



RESEARCH PAPER

It Takes Two to Tango: Relative Influence of Male and Female Identity and Morphology on Complex Courtship Display in a Newt Species

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Abstract

Consistency in behaviour is currently receiving a renewed interest. Although courtship display is generally consistent in terms of behavioural sequence and structure, there is also commonly important variation in the intensity of courtship display between and within males of a given species. Indeed, not all males have the same ability to perform courtship display (variation between males), and each male can potentially adjust his courtship effort in response to the environment (variation within a male). Although the study of male courtship display has received considerable attention in recent years, it is still unclear which part of the variation can be explained by male ability or motivation. We investigated this issue on two phases of the complex courtship display of the palmate newt *Lissotriton helveticus*. Overall, we found that both male and female identities affected courtship behaviour, but the relative influence of each sex depended on the courtship phase. Male identity explained variation in fan and creep-quiver display, whereas female identity explained variation in creep-quiver only. Interestingly, we did not find any link between the expression of courtship display and male or female morphological traits. Our study showed consistency of male courtship display in newts and successfully dissects the different sources of variation that can affect behavioural repeatability/consistency of courtship display.

Introduction

The evolutionary potential of sexual selection is largely driven by mate choice; therefore, the role played by female sexual preferences on shaping male secondary sexual traits has received considerable attention over the past century. Much focus has been put on male ornaments, while behavioural components of courtship displays have received much less attention. Behavioural courtship displays consist of a series of stereotyped behaviours, which are both consistent in terms of behavioural sequence and structure within a species and that are used in sexual communication.

Despite its importance in promoting mate choice, courtship is sometimes not considered as a sexual trait *per se*, but only as an attracter of the female's attention on male ornaments (Rowe 1999) or an ornament amplifier because most morphological traits can be fully assessed only when displayed during courtship (Loyau et al. 2005a). However, several studies have pointed out that courtship display can contribute to female mate choice in addition to and independently of ornaments (e.g. H glund & Lundberg 1987; reviewed by Andersson 1994; see also Loyau et al. 2005a; Lehtonen 2012) or can even be the main determinant of female sexual preferences (e.g.

Vehrencamp et al. 1989; Cornuau et al. 2012). For a behavioural courtship display to be informative, variation in its intensity should be larger between than within males. This implies that (1) the behaviour should be at least partially consistent within a given individual (consistent on a short timescale when individual state and external conditions remain constant) and (2) individuals of the population behave differently from one another.

The fact that females prefer males that express the most intense courtship displays is likely to be evolutionarily rooted in the costs paid by the displaying males in terms of time, energy and exposure to higher predation risks. Generally, only males in good condition, of high quality or that are extremely motivated can maintain a high courtship display effort (Bradbury & Vehrencamp 2011; Mowles & Ord 2012; but see e.g. Lehtonen 2012). In this case, male sexual behaviour is affected by male internal factors. When the internal factors remain constant over the breeding season (e.g. male body condition, phenotypic quality) or even the lifetime of the individuals (e.g. genetic quality, 'good genes', immune capacities, ontogenetic development and condition at metamorphosis), courtship display will also remain constant. For example, more ornamented peacocks (*Pavo cristatus*) were better able to maintain high rates of courtship display when facing an immune challenge (Loyau et al. 2005b; but see Cornuau et al. 2014 for a counterexample in the Palmate newt *Lissotriton helveticus*), and low-quality males depleted their energy reserves in a terminal effort in the sand goby *Pomatoschistus minutus* (Lehtonen 2012). Here, the male's intrinsic properties (i.e. ability or quality) are important factors determining courtship behaviour and reproductive success and therefore will be statistically captured by the inclusion of 'individual identity' (i.e. female 1, female 2, male 1, male 2 and so on, which include unmeasured intrinsic properties).

Other internal factors may vary on a shorter timescale, such as levels of reproductive hormones or health status, influencing male ability to display, consequently altering the consistency of courtship displays across observations. Males may also be sensitive to their environment and adjust their courtship effort in response to environmental pressures such as predation, environmental condition or the presence of rivals that alter male motivation. For example, male alpine newts *Ichthyosaura alpestris* and guppy *Poecilia reticulata* decrease their visual courtship displays in darker environments (Chapman et al. 2009; Denoël & Doellen 2010), male wolf spiders reduce their likelihood to court in response to predator cues

(Fowler-Finn & Hebets 2011), and male Siamese fighting fish *Betta splendens* increase their courtship effort in the presence of a rival (Dzieczynski et al. 2009). Moreover, male courtship effort can also be adjusted to spatial and temporal partner availability (Lindström et al. 2009), as well as female quality or receptivity (Reading & Backwell 2007). Males can spend more time in courtship display towards larger females (Wong & Svensson 2009) or modify their courtship display activity in response to a specific positive female feedback cue (Santangelo 2005; Sullivan-Beckers & Hebets 2011). Here, female intrinsic properties are equally important factors (Patricelli et al. 2002, 2006). All these examples show that courtship display effort can be driven by both male and female attributes, but their respective magnitude is not yet disentangled. Therefore, it is important to understand the sources of behavioural variation in courtship display, their timescale of variation and their influence on mate choice (Lehtonen et al. 2011).

In this study, we investigated the importance of both male and female identity on the elaboration of complex courtship displays with the aim to better understand how courtship display can affect the regime of sexual selection (Jaquière et al. 2009; Schneider & Lesmono 2009; Loyau & Lacroix 2010). We examined the temporal variation amongst and within males by performing three successive mate choice trials in a population of palmate newts *Lissotriton helveticus*. Male newts express a complex, stereotyped, elaborated courtship display that is the main determinant of female mate choice (Cornuau et al. 2012). Palmate newt courtship display combines multimodal cues including visual, chemical and tactile ones (Wells 2007). The male first approaches the female, smells her cloaca and follows her before moving to her front. Then, courtship activity *per se* begins, characterized by the male newt performing fan, whip and wave behaviours (Table 1). The fan behaviour represents the longest and the most frequent behaviour in palmate newt display. It consists in displaying the tail and the filament to the female in a rapid vibrating fan movement. Before spermatophore deposition, the male creeps in front of the female and performs a creep-quiver behaviour (Table 1), which corresponds to an offer to deposit a spermatophore for the female. The female then touches the male's tail to motivate spermatophore deposition on the ground. To transfer the spermatophore, the female follows the male until her cloaca is above the spermatophore, allowing her to take it up. In this and other urodele species, reproduction requires a close coordination between males and females because internal

Table 1: Courtship display behaviours of male palmate newts

Behaviours	Description
Fan	The male folds his tail along his flank and vibrates the distal portion of his tail in front of the female
Whip	The male suddenly lashes his tail against his flank
Wave	The male holds his tail up for a few seconds, to present it in a full lateral view to the female
Creep-quiver	The male turns away from the female and begins to creep. He holds his tail straight in front of the female snout and moves his tail slowly (quiver). This behaviour could be viewed as an offer to deposit a spermatophore to the female

fertilization occurs without copulation by means of spermatophore transfer without prolonged physical contact (Wells 2007). We therefore suspected that both male and female identity may affect courtship behaviour. We observed courtship activity consistency after 1 d and again after 4 d, for fan, whip, wave and creep-quiver behaviours and predicted that consistency should be higher when the interval between observations was shorter (Bell et al. 2009; Garamszegi et al. 2012).

Methods

Laboratory Experiment

All the individuals (24 male and 24 female adult newts) were captured by dip netting in one pond near Caumont (Ariège, France) at an early stage of the breeding season (3rd April 2012) and were immediately taken to our animal facility (catching permit no. 2009-13, Préfecture de l'Ariège). All the females were sexually mature and gravid, all potentially having a similar motivation to reproduce. As females usually come later than males to the pond, monitoring males' arrival allowed us to capture the females at an early stage of the breeding season, to maximize the probability that the females were still unmated. Even though we cannot discard the possibility that some of the females already mated, we are confident that these females represented only a small proportion of the females involved in our study. As female palmate newts usually mate multiple times with multiple males over the breeding season (Cornuau et al. 2012; J. H. Cornuau, pers. obs.), previous matings should not alter the results of our study. The day following capture, each individual was marked with a subcutaneous coloured visible elastomer (VIE, Northwest Marine Technology, Washington, Shaw Island, WA,

USA) at the base of one of the four legs allowing individual identification (see Cornuau et al. 2014 for details).

The newts were maintained in unisex groups of six for 1 wk before the start of the experiment. They were kept in tanks (52 × 33.5 × 29.5 cm), each filled with a mix of approximately half environmental water from their native pond and half aged tap water. We also placed plants collected from their native pond to keep the water environment familiar and close to natural conditions. A perforated clay brick was placed in each tank to ensure shelter. The newts were maintained at 18°C (±1) under fluorescent tubes (Repti-Sun 2.0, ZooMed) to simulate natural light with a cycle of 12 h light/12 h dark. They were fed *ad libitum* by daily provision of living daphnia collected from a semi-natural pond, which maintained the newts' natural predation behaviour. The newts were released in their native pond immediately after the experiment. They were kept in captivity for 2 wk, which represents only a small part of the breeding season (up to 3 mo) and should not have any impact on the population of origin. All the individuals maintained their weights during captivity and were healthy upon release.

Measurement of Morphological Traits

The day after capture in the field, we recorded body mass (accuracy: 0.01 g), filament length (only for males) and snout-vent length (SVL) as a measure of body size (Table S1). We took photographs of the individuals on a millimetre paper background (grid 1 mm²) to obtain SVL and filament length with licence-free software IMAGEJ v.1.28 (<http://rsb.info.nih.gov/ij/>), which yields highly reliable and repeatable measures (Cornuau et al. 2012). We calculated the body condition index (BCI) of males and females using the residuals of the linear regression of the square root of weight on SVL for each sex separately (Băncilă et al. 2010; Table S1). In male palmate newts, morphological sexual traits are composed of one filament at the extremity of the tail, two hind-foot-webs and a small crest on the back. These ornaments are only expressed during the reproductive period and their developments are highly correlated (Cornuau et al. 2014); therefore, we used only filament length in the present study.

Experimental Design

We aimed to investigate the consistency of male and female behaviour as well as the relative contribution

of both males and females on several aspects of palmate newt courtship display. One week after capture, courtship display behaviours were assessed during dyadic encounters between one male and one female. Pairs of individuals were randomly formed in respect to morphological variables. The behaviours of each individual were observed in three instances: on day 1 (10th April 2012), day 2 (11th April) and finally 4 d after the second measure (day 6, 16th April). All encounters were unique, that is each male encountered three different females, and each female encountered three different males. To avoid changes in female receptivity over the course of the experiment, we did not allow the females to take male spermatophores. Indeed, in the palmate newt, female mate choice and female choosiness may change after a first mating, as shown in the smooth newt *Lissotriton vulgaris* (Gabor & Halliday 1997). Therefore, when a female appeared to be willing to transfer a deposited spermatophore (by starting to follow the male), we gently prevented the female from placing her cloaca above the spermatophore by positioning a glass rod between her body and the spermatophore. Both male and female still performed courtship behaviour immediately after this intervention (J.H. Cornuau, pers. obs.).

The trials were performed in an experimental tank (26 × 33.5 × 29.5 cm), from 08:00 am to 12:00 noon. Six mate choice trials were simultaneously performed, each in a separate tank, so that all 24 trials were conducted on the same day. Each experimental tank contained 3 cm of sand and 8 cm of water. The tank water was changed, and the tanks and sand were cleaned between trials to remove chemical cues. Before the trial, each experimental tank was divided into two parts, one for each sex, with an opaque separator. The male and the female were placed in each part of the experimental tank for a 5 min to allow acclimatization before the visual barrier was eventually removed. Then, the individuals were able to interact freely for 40 min, a period of time found to be sufficient for the observation of sexual behaviours (Cornuau et al. 2012).

Measurement of Behaviour

Each mate choice trial was recorded using a video camera placed above the experimental tank. The videos were analysed with the software The Observer 7.0 (Noldus Information Technology). We recorded the number of fan, whip and wave events performed by a given male over the 40 min of the trial. As fan behaviour can last several minutes, so we also recorded the

time spent in fan. The numbers of fans, whips, waves as well as the time spent in fan were all strongly correlated (Tables S1 and S2). Therefore, we subsequently used only the time spent in fan behaviour as a proxy of display activity as previously performed (Cornuau et al. 2012). However, we checked that we obtained identical results when we used the number of fans, waves or whips instead of the time spent in fan. In addition, we counted the number of creep-quivers.

Statistical Analyses

The tests were performed using the R 3.0.1 software (R Development Core Team). First, we examined the effects of the day, as well as both male and female identity on the time spent in fan display. No fan display behaviour was observed in 13 of the 72 trials. To account for this potential bias in our analysis, we analysed this parameter in two steps. In a first step, we used the whole data set and performed nonparametric statistics because the time spent in fan display was not normally distributed. We used a Cox regression model with the package *coxme* as this model does not assume a specific probability distribution, but unlike most nonparametric approaches it takes into account the influence of mixed effects, that is both covariates and random factors, as GLMMs do (Therneau 2012). In a second step, we discarded the trials in which the fan display was not observed. In the reduced data set, the fan display was normally distributed and we performed GLMMs with the *lme4* package using a Gaussian distribution of error terms. Secondly, we examined the effects of the day, as well as both male and female identity on the number of creep-quivers, as performed by Lehtonen et al. (2011). We built GLMMs with the *lme4* package using a Poisson distribution of error terms and the log link function.

In all the models (Cox mixed models and GLMMs), the day was set as a fixed factor, and both male and female identities were included as random factors. We built 4 models: model 1 (full model) including day, male identity and female identity; model 2 with male identity and female identity; model 3 with day and female identity; and model 4 including day and male identity. We assessed the statistical significance of fixed and random factors using log-likelihood tests by comparing a model including the factor of interest with a reduced model without this factor. We obtained the contribution of male identity by comparing model 1 and model 3, female identity by comparing model 1 and model 4 and day by comparing model 1 and model 2.

In addition, we calculated the repeatability of the time spent in fan display and the number of creep-quivers. We calculated R and 95% confidence intervals using Nakagawa & Schielzeth's (2010) method with the *rptR* package. We used the function for Gaussian data for the time spent in fan display and the function for count data for the number of creep-quivers.

Finally, we assessed the influence of both female and male morphological traits on both the time spent in fan display and the number of creep-quivers in the same way as described above, with both male and female identities set as random factors and morphological traits as fixed factors. The interaction between fixed factors was initially included but was always non-significant. We built one model for male traits (body size, BCI, filament length) and one model for female traits (body size, BCI) so as not to overload the models, given the sample size. Again, we assessed the statistical significance of the fixed factors using log-likelihood tests by comparing a full model with reduced models without the fixed factor of interest.

Results

Only male identity explained a significant proportion of the time spent in fan display (Table 2, Fig. 1). Female identity and day did not significantly contribute to explaining the time in fan display (Table 2). The results were similar irrespective of whether all data or only trials in which fan displays were observed were included in the analysis (Table 2).

The number of creep-quivers was significantly explained by male identity, day and female identity (Table 2, Fig. 2). Male identity better explained the number of creep-quivers, and female identity and day

also contributed significantly to this behaviour (Table 2). We found that the number of creep-quivers significantly decreased between day 1 and day 2 (Wilcoxon matched-pairs signed-ranks test: $V = 246$, $df = 22$, $p = 0.001$) and between day 1 and day 6 (Paired Wilcoxon test: $V = 148$, $df = 22$, $p = 0.007$), but remained constant between day 2 and day 6 (Paired Wilcoxon test: $V = 70.5$, $df = 22$, $p = 0.33$).

The time spent in fan display and the number of male creep-quivers was not explained by any of our male or female morphological parameters (Table 3).

Discussion

Consistent behavioural differences amongst individuals of the same species have been recognized as important for selection (Bell et al. 2009). Here, we tested in a series of experimental trials whether two phases of a complex courtship display could be explained by both male and female identity and morphological traits in the palmate newt *Lissotriton helveticus*. Our study provides evidence that both male and female identity influenced complex courtship behaviours, but interestingly, the relative influence of sex depended on the courtship phase. More precisely, we found that the time spent in fan display, a major determinant of female mate choice, was explained only by male identity. The day of observation and female identity had no influence on this particular behaviour. The number of creep-quiver displays (corresponding to the male's offer to deposit a spermatophore) was explained by both male and female identity, but the influence of female identity was lower than that of male identity. Surprisingly, none of the measured male and female morphological traits contributed to explain variation in courtship behav-

Table 2: Effects of male and female identities and day on male behavioural sexual traits (fan display and creep-quiver). Male and female identities were set as random factors and day as a fixed factor

Response	Factor of interest	χ^2_1	Variance explained ^a	p	Repeatability ^b
Fan display (total)	Male identity	5.42	34.629	0.019	0.33 (0.055, 0.605)
	Female identity	0.014	0	0.906	-0.055 (-0.287, 0.178)
	Day	0.654	7.422	0.418	
Fan display (without 0)	Male identity	5.514	32.535	0.019	0.291 (-0.016, 0.599)
	Female identity	0.347	6.458	0.556	-0.023 (-0.318, 0.273)
	Day	2.366	0.847	0.124	
Creep-quiver	Male identity	22.03	28.256	<0.001	0.329 (0.139, 0.583)
	Female identity	5.02	7.754	0.025	0.173 (0.082, 0.431)
	Day	19.95	10.073	<0.001	

^aCalculated after Lehtonen et al. 2011.

^bR and 95% confidence intervals in brackets calculated after Nakagawa & Schielzeth 2010.

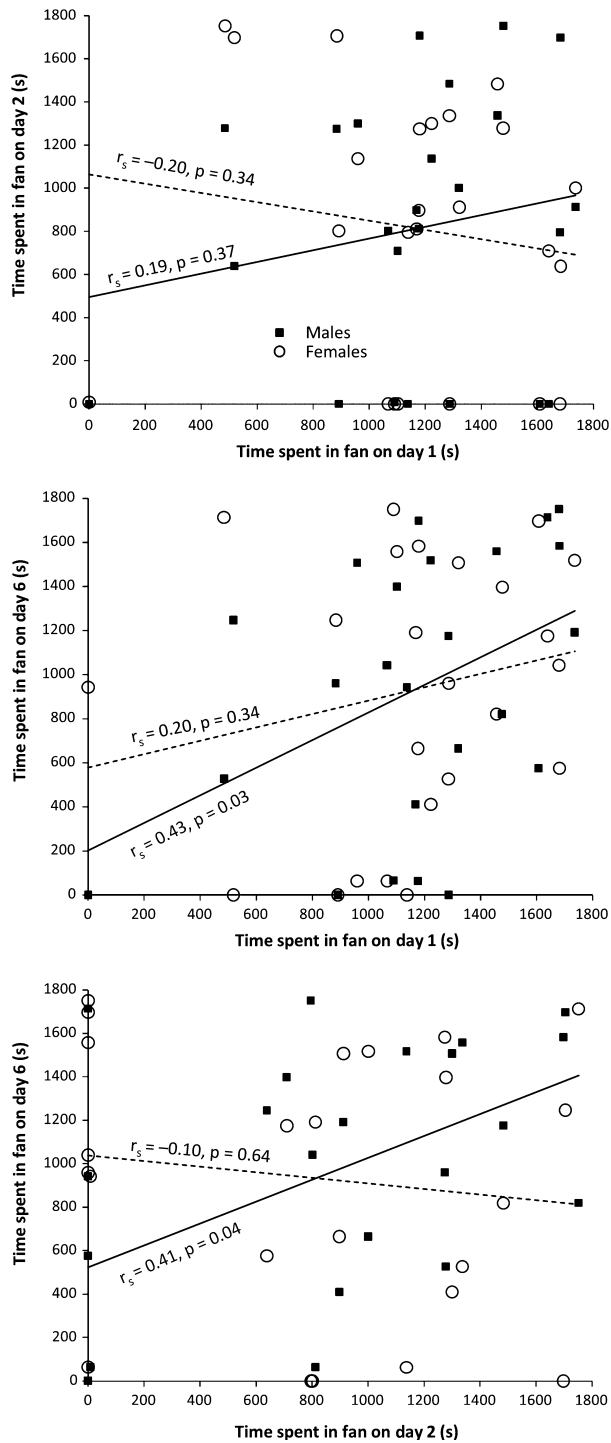


Fig. 1: Correlations between observations on day 1, day 2 and day 6 for the time spent in fan display for males (black squares and solid lines), and the time the females were displayed to for (empty circles and broken lines).

our. In palmate newts, the behavioural fan display is the main determinant of female mate choice (Cornuau et al. 2012). Here, the expression of behavioural

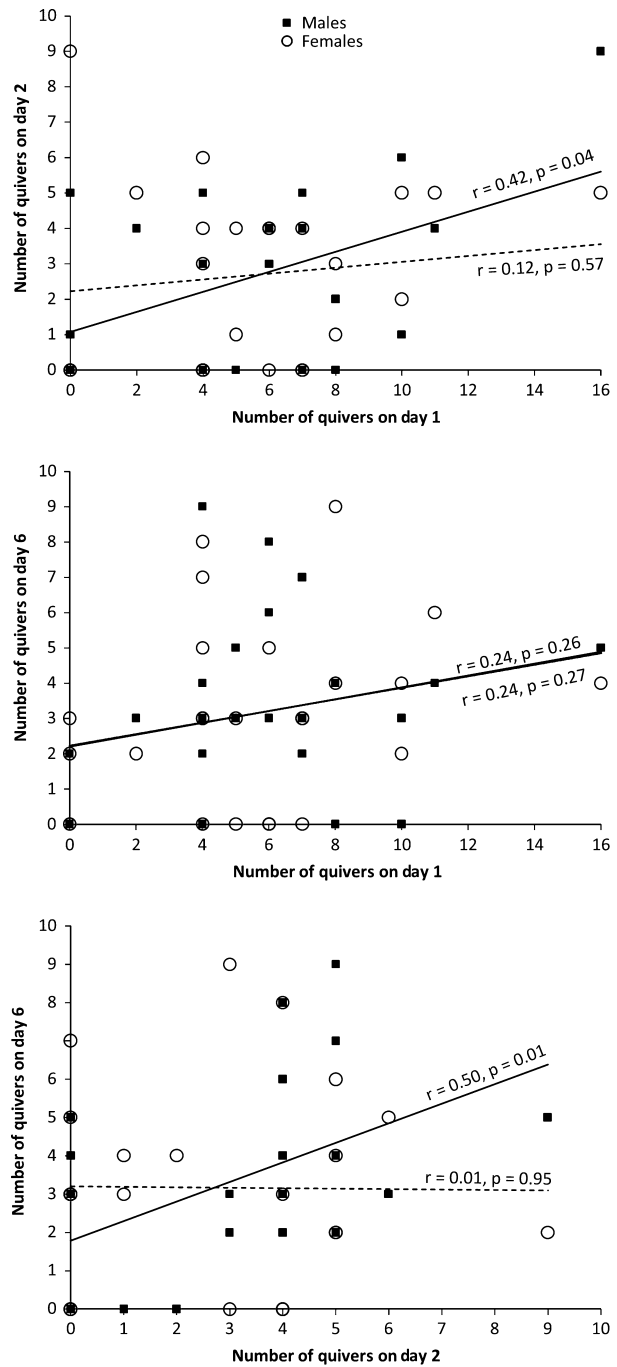


Fig. 2: Correlations between observations on day 1, day 2 and day 6 for the number of creep-quivers for males (black squares and solid lines) and females (empty circles and broken lines).

fan display was explained only by male identity meaning that females can potentially extract reliable information concerning male quality based on the courtship display effort. Generally, extravagant courtship displays are assumed to be costly for males

Table 3: Effects of male and female morphological traits on male behavioural sexual traits (fan display and creep-quiver). Male and female identities were included in each model as random factors. All the interactions were non-significant

Response	Factor of interest	χ^2_1	p
Fan display	Male body size	0.74	0.39
	Male BCI	0.01	0.97
	Filament length	0.48	0.49
Fan display	Female body size	1.19	0.27
	Female BCI	2.87	0.09
Creep-quiver	Male body size	0.02	0.89
	Male BCI	0.16	0.93
	Filament length	0.04	0.85
Creep-quiver	Female body size	0.39	0.53
	Female BCI	0.53	0.47

implying that these displays can only be maintained by males in good condition. However, we did not find any impact of male ornamentation, body size or condition on the courtship effort. This result is consistent with previous results suggesting that the fan display is probably not a condition-dependent sexual trait (Cornuau et al. 2014).

Recent studies have stressed that males can adjust their behavioural courtship display according to female characteristics, especially when females vary greatly in their reproductive value such as receptivity or body size (Reading & Backwell 2007). Such behavioural adjustment can affect the reliability of courtship display and could blur our assessment of female mating preferences (Widemo & Saether 1999; Lehtonen et al. 2011). In our study, we did not find evidence of any kind of behavioural adjustment for the fan display. Our finding, however, is in agreement with other studies which showed that courtship displays were more driven by internal male properties or male state and less by the external environment (Ruiz et al. 2008; Lehtonen et al. 2011). Limited behavioural flexibility could be driven by genes, prior experience, environmental factors and/or physiology, such as metabolism or hormones (Sih et al. 2004; Sih & Bell 2008; Wolf & Weissing 2010; Garamszegi et al. 2012). Further studies are needed to explore the contribution of these parameters on behavioural flexibility.

In this study, another component of the male behavioural courtship, the creep-quiver behaviour, was driven by both male and female identity. However, none of the female morphological traits measured explained the observed variation. A creep-quiver represents a male's offer to deposit a spermatophore; thus, it is likely adaptive to adjust that behaviour to female receptivity (Halliday 1975). Yet,

the influence of male identity on creep-quiver was more important than female identity, suggesting that this behaviour is more strongly determined by male internal factors.

Behavioural consistency can drastically vary from one species to another and can also depend on the experimental set-up. For example, in a meta-analysis of behavioural consistency, Bell et al. (2009) found that, on average, 35% of the variation amongst individuals is attributed to individual differences. This is consistent with the 33% of variance in fan display and creep-quiver behaviour explained by male identity. However, more recent studies have reported higher values of repeatability (e.g. Dzieczynski et al. 2014; $\leq 25\%$, Garamszegi et al. 2012: 48%; %, Lehtonen 2012: 51–52%; %, Dzieczynski & Leopard 2010: 57–83%; %, Lehtonen et al. 2011: 84%; %). With regard to consistency in other species, an important part of variation of both components of the display behaviour measured in this study remained unexplained despite the inclusion of female identity and day as potential explanatory variables. Therefore, further work should be conducted to unravel additional factors promoting behavioural variation of male courtship. In line with this idea, we found an impact of the observation day on the creep-quiver behaviour, and the strength of the correlation also varied for the fan display between observation days. Due to their very nature, studies on behavioural consistency allow the individuals to collect information on the experimental environment during the first test (Bell et al. 2009). While we tried to minimize this problem by preventing the females from transferring spermatophores, our experimental design might still have led to a modification in the experimental situation for both males and females. Indeed, female selectivity may have increased after a first encounter (Gabor & Halliday 1997), or female motivation may have decreased because they could not take the spermatophores deposited by the males. This could also explain why, contrary to our expectation, the consistency of the creep-quiver behaviour was stronger between day 2 and 6 than between day 1 and 2, despite the interval between observations being longer (Bell et al. 2009; Garamszegi et al. 2012).

To conclude, we measured two aspects of male behavioural courtship display and found that this courtship display effort was explained by male identity, especially for the fan display, which is the main determinant of female mate choice in this species. Male identity, female identity and day of observation all had an impact on one of the two measured behaviours (creep-quiver). Morphological traits measured in this study (body size, body condition and orna-

ment) did not contribute to explain within-male variation in behaviour. Why some males consistently perform more numerous and intensive courtship displays compared to other males remains an open question for future studies. Our study is one of a few that experimentally dissected the different sources of variation that can affect behavioural repeatability/consistency of courtship display (Lehtonen et al. 2011), and provides the first example of a significant within-male variation in newt courtship display. Our study shows that two aspects of a complex courtship display can differ greatly in their consistency, providing males with a signalling ability highly consistent within a male and therefore highly informative to the females, and a behaviour that can be partly adjusted by the male to the context (female intrinsic properties and seasonality). Male variation in both behaviours can contribute to variance in reproductive success and consequently modify the evolutionary potential of sexual selection (Lehtonen et al. 2011).

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1: Descriptive statistics of morphological and behavioural courtship display.

Table S2: Coefficients of Spearman correlations between behavioural measures in male palmate newts. All *p*-values <0.001.