



Ontogenetic colour changes and male polymorphism in *Mnais andersoni* (Odonata: Calopterygidae)

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(Received 21 January 2017; final version received 8 May 2017)

Colour-based traits are widespread in flying species due to the importance of visual perception in their communication. Ontogenetic colour changes and reversible physiological colours occur in some species and are used as communication signals to conspecifics. The genus *Mnais* (Zygoptera: Calopterygidae) shows both genetic colour polymorphism and age-related colour changes, making challenging even the identification of species. Here we study three Chinese populations of *Mnais andersoni* during one month by mark-resighting methods. We describe the ontogenetic body and wing colour changes of male morphs (orange-winged and hyaline-winged) and females. With maturity, thoracic colour changes from metallic green to copper. The initially transparent wings of the hyaline winged males and females became light amber with age, while the orange-winged males show this colour since emergence to maturity. Whitish pruinosity covered all thorax in orange-winged males, while it remained limited to the ventral part of the thorax in hyaline-winged males and females. Hyaline-winged males presented less abdominal pruinosity than the rest of individuals. Our observations suggest that male morphs of *M. andersoni* are analogous to other species of the genus.

Keywords: colour polymorphism; age; maturation; pruinescence; China; dragonfly

Introduction

Animals with aerial locomotion, with the exception of bats, possess a developed visual system. In these species, visual stimuli used in communication can be found in special body structures, and usually they exhibit a great colour diversity. Colour can communicate hierarchy (e.g. Cuthill, Hunt, Cleary, & Clark, 1997; Gerald, 2001), condition (Johnsen, Delhey, Andersson, & Kempenaers, 2003; Thompson & Moore, 1991), sexual attraction (Blount, Metcalfe, Birkhead, & Surai, 2003; Gilbert, Williamson, Hazon, & Graves, 2006), or danger (Beeching, 1995; Summers & Clough, 2001). As with other communication signals, the message transmitted with colours can be enhanced with the exhibition of behavioural displays (e.g. Guillermo-Ferreira, Neiss, Hamada, & Bispo, 2014; Sanmartín-Villar & Cordero-Rivera, 2016a).

Intraspecific colour diversity is a common trait among damselflies. They may present colour variability within the day (Bick & Bick, 1965; Conrad & Pritchard, 1989), across maturity

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(Cordero, 1990; Sanmartín-Villar & Cordero-Rivera, 2016b) or between colour morphotypes (polymorphism; Van Gossum, Sherratt, & Cordero-Rivera, 2008). Daily and ontogenetic colour changes are temporal signals, while colour polymorphism constitutes a pattern of variation that is genetically determined (e.g. Cordero, 1990; Sánchez-Guillén, Van Gossum, & Cordero-Rivera, 2005; Sanmartín-Villar & Cordero-Rivera, 2016b). In some species, both age-related colour changes and polymorphism co-occur, creating large phenotypic variation, which can be erroneously considered of taxonomic significance (Sanmartín-Villar, Zhang, & Cordero-Rivera, 2016).

The identification of the species of the genus *Mnais* is an example of a challenging subject in damselfly taxonomy due to the morphological similarity between species, the absence of data from large geographical regions and the existence of extreme intra-population colour variability. For example, there are two male morphs and one female morph described in the literature for *Mnais costalis* (Selys, 1869) (e.g. Watanabe, 1990), while five different colorations are known for males and two for females in the whole of Japan (Ozono, Kawashima, & Futahiashi, 2012). In addition, *Mnais* species show geographic variation in the number of morphs per population (Tsubaki & Okuyama, 2015).

Our aim was to characterize and describe the intraspecific colour variation of *Mnais andersoni* (McLachlan in Selys, 1873) in three Chinese populations. Our findings provide a simple and practical guide to understand colour diversity in this species.

Material and methods

Field observations were performed between 9 and 18 May and between 15 and 18 June 2015 in three populations of the Yunnan province (China). One population was in Gengma (23.591358 N, 99.364905 E, 1320 m) and two in Ximeng (Ximeng 1: 22.716377 N, 99.612178 E, 824 m; Ximeng 2: 22.818943 N, 99.603052 E, 987 m). Damselflies fly early in Ximeng populations due to the southern latitude, lower altitude and warmer weather (HZ pers. obs.). Capture, marking and resighting were performed by one researcher during 65.6 h. Individuals were collected with an entomological hand net and marked on the right forewing with a xylene-free white permanent marker (Pilot Super Colour EF; www.pilotpen.com). Teneral were not studied to avoid damaging them. Resightings were performed by naked eye or employing a close-focusing monocular (range = 0.60–9.00 h day⁻¹). Avoiding the recapture of the animals minimizes the effect of handling and does not affect behaviour. Total body length (between head until the end of the anal appendages) and hind wing length were measured with a calliper to the nearest 0.1 mm. The age of the specimens was estimated by the bend of their wings (Plais-tow & Siva-Jothy, 1996), the thoracic coloration, the body pruinescence and the colour of the wings.

Specimens showed transparent wings, light amber wings or orange wings. The resighting of individuals through time allowed us to determine if this variability was due to an ontogenetic colour change (colour differences between successive resightings of the same individual) or a polymorphism (consistency of the coloration pattern). Body sizes were compared among wing coloration categories. Transparent-winged females were rare, and were only resighted in the same month of capture, limiting the analysis of their ontogenetic changes. The morphological and behavioural comparison between orange and light amber-winged males was analysed in a parallel study (Sanmartín-Villar, 2017). Body and wing lengths were compared between males with transparent and light amber wings by t-tests to analyse if both colorations belonged to the same morphotype. The same morphological traits were used as response variables in different general linear models (GLM) with wing colour, month (May/June) and population as fixed factors to analyse possible fluctuations across the time and space. Sexes were analysed separately.

Sex-ratio was calculated as the proportion of the number of males to the number of females for each population and time. Morph-ratio was calculated following the same method, dividing the number of orange-winged males by the number of hyaline-winged males.

Results

Population frequencies

Three wing colorations were observed in males and two in females. Males presented orange, light amber or transparent wings while females showed light amber or transparent wings. We will refer to all light amber and transparent-winged males as hyaline-winged males.

The sex ratio was always biased to males but there is no evidence for a change over time and among populations (contingency chi-square; $\chi^2_4 = 6.728$, $p = 0.151$; Table 1). The flight period had apparently ended in Ximeng 1 by June, as no individuals were found. Male morph ratio (orange:hyaline-winged) also did not change over time for the populations sampled in May and June (contingency chi-square with Yates correction, Gengma: $\chi^2_1 = 1.045$, $p = 0.307$; Ximeng 2: $\chi^2_1 = 1.235$, $p = 0.267$; Table 1). The resighting rate was low for all colorations except for Gengma orange-winged males (92.86%) and transparent-winged females in May (86.36%, Table 1).

Table 1. *Mnais andersoni* populations. No individuals were found in Ximeng 1 in June. Thoracic pruinescence: every level includes the previous one. The number of recaptured individuals is indicated between parentheses. Hyaline individuals are the sum of light amber and transparent categories.

Population	Gengma		Ximeng 1		Ximeng 2	
	May	June	May	May	June	
Sex ratio ($\sigma^{\circ}:\varphi$)	1.13	2.75	1.93	4.50	2.25	
Morph ratio (orange:hyaline)	1.08	0.38	1.25	4.40	1.25	
σ°						
Orange	14 (13)	3 (2)	15 (2)	22 (3)	5	
Light amber	3 (1)	8 (1)	12 (3)	5 (0)	4	
Transparent	10 (3)	0	0	0	0	
φ						
Light amber	0	4 (1)	14 (4)	5 (1)	4	
Transparent	22 (19)	0	0	1(0)	0	
Thorax						
Green	15	0	0	2	0	
Intermedium	35	5	19	22	4	
Copper	1	10	22	9	9	
Thoracic pruinescence						
No	9	0	0	1	0	
Basal	33	12	26	11	8	
Dorsal	9	3	7	15	0	
Lateral	0	0	8	6	5	
Abdominal pruinescence						
No	3	0	0	1	0	
Low	0	4	12	5	4	
S8-10	24	1	3	2	2	
S7-10	24	10	26	25	7	
Wing discoloration						
No	5	0	0	4	0	
Dots	4	0	10	15	1	
Groups	0	3	1	0	1	
Extensive	4	0	5	2	2	
Wing stiffness						
Basal	12	5	7	5	0	
Medium	35	10	31	27	12	
Apical	2	0	2	1	0	
Fieldwork days	3	2	6	3	1	
Total time employed (h)	19.55	9.82	21.27	9.58	6.33	

Ontogenetic changes

Three different thoracic colours were observed: green, green-copper (hereafter, intermediate), and copper (Figure 1; Table 1). All thoracic colorations were observed in May while green individuals were not observed in June. Light amber-winged males and females never presented green thoraxes. Intermediate thoraxes were observed in all kind of individuals of both populations and times. No transparent-winged individuals showed copper thoraxes. Five individuals (four orange-coloured males and one female) were marked in May and resighted in June after 37 (Gengma) and 28 (Ximeng 2) days. These resighted specimens revealed a thoracic colour change across maturity. Greenish individuals became intermediate, while intermediate individuals presented copper thoraxes. Most of the individuals observed in May on Gengma population showed green and intermediate thoracic colours, while in June they showed intermediate and copper thoraxes (Table 1). Similar results were obtained from Ximeng 2 population but more biased towards copper thoraxes in both months. Individuals from Ximeng 1 showed intermediate and copper thoraxes in May, while no individuals were found in June.

Four different levels of pruinosity were identified in the thoracic region (without pruinosity; ventral thorax and coxae; the previous level plus dorsal thorax; the previous level plus lateral thorax; Figure 1). Individuals without thoracic pruinosity were only observed in May and showed green thoraxes (except for one female). Only orange-winged males presented dorsal and lateral thoracic pruinosity. It was present in the ventral region of the thorax and covered the whole thorax in orange-winged males. Pruinosity covered the last three abdominal segments of hyaline males and the last four in orange-winged males and females. All five males and the only female resighted in June increased their level of pruinosity.

Four levels of pruinosity were observed in the dorsal part of the abdominal tip (without pruinosity; spots between the last three segments; last three segments; last four segments). Individuals resighted after one month showed a progression of pruinosity expansion across the abdominal segments. No individuals without pruinosity were observed in populations visited in June.

Wing colour suffered modifications in the individuals resighted in June (Figure 2). The light amber colour of the only resighted female showed a darkening process, but her coloration continued to be lighter than orange. Two of the four orange-winged males resighted in June presented more intensity of the orange colour at the core of the wings, as well as in the principal veins through the edge of the wings (Figure 2B), so that they seemed discoloured at the edges.

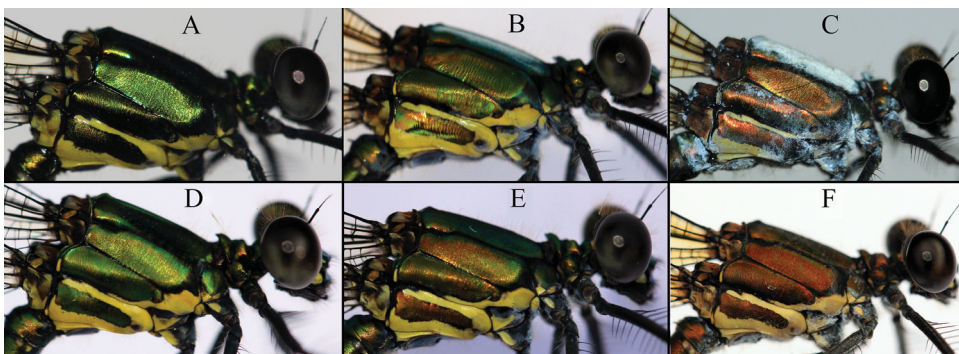


Figure 1. Ontogenetic colour change and pruinosity expansion in *Mnais andersoni* thorax. (A) immature male with green thorax. (B) mature male with “intermediate” thorax colour and pruinosity in the dorsal and ventral part of the thorax and in the coxae. (C) old male with copper thorax and pruinosity covering all thorax sides. (D) immature female with green thorax. (E) mature female with “intermediate” thorax colour and pruinosity in the ventral region and coxae. (F) old female with copper thorax and pruinosity in the ventral region and coxae.

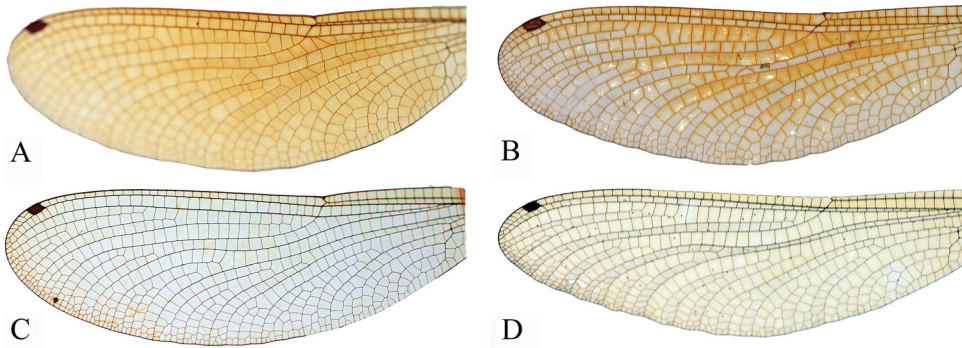


Figure 2. Ontogenetic wing colour change in *Mnais andersoni*. The wing shape seems different due to the different orientation of the camera. Hind wing of an orange-winged male captured in May (A) and recaptured in June (B); hind wing of a light amber wing female captured in May (C) and recaptured in June (D). Both individuals belonged to Gengma population.

Orange-winged males also presented individual or grouped discoloured cells in old resighted specimens.

Individuals with green thoraxes did not present apical bend. However, no more unambiguous information was obtained from the wing stiffness. This suggests that almost all captured individuals were several days old. Almost all individuals showed medial wing bend independently of the sex, thoracic colour, pruinosity level, population, and time of observation.

Body measurements

The only population where transparent and coloured males were found simultaneously was Gengma in May. In this population, body measurements of transparent-winged males did not differ from light amber-winged males (body: $t = 0.78$, $df = 2.76$, $p = 0.495$; hind wing: $t = 0.27$, $df = 3.10$, $p = 0.804$; Table 2) but they were smaller than orange-winged males (body: $t = 4.58$, $df = 16.84$, $p < 0.001$; hind wing: $t = 3.84$, $df = 18.06$, $p = 0.001$).

Male size differed among months and populations, but no significant interactions were detected between these factors (Table 3, Supplementary table). Due to the distribution of the female data (see Table 1), body sizes were not analysed among female wing colorations. Females presented longer bodies and hind wings in Gengma population (Tables 2, 3). Female body sizes were similar across time (Table 3). There was a significant interaction between month and population for female hind wing length (Table 3).

Table 2. Body measures of each kind of *Mnais andersoni* individual in relation to their wing and thorax colour. Mean \pm SE values.

Measure	Sex	Wing colour	Gengma		Ximeng 1	Ximeng 2	
			May	June	May	May	June
Body	♂	Orange	56.19 \pm 0.24	54.20 \pm 0.82	54.23 \pm 0.52	53.28 \pm 0.34	51.90 \pm 0.48
		Light amber	54.93 \pm 0.84	52.49 \pm 0.64	51.93 \pm 0.40	50.10 \pm 0.62	50.80 \pm 0.56
		Transparent	54.22 \pm 0.36	—	—	—	—
Body	♀	Light amber	—	51.08 \pm 0.59	48.66 \pm 0.43	46.94 \pm 0.47	46.10 \pm 1.40
		Transparent	50.81 \pm 0.23	—	—	48.40	—
		Transparent	—	—	—	—	—
Hind wing	♂	Orange	35.91 \pm 0.26	34.10 \pm 0.50	34.51 \pm 0.24	33.79 \pm 0.23	32.14 \pm 0.50
		Light amber	34.47 \pm 0.68	33.14 \pm 0.36	32.97 \pm 0.24	31.46 \pm 0.69	30.30 \pm 0.21
		Transparent	34.26 \pm 0.34	—	—	—	—
Hind wing	♀	Light amber	—	37.10 \pm 0.27	35.13 \pm 0.25	34.66 \pm 0.30	33.08 \pm 0.86
		Transparent	37.13 \pm 0.18	—	—	35.30	—
		Transparent	—	—	—	—	—

Table 3. *Mnais andersoni* body differences obtained by GLM analyses. Note that the interaction between female colour and month cannot be analysed because colours were found in different months.

Sex	Factors	Body			Hind wing		
		F	df	<i>p</i>	F	df	<i>p</i>
♂	Colour	24.25	2	< 0.001	33.30	2	< 0.001
	Month	8.40	1	0.005	25.57	1	< 0.001
	Population	26.69	2	< 0.001	38.71	2	< 0.001
	Colour × month	0.66	1	0.418	0.57	1	0.453
	Colour × population	0.10	1	0.909	1.35	1	0.265
	Month × population	3.29	1	0.073	0.07	1	0.790
	Colour × month*pop	1.83	1	0.179	0.00	1	0.996
♀	Month	0.17	1	0.683	2.88	1	0.096
	Population	32.95	2	< 0.001	43.60	2	< 0.001
	Month × population	1.46	1	0.233	7.68	5.00	0.030

Discussion

Our results indicate the existence of two male morphotypes and one female morph in *Mnais andersoni* that show ontogenetic colour changes. Using capture-resighting instead of capture-recapture is more appropriate for behavioural studies of species that are easily affected by the presence of observers, like the *Mnais* species studied here.

We can conclude that males with transparent and light amber wings belong to the same male morphotype due to (i) the darkening process of wing during development; (ii) lack of morphological differences among these colorations, when there were differences between both forms and orange-winged males (Sanmartín-Villar, 2017); (iii) transparent-winged males were not observed at the end of the flight period. Orange colour was maintained throughout the life of orange-winged males (soft orange-winged males were seen) while hyaline-winged males and females showed a darkening process with maturity (from transparent to light amber wings; Figure 2). Similar processes may occur in other *Mnais* species in the region. In a parallel study (Sanmartín-Villar, 2017), we observed three wing colorations in males (black and white, light amber and transparent) and two wing colours in females (orange and light amber) of *Mnais gregoryi* (Fraser, 1924) and one transparent male in *Mnais mneme* (Ris, 1916) (as well as the common orange and light amber-winged males).

Wing colour changes are commonly found in odonates (Corbet 1999). The ontogenetic wing colour change here described is similar to the differences in colour intensity found in *Mnais costalis*. This species shows different wing coloration as an effect of the diet and the progress of the season (Hooper, Tsubaki, & Silva-Jothy, 1999). The loss of efficiency of coloured-winged males to establish a territory at old ages (Tsubaki, Hooper, & Siva-Jothy, 1997) might be related to the wing discoloration here described. Some calopterygids only require a few days after metamorphosis for the almost complete development of the wing coloration (Dumont, 1972; Corbet, 1999) while others need five (Dumont, 1972) or 10 days (Heymer, 1973).

Along their ontogeny, individuals of both sexes and morphs changed their thoracic colour from green to copper. As is typical of odonates, immature individuals did not show pruinosity (Corbet, 1999). The fact that the more conspicuous and territorial male morph (described in Sanmartín-Villar, 2017) possessed higher intensity of pruinosity agrees with a possible function of this wax as a pattern for intraspecific communication (Gorb, 1995). The lack of pruinosity in immatures, females and sneakers suggests that pruinosity is widely used in intraspecific interactions due to its UV reflection (Robertson, 1984). On the other hand, pruinosity has also been interpreted as a defence against solar light (Paulson, 1983). In fact, in some species, hyaline-winged males develop higher thoracic temperatures than orange-winged males (Samejima & Tsubaki, 2010).

Males exposed to sunlight increase their thoracic temperature and court with more intensity, while sun exposed females oviposit for longer (Tsubaki, Samejima, & Siva-Jothy, 2010). From this point of view, pruinosity may possess a thermoregulatory function that allows continuous solar exposure in territorial males.

The observed colour change in both body and wings throughout time consisted in a darkening process as was found in other damselflies (e.g. Sanmartín-Villar & Cordero-Rivera, 2016a, 2016b; Sanmartín-Villar et al., 2016). This could be in concordance with (i) the communicative function of colour to indicate immaturity with conspicuous colorations (Hammers, Sánchez-Guillén, & Van Gossum, 2009); (ii) the maintenance cost of conspicuous colorations (Hooper et al. 1999); or (iii) the age-dependent dehydration (Corbet, 1999). The first two arguments are not mutually exclusive. Under the assumption that lighter colours are more conspicuous, the costs of producing and maintaining conspicuous colorations towards conspecifics could be lower than the costs derived from male harassment towards individuals of cryptic coloration that do not signal immaturity. However, immatures that present conspicuous colours might attract predators. In *M. andersoni*, immature colorations might be more similar in reflectance to the background than the adult coloration (see Schultz & Fincke, 2013), and therefore their coloration could be cryptic. Future studies are needed to understand this process and to link the ontogenetic colour change with possible colour variations in the background throughout the flight season.

Although not significant, there was a tendency for morph ratio to change over time (Table 1). This could be due to higher longevity of hyaline-winged males (Tsubaki et al., 1997) or to differences in the mean time of emergence between morphs (Watanabe & Taguchi, 2000). In other *Mnais* species, both male morphs gain similar lifetime fitness by a balance between longevity and daily reproductive success (Tsubaki & Hooper, 2004). The high resighting of orange-winged males and females, in contrast with hyaline-winged males, may be explained by their contrasting behavioural strategies. Orange males and females might be encountered easily in the same place due to their territoriality and their high site fidelity respectively (see Watanabe & Taguchi, 2000). Hyaline-winged males might spend more time far from the water mass due to the costs of the harassment from the other male morph (Watanabe, 1990).

Differences in body length may contribute to the behavioural dominance of orange males over hyaline winged males. Orange-winged males might increase the effectiveness of their dominant behaviour and territoriality due to their larger sizes (higher muscle power, more conspicuous) while hyaline-winged males might be more cryptic or mimic females by being smaller (Watanabe, 1990).

The male-biased sex-ratio across the season in absence of protandry (see also Watanabe and Taguchi, 2000), can be explained by different spatial distribution of the sexes and/or differences in longevity. Behavioural observations indicate that females have a tendency to return to the same spot of the stream, but more data are needed to document their distribution in the forests. The low number of females in the reproductive population could explain the low number of matings observed in this species (Sanmartín-Villar, 2017). Future studies should clarify this topic by the study of the sex-ratio in the larval stage.

In conclusion, *M. andersoni* presented high morphological variability (in body length and colour) between morphs, over time and across populations. These facts challenge species identification in *Mnais* populations and highlight the need for long-term studies of marked individuals.

Acknowledgements

Many thanks to Professor Quinghua Cai, director of the State Key Laboratory of Freshwater Ecology and Biotechnology of the Institute of Hydrobiology (Wuhan) and his team, for their help to ISV during his stay in China. Thanks to Yoshitaka Tsubaki and to Matti Hämäläinen for their comments.

Funding

This work was supported by the Spanish Ministry with competences in Science [Grant BES2012-052005 and EEBB-I-15-09382]; and by projects CGL2011-22629 and CGL2014-53140-P, including FEDER funds.

Supplemental data

Supplemental data for this article can be accessed at <https://doi.org/10.1080/13887890.2017.1329754>.

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