

Body temperature, size, nuptial colouration and mating success in male Moor Frogs (*Rana arvalis*)

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Abstract. Variation in colouration has rarely been related to sexual selection in anuran amphibians, even though such a relationship has been proven for many other vertebrate taxa. Male and female Moor Frogs (*Rana arvalis*) have a cryptic brown colour pattern, but males develop a conspicuous blue nuptial colouration during the reproductive season. To investigate the possibility that colouration plays a role in sexual selection in this species, we studied the temporal variation in blue colouration, determined if body size or body temperature affected blueness and investigated if blueness of males could be related to their mating success. Results confirmed previous observations that males develop and maintain blue colouration for only a very few nights during peak reproductive activity. Colouration of males was unrelated to body size, but males exhibiting higher body temperatures were somewhat bluer than males with lower body temperatures. Further, males in amplexus had higher body temperatures than non-mated males. Finally, mating success was positively related to blueness in small males, whereas in large males no such relationship was detected. While our results align with the hypothesis that the bright blue colouration of males may be a target of sexual selection, alternative explanations are also discussed.

Keywords: male-male competition, mate choice, natural history, reproduction, sexual selection.

Introduction

Visual signals including both colouration and behaviour-mediated displays play important roles in foraging, anti-predator defence and social interactions in many vertebrates (Andersson, 1994). Conspicuous colouration present in one sex only is often assumed to play a role in sexual selection (Andersson and Simmons, 2006), especially if the colouration is expressed only during the reproductive season (Amundsen and Forsgren, 2001). Brightly coloured males may confer direct and indirect benefits

to their mates (Trivers, 1972; Møller and Jennions, 2001) and male colouration may facilitate sexual isolation when closely related, syntopic species breed simultaneously (Seehausen and van Alphen, 1998). The information content of male colouration may thus be exploited by female choice, resulting in fitness gains for choosy females and for brightly coloured males. Furthermore, colouration of contestants may also play a role in male-male competition for mates, territories or other resources (Olsson, 1994). Using these visual cues, males may avoid costs arising from strenuous behavioural displays and direct aggressive interactions (Maynard-Smith and Price, 1973). The question of how generally sexual selection is involved in the evolution of temporal sexual dimorphism in colouration has remained largely unexplored in anuran amphibians.

Only a few studies have demonstrated colouration to be associated with sexual selection in anurans (Summers et al., 1999; Taylor, Buchanan and Doherty, 2007; Vasquez and Pfennig, 2007). One explanation for the scarce documentation of such a relationship may be that female choice is often based on acoustic

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signals in anuran amphibians (e.g. Ryan, 1980; Roesli and Reyer, 2000; Hobel and Gerhardt, 2003) whereas fights for receptive females are generally decided by the body size of rivals (e.g. Davies and Halliday, 1977, 1979; Arak, 1983; Byrne and Roberts, 2004). Nonetheless, the rarity of studies suggesting the use of visual signals in reproduction-related behavioural processes may partly be the result of a tradition-mediated bias in herpetology (for a similar bias see chemical communication in frogs, Waldman and Bishop, 2004). It may also be due to observer bias, as humans (but not frogs, see Larsen and Pedersen, 1982; Buchanan, 1998) see poorly at night, when most reproductive activity takes place in the majority of anuran species. Thus, the importance of colouration for sexual selection in anurans may currently be underestimated (Hoffman and Blouin, 2000). This may especially be true if anurans use multiple cues in communication for which there is some support (Narins, Hödl and Grabul, 2003; Rosenthal, Rand and Ryan, 2004; Taylor et al., 2007; Vasquez and Pfennig, 2007).

While the bright blue colouration of male Moor Frogs (*Rana arvalis* Nilsson, 1842) during the breeding season has puzzled naturalists for more than a century (Brehm, Boettger and Pechuel-Loesche, 1892), virtually nothing is known about its temporal variability, physiological background and functional significance. As the conspicuous colouration only develops in males and only during the breeding season (Nöllert and Nöllert, 1992; Ries et al., 2008), it seems straightforward to assume that male colour plays a role either in female mate choice and/or intrasexual competition for mates. The only published study (Sheldon et al., 2003) that has focused on male colouration in the Moor Frog assumed that colouration could play a role in sexual selection and tested if bluer males produced offspring with lower mortality rates when exposed to predation. Sheldon and colleagues (2003) indeed found a positive relationship between sire colouration and tadpole survival and

concluded that male colouration may provide a basis for female choice.

In the present paper, we tested the hypothesis that blue male nuptial colouration may be a sexually selected trait in Moor Frogs. As a first step towards testing this hypothesis, we investigated whether male colouration is related to male mating success, i.e. whether bluer males are more likely to be found in amplexus than paler or brown males. We also tested the significance of body size and temperature, both factors predicted to positively affect mating success of males. To investigate what may affect blueness of males, we tested if larger, usually older males (Söderman, 2006) are bluer than smaller, younger males. We also explored whether male colouration correlates with body temperature (as suggested by Hedengren, 1987) which is a significant factor determining physiological and thus behavioural performance of ectotherms.

Materials and methods

The study species

The Moor Frog is a medium-sized frog that occupies large areas of eastern and northern Europe and western Asia. Its colouration is typically brown, often with darker and lighter lengthwise stripes on the back and hind legs and black blotches distributed all over the body apart from the whitish ventral side. During the reproductive season, males develop dark thumb pads and a more or less blue body-colouration while females remain brown (Nöllert and Nöllert, 1992). Despite the wide distribution range and extensive studies on various aspects of the biology of this species (e.g. Räsänen, Laurila and Merilä, 2003; Loman and Lardner, 2006; Söderman et al., 2007), very little is known about its reproductive behaviour (but see Hedengren, 1987). The reproductive season is extremely short and starts early in the year, as soon as the water temperature reaches about 10°C (Kuzmin, 1999). Males arrive at the breeding pond first, while most females arrive simultaneously during two to three nights and leave the pond after having laid their eggs (Hedengren, 1987). Males form dense choruses and call persistently. Females usually get amplexed in the water and deposit their clutch within the male chorus. Animals are active day and night during the reproductive season (Nöllert and Nöllert, 1992).

Data collection

In April 1999, we surveyed two Moor Frog populations located in mid-Sweden (Lindrågen: 59°28'N, 13°31'E,

Häggedal: 59°40'N, 17°15'E) over one and five nights, respectively. Both populations were very large with the number of calling males exceeding 1000 individuals. In Lindrängen the survey night was chosen to be the one with highest mating activity and in Häggedal, survey nights covered the peak of the reproductive season. On a survey night, we moved around in the pond for several hours and hand-collected amplexed and non-amplexed adult males opportunistically while visiting different parts of the pond to avoid recapturing the same individuals. Immediately after capture, we noted time, mating status, measured cloacal temperature with a portable thermometer (to the nearest 0.1°C) for estimating body temperature, snout-vent length (SVL) with a digital calliper (to the nearest 0.1 mm), and scored colouration of males. To obtain representative scores on blueness of males, we scored male colouration by dividing up the dorsal part of the body into seven areas adopting the highly repeatable scoring method (unpublished data) of Sheldon et al. (2003). The areas were (1) the upper head; (2) the two sides of the head; (3) the forelimbs; (4) the upper back; (5) the lower back; (6) the left and right flanks and (7) the hind limbs. Each area was given a score for the extent and for the intensity of blue colour within them, scores ranged from one (least) to five (most). Scores were subsequently mathematically combined into one measure of overall blueness (see below). Captured animals were released back into the pond after each night's field work.

Statistical analyses

Scores on the extent and intensity of blue colour for seven areas of the upper body were first subjected to a principal components analysis (PCA) to collapse the seven variables into a composite measure of 'blueness'. The correlation matrix revealed strong positive within-individual relationships between the extent covered by blue colouration and the colour intensities between and within these areas (all $R > 0.42$). The value of the Kaiser-Meyer-Olkin Measure of Sampling Adequacy was 0.89 and the Bartlett's Test of Sphericity was significant ($\chi^2 = 3878$, $n = 91$, $P < 0.001$). Consequently, we could proceed with the PCA. The first component explained 68.1% of the total variance and all variables loaded strongly and positively onto this component (all loadings > 0.72). We thus decided to use the scores on PC1 as an overall measure of 'blueness'.

As body temperature decreased with time within sampling nights (Partial correlation, $r = -0.24$, $n = 191$, $P = 0.001$), and amplexed males were not encountered randomly in respect to time (Generalized Linear Model, time nested within dates, Wald $\chi^2 = 10.57$, $n = 191$, $P = 0.032$), we calculated standardized residuals from the regression of body temperature on time for each night and used these as measures of temperature. This was also necessary as body temperature was in a strong non-linear relationship with date of sampling (fig. 1a). There was a similarly strong relationship between the date of sampling and SVL and males' overall blueness (fig. 1b and 1c), consequently, we standardized SVL and 'blueness' within every night and used these standardized values in the analyses to avoid strong correlations between independent variables.

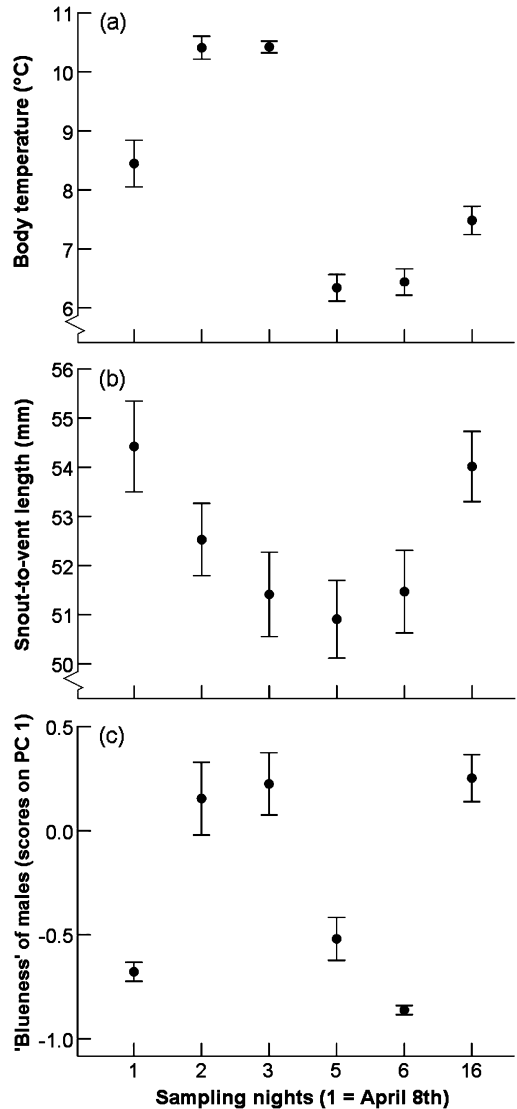


Figure 1. Body temperature (a), SVL (b) and 'blueness' (c) of sampled males on the six nights. Nights 1 to 6 covered the reproductive season in the Häggedal population, night 4 was a cold night with no reproductive activity. Night 16 was the night the Lindrängen population was sampled, which was one of the nights with most mating activity. For the ease of interpretation, untransformed data are shown. 'Blueness' of males refers to scores on PC1 from a PCA on extent and intensity of blue colouration, larger values mean bluer males. Bars represent 1 SE.

As variables were standardized within sampling nights, we could pool data for each population across nights to simplify the structure of models and to aid interpretation of the results. In Häggedal, where samplings occurred over five nights, we excluded the first and last survey night from the

analyses as no mating activity was detected on these occasions.

To test for factors acting on male colouration, we performed a General Linear Model (GLM) ANCOVA by entering 'blueness' as the dependent variable, population as a random factor, body temperature and SVL as covariates. We explored the factors potentially affecting mating success of males by Generalized Linear Modelling procedures with binomial error distribution and logit-link function. Mating status (amplexed or not) was entered as the response variable, population was entered as a factor to control for the non-independence of data collected within each of the two populations, whereas body temperature, SVL and 'blueness' were entered as continuous covariates. We included all the biologically interpretable two-way interactions in our initial models and applied backward removal model selection to avoid problems due to the inclusion of non-significant terms (Engqvist, 2005). Statistics were calculated using SPSS 15.0 for Windows.

Results

When analyzing if male body size and body temperature affected male colouration, GLM ANCOVA revealed a significant effect of body temperature ($F_{1,173} = 5.36$, $P = 0.022$). The variation explained by body temperature was, however, only 3% of the total variation in blueness ($R^2 = 0.03$). Effects of SVL ($F_{1,85} = 0.1$, $P = 0.75$) population ($F_{1,172} = 0.05$, $P = 0.83$) and all interactions were non-significant ($P > 0.08$).

Generalized Linear Model analysis of the background of male mating success indicated a significant positive effect of body temperature (Wald $\chi^2 = 10.44$, $n = 86$, $P = 0.001$, fig. 2), and a negative effect of SVL (Wald $\chi^2 = 5.07$, $n = 86$, $P = 0.024$) whereas the main effects of 'blueness' (Wald $\chi^2 = 2.24$, $n = 86$, $P = 0.14$) and population (Wald $\chi^2 = 0.17$, $n = 86$, $P = 0.69$) were non-significant. The interaction between SVL and 'blueness' of males was, however, significant (Wald $\chi^2 = 6.46$, $n = 86$, $P = 0.011$), indicating that while among small males the bluer ones are more successful in obtaining a mate, this difference disappears among larger males (fig. 3). All other interactions were non-significant ($P > 0.1$). Removing three extremely blue males (fig. 3) did not qualitatively change results.

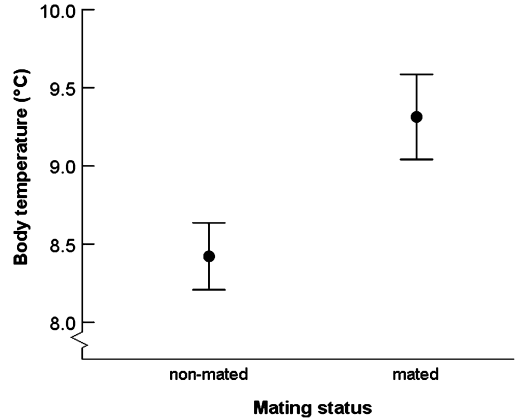


Figure 2. The relationship between mating status and body temperature. For the ease of interpretation, untransformed data are shown. Bars represent 1 SE.

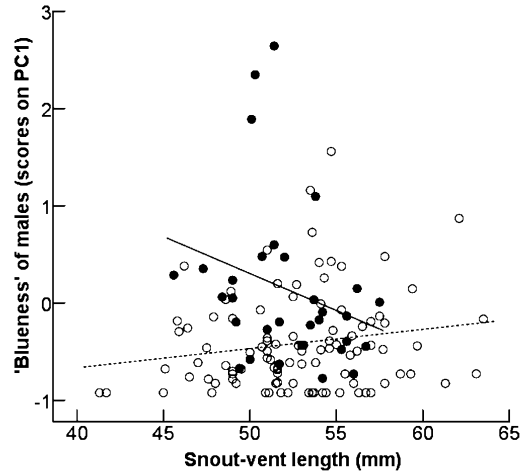


Figure 3. The relationship between SVL, 'blueness' and mating status of males (○: non-mated males, ●: mated males). Removing the three very blue mated males did not change results substantially.

Discussion

From our results we may conclude that blueness of males is influenced by their body temperature to some degree: males exhibiting higher body temperatures were bluer than males exhibiting lower body temperatures (also see Hedengren, 1987). This relationship is not a statistical artefact due to the similar temporal pattern in body temperatures and colouration (see fig. 1a and c), as males with higher body temperatures still appeared to be bluer after we corrected for the

among-night differences in body temperature and colouration. Blueness of males did not vary according to body size of males and may thus be independent of both size and age. Patterns did not differ between the two populations.

The coincidence of a peak in blueness and body temperatures may at least partly be due to the alignment of reproductive activities to the first warm nights. With rising water temperatures, males become increasingly blue, also paralleling rising intensities of reproductive activities (also see Hedengren, 1987). After the mating peak, when mating activity declines and finally ceases, males gradually lose their nuptial colouration even if mild weather persists (personal observation of the authors from other years and populations). This, and the fact that body temperature only explained about 3% of the variation in colouration, however, suggests that the switch in colouration largely depends on other factors than temperature. While it is known that some anurans become lighter at higher temperatures (e.g. King, Hauff and Phillips, 1994; Stegen, Gienger and Sun, 2004; Tattersall, Eterovick and de Andrade, 2006), a complete switch in colour, as that observed in male Moor Frogs from brown to blue, is probably affected by changes in sex-hormone levels (Hayes and Menendez, 1999). Nonetheless, colouration of individual males may to some extent depend on their ability to maintain high body temperatures (Stevenson, 1985a), even if physiological heat production is expected to be negligible in Moor Frog sized ectotherms (Stevenson, 1985b), and behavioural options are limited at night, when almost all males reside in the water and radiant heat is absent.

Mating status of males was associated with their body temperature: males found in amplexus had higher body temperatures than non-amplexus males. This relationship may have resulted from at least four different but non-exclusive mechanisms. (1) Males that could maintain higher body temperatures and, thus, elevated physiological performance, may have had an advantage in the intensive scramble com-

petition for favourable places within the lek or for females. (2) Mated males may have had higher body temperatures if the centres of leks, where most females moved towards to mate and spawn, were in warmer areas of ponds. (3) Elevated body temperature of amplexed males may also be a result of getting into close contact with warmer, recently arrived females. (4) Moor Frog males successful in searching for females and amplexing them on the shore may be warmer than males that have stayed in the water. While we think that the third and fourth explanation may be less important as body temperature accommodation to the environment may be rapid in Moor Frogs due to their small body size (Grigg, Drane and Courtice, 1979), it remains to be tested which of these mechanisms have contributed most to the observed differences in body temperatures of mated and non-mated males.

Mating status of males was affected by the interaction of body size and blueness (fig. 3). While it is unclear how colouration by itself affects mating success in the two study populations (Engqvist, 2005), this result indicates that blueness of males may have an effect on their mating success which would accord to previous results on other populations (Hedengren, 1987; Sheldon et al., 2003). Females may prefer to mate with bluer males as colour may signal additive genetic quality (Sheldon et al., 2003). Females may be attracted to bluer males simply because these are more conspicuous than other, more cryptic-coloured males (*sensu* Arak, 1988). Blue colour may also advertise enhanced fighting ability (*sensu* Olsson, 1994) facilitating bluer males to gain access to more favourable positions within the lek which may lead to higher mating success by itself (e.g. Bro-Jørgensen, 2002). However, it is also possible that males that are in amplexus have become bluer because they are in amplexus. Blueness may be a side-effect of elevated sexual hormone levels which are likely to peak before and around ejaculation, that is when males are in amplexus with females. Which mechanism

has actually led to the observed relationship between body size, blueness and mating success needs targeted experiments to clarify.

Interestingly, small males were more likely to be found in amplexus than large males. In anurans, large males are generally superior competitors when compared to smaller males (e.g. Davies and Halliday, 1979; Berven, 1981; Byrne and Roberts, 2004) and are usually preferred as mates by females (e.g. Howard, 1978; Ryan, 1980; Howard and Young, 1998). We do not know what could have caused the observed pattern in our study, but the unusual sexual dimorphism in body size with males being larger than females (Söderman, 2006) might be of importance to the origin of this phenomenon. Smaller males may be better aligned to the body size of females and may as a consequence get a better grip on the female which could enhance their ability to resist overtaking attempts of other males. However, contrary to our findings, Hedengren (1987) observed a mating advantage for large males in her study population and suggested that this might have been caused by a higher success of large males in struggles for females. Under which circumstances male body size affects reproductive success positively or negatively, and how it does so, remains to be shown.

In summary, our results imply that the blue nuptial colouration of Moor Frog males may be affected by temperature. Also, blueness can be related to the mating status of males and may thus be under sexual selection. This study is part of the first step towards understanding the background and evolutionary role of nuptial colouration in Moor Frog males as questions arising from it are more numerous than ones we could answer. However, our results should facilitate the design and performance of more specific surveys and experiments which may finally resolve the puzzling – and for anuran amphibians rare – phenomenon of male nuptial colouration in Moor Frogs.

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