immature individuals (*violacea* and *rufescens* forms: Sánchez-Guillén et al. 2005). Immature individuals showed a high parasitization rate (parasitized immatures: 36.1%, N = 379; adults: 7.8%, N = 793), and were rarely found mating (mating immatures: 5.0%, N = 379; adults: 37.0%, N = 956).

Mate choice

We studied mate choice both by assessing the number of individuals of different morphs that were found unpaired or found mating (wheel position) in the field, and conducting mate choice standardized tests (van Gossum et al. 1999, 2001; see Cordero-Rivera and Andrés 2001 cautionary note on choice experiments). To compare the body length of damselfly morphs, at each visit to a site we randomly captured a sample (mean 30 ind., range 7–124 ind.) of non-paired individuals and of individuals engaged in mating pairs.

Mate choice tests were performed in field in the same area of capture using an insectary formed by a squared iron framework (60 × 100 × 100 cm), laid down on the grass and covered by a mosquito net. One male and two females of different morphs (androchrome and *infuscans*) were placed at the same time inside the insectary and observed for 30 min. During this time, any interaction (grasping, tandem, wheel mating) between the male and one of the two females was considered as an indication of choice. In this study, males never tried to approach two different females during the test session.

Growth and survival of progeny

We utilized a standard lab method to assess growth and survival of the progeny (Cordero 1990; Bots et al. 2010a; Bouton et al. 2011; Locklin 2012; Piersanti et al. 2015). Females actively engaged in mating activity (wheel position) were captured in the field and successively transported to the laboratory. Mating males were immediately released. We only captured androchrome and *infuscans* females, because *rufescens-obsoleta* females were very uncommon in our study area. In the laboratory, each female was photographed, then placed individually in a plastic cup containing a small piece of wet tissue paper and a small amount of water to stimulate the oviposition (Fincke 1984; Abbott and Svensson 2005; Subrero et al. 2019). Each plastic cup was closed with a mosquito net and females were left for about 20 h with an artificial photoperiod 16–8 L-D during which females usually laid their eggs on the tissue paper. After egg deposition (1937 eggs from 18 androchrome and

3323 eggs from 39 *infuscans* females, all from unparasitized individuals), each tissue paper was placed in a separate tray containing natural water under the same lighting conditions, and females were released in their original capture area.

After about 12–15 days, the eggs began to hatch and the larvae were fed daily with *Artemia salina* nauplii. In line with other studies (De Block and Stoks 2008; Abbott 2013; Álvarez et al. 2013), *Artemia* shrimps were the only food item used throughout the rearing period. Once a week, larvae were placed in a petri dish with graph paper and measured to the nearest 0.25 mm under a stereo microscope to evaluate growth. To assess mortality rates, larvae were counted three times a week. In the last part of the rearing period, the trays containing the developing larvae were covered by a light perforated veil and a small stick was inserted to allow the ones that had to transform to rise out of the water. Once damselflies emerged, they were counted to establish emergence success.

Statistics

The difference in adult body length throughout the season was investigated with a general mixed model *lme4* package (Bates et al. 2015) with length as the dependent variable and Julian date, study site, year, and morph as predictors. Site and year were added as random effects. The relationship between sex-ratio and Julian date and site were independent variables.

The effect of parasites on body length was analyzed by general mixed models only in males and in two female morphs, i.e. androchrome and *infuscans*, due to the low sample size of the *rufescens-obsoleta* morph.

Mortality was compared for androchrome and *infuscans* progeny using survival analyses (Kaplan–Meier estimates) with the *survival* packages (Fox and Carvalho 2012; Therneau 2020) implemented in the R Commander plugin (Fox 2005) for the R software (R Core Team 2016). In the models, female ID was entered as a random effect using the "frailty" function.

Results

Abundance and size of morphs in the field

The sex ratio observed in the field was always male biased. There were about twice as many males per female at the beginning of the reproductive seasons, from June to July, with a significant increase in the sex ratio toward the end of the season, from August to September (Fig. 1a; $\chi^2 = 41.58$; d.f. = 4; $P < 0.001$).

There was a significantly different frequency of the three female morphs ($\chi^2 = 203.2$; d.f. = 2; $P < 0.001$, N = 410). The androchrome and *infuscans* morphs were the most abundant, while the *rufescens-obsoleta* was rarely found (3.4%).

Males were significantly smaller than females ($F_{3,1000} = 9.58$, $P < 0.001$, N = 1004). There was a tendency for *infuscans* females to be larger than androchrome females ($F_{2,256} = 1.805$, $P < 0.07$). The few *rufescens-obsoleta* females showed a conspicuous size variability (Fig. 2).

The size of males and all female morphs decreased across the season (Fig. 3), with early-season individuals larger than end-season ones (Males: length = 32.61–0.0291 * day,

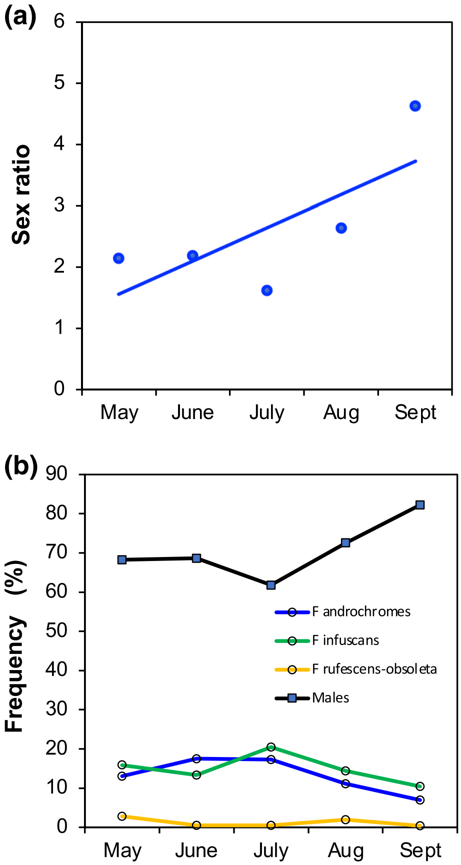


Fig. 1 Seasonal trend along the reproductive season of (**a**) sex ratio, and (**b**) frequency of the three female morphs

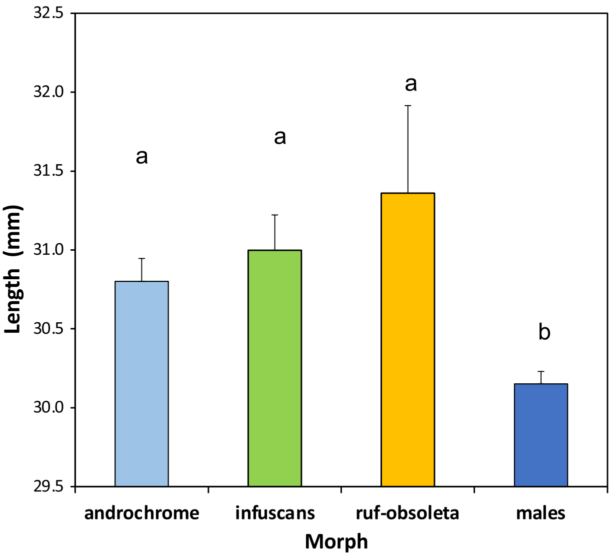


Fig. 2 Sizes of males (M) and females of three different morphs (androchrome, *infuscans* and *rufescens-obsoleta*). Different letters indicate significant differences among types

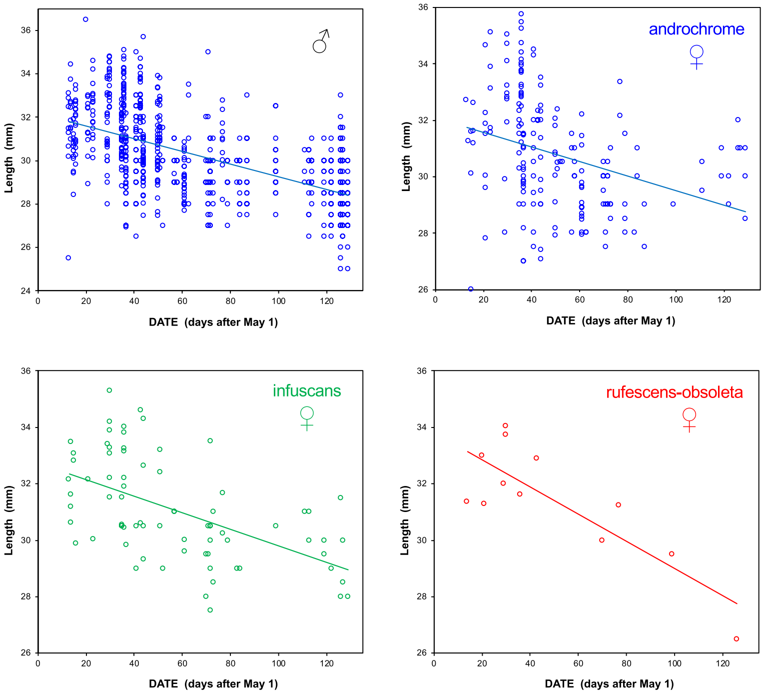


Fig. 3 Seasonal size trend for males and the three female morphs

$t_{1,490}=336.9$, $P<0.001$; Androchomes: length $=32.14–0.0177$ *day, $t_{1,58}=4.92$, $P<0.03$; *infuscans*: length $=32.84–0.0302$ *day, $t_{1,67}=29.16$, $P<0.001$; *rufescens-obsoleta*: length $=33.99–0.0527$ *day, $t_{1,5}=15.45$, $P<0.011$).

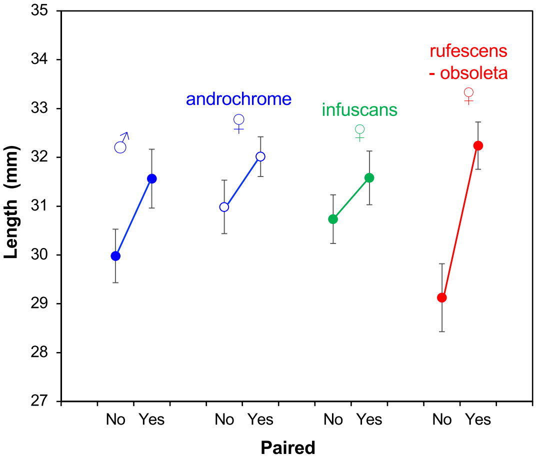
Mate choice

Under field conditions, gynochrome *infuscans* were found mating significantly more than androchrome females (Logit unpaired $=0$, paired $=1$; effect of morph: androchrome $=-1.654$, $Z=-7.308$; $P<0.001$). The *rufescens-obsoleta* females were excluded from the analysis, because they were very uncommon in the study area. In relation to the increased proportion of males as the season progressed, the mating frequency of both androchrome and *infuscans* females increased along the reproductive period (Logit effect of Julian date: androchrome: effect $=0.0370$, $Z=6.611$, $P<0.001$. *Infuscans*: effect $=0.0150$, $Z=2.742$, $P<0.001$).

Paired males and paired androchrome females were larger than unpaired individuals, while *infuscans* females had similar sizes regardless of their pairing status (Fig. 4. Males: $t_{2,491}=3.139$, $P<0.002$; androchrome: $t_{2,57}=2.28$, $P=0.02$; *infuscans*: $t_{2,66}=1.071$, $P=0.29$ n.s.; *rufescens-obsoleta*: $t_{2,4}=1.43$, $P=0.23$ n.s.).

In the binary choice test, *infuscans* were preferred over androchrome females (only 3 androchrome preferred out of 17 tests, Binomial test $P<0.0064$). The time elapsed from

Fig. 4 Sizes of paired *vs* unpaired individuals



the beginning of the test to the first mating interaction was significantly lower for *infuscans* females (10.0 ± 5.77 min vs 25.0 ± 5.0 min; $t_{1,10} = 3.09$; $P = 0.011$).

Parasites

Males were less parisitized than females (Yates corrected chi-square = 16.82, d.f. = 1; $P < 0.001$), and this difference was largely due to androchrome females that were significantly more parasitized than both males and the other female morphs (Fig. 5; chi-square = 28.4, d.f. = 3; $P < 0.001$).

Parasitized individuals of both sexes were significantly smaller than non-parasitized one (Table 1). The small sample size prevented any comparison for the *rufescens-obsoleta* morph.

Mating success of unparasitized individuals was higher than that of parasitized individuals (androchrome females: 57.0% *vs* 10.5%, N = 98, chi-square = 13.2, $P = 0.0003$;

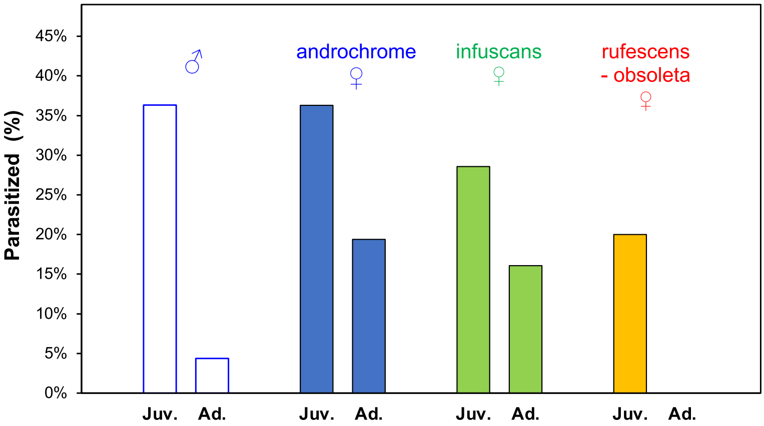


Fig. 5 Percentage of parasitized individuals for males and three female morphs

Table 1 Sizes of parasitized versus unparasitized individuals in relation to Julian date and presence/absence of parasites

Morph	Constant	Julian date	Parasites	t	p
Males	32.878	−0.0340	−1.667	5.142	<0.001
Androchromes	33.456	−0.0280	−2.458	5.696	<0.001
Gynochrome *infuscans*	33.257	−0.0333	−0.889	2.032	<0.046

infuscans females: 69.1% *vs* 33.3%, N = 112, chi-square = 8.35, $P = 0.0039$; non-significant tendency for males: 21.4% *vs* 12.0%, N = 572, chi-square = 1.27, $P = 0.25$).

Hatching rate, growth and survival of progeny

The number of eggs laid by captured females of the two morphs did not significantly differ (androchrome: 107.6 ± 81.7 SD, N = 18; *infuscans*: 85.2 ± 90.7 SD, N = 39 females; Mann–Whitney test: W = 442; $P = 0.12$ n.s.).

The hatching rate of eggs laid by androchromes were similar to that of eggs laid by *infuscans* females (75.1% *vs* 71.6%; z value = 0.609, $P = 0.543$ n.s.).

Growth of larvae born from *infuscans* females was slightly higher than that of larvae born from androchrome females (Fig. 6a; mixed model with female identity as random effect: N observations = 6198, groups = 48, t = 2.433, $P = 0.015$). On the contrary, survival of progeny was significantly higher in larvae born from androchrome females (Fig. 6b; chi-square = 31.0, d.f. = 1, $P < 0.001$).

Success at emergence was significantly higher for progeny of androchrome females than for progeny of *infuscans* females (androchrome: 2.57%, N = 75/2918; *infuscans*: 1.77%, N = 96/5435; chi-square = 5.86, $P = 0.015$).

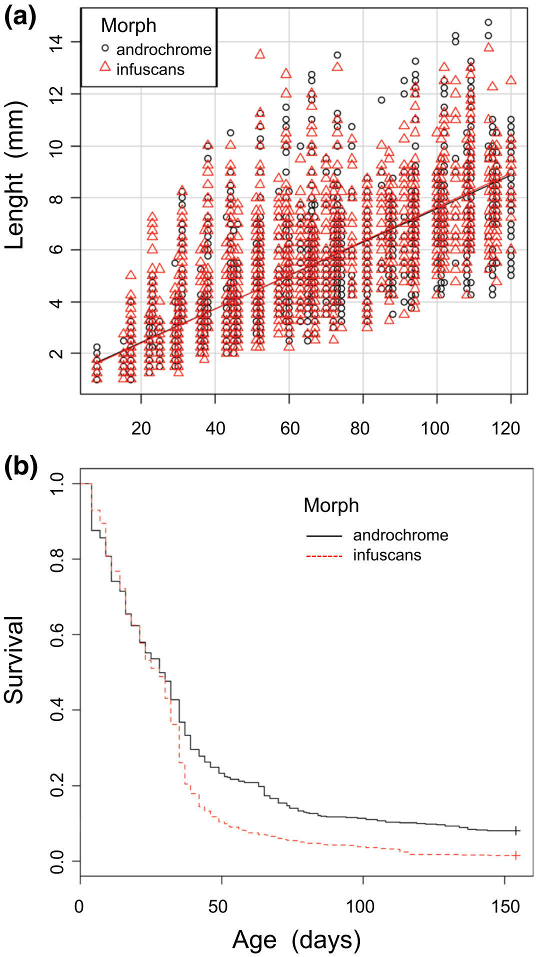
Discussion

In this study we compared mate choice and survival of the progeny of different female morphs of the Blue-tailed damselfly. We found that androchrome females were slightly more frequent in nature and their progeny had better survival, while *infuscans* females were more chosen by males and less parasitized.

Sex ratio and morphs frequency

In our study area, sex ratio was always male-biased. Adult Odonates populations often have male-biased sex ratios at the breeding habitat (Corbet and Hoess 1998; Foster and Soluk 2006; Cordoba-Aguilar 2008). This bias could be attributed to a high female mortality, to females using alternative habitats (Stoks 2001; Johansson et al. 2005; Torres-Cambas and Fonseca-Rodríguez 2011), or to higher female mortality in the larval stage (Johansson et al. 2005). In some cases, it has been questioned as to whether male-biased sex ratios in Odonate populations are real or artificial, but current data suggest that the biased sex ratios are real (Stoks 2001). The continuous occurrence of a large number of males in our study species poses the basis for the presence of both intrasexual (male-male) and intersexual competitions.

Fig. 6 Larval growth (**a**) and mortality of progeny (**b**) from androchrome and *infuscans* gynochrome females



We found a different frequency of the three female morphs, with the andromorph slightly more abundant, the gynomorph *infuscans* rather frequent, and the gynomorph *rufescens-obsoleta* very rare. The morph frequency of female Odonates can vary across environmental gradients (Inomata et al. 2015; Bybee et al. 2016) or can vary cyclically when there is a fitness advantage of the rarer morph (Takahashi and Kawata 2013). In one study of *Ischnura elegans,* the morph frequencies had a pattern similar to those found in our study area, and were found to be stable over ten generations (Le Rouzic et al. 2015), while in other studies the proportion of the morphs varies between years, with more androchrome females in younger populations (Svensson and Abbott 2005), or with very large differences among nearby populations (Fincke et al. 2005; Sánchez-Guillén et al. 2005; Svensson et al. 2005).

Mate choice

We found that androchrome females had a lower probability of being found in copula compared to the gynochrome morph: androchromes represented 55% of females but were involved in 43% of matings. Our result is similar to that reported for other populations of the same species (Cordero et al. 1998; Cordero-Rivera and Sánchez-Guillén 2007; Gosden and Svensson 2007, 2009; Hammers and Van Gossum 2008; Gosden et al. 2011). In the congeneric species *Ischnura graellsii,* mating success was similar for andro- and gynochrome morphs at high population densities, but the proportion of mated females was greater in gynochromes at low densities (Cordero 1992a). In *Ischnura ramburi*, andromorphs were less likely than gynomorphs to receive mating attempts by males, but did not mate less frequently than other females (Sirot et al. 2003).

The larger proportion of gynochrome females copulating in the field likely reflects the preference of males for that morph. The results of our experimental binary choice test confirm this hypothesis: the males preferred the gynochrome female when allowed to choose between the androchrome and *infuscans*. Our results on female pairing are in line with two other studies on the Blue-tailed damselfly, where a preference for gynochrome females was also found (Svensson et al. 2005; Sánchez-Guillén et al. 2017), but differs from other studies where males did not prefer gynochrome females but mated predominantly with the most common morph in the population (van Gossum et al. 1999). In general, male–female interactions may be very complex (Cordero et al. 1998; Cordero-Rivera and Sánchez-Guillén 2007; Sánchez-Guillén et al. 2013a), and may involve image search ability and learning (Punzalan et al. 2005; Nityananda 2016; but see Piersanti et al. 2021), multiple sensory cues (Van Gossum et al. 2008; Winfrey & Fincke 2017; review in Rebora et al. 2018), and female behaviour in responding to mating attempts by males. Recent studies report that the preference for a specific morph may not be innate, but that male preference can be influenced by experience, i.e. naive males at their first encounter with a female did not show a clear preference for gynomorph individuals but the preference is shown later (Sánchez-Guillén et al. 2013a), and there is no long term memorization of preference because choice can vary the following day (Takahashi and Watanabe 2009).

A higher pairing success of gynochrome morphs was found in several damselfly species too. Indeed, male preference for gynochrome females seems to be a widespread pattern in Odonates (Cordero-Rivera and Andrés 2001).

Size

We found a strong sexual size dimorphism, with females larger than males. Sexual size dimorphism has been observed in several insect taxa. Fecundity selection acting on female body size usually produces female-biased dimorphism through increasing fecundity in larger females, but variations with respect to this pattern have been frequently found. For example, male-male competition can end with male-biased size dimorphism in species in which males compete for females on the ground, or female biased size dimorphism in species in which males compete in the air and manoeuvrability is favoured by small size (Serrano-Meneses et al. 2008). In Odonates, a female-biased sexual size dimorphism in non-territorial species and monomorphism for territorial species has been shown (Wong-Muñoz et al. 2011). Dimorphism can progress even from the early stages of life in eggs (Takahashi and Watanabe 2010a; Iserbyt et al. 2013).

In our study, we found that gynochrome females were larger that androchrome females. Hence, androchrome females were somehow similar to the males even for size besides colour. A similar pattern was found in the same species in Sweden (Abbott and Gosden 2009), but this is not a general pattern of our study species (Cordero et al. 1998), nor within this damselfly genus, because in *Ischnura graellsii* either no difference or the reverse pattern was found (Cordero 1992a), nor is it a general pattern in other damselflies (Lajeunesse and Forbes 2003).

Our results indicated that both female and male Blue-tailed damselflies reached a smaller body size as the season progressed. The decrease in size within season is a common pattern in Odonates with the opposite having been found in a few species only (Wong-Muñoz et al. 2011).

Interestingly, paired males were larger than unpaired males. The morphometric difference between mated and unmated males suggests the presence of sexual selection acting on this trait. Our result contrasts with the small-male mating advantage hypothesis (Stoks 2000; De Block and Stoks 2007) which predicts that small males are advantaged by better manoeuvrability in flight. In Sweden's Blue-tailed damselflies, it has been reported that sexual selection on the male body size is mediated by densities of the two common female morphs, androchromes and gynochromes. High densities of androchrome females selected for small male body sizes, whereas high densities of gynochrome females selected for larger males (Gosden and Svensson 2008). Adult size is a highly hereditable trait in the Blue-tailed damselfly morphs (Abbott and Svensson 2010), as well as in other species (Cordero 1992b; Andrés and Cordero 1999; Abbott and Svensson 2005; Sánchez-Guillén et al. 2005). If larger males enjoy a higher pairing success, then a selective trend toward larger sizes should be at work. However, this predicted trend may hold only in gynochrome-rich populations. Moreover, it is difficult to predict pressures acting on adult size by considering just a single behavioural trait. Indeed, in the Common blue damselfly *Enallagma cyathigerum*, studies have failed to observe morph differences in size despite highly different levels of a behavioural trait in the form of male harassment (Bots et al. 2009).

Parasites

In our study, we found a noticeable difference between sexes and morphs in water mite parasitization rate. Males were less intensely parasitized than androchrome females which, in turn, were more parasitized than gynochrome females. Our result contrasts with the trend outlined in a recent review on parasite infestation, according to which the two sexes are generally equally parasitized in both dragonflies and damselflies (Ilvonen et al. 2016). However, a study on six species of damselflies showed that androchrome females suffer from a higher degree of parasitism than gynochrome females and males (Sánchez-Guillén et al. 2013b). Furthermore, a study on the Blue-tailed damselfly found that males were less parasitized than both gynochrome and androchrome females (Willink and Svensson 2017). From these contrasting findings, it appears that a general pattern of parasitic infestation in relation to sex and morph is difficult to extract from Odonate research. Probably, parasitization condition is mainly shaped by large between-species and between-populations differences. Parasite resistance too can differ between sexes and morphs. Recently, a comparison between male and female immunity identified genes with sex-biased expression, and gynochromes differed more from males than the androchrome females (Chauhan et al. 2016).

In our study, parasitized damselflies were smaller than non-parasitized. Our result is similar to findings on males of the Variable damselfly *Coenagrion pulchellum*

(Hughes et al. 2016). Reduced size could be related to the negative effects of parasites, because water mites extract body fluids from their hosts. However, mites are acquired when tenerals leave the water during emergence (Forbes and Robb 2008; Stoks and Cordoba-Aguilar 2012). Therefore, a negative effect of parasites on size seems to be unlikely in damselflies, which had already developed to their full body size after emergence (Hughes et al. 2016). Other possible explanations include the behavioural and the immune reactions of damselflies to parasites. Water mites attach themselves on to the ventral side of the host, and larval damselflies have been found to get rid of attached mites by grooming. It is possible that larger individuals can free themselves of the mites more effectively (Forbes and Baker 1990). Besides, body size could also be related to immunity. If larger individuals are able to allocate more resources towards their immune reaction, then their response (mite encapsulation) may be more efficient and the observed parasitization rate lower (Hughes et al. 2016). Lastly, the difference in size could be related to the age of damselflies. *Arrenurus* mites are found mainly in young individuals, and usually drop-off from the damselflies when they start to reproduce (Rolff 1999). Larger individuals may be able to survive longer and will also have less parasites, because they detach when the damselflies begin to reproduce. In this study, we excluded immature individuals (*violacea* and *rufescens* forms: Sánchez-Guillén et al. 2005), but in adults we did not control whether the unparasitized and larger individuals were older than parasitized ones. This hypothesis needs detailed studies in the future.

In Odonates, negative effects of parasites have also shown to be related to reduced egg production (Forbes and Baker 1991; Rolff 1999; Canales-Lazcano et al. 2005; but see Kaunisto et al. 2017), reduced mating success (this study; Forbes and Baker 1991; Andrés and Cordero 1998; Rolff 1999; Canales-Lazcano et al. 2005), or to increased mortality. In the Azure damselfly *Coenagrion puella*, mite load influenced the probability of daily re-sighting (Sherratt et al. 2010), or increased the likelihood of dispersal (Conrad et al. 2002).

Larval growth

In order to compare the two female morphs fitness, aside from pairing success and parasitisation rate, it is important to consider other fitness-related parameters, e.g. clutch size, egg hatching rate, and growth of the progeny.

In previous studies, female morphs of some species have been shown to differ in clutch size (Bots et al. 2009, 2010b; Bouton et al. 2011; Sánchez-Guillén et al. 2017; Khan 2020) and egg size (Takahashi and Watanabe 2010b; Takahashi and Kawata 2013), but in other species there was no difference (Iserbyt et al. 2013). In our study, we found a similar growth of larvae born from andromorph and gynomorph B-females. This result on growth rate is in line with the findings of (Abbott and Svensson 2008), who found that offspring from androchrome and *infuscans* have similar growth rates, but a different growth rate was found for offspring of the rare *rufescens-obsoleta* morph. However, we found that survival of the progeny during the growing period and the emergence rate differed between the two morphs, with a higher mortality of gynomorph progeny.

In conclusion, our results suggest that a higher survival of progeny of andromorph females at the larval stage could counterbalance the higher parasitization and the lower pairing success of andromorph adult females. Indeed, female fitness is related to adult mating behaviour and to ectoparasite burden (Thompson et al. 2011), but our results highlight the importance of considering the whole life-cycle in polymorphism studies (Cordoba-Aguilar 2008).

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