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# Looks or personality: what drives damselfly male mating success in the wild?

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## Abstract

Understanding the connection between personality and fitness is an important topic in both behavioural and evolutionary ecology. Most of our current knowledge stems from lab-studies despite that studies in natural populations for most parts generate more ecologically relevant information on behavioural variation and mating success. Here, we quantified *Calopteryx splendens* male mating success across two behavioural axes: courtship and boldness-aggression, testing personality and plasticity of behavioural traits in a natural population situated in the central-core of the species distribution. We also measured wing patch area and body size as these traits are important in damselfly sexual selection. The only behavioural trait that positively affected mating success was consistency in courtship effort. Among morphological traits, smaller wing patch size was associated with greater male mating success, while thorax size was a better predictor of male mating success than either personality or plasticity in boldness and activity. Our results demonstrate the importance of behavioural consistency over plasticity in a wild insect population and support prior studies showing the importance of body size for mating success.

**Keywords:** *Calopteryx splendens*, boldness, activity, courtship, behavioural syndrome, wild population

## Introduction

Animals have been shown to differ consistently in their individual behaviour (Sih et al. 2004a, 2004b; Bell 2007). This is known as animal personality and can substantially affect ecological and evolutionary processes (Réale et al. 2007; Wolf & Weissing 2012). Further, personality traits are often correlated with other behavioural traits leading to behavioural syndromes (BS, Sih et al. 2004b). For example, bold individuals are usually more active (boldness/activity BS, Golab et al. 2022), aggressive (boldness/aggression BS, Bell & Sih 2007), prone to take risk (boldness/risk-taking BS, van Oers et al. 2004) and/or more likely to explore new environments (boldness/exploration BS, Mazué et al. 2015). Individual behavioural variation, however, is not only determined by personality but is also influenced by individual plasticity, which governs the behavioural response of an animal to changing

environmental and/or social conditions (Mathot & Dingemanse 2014).

Individual differences in behavioural traits play important roles in population dynamics (Dall et al. 2012), dispersal and spatial distribution (Cote et al. 2010; Baguette et al. 2013), tendency to be invasive (Fogarty et al. 2011; Chapple et al. 2012) and inter-specific interactions (Pettorelli et al. 2015; Lichtenstein et al. 2018). Personality traits are also suggested to affect fitness (Dingemanse & Reale 2005; Smith & Blumstein 2007). Mating success is a good predictor of fitness (Andersson 1994) and in many cases strictly depends on animal behaviour (Bangham et al. 2002; Reaney & Backwell 2007; Rayner et al. 2020 but see Thompson et al. 2011). Yet, it is unclear to what extent consistent between-individual behavioural variation shape mating success in different environmental conditions (Schuett et al. 2010).

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In general, consistent behaviour is favoured in predictable environments (Lytle et al. 2008). It is also possible that consistent behaviours are present if individuals are unresponsive to environmental stimuli (Dingemanse et al. 2010; Mathot & Dingemanse 2014) or if animals consistently differ from each other in their adjustment to ambient conditions (Dingemanse et al. 2010). However, most studies focus on one of the two components of behavioural variation. One of the first studies comparing the strength of behavioural plasticity and personality in an invertebrate species investigated startle response in hermit crab (*Pagurus bernhardus*). The authors found that personality was more important than plasticity (Briffa et al. 2008), which confirms that these two components together determine variation in behaviour and should be studied together (Briffa et al. 2008; Dingemanse et al. 2010).

Compared to the large number of laboratory experiments on captive (or captive-bred) animals, relatively few studies have focused on personality in the wild. This despite the many limitations with studying animal behaviour under laboratory conditions (e.g. captivity stress, selective trapping, scale effects, homogeneity of the laboratory environment, artificial and relaxed selection, reduced pool of potential mates, etc.; Archard & Braithwaite 2010). Assessments of personality under artificial conditions might generate results and conclusions that can be ecologically or evolutionary misleading compared to what happens in the wild (Niemełä & Dingemanse 2014). While some studies do confirm similar personality estimates both in the lab and natural populations (e.g. studies on African striped mice *Rhabdomys pumilio*, Yuen et al. 2016; and blue tits *Cyanistes caeruleus*,; Herborn et al. 2010), other studies show differences between personality assessment in laboratory and field conditions (Fisher et al. 2015; Osborn & Briffa 2017). Further, some authors assume that laboratory vs field conditions can be considered as different contexts and as such generate different behavioural responses driven by alternative experimental conditions (Yuen et al. 2017; Mouchet et al. 2021).

The aim of our study was to determine if variation in male mating success depends on personality, plasticity and/or morphology in a wild insect population. We chose the damselfly *Calopteryx splendens* as a model organism for two main reasons. First, to fill a current knowledge gap in animal personality research, where insects – the most numerous taxonomic group on Earth – receive relatively limited attention (Mather & Logue 2013; Kralj-Fišer & Schuett 2014; Amat et al. 2018). Second, odonates have already been identified as good models for testing ecological and evolutionary

hypotheses (Córdoba-Aguilar 2008) and because the behavioural repertoire of *C. splendens* is very suitable for behavioural experiments in the wild (Golab et al. 2021). We formulated four main hypotheses: (i) males devoting more time to courtship display have higher mating success than males chasing females, as previously demonstrated in wolf spiders (Shamble et al. 2009) and dung beetles (Kotiaho 2002), (ii) males with more bold-aggressive personality have higher mating success than shy and less aggressive males, as previous research on water striders suggest (Sih et al. 2014), (iii) the most successful males show a balance between personality and plasticity in the studied traits, because these two components of behavioural diversity often complement each other – especially in moderately predictable environments (Dingemanse et al. 2010), (iv) wing spot area and thorax length will positively affect mating success, because it has been previously suggested that male wing coloration affects female reproductive decisions in *C. splendens* (Fitzstephens & Getty 2000), and body size is important for sexual selection in insects (Thornhill & Alcock 1983). We tested these hypotheses by measuring courtship effort, boldness and aggression all the while controlling for important sexually selected morphological traits (wing patch and body size) (Córdoba-Aguilar 2008).

## Methods

### *Study organism*

*Calopteryx splendens* (Figure 1) is a damselfly commonly found along slow flowing rivers in Europe (Dijkstra et al. 2020). Sexually mature males and females inhabit the shores of running waters where mating and oviposition take place (Rüppell et al. 2005). Males are territorial and polygynous and have an average life span, as mature, of approx. 1 week (Svensson et al. 2006). During the peak of the flying season (July in South Poland) many males adopt a non-territorial tactic attempting to take over already occupied territories (Rüppell et al. 2005; Golab et al. 2013). Males fight to gain access to territories (floating vegetation rafts) suitable for oviposition. A territory owner (resident) defends his patch for a few consecutive days, primarily by chasing away intruders; escalated male contests include biting (Rüppell et al. 2005). While holding a territory, the resident male patrols along the territory borders in order to detect and chase away intruders and to attract females with an elaborated courtship display (Corbet 2004). Copulation takes place after male courtship and female acceptance



Figure 1. *Calopteryx splendens* - mature male.

(Corbet 2004). After mating, the territorial male guards the female, while she oviposits eggs on his territory (Marden & Waage 1990; Córdoba-Aguilar & Cordero-Rivera 2005; Golab & Sniegula 2012). Vision is the only sense used during mate choice in odonates (Corbet 2004). Wing pigmentation communicates the male condition (reviewed by Córdoba-Aguilar & Cordero-Rivera 2005), and wings play an important role in courtships display (Rüppell et al. 2005). Previous studies have shown that *C. splendens* males can be safely observed from 2 m distance without influencing its behaviour (e.g. Golab et al. 2013, 2017). Also, neither the time of day (between 11.00 h and 15.00 h) nor habitat disturbance affects the territorial behaviours of territorial males in the studied population (Golab et al. 2013).

#### Field study

The studies were conducted between 1 June and 31 August 2020 and 2021 along a 50 m section of the river Biala Nida, South Poland (50.712860 N, 20.194094 E), located in the centre of the species distribution (Figure 2c; Dijkstra et al. 2020). The river section chosen for the study is regulated and located in a homogeneous landscape; therefore, its hydrological conditions are stable. Riparian vegetation was cut regularly to standardize vegetation height and to avoid shading of the water. Aquatic vegetation used by the damselfly as territories and oviposition substrates was manipulated (cut with scissors) so that floating vegetation rafts (territories) were equal in size, shape and plant composition (Figure 2a). An earlier study showed that the size of a vegetation patch correlates with the territorial strategy of resident males (Golab et al. 2013). At the

studied river section, a conspecific damselfly species, *C. virgo*, was also present, but only at low densities, 5–15 individuals per 50 m. To avoid interspecific aggression during the experiments, all *C. virgo* individuals were collected and relocated at least 4 km upstream each morning (usually less than 10 individuals). Field experiments were conducted under comparable weather conditions (sunny days, air temperature 23–28°C; wind 0–4 m/s) and time of day (10.00 h–11.00 h individual marking, 11.00 h–15.00 h experiments and 16.00 h–17.00 h collecting males for morphological measurements, details below). Birds, mostly white wagtails, have been seen hunting odonates along the study river. However, no bird-predation was observed during the conducted research. Presumably, the presence of 2–3 researchers along the river scared the birds away. At the beginning of every field work day, all males present at the studied section of the river were caught with an insect net and individually marked with a unique combination of three digits written on both hindwings (white marker) in order to recognize individuals without recapturing them. Each male had the same wing surface marked to ensure that the potential impact of the marking was consistent for every individual (Anderson et al. 2011). After marking, individuals were released at their respective capture site. Every morning, prior to the start of the data collection, a 10 min observation of studied territories was performed in order to assign resident males to their respective territories. Next, at least six randomly chosen mature males (to serve as intruders in the following experiments) and females were caught and glued to a fishing-line (Figure 2c,d; Tynkkynen et al. 2008; Golab et al. 2021), placed in a cooler to prevent energy expenditure and kept until experiments began. After each day of data collection, the studied residents were caught and preserved in 70% ethanol. Morphological features (abdomen and thorax length) of the males were measured to the nearest 0.1 mm using a digital caliper. Wings were photographed, and patch size was subsequently measured with the software ImageJ.

*Courtship effort experiment.* One of the collected females was attached to a fishing-line anchored to a rod (Figure 2c) and presented to a focal resident male for 2 min. Female presentation was video-recorded in order to quantify the following male traits: (1) courtship – time [s] the courtship display was performed by the resident male; (2) female chasing – the time [s] the resident male devoted for chasing female without courtship display (hereafter, female chasing) – a behaviour related to sexual coercion. In order to avoid female exhaustion and to



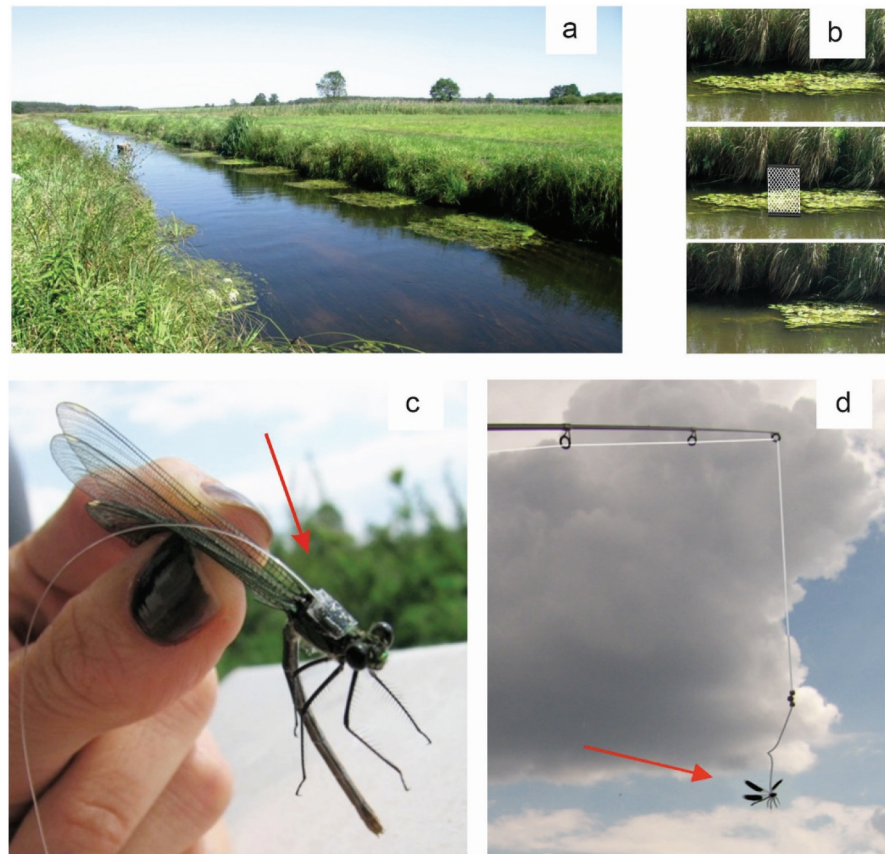


Figure 2. Study site and experimental methods in Biala Nida river, Poland. Floating vegetation (*potamogeton natans*) rafts (territories) (a), territory manipulation by sinking the floating vegetation with ballast (b), *Calopteryx splendens* female attached to a fishing line (c-d).

reduce risk of females displaying rejection signals, females presented to the resident males were replaced every 10 min. The video-recordings were analysed in slow motion in order to quantify the traits listed above. This method has successfully been used in previous behavioural studies on this damselfly species (Rüppell & Hilfert-Rüppell 2013). The procedure was carried out, to each of the focal residents, both in the morning (10.00–12.00 h, before territory manipulation) and in the afternoon (13.00–15.00 h, after territory manipulation). In the afternoon trial, the quality of the territory (vegetation raft) was manipulated by reducing its size by sinking ca. 25% of the floating vegetation with ballast (two steel pipes connected with a fishing net) (Golab et al. 2013, 2021; Figure 2b)

**Boldness experiment.** A bird decoy, with real feathers, dimensions similar to a wagtail and in a spread-wing posture, was moved from a distance of 4 m with a speed ca. 2 m/s (which is 2 times faster than *Calopteryx* spp. flight speed; Rüppell & Hilfert-Rüppell 2020) towards a perching resident male until he flew away. Time until the resident returned

to his territory was recorded. The observation was terminated after 200 s and individual that had not returned was assigned a maximum value of 200 s. As above, the trial was repeated in the morning and afternoon with the same habitat manipulation, as described above, carried out. Boldness was measured as latency to return to the territory – the bolder an individual was, the faster he returned. To make the interpretation of the result presentation more intuitive (i.e. higher values = higher boldness), boldness values were inverted. A similar method for quantifying damselfly boldness was successfully used in previous studies (Brodin 2009; Golab et al. 2021).

**Aggression experiment.** One of the collected intruder-males was attached to a fishing-line and presented to a focal resident male for 2 min (the intruder was moved towards the resident while flying). Again, each assay was recorded and analysed analogously to the courtship trials. The following traits were quantified: (1) male chasing – time [s] a resident male spent chasing an intruder without a fighting attempt, which denotes a less aggressive response to

an intruder (2) escalated fight – time [s] a resident male spent on heavy/escalated fighting, which represents the most aggressive behaviour. This treatment was repeated to each of the resident males, similarly to the courtship experiment. As with stimuli females, intruder males were replaced every 10 min.

**Mating efficiency.** Observations were made from the centre of the river channel, over a distance of 50 m along the river. Each set lasted 15–25 min during which territorial males and their territories were observed. If experiments were being conducted on the particular territory, observation of that, and the two adjacent, territories was skipped. Since egg-laying in *C. splendens* usually takes less than an hour (Rüppell et al. 2005), it was possible to observe most of the females laying eggs in a given territory. The number of females that laid eggs on a given male territory were counted and used as a proxy of male mating success. We only included females that were previously seen copulating with the focal residents.

**Analyses.** The R software (R Development Core Team 2022) was used for data analyses. Spearman's correlations between mean boldness and mean aggression traits (chasing male, heavy fights) were calculated to test for the existence of bold-aggressive syndrome.

A behavioural reaction norm approach was used to assess plasticity and personality of the studied traits. The plasticity of the studied traits was computed as the slope of the behavioural traits measured in the two experimental trials (absolute value of the difference between second and first measurement). Personality (consistency of traits) was computed as an average trait value from the two experimental trials (Gosling 2001; Pigliucci 2001; Schuett et al. 2010). It was previously shown that the traits related to activity, boldness and sexual behaviours are repeatable in *C. splendens* in the studied population (Golab et al. 2021). In the present study, we again tested for consistency of behavioural traits by comparing the differences between the two territory manipulations (before and after manipulation). We used generalized linear mixed-effects models (GLMMs; glmmTMB function) with treatment (i.e. before and after manipulations) as fixed effect and the ID of male as a random effect to control for the repeated measures.

A generalized linear model (GLM; glmmTMB function) was constructed to test how mating success (negative binomial distribution) in resident males was affected by behaviours with the following explanatory variables: year, plasticity (slope values)

of: aggression (chasing male, heavy fights), boldness and courtship (courtship effort, chasing female) and consistency (mean values) of the above traits. Wing patch size and thorax length were used as covariates. Courtship-related traits were analysed in a separate model, since we wanted to analyse sexual and non-sexual behaviours separately (Golab et al. 2022). Statistical significance was established at  $p < 0.05$ .

## Results

In this study, we assayed in total 87 males: 31 males in 2020 and 56 in 2021 (Table I).

None of the tested behavioural traits were significantly different between the two territory manipulations (Courtship effort: Estimate =  $-0.44$ ,  $Z = -1.64$ ,  $P = 0.101$ ; Chasing female: Estimate =  $-0.12$ ,  $Z = -0.4$ ,  $P = 0.692$ ; Boldness: Estimate =  $0.39$ ,  $Z = 0.94$ ,  $P = 0.347$ ; Chasing male: Estimate =  $<-0.01$ ,  $Z = <-0.01$ ,  $P = 0.997$ ; Heavy fights: Estimate =  $1.02$ ,  $Z = 0.24$ ,  $P = 0.811$ ), showing that males in the studied population behaved consistently over the two trials and the average trait value can be used as a proxy for trait consistency. Also, there were no differences in male success between the 2 years in all models (courtship consistency:  $P = 0.142$ , courtship plasticity:  $P = 0.631$ , boldness-aggression consistency:  $P = 0.061$ , boldness-aggression plasticity:  $P = 0.095$ ); hence, year was removed from the models.

Average courtship effort (consistency, proxy for personality) was positively correlated to male mating success, while wing patch size was not related to mating success (Table II, Figure 3a,e). In contrast, neither chasing females nor thorax length affected male mating success (Figure 3b,f).

Plasticity of courtship effort and of chasing females did not affect male mating success (Figure 3c,d). Wing patch size was negatively correlated to male mating success (Table II, Figure 3e).

Average boldness, chasing male and heavy fights (consistency measures) did not influence male mating success (Table III, Figure 4a,b,e). However, also

Table I. Number of *Calopteryx splendens* males used in experiments on Biala Nida river, Poland.

Trait measured	Number of individuals
Mating success	52
Courtship effort, Chasing female	79
Boldness	45
Chasing male, Heavy fights	72
Patch size, Thorax	78

Table II. Effects of personality and plasticity of courtship-related behaviours and body size on male mating success in *Calopteryx splendens*.

	Variable	Estimate	Z value	P
Personality (consistency)	Courtship effort	0.02	2.78	<b>0.006*</b>
	Chasing female	<0.01	0.39	0.699
	Patch size	-0.01	-1.71	0.087
	Thorax	0.33	1.51	0.130
Plasticity	Courtship effort	0.01	1.70	0.089
	Chasing female	<0.01	0.45	0.651
	Patch size	-0.02	-2.81	<b>0.005*</b>
	Thorax	0.22	0.71	0.478

here wing patch size affected mating success negatively, whereas thorax length had a positive effect on male mating success (Table III, Figure 3f).

Plasticity of boldness and aggression-related traits did not affect male mating success (Table III, Figure 4c,d,f). Nevertheless, here, in contrast to the other models, wing patch size did not correlate with male mating success (Table III).

Finally, there was a significant negative correlation between average boldness and average chasing male ( $r = -0.34$ ,  $p = 0.038$ ; Figure 5a). In contrast, average boldness was not correlated with average heavy fights ( $r = -0.08$ ,  $p = 0.641$ ; Figure 5b).

## Discussion

In this study, we investigated the impact of personality (consistency), plasticity and morphology on male mating success in a wild insect population. Our results supported the hypothesis that males devoting more time to courtship would get higher mating success. We showed, however, that the bold-aggressive syndrome does not seem to affect mating success. In addition, we did not find support for our third hypothesis that intermediate personality and plasticity lead to the highest mating success. Finally, we can conclude that our results were in line with the long-standing assumption that sexually selected morphological traits affect male mating success (Andersson 1994), although the effect is not always positive.

In general, the connections between body metrics and male mating success were not clear in our study. The negative effect of patch size on male mating success seen here can have several explanations. Usually, sexual selection favours larger wing pigmentation in calopterygids (Siva-Jothy 1999; Córdoba-Aguilar 2002). However, interspecific interactions might interfere with sexual selection. Co-occurrence of *C. virgo* at the studied river might have been selected for smaller patch size in *C. splendens* through reduced interspecific

aggression. *C. splendens* with larger wing patches are more often attacked and deprived of territory by *C. virgo* males than males with smaller wing patches (Tynkkynen et al. 2004; Kuitunen et al. 2011). Yet, the experiment was conducted in a river section where *C. virgo* was relatively rare. The congeneric species was more numerous in the lower parts of the river (ca. 4 km downstream). Another possible explanation to the negative effects of patch size on mating success found here could be that the individuals in our study area were migrants from the lower sections of the river and hence had a history of high interspecific interaction with *C. virgo*, which is very plausible since calopterygid damselflies tend to migrate upstream (Stettmer 1996; Schutte et al. 1997). Also, an increased predation-risk for large-spotted males could be another force selecting for smaller wing patch and acting antagonistically to sexual selection. Such decoupled sexual and natural selections have been suggested for *C. splendens* (Kuchta & Svensson 2014; Outomuro & Johansson 2015) and other species such as swordtails (*Xiphophorus hellerii*; Rosenthal et al. 2001) or several agamid lizard species (Stuart-Fox & Ord 2004). It is also important to note that the wing marking method itself can impact the mating efficiency of odonates, as has been demonstrated in the species *Hetaerina americana*, where increasing the red pigment area affected mating success (Grether 1996). In our study, we had to compromise between reducing time in captivity (minimizing stress) and reducing identification time in the field to avoid disrupting the natural behaviour of the males during experiments. Wing marking allowed us to balance these two goals. As we ensured that the wing surface covered by the code was comparable across all studied males, we assume that the experimental procedure's impact was uniform for all damselflies. This approach allowed us to reveal real behavioural differences among them. However, caution should be exercised in directly relating the absolute number of matings

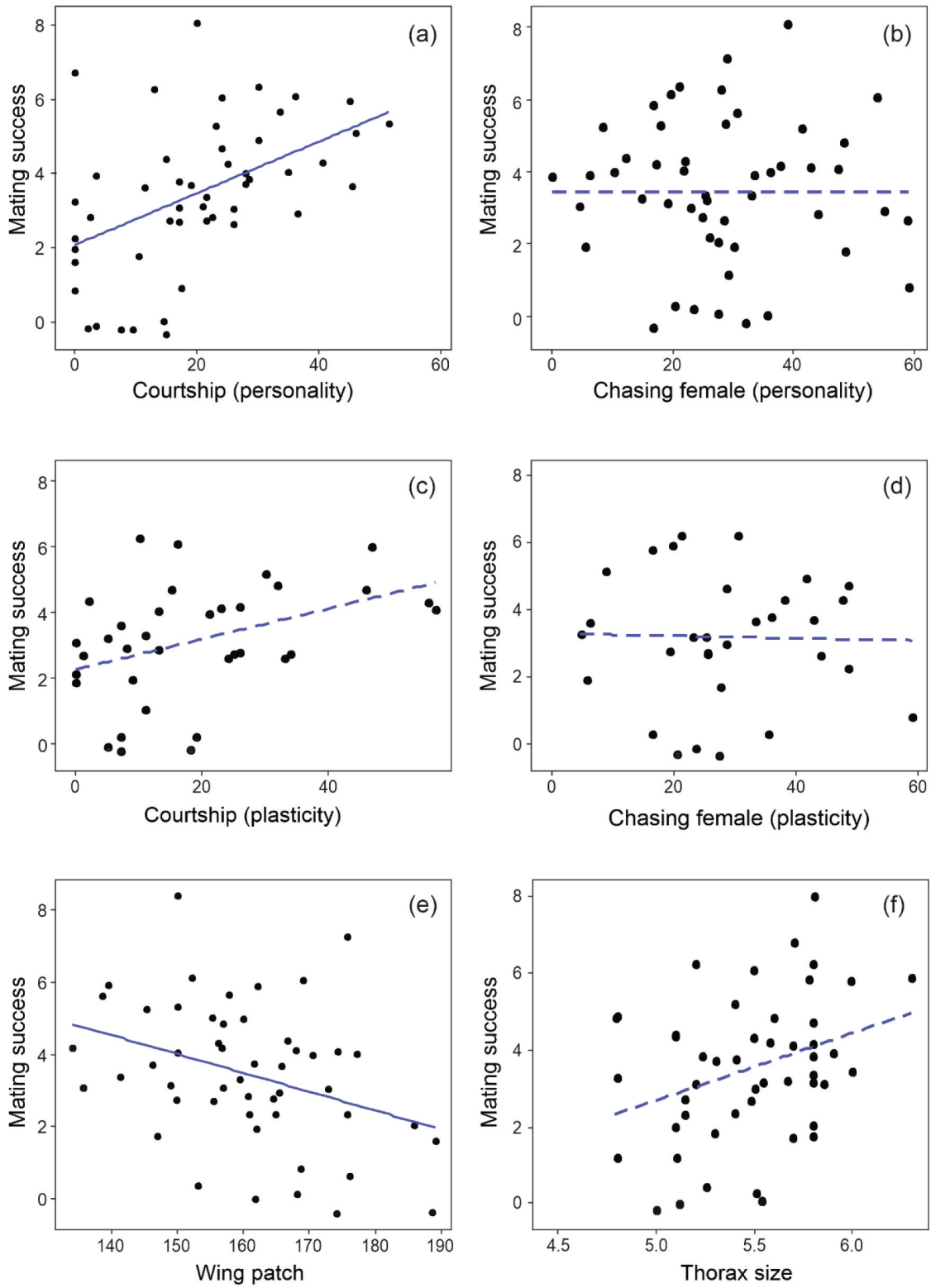


Figure 3. Correlation between plasticity and personality of courtship related traits and mating success (a–d). Correlation between body dimensions (wing patch size and thorax width) and male mating success in *Calopteryx splendens* males (e–f). Non-significant relationships are shown with dashed lines.



Table III. Effects of personality and plasticity in boldness-aggression related traits and body size on male mating success in *Calopteryx splendens*.

	Variable	Estimate	Z value	P
Personality (consistency)	Boldness	<0.01	0.13	0.893
	Chasing male	<-0.01	-0.38	0.630
	Heavy fights	<0.01	0.50	0.617
	Patch size	-0.01	-2.21	<b>0.028*</b>
	Thorax	0.51	2.03	<b>0.042*</b>
Plasticity	Boldness	<0.01	0.84	0.397
	Chasing male	<-0.01	-0.72	0.468
	Heavy fights	<0.01	0.73	0.466
	Patch size	-0.02	-1.82	0.069
	Thorax	0.93	2.44	<b>0.015*</b>

obtained by the studied males to un-manipulated males under natural conditions. Altogether, male secondary sexual character (wing patch size) maintenance was probably disrupted by different selection pressures (Andersson 1994) in our study, suggesting that the trait plays a minor role for male mating success in this particular population, especially when compared to male courtship effort. A similar pattern was observed in a wolf spider (*Schizocosa uetzi*) where body ornamentation was condition dependent and only male courtship intensity increased mating success (Shamble et al. 2009).

Courtship effort consistency affected male mating success positively, whereas plasticity of courtship effort only tended to affect male mating success. As such, courtship effort consistency seems to be more important than plasticity for male mating success in our study population. The advantage of consistency over plasticity might be explained by predictability of environmental conditions (both physical and social; Dall et al. 2012) and a balance between sexual and natural selection (Gadgil 1972; Burk 1982; Andersson 1994). The studied population was located in the central area of the *C. splendens* distribution, and we assume that the environmental variation in this area is highly predictable and suitable for the species (Lytle et al. 2008; Dijkstra et al. 2020; Riotte-Lambert & Matthiopoulos 2020), which should favour personality over plasticity (Dingemanse et al. 2010). Current results correspond with previous findings showing the highest courtship values in *C. splendens* populations central in the species range, where local factors favour selection on courtship rather than boldness (Golab et al. 2022). Calopterygid females mate discriminately and refuse forced copulations with males that do not adopt pre-copulatory courtship (Waage 1987; Cordero 1999; Arnqvist & Nilsson 2000). Therefore, at stable environmental conditions, partners devoting much time to

courtship should experience higher mating success. Forced copulations may be accepted only in unfavourable environments, like in very high population densities (Cordero Rivera & Andrés 2002) or when habitats are disrupted (Golab & Sniegula 2012), which was not the case in our study system. Also, since personality can be heritable (Réale et al. 2007; Korsten et al. 2013) females may choose partners with a given behavioural profile which would be adaptive for their offspring (Dingemanse et al. 2010). Similar results, personality being more important than behavioural plasticity, were shown in a study on mosquitofish (*Gambusia holbrooki*), where increasing personality and decreasing plasticity over ontogeny were attributed to a reduction in environmental uncertainty (Polverino et al. 2016).

Finally, Fowler-Finn and Hebets (2011) showed that wolf spider (*Hogna georgicola*) males with conspicuous body ornamentation showed greater degree of plasticity in courtship under predation risk. This observation corresponds with the pattern found in our courtship model, where smaller and less conspicuous wing ornamentation was related to higher mating success and consistency of courtship effort.

We found no effect of boldness-aggression traits on male mating success. Instead, the models showed significant effects, albeit in opposite direction, of both wing patch size and thorax length. The reasoning for the negative relationship between wing patch size and male mating success here would be similar as for the patch size and courtship relation discussed above, whereas the positive effect of body size (thorax length) on male mating success is in line with results in other studies of both invertebrates and vertebrates (Thornhill & Alcock 1983; Reiss 1989; Stearns 1992). This has mainly been explained by that sexual selection can enhance body dimensions that are beneficial for fighting for territories and mates, resisting predators, etc. (e.g. Partridge et al. 1987; Karsten et al. 2009). With

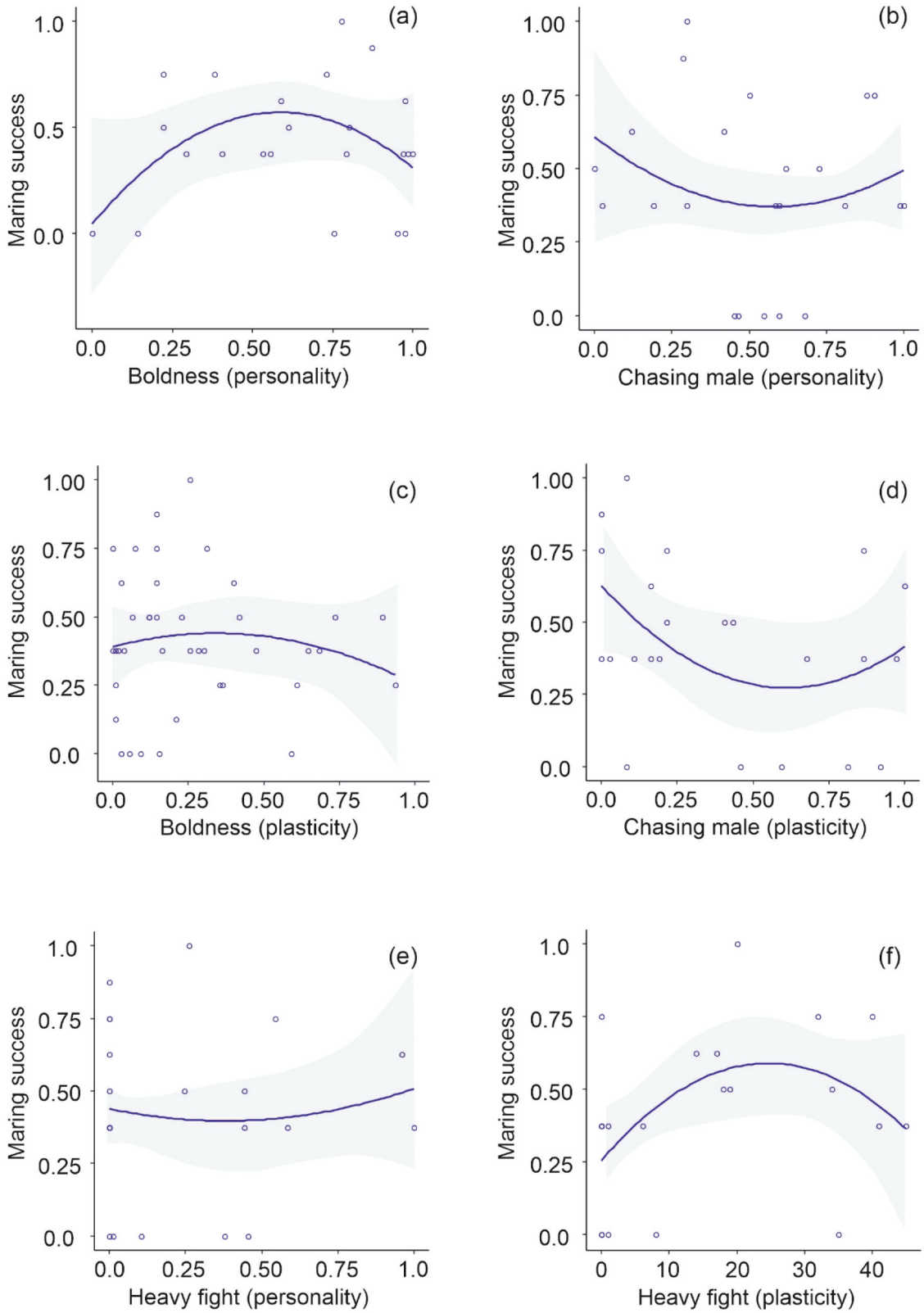


Figure 4. Polynomial relation between: personality in boldness and aggression related traits and mating success of *Calopteryx splendens* males (a, b, e) and between plasticity of boldness and aggression related traits and mating success (c, d, f); standard error (shaded area).

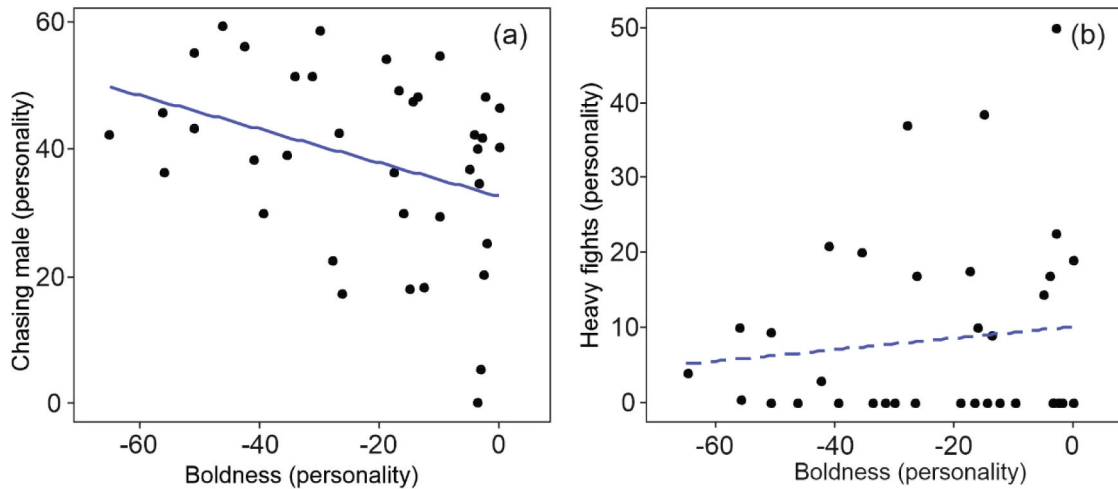


Figure 5. Correlations between boldness and aggression related traits: a – chasing male, and b – heavy fights. Non-significant relationship is shown with dashed line.

regard to damselfly biology, the muscles located in thorax influence both flight ability and endurance (Corbet 2004). Higher investment into muscle mass increases the chance of escaping predators and congeneric avoidance, resisting wind gusts and allows for more effective territory patrolling (Corbet 2004; Ruppell et al. 2005; Golab et al. 2017). In some populations high aggression and boldness might be a bad fit for the social context and reduce male mating success as has been shown for instance in water striders (Sih et al. 2014).

We found no evidence that the most successful males show intermediate values of consistency and plasticity in boldness and aggression. Also, unlike most studies (Bell 2007) the boldness-aggression correlation was rather weak with significant correlation only between boldness and mild aggression (chasing male), but not between boldness and heavy fights. Since male chasing is a safe and short social interaction which in fact may reduce costs of open aggression (Briffa & Sneddon 2010) we suggest that our study are not showing a classic boldness-aggression correlation. It is probable that the favourable environmental conditions that these damselflies experience at the centre of species distribution (Sagarin & Gaines 2002) are not selected for bolder and/or more aggressive behaviours in general, and therefore neither plasticity nor consistency in boldness or heavy fights affects male mating success directly. Similar results were shown in previous studies on, e.g. stickleback *Gasterosteus aculeatus* (Bell 2005) and zebrafish *Danio rerio* (Way et al. 2015), where the authors failed to detect a correlation between aggression and boldness under conditions without severe stressors.

Order effects, which arise when the order in which experimental treatments are administered affects the response, can be a potential confounding factor in personality studies (Schuett et al. 2010). However, it is unlikely that order effects were present in our study, as previous research has shown that neither time of day nor habitat disturbance affected the territorial behaviours of the studied population (Golab et al. 2013).

In summary, our study provides insights into how personality, morphology and behavioural correlations affect mating success in a wild insect population. Our results demonstrate the importance of consistency over plasticity in the context of environmental change. Further studies on how behavioural profiles affect insect fitness over time and space (i.e. larger geographic gradients) are needed to test the generality of found results and to support/reject their suggested explanations.

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