

## Displaying in the dark: light-dependent alternative mating tactics in the Alpine newt

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### Abstract

Environment plays a major role for determining the kind of courtship behaviours or alternative mating tactics employed, but the effect of physical variables on fitness has received little attention. The Alpine newt courts during both day and night times and exhibits a complex suite of behaviours involving olfactory, visual and tactile cues. Displaying in both dark and light conditions may increase the number of mating opportunities and alleviate predation risk, but the frequency and efficacy of the various tactics deployed may vary across light conditions, leading males to vary their use of these tactics across different light regimes. To test this hypothesis, we video-recorded sexual encounters at two light intensities in a controlled experimental design. When courting in the dark, males used comparatively more olfactory rather than visual displays. They also relied more on positive feedback from the female before releasing a spermatophore for her to pick up. The particular mix of tactics used under each light condition is likely to be adaptive because in the dark (1) visual communication is hampered, making olfactory displays possibly more effective and (2) males depositing spermatophores are more likely to lose fertilizations to competitors. Mating in light and dark conditions has similar reproductive payoffs, which shows that displaying in the dark is not detrimental and may even be advantageous if predation risk is reduced at night. These results confirm the importance of taking into account physical variables to understand the evolution of sexual communication in animals.

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### Introduction

The environment plays a major role in the expression of alternative mating tactics. Most research has focused on intrinsic mate qualities, such as relative body condition or size, i.e., individual status (Gross 1996). However, extrinsic environmental features, such as ambient abiotic conditions, relative frequency of expressed alternative phenotypes, mate responsiveness and density all affect the tactics adopted by an individual animal (Emlen 2008). Temporal heterogeneity is a key feature of environments that provides opportunities for the diversification of behavioural patterns. Many environmental features vary temporally, including light, temperature, oxygen, humidity and habitat structure.

In organisms that court in both dark and light conditions, it is unlikely to be adaptive to use the same behaviours in both (Endler 1987; Reynolds et al. 1993; Houde 1997). First, conspicuous displays might attract mates, but also male competitors, predators or parasites. Second, it would be useless to exhibit signals that could not be perceived or would be perceived poorly by partners or conspecifics (Butlin and Ritchie 1994; Plath et al. 2004; Kemp and Williams 2009). It is thus important to understand the success of alternative behavioural strategies as a function of environmental conditions (Łukasic et al. 2006). For instance, Larison (2009) found that the payoffs of the perching (i.e., sitting in the vegetation) and hovering (i.e., moving over the water surface) tactics in damselflies were greater

in low and high light conditions, respectively. This suggests that more empirical work is needed to understand how environmental heterogeneity could act as a key factor in shaping behavioural diversity (West-Eberhard 2003). However, very few studies have examined the payoffs of such alternatives in contrasting abiotic environmental situations.

Some sexual displays are visual, olfactory or mechanoreceptive, whereas others use a combination of these sensory modalities (Himstedt 1979; Denoël 1999). In newts, the fanning movement, a tail undulation which is exhibited in all encounters, carries a water current towards the female (Denoël 1996). It provides visual and mechanical stimuli (Grüsser-Cornehls and Himstedt 1976; Martin 1982), but another important function is olfactory because the cloaca contains dorsal glands that secrete pheromones which are conducted to the female's nostril by this water current (Sever 2003). This can explain their ability to court across a large range of environmental conditions. Although there is variation among populations and species in the timing of courtship in relation to light intensity, courtship is commonly observed in both light and dark conditions. However, it remains unknown whether reproductive payoffs and courtship tactics are similar under different light conditions.

Many newts, such as the Alpine newt *Mesotriton alpestris*, show a conspicuous sexual dimorphism which involves both morphology (dorsal crests, swollen cloaca in males) and coloration (e.g., blue back in males; Thorn and Raffaëlli 2001). Their courtship behaviour is complex (Arntzen and Spar-

reboom 1989; Denoël 1996; Houck and Arnold 2003). A sexual encounter starts with orientation behaviours during which the male tries to place himself in front of the female. Once the female stops moving away from him, the male exhibits varied courtship displays and deposits a spermatophore on the substrate where it may be picked up by a female. This does not end the encounter as males can exhibit additional tail displays and may deposit additional spermatophores. In addition to the species-specific pattern of courtship displays, alternative mating tactics are common in newts. Tactics used include sneaking (sexual interference: Verrell 1988), amplexus (Verrell 1983), and a changed rate of courtship displays (Denoël et al. 2001, 2005). In the Alpine newt, males can use two alternative behavioural sequences. In one, males wait for a positive response of the female to start spermatophore deposition; this is facilitated by the exhibition of a movement, which increases female responsiveness before sperm transfer (Denoël 1996; Denoël et al. 2001, 2005). In the other, males deposit a spermatophore without positive feedback from the females. They can achieve mating success by using post-deposition luring movements of the tail. Although the payoff of the luring tactic is low, luring is frequently used by males and is considered to be a sidepayment strategy (sensu Dunbar 1982).

We experimentally manipulated light intensity to assess the effect of light on the use of alternative mating tactics in the Alpine newt. Our hypothesis was that males should exhibit displays that rely on different combinations of sensory modes depending upon the light conditions in order to optimise signal reception by females.

## Materials and methods

### Field sampling

One hundred adult Alpine newts (*M. alpestris*, formerly *Triturus alpestris*) of each sex were caught on a road during pre-reproductive migration between their overwintering woodland and breeding pond (Boirs, Province of Liège, Belgium; 50°45'N–5°36'E, 70 m elevation a.s.l.). There were no other ponds between these sites. Thus, they had not yet reproduced. Newts were carried in boxes with humid substrates (hydrophilous cotton) directly to the laboratory by car (about a 20-min drive) upon capture.

### Maintenance

In the laboratory, we separated males and females and placed them in four independent aquaria at a density of 25 individuals per aquarium (200 l each; 250×30×40 cm lwh). We kept the environmental conditions within the range of values encountered by the newts during the reproductive period in nature (Denoël 2003). Ambient air temperature was regulated to maintain each aquarium at the same temperature (mean  $\pm$  SE=12.8 $\pm$ 0.3°C). Aquaria were oxygenated with airstones (O<sub>2</sub>:10mg/l). We set the photoperiod at 13.5/10.5 LD (four daylight fluorescent tubes Luminux de Luxe 2,350 lm, L 36W/12–950 to simulate the natural light spectrum during the breeding season; four normal fluorescent tubes Sylvania Professional, 36W decor 183 to give a higher light intensity in the room). Each afternoon, we fed newts a fixed quantity of chironomid larvae (*Chironomus*, 60 mg/newt). We provided shelters (rocks) in each aquarium. After the observation of behavioural patterns, we transferred the newts to

other aquaria (one of 200×100×40 cm lwh, two of 100×100×40 cm lwh) before releasing them back into their native habitat. We conducted the experiment within 8 to 40 days of capture, i.e., during the usual main breeding period of the species (von Lindeiner 1992; Denoël 1996).

### Experimental design

The experiment consisted of staged sexual encounters between pairs of newts in light and dark conditions. We selected the first male and female showing movement from the maintenance aquariums and placed them together in an observation aquarium (50×25×25cm; 20 cm water depth). Alpine newts breed naturally in small aquatic habitats devoid of vegetation, such as pools (Denoël 2007). Their behaviour can thus be recorded adequately in such aquaria. We carried out fifty trials in aquaria illuminated with two fluorescent tubes (hereafter, high light treatment: 303 lx; Luminux de Luxe 2,350 lm, L 36W/12–950) and 50 others in a darkened room (hereafter low light treatment, 0.04 lx). Newts were found to court in natural ponds within this range of luminosity values (M. Denoël, pers. obs.). The experiment took place in the same room in which the newts were maintained. The dark treatment began 3 h before the lights were turned on and the light treatment began just after the lights were turned on. Males and females used in the two light treatments did not differ in body size (mean  $\pm$  SE=51.6 $\pm$ 0.4 mm in the light and 51.3 $\pm$ 0.4 mm in the dark,  $t_{98}$ =0.492,  $P$ =0.62) or mass (3.6 $\pm$ 0.1 g in the light and 3.5 $\pm$ 0.1 g in the dark,  $t_{98}$ =0.131,  $P$ =0.90). We used each individual only once. We took the water of the observation aquarium from another tank in the laboratory that had not contained newts in order to obtain the same water temperature as the aquaria where the newts had been held. We changed the water between each trial.

We recorded courtship with a Sony Hi8 video camera. For the recording in low light treatment, we used infrared light with the Sony night-shot system (HVL-IRM). We considered that a sexual encounter failed when no courtship interactions were seen within 40 min. Otherwise, we conducted observations until no further courtship displays or interactions were exhibited for more than 1 min.

We then compressed videotapes using an mpeg-1 encoder and subsequently viewed and analysed them by using Noldus Observer Video Pro 4.1. software (Noldus 2002). We recorded sequencing and timing by typing keys on the keyboard of a computer; each key corresponding to a behaviour of males (see Table 1 for the list of courtship displays) or females (see next paragraph for more details). Because this software allows cross-referencing between digital images and encoded behavioural patterns (i.e., each encoded behaviour is connected with its exhibition on the video), it was possible to encode the behavioural patterns of males and females separately.

### Behavioural and statistical analysis

The descriptions and associated inter-sexual signalling functions are presented in Table 1. To obtain relative frequencies of courtship displays, we divided the absolute frequencies of each of the seven courtship behaviours by the sum of the numbers of all displays exhibited during each encounter. As behaviours, we considered bouts as unit. For instance, the fanning display consists of several bouts that can be separated from each other by pauses or other courtship displays such as the wiggle-tail-bent or the

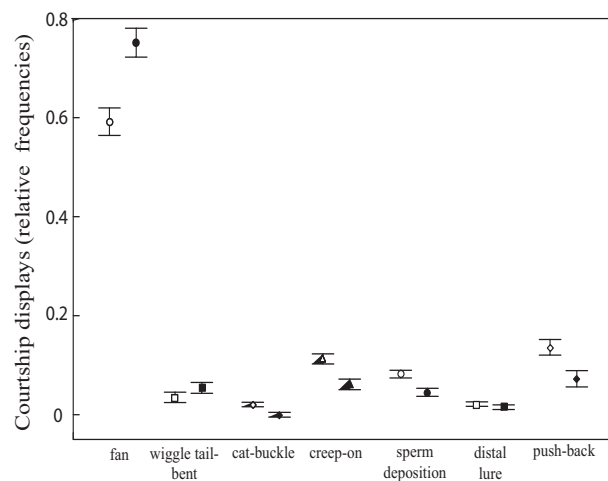
catbuckle with lean-in (Denoël 1996). In addition, we took into account the success of sperm transfer, the duration of encounters (from the first to last courtship events), the time from which the pair was introduced in the aquarium and the first courtship display and the proportion of exhibition of two behaviours (creep-on and sperm deposition) exhibited in front of unresponsive females. We considered a female responsive when she moved towards the male or turned her head in his direction. During spermatophore deposition (starting from the behaviour 'creep-on': Table 1), the male cannot see the female. The responsiveness of the female is then expressed by a tactile stimulus: the female touches the male's tail with her snout.

We tested the effect of light treatment (high vs low) on the frequencies of courtship displays using a multivariate analysis of variance. To achieve normality and homogeneity of variance, we normalised proportions by arcsin transformations, other continuous data by log transformations and counts by square-root transformation before calculating the parametric significance tests (Sokal and Rohlf 1995). We computed chi-square tests ( $2 \times 2$  contingency tables) to compare the success of sperm transfer (binary variable) in light and dark conditions (Siegel and Castellan 1988). All statistical tests were two-tailed and run in Statistica 8.0 (Statsoft-France 2007).

## Results

### Encounter success and female responsiveness

Males exhibited courtship display in 87% of the trials ( $n = 100$ ). The proportion of males that displayed did not differ significantly between the high and low light treatments (90% vs 84%,  $\chi^2 = 0.8$ ,  $P = 0.37$ ). Among these 87 encounters including displays, 28% were successful in terms of sperm transfer (i.e., at least one spermatophore picked up by the female). The light treatment did not significantly affect this success (high light: 33%, low light: 24%;  $\chi^2 = 0.6$ ,  $P = 0.45$ ). Similarly, there were no differences in average numbers of spermatophores picked up by the females during each trial in the two treatments (high light:  $0.34 \pm 4.3$  vs low light:  $0.26 \pm 0.08$ ;  $F_{1,79} = 0.64$ ,  $P = 0.64$ ). However, female responsiveness, i.e., the proportion of time a female



**Fig. 1.** Mean relative frequencies ( $\pm$ SE) of courtship displays in male Alpine newt in light (open symbols) and dark (full symbols) treatments. See table 1 for a description of the behavioural patterns.

was responsive to a male, was significantly affected by light treatment. Females reacted more positively to the males in the low light treatment ( $53.4 \pm 4.3\%$  vs  $35.8 \pm 3.9\%$ ;  $F_{1,79} = 11.71$ ,  $P < 0.001$ ). This variable was not affected by the size of males ( $F_{1,83} = 6.542$ ,  $P = 0.08$ ).

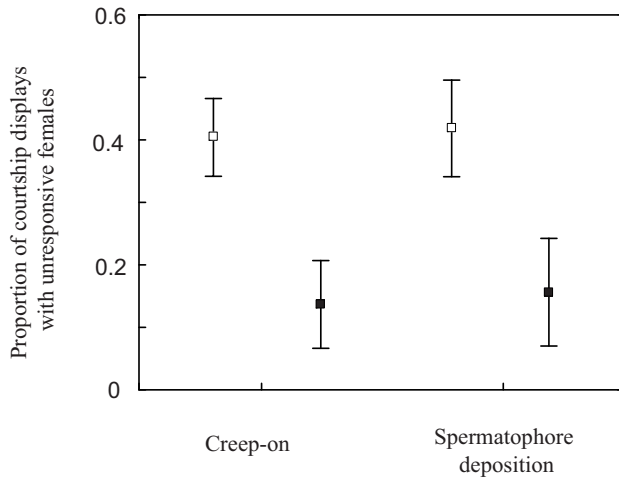
### Male courtship display

Because female responsiveness differed in the two treatments, we controlled for the effect of light on female responsiveness by adding it as a covariate in a MANCOVA model. Males used all courtship displays in both light treatments, but relative frequencies with which different tactics were used was different. Effects of both light and female responsiveness on the courtship displayed by males were significant (light,  $\lambda = 0.655$ ,  $F_{7,77} = 5.784$ ,  $P < 0.001$ ; female responsiveness:  $\lambda = 0.605$ ,  $F_{7,77} = 7.196$ ,  $P < 0.001$ ). In the high light treatment, males exhibited the cat-buckle with lean-in ( $F_{1,83} = 11.187$ ,  $P = 0.001$ ), creep-on ( $F_{1,83} = 18.138$ ,  $P < 0.001$ ), deposition ( $F_{1,83} = 14.243$ ,  $P < 0.001$ ) and push-back ( $F_{1,83} = 8.046$ ,  $P = 0.006$ ) more than at the low light treatment (Fig. 1). In contrast, they used the fanning display less in the light than

**Table 1.** Male courtship patterns: description and respective main inter-sexual signal.

Behaviour	Description	Sensory modality targeted
Fan	The most frequent courtship act: beating tail movement in direction of female's snout	Olfactive, mechanoreceptive, visual
Wiggle-tail-bent	Slow oscillation of the tip of the tail	Visual
Cat-buckle with lean-in	The male raises his body by extending his legs and arching his back, and moves his tail toward the female	Visual
Creep-on	Initiation of the sperm transfer during which the male loses the sight of the female	Visual
Sperm deposition	Deposition of a spermatophore on the substratum, possibly following a touch from the female	Visual
Distal lure	Slow and large movement of the distal part of the tail after sperm deposition, particularly used to attract unresponsive females	Visual
Push-back	Tail contact with the female which pushes her back to the spermatophore after deposition. This behaviour favours spermatophore pick-up when females missed it.	Tactile

For a more detailed description of the behaviours, see Denoël 1996.



**Fig. 2.** Proportion (mean $\pm$ SE) of sperm transfer phase initiations (creep-on) and spermatophore deposition with unresponsive females in male Alpine newts in light (open symbols) and dark (full symbols) treatments.

in the dark ( $F_{1,83} = 17.452$ ,  $P < 0.001$ ; Fig. 1). No significant effects were found for the wiggle-tail-bent ( $F_{1,83} = 2.038$ ,  $P = 0.16$ ) or the distal lure ( $F_{1,83} = 1.279$ ,  $P = 0.26$ ; Fig. 1). During an encounter, males and females were more engaged in orientation behaviours (i.e., in activity patterns without courtship displays) in the low ( $34.27 \pm 0.03\%$ ) than in the high ( $30.01 \pm 0.02\%$ ) light treatment ( $F_{1,83} = 6.392$ ,  $P = 0.01$ ).

The duration of encounter was significantly similar in the light and dark treatments (mean  $\pm$  SE =  $766 \pm 109$  s and  $811 \pm 100$  s respectively,  $t_{85} = 0.471$ ,  $P = 0.64$ ). The time needed by males to start courtship from the time the pair was introduced in the observation aquarium was not significantly different in the two treatments (light,  $492 \pm 61$  s and dark,  $519 \pm 55$  s;  $t_{85} = 0.326$ ,  $P = 0.75$ ).

Male Alpine newts can start a sperm-transfer phase by deposition, which occurs when the male cannot see the female). Males started a sperm-transfer phase and a sperm deposition without a positive behavioural action from the female more often in the high light treatment than in the low light treatment (creep-on:  $F_{1,73} = 8.119$ ;  $P = 0.006$ ; sperm deposition:  $F_{1,72} = 5.131$ ;  $P = 0.03$ ; Fig. 2).

## Discussion

We showed that male Alpine newts exhibited courtship behaviour in both dark and light conditions, but depending on light intensity, they used different behavioural patterns. *Sensu* Gross (1996), this is an example of a conditional strategy with alternative phenotypes dependent on environmental cues. Whereas males more often used visual tactics in the light, they exhibited more olfactory behaviours and needed more positive feedback from the females in the dark. The two tactics had similar payoffs because the same number of spermatophores was picked up by females in the two conditions. The time investment by males in courtship and searching for females was also similar in light and dark environments. This confirms the importance of physical factors in the exhibition of sexual displays and shows how reproductive success can be maintained under variable environmental conditions.

In the dark, males exhibited fewer cat-buckle with lean-in displays. Although this behavioural pattern is never exhibited at a high frequency dur-

ring an encounter, it is the most conspicuous and effective form of courtship and often makes females responsive (Denoël 1996). It allows a male to show its whole body, including the red belly, while it arches its back and extends its tail toward the female. Alpine newts can perceive different colours and are sexually attracted by the red colour (Himstedt 1979). However, although Alpine newts are known to have good diurnal visual acuities, it is not known whether they can perceive and discriminate between colours at night. From our behavioural results, it seems that belly colours are less exhibited at night than during daylight. In contrast, male Alpine newts needed more tactile feedback from the female in the dark than in the light, in which some males started the sperm-transfer phase and even sperm deposition with both responsive and unresponsive females, i.e., females that did not give any tail-touch response to the male (Denoël et al. 2001). This alternative mating tactic fits well with the environmental conditions. In the dark, male Alpine newts are expected to be less able to efficiently perceive females by visual cues, as only 21% of retinal sensory cells are rods, i.e., half the amount of more nocturnal species such as the crested newt or the fire salamander (Grüsser-Cornehls and Himstedt 1976). Males also spent more time moving near females without courting (i.e., orientation behaviours) in the dark, which suggests that males may need more positive feedback from the female in such conditions and that it takes more time to identify them in dark than in light conditions. Indeed, during orientation behaviours, males spent a large part of the time exhibiting sniffing behaviours (Denoël 1996). Depositing sperm in front of unresponsive females in the dark may be more risky than in daylight because attempts to attract the female through the luring visual tactic may be ineffective. On the other hand, males are also at risk of intrasexual competition during this courting phase. Opportunistic males can interfere with the courting pair and transfer their own sperm to the females (Verrell 1988; Denoël 2003). Waiting for a tactile response of the female before starting the key phase of the encounter, i.e., the sperm transfer, may thus avoid the risk of losing contact with the courted female. This does not mean that females were less responsive in the dark, as the opposite was observed. But when females did not show responsiveness, males were more cautious. As previous work showed that females were more choosy late in the season (Gabor and Halliday 1997), the impact of darkness might change in the favour of less visually attractive males, but testing this hypothesis would require further experiments using fertilised females. During our experiment with unfertilised females, choosiness was not affected as the same number of successful encounters occurred in light and dark treatments and no change in encounter duration was found. Similarly the size of males did not explain their success in terms of female responsiveness.

In the light, males used the fanning display proportionally more than in the dark, but this behaviour constituted more than 80% of the courtship displays in both light conditions. Fanning behaviour is primarily a form of olfactory communication (Denoël 1996), which appears to remain important both in light and in the dark. It functions at close proximity during sexual communication, but also at longer distances in mate location (Cogalniceanu 1994). The peptide pheromones were identified in two related species which also use the fanning movement during courtship (*Cynops pyrrhogaster* and *Cynops ensicauda*) and were shown to be effective in attracting conspecific females (Kikuyama et al.

1995; Toyoda et al. 2004). Although our study focused on dark versus light conditions in clear waters, clear water is not always available in the field because newts also breed in muddy waters in which visual communication is probably reduced (Cogalniceanu 1994; Secondi 2007). Thus, there may be strong selection for the use of olfactory signals in courtship, even in daylight. Similarly, cave salamanders, such as *Proteus anguinus*, are attracted by conspecific odours in a habitat fully devoid of visual cues (Richard et al. 1982). Species, which can inhabit both hypogean and epigean habitats, such as the cavedwelling fish primarily exhibit olfactory communication, whereas those in light environments exhibit primarily visual communication. However, this reflects a fixed, rather than variable, difference in light environment (Plath et al. 2004).

Exhibiting courtship in both high and low light conditions may be adaptive for Alpine newts, allowing males and females to have a higher fitness through an increasing number of mating events. Similarly, breeding in a wide range of conditions such as low oxygen (Halliday 1976) and low temperature waters (Denoël et al. 2005) or under a high risk of competition (Verrell 1983) is clearly adaptive. This is especially important in newts, for which multiple mating is the rule (Rafinski and Osikowski 2002) and is associated with a higher number of eggs laid by females (Osikowski and Rafinski 2001).

Being able to court in the dark could be an adaptation to avoid predation risk. In guppies, light level is correlated with predation by large fish species, which creates a fitness advantage for crepuscular and night courtiers (Endler 1987; Reynolds et al. 1993). Similarly, in newts, displaying in the dark could alleviate the risks posed by diurnal predators such as water birds (Schmitz 1985) and snakes (Luiselli et al. 2007). Experimental studies on the effects of predators, such as those done with guppies, would help us to understand the evolution of courtship activity in newts.

In conclusion, although caudate amphibians, such the Alpine newts, exhibit a common sequence of behavioural patterns (Denoël 2002), the details vary under different environmental conditions. Moreover, as emphasised by Candolin (2003), use of multiple cues could reduce the costs of identification mistakes by sexual partners in mate choice. We do not know the relative importance of each sensory mechanism in Alpine newts, but the observed variation of patterns suggest that newts can take advantage of multiple cues should some be temporarily unavailable (e.g., colour vision at night). These results also indicate that physical variables are of great importance in shaping behavioural patterns and that failure to take them into account may affect our understanding of the evolution of behavioural tactics.

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## References

- Arntzen JW, Sparreboom M (1989) A phylogeny for the old world newts, genus *Triturus*: biochemical and behavioral data. *J Zool, Lond* 219:645–664
- Butlin RK, Ritchie MG (1994) Behaviour and speciation. In: Slater PJB, Halliday TR (eds) Behaviour and evolution. Cambridge University Press, Cambridge, pp 43–79
- Candolin U (2003) The use of multiple cues in mate choice. *Biol Rev* 78:575–595
- Cogalniceanu D (1994) The relative importance of vision and olfaction in mate recognition in male newts (Genus *Triturus*). *Herpetologica* 50:344–349
- Denoël M (1996) Etude comparée du comportement de cour de *Triturus alpestris* (Laurenti, 1768) et *Triturus alpestris cyreni* (Wolterstorff, 1932) (Amphibia, Caudata): approche évolutive. *Cah Ethol* 16:133–258
- Denoël M (1999) Le comportement social des urodèles. *Cah Ethol* 19:221–258
- Denoël M (2002) Pedomorphosis in the Alpine newt (*Triturus alpestris*): decoupling behavioural and morphological change. *Behav Ecol Sociobiol* 52:394–399
- Denoël M (2003) Effect of rival males on the courtship of paedomorphic and metamorphic *Triturus alpestris*. *Copeia* 2003:618–623
- Denoël M (2007) Le Triton alpestre, *Triturus alpestris* (Laurenti, 1768). In: Jacob JP, Percsy C, De Wavrin H, Graitson E, Kinet T, Denoël M, Paquay M, Percsy N, Remacle A (eds) Amphibiens et reptiles de Wallonie. Aves-Rainne & Région wallonne, Namur, pp 62–71
- Denoël M, Poncin P, Ruwet JC (2001) Alternative mating tactics in the Alpine newt *Triturus alpestris alpestris*. *J Herpetol* 35:62–67
- Denoël M, Mathieu M, Poncin P (2005) Effect of water temperature on the courtship behavior of the Alpine newt *Triturus alpestris*. *Behav Ecol Sociobiol* 58:121–127
- Dunbar RIM (1982) Intraspecific variations in mating strategy. In: Bateson PPG, Klopfer PH (eds) Perspectives in ethology. Plenum Press, New York, pp 385–431
- Emlen DJ (2008) The role of genes and the environment in the expression and evolution of alternative tactics. In: Oliveira RF, Taborsky M, Brockmann HJ (eds) Alternative reproductive tactics: An integrative approach. Cambridge University Press, pp 85–108
- Endler JA (1987) Predation, light intensity and courtship behaviour in *Poecilia reticulata* (Pisces, Poeciliidae). *Anim Behav* 35:1376–1385
- Gabor CR, Halliday TR (1997) Sequential mate choice by multiply mating smooth newts: females become more choosy. *Behav Ecol* 8:162–166
- Gross MR (1996) Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol Evol* 11:92–98
- Grüsser-Cornehls U, Himstedt W (1976) The urodele visual system. In: Fite KV (ed) The amphibian visual system—a multidisciplinary approach. Academic Press, pp 203–267
- Halliday TR (1976) To breathe or not to breathe; the newt's problem. *Anim Behav* 24:551–561
- Himstedt W (1979) The significance of color signals in partner recognition of the newt *Triturus alpestris*. *Copeia* 1979:40–43
- Houck LD, Arnold SJ (2003) Courtship and mating behavior. In: Sever DM (ed) Reproductive biology and phylogeny of urodela. Science Publ., Enfield, New Hampshire, pp 383–424
- Houde AE (1997) Sex, color, and mate choice in guppies. Princeton University Press, New Jersey
- Kemp PS, Williams JG (2009) Illumination influences the ability of migrating juvenile salmonids to pass a submerged experimental weir. *Ecol Freshwat Fish* 18:297–304
- Kikuyama S, Toyoda F, Ohmiya Y, Matsuda K, Tanaka S, Hayashi H (1995) Sodefrin: a female-attracting peptide pheromone in newt cloacal glands. *Science* 267:1643–1645

- Larison B (2009) Impacts of environmental heterogeneity on alternative mating tactics in the threadtail damselfly. *Behav Ecol Sociobiol* 63:531–536
- Luiselli L, Capizzi D, Filippi E, Anibaldi C, Rugiero L, Capula M (2007) Comparative diets of three populations of an aquatic snake (*Natrix tessellata*, Colubridae) from Mediterranean streams with different hydric regimes. *Copeia* 2007:426–435
- Lukasic P, Radwan J, Tomkins JL (2006) Structural complexity of the environment affects the survival of alternative male reproductive tactics. *Evolution* 60:399–403
- Martin E (1982) Distribution des activités comportementales chez le Triton alpestre *Triturus alpestris* (Amphibien, Urodèle) en phase aquatique : étude de la variabilité interindividuelle et de l'intensification locale. PhD Thesis. Université Claude Bernard Lyon 1
- Noldus (2002) The Observer. Reference manual version 4.1. Noldus Information Technology, Wageningen
- Osikowski A, Rafinski J (2001) Multiple insemination increases reproductive success of female Montandon's newt (*Triturus montandoni*, Caudata, Salamandridae). *Behav Ecol Sociobiol* 49:145–149
- Plath M, Parzefall J, Körner KE, Schlupp I (2004) Sexual selection in darkness? Female mating preferences in surface- and cave-dwelling Atlantic mollies, *Poecilia mexicana* (Poeciliidae, Teleostei). *Behav Ecol Sociobiol* 55:596–601
- Rafinski J, Osikowski A (2002) Sperm mixing in the Alpine newt (*Triturus alpestris*). *Can J Zool* 80:1293–1298
- Reynolds JD, Gross MR, Coombs MJ (1993) Environmental conditions and male morphology determine alternative mating behaviour in Trinidadian guppies. *Anim Behav* 45:145–152
- Richard PB, Parzefall J, Durand J (1982) Communication chimique chez deux proteïdes, *Proteus anguinus* et *Necturus maculosus*. Premiers résultats. *Bull Soc Zool Fr* 107:597–605
- Schmitz L (1985) Consommation de Tritons alpestres (*Triturus alpestris*) par le Grèbe castagneux (*Tachybaptus ruficollis*). *Aves* 22:213
- Secondi J (2007) Water turbidity affects the development of sexual morphology in the palmate newt. *Ethology* 113:711–720
- Sever DM (2003) Courtship and mating glands. In: Sever DM (ed) *Reproductive biology and phylogeny of Urodela*. Science Publ., Enfield, New Hampshire, pp 323–381
- Siegel S, Castellan NJ (1988) *Nonparametric statistics for the behavioral sciences*. McGraw-Hill, New York
- Sokal RR, Rohlf FJ (1995) *Biometry*. Freeman and Co, New York
- Statsoft-France (2007) *Statistica (logiciel d'analyse des données)*, version 8.0., Maisons-Alfort
- Thorn R, Raffaëlli J (2001) *Les salamandres de l'ancien monde*. Boubée, Paris
- Toyoda F, Yamamoto K, Iwata T, Hasunuma I, Cardinali M, Mosconi G, Polzonetti-Magni AM, Kikuyama S (2004) Peptide pheromones in newts. *Peptides* 25:1531–1536
- Verrell PA (1983) The influence of the ambient sex ratio and intermale competition on the sexual behavior of the red-spotted newt, *Notophthalmus viridescens* (Amphibia: Urodela: Salamandridae). *Behav Ecol Sociobiol* 13:307–313
- Verrell PA (1988) Sexual interference in the Alpine newt, *Triturus alpestris* (Amphibia, Urodela, Salamandridae). *Zool Sci* 5:159–164
- von Lindeiner A (1992) Untersuchungen zur Populationsökologie von Berg-, Faden- und Teichmolch (*Triturus alpestris* L., *T. helveticus* Razoumowski, *T. vulgaris* L.) an ausgewählten Gewässern im Naturpark Schönbuch (Tübingen). *Jahrb Feldherpetol* 3:1–117
- West-Eberhard MJ (2003) *Developmental plasticity and evolution*. Oxford University Press

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