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Effect of water temperature on the courtship behavior of the Alpine newt *Triturus alpestris*

Abstract Temperature is expected to have an effect on the behavioral patterns of all organisms, especially ectotherms. However, although several studies focused on the effect of temperature on acoustic displays in both insects and anurans, almost nothing is known about how environmental temperature may affect ectotherm visual courtship displays and sexual performance. The purpose of this study was to determine the effect of environmental temperature on the sexual behavior of Alpine newts (*Triturus alpestris*). We subjected *T. alpestris* to two different temperatures in controlled laboratory conditions. Temperature had a major effect on both male and female behaviors: at low temperature, the frequencies of several displays, including tail-raising during sperm deposition, are lowered. This variation is caused indirectly by temperature because it is due to female responsiveness, which is temperature-dependent. However, the fanning movement of the male's tail during its main courtship display is independent of female behavior: at lower temperatures, the tail beats at a lower rate, but for a longer time. The similar reproductive success (i.e. sperm transfer) at the two temperature ranges indicates that breeding in cold water is not costly but instead allows males and females to mate early in the season. This is particularly adaptive because, in many habitats, the reproductive period is shortened by drying or freezing conditions, which may impair survival of branchiate offspring. This study also demonstrates the necessity of considering environmental parameters when modeling optimality and characteristics of ectotherm behaviors.

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Introduction

Environmental factors have a major effect on behavioral patterns of organisms (Davenport 1992; Hutchinson and Dupré 1992). Among these factors, the social environment is of primary importance in determining the intensity of sexual selection. Variation in population density, operational sex ratio, and predation risk stimulate individuals to exhibit alternative courtship tactics to maximize their fitness (Endler 1995; Gross 1996; Kvarnemo and Ahnesjö 1996; Wong et al. 2004). Abiotic factors, which are mainly known to affect morphology or physiology (Rome et al. 1992), are also proximate mechanisms affecting behavioral patterns (Kvarnemo 1996; Ruano et al. 1999; Shine et al. 2000).

Temperature affects both ectotherms and endotherms, but is expected to have a greater effect on animals whose body temperature is directly dependent on ambient temperature. Ectotherms can experience large variations in body temperature during their life-cycle or even during a single day. The rate of physiological functions is considerably reduced as temperatures decrease (Rome et al. 1992; Gerhardt and Huber 2002). Locomotory patterns are particularly affected: swimming and jumping performance in frogs (Hirano and Rome 1984; John-Alder et al. 1989; Whitehead et al. 1989) and anti-predator responses in snakes (Kissner and Forbes 1997; Mori and Burghardt 2001) are decreased at low temperatures. Chemical signaling is also believed to be altered at low temperature (Lass and Spaak 2003).

Ambient temperatures vary during the animal's breeding seasons and therefore should have an impact on courtship (Ward and Stanford 1982; Davenport 1992). This may be particularly relevant to ectotherms as they may be forced to endure suboptimal temperatures if they are to maximize their opportunity to mate. Alternatively, ectotherms may wait for better environmental conditions, but then run the risk of missing reproduction. Temperatures vary among

breeding places depending on the local climatic conditions (e.g., lowland pond vs alpine lake), but also during the course of the reproductive season (Ward and Stanford 1982; Davenport 1992). In fish, such as sand gobies and pipefish, mating competition is temperature-dependent (Ahnesjo 1994; Kvarnemo 1996, 1998). Calling-related traits (e.g. sound pressure level, pulse rate and duration) are also affected by temperature in insects (Walker 2000; Gerhardt and Huber 2002; Sueur and Sanborn 2003), fish (Connaughton et al. 2002) and anurans (Vasara et al. 1991; Sullivan and Malmos 1994; Wells et al. 1996; Howard and Young 1998; Navas and Bevier 2001; Gerhardt and Huber 2002; Wong et al. 2004).

Even though the effect of ambient temperature on migration, hibernation, and thermoregulation are well documented (Ward and Stanford 1982; Davenport 1992), the potential effects of temperature on non-acoustic aspects of courtship behavior remain largely unexplored. In urodeles, although dozens of experiments characterize in detail the courtship behavior of many species, including those in the genus *Triturus* (e.g., see reviews in Denoël 1999; Houck and Arnold 2003), only one preliminary study examined the effect of low temperature on courtship (Denoël 1998). However, only one male display was examined, and nothing is known on the consequences of low temperatures on all sexual interactions, including partners' responsiveness and sperm-transfer success.

From the results of experiments on temperature-dependence in ectotherm species (e.g., Rome et al. 1992; Connaughton et al. 2002; Gerhardt and Huber 2002), it can be expected that sexual behavior in newts is also strongly dependent on water temperature. Indeed, newts' courtship is complex and composed of many tail movements that males exhibit to females (Arntzen and Sparreboom 1989; Denoël 1999, 2002). At low temperatures, the rate and duration of these displays may change similarly to what was found for the call in frogs and fish (Connaughton et al. 2002; Gerhardt and Huber 2002). In addition, although nothing is known about the energetics of the different male courtship behaviors, it is likely that some acts are more costly than others. Males might then use alternative mating tactics to maximize their success in such environmental conditions. Because female behavior is affected by male courtship (Teyssedre and Halliday 1986), any changes in the courtship of males are likely to affect the responsiveness of the female and thus reproductive success. At low temperatures, mate choice might be altered, individuals thus becoming either less or more selective on body traits. If courtship behavior is indeed temperature-dependent, all future studies should control this factor to avoid biased results and to provide valuable raw data for comparative studies that help our understanding of phylogeny (Arntzen and Sparreboom 1989).

The aim of our study was to determine the effect of two different water temperatures on: (1) the courtship behavior of males, with special attention to alternative mating tactics such as luring behaviors, (2) the responsiveness of females and its effect on the courtship behavior of males, (3) the effect of male body traits on female responsiveness, and (4) the success of sexual encounters between males and females in terms of sperm transfer.

Methods

Courtship behavior of the Alpine newt

In the Alpine newt (*Triturus alpestris*), breeding occurs underwater after the cold winter period (end of winter or in early spring in lowlands) and lasts from several weeks to several months (Halliday 1977; Denoël 1996). Sexual interactions consist of varied male courtship displays directed towards the female, which can respond negatively or positively to the approaching male. A sexual encounter can include both a display phase, in which the male exhibits foreplay behaviors, and a sperm-transfer phase, in which the male tries to attract a female using different caudal displays, and to transfer sperm to her (Table 1) (Halliday 1977; Denoël et al. 2001a; Denoël 2002). Some of these behaviors (i.e., quiver and distal lure) are alternative mating tactics that include luring movements and are mainly exhibited to unresponsive females (Denoël et al. 2001b; Denoël 2002).

Sampling and laboratory maintenance

Adult Alpine newts were caught on a road in Boirs, Liège Province, Belgium (50°45′N–5°36′E, 70 m elevation a.s.l.), during their migration from their hibernation place to the pond where they reproduce. Collection took place during the 1st week of March 2003 (females, $n=80$; males, $n=80$). Because newts were caught before they entered the pond at the start of the breeding season, they had not yet reproduced that year. The specimens were brought directly to the laboratory (20 min drive) after their capture.

Males and females were kept separately in 4 different aquaria (300 l each; 40 individuals/aquarium). The newts were fed *Chironomus* larvae (50 mg/newt) every day in the afternoon. Two of the aquaria were maintained at a mean±SE temperature of 13.1±0.1°C, whereas the other two were maintained at 6.9±0.1°C. Photoperiod was 13.5/10.5 LD (four daylight neon tubes Lumilux de lux 2,350 lm, L 36 W/12–950 to simulate the natural light spectrum; four normal neon tubes: Sylvania Professional, 36 W DECOR183 to give a higher light intensity in the room). These laboratory conditions are within the range encountered by *T. alpestris* in the field during the reproductive period. All newts were released in their native habitat after completion of the experiment.

Experimental procedures

Dyadic encounters ($n=80$) were staged within the month of capture (11–28 March 2003), i.e. within the normal breeding period of the species (von Lindeiner 1992; Denoël 1996). All encounters are unique, as each individual was used only once (after the experiment, the newts were placed

in another aquarium and not used subsequently). In each experiment, a male and a female, both randomly chosen, were placed in an aquarium (45×30 cm and 25 cm high) floored with a slab of stone. Half of the trials were conducted at low water temperature (mean±SE=7.4±0.05°C), while the other half were conducted at high water temperature (12.7±0.05°C) (t_{78}=74.65, $P<0.001$). The animals placed in the observation aquarium at low temperature came from the maintenance aquarium at low temperature and vice versa for the high temperature treatment. The light intensity was 5,000 lx at the bottom of the aquarium (1 day light neon tube Lumilux de lux 2,350 lm, L 36 W/12–950; one normal neon tube Sylvania Professional, 36 W DECOR183). The tank water was replaced after each trial. Encounters were staged in the morning and recorded with a Sony digital 8 camcorder (TRV-510).

Observations were conducted until sexual activities between the two partners ceased (no courtship displays or interactions exhibited for more than 1 min). The trial was stopped if the male or the female surfaced to breathe, because the probability of a male finding a female again in natural conditions is considered to be low after this event (Halliday 1977). However, the trial was not stopped when females surfaced during sperm transfer because males are stationary during this phase and may attract distant females in using luring displays (Denoël et al. 2001b). At the end of the encounter, the snout-vent length (SVL) and body mass (BM) were measured to the nearest millimeter and tenth of gram, respectively. Males and females used in the two treatments (low and high temperature) did not differ significantly in the extent of these morphological traits (low temperatures: males, mean SVL±SE=51.4±0.4 mm, BM=3.5±0.1 g, females, SVL=59.9±1.3 mm, BM=6.4±0.2 g, high temperatures: males, SVL=51.4±0.4 mm, BM=3.5±0.1 g, females, SVL=59.1±0.4 mm, BM=6.1±0.2 g; MANOVA: males, λ=0.999, $F_{2,77}$=0, P=1; females, λ=0.986, $F_{2,77}$=0.6, P=0.57).

Videotapes were then compressed using an MPEG-1 encoder and screened and analyzed using Noldus Observer Video Pro 4.1 software (Noldus 2002). Sequencing and timing (precision of 0.01 s) were obtained in typing keys on the keyboard of a computer. Because this software allows cross-referencing between digital images and encoded behavioral patterns, it was possible to encode separately the behavioral patterns of males and females.

In this study, we took into account the following variables:

– The absolute frequencies (i.e. the number of times a behavioral pattern was exhibited by an individual during an encounter) of the main male courtship displays (Table 1);
– The male display index (i.e. the proportion of time during which the male was courting during a sexual interaction: from the first to the last interaction with the female during a trial);
– The mean duration and tail-beating rates (i.e. the number of times per second the tails come back to the same

Table 1 Description of the main courtship displays of male Alpine newts. Terminology follows Denoël et al. (2001a) and Denoël (2002)

Behavior	Description
Display phase	
Fan	The male folds his tail against his flank and beats it rapidly
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
Sperm-transfer phase	
Quiver	The creeping male quivers his tail in the same axis as his body
Sperm deposition	The male deposits a spermatophore on the substratum while raising his tail above his back
Distal lure	The male holds his tail perpendicular to the body, initially moving the tip of the tail slowly, then exhibiting a wider movement, before bringing it again parallel to his body
Pushback	As the male stands in front of the female, she can push hard with her snout against his tail. In reaction, he bends his body toward the female and flexes his tail away from his flank, so that the female is pushed back

position during the beating movement) of the fanning bouts;
– The number of encounters (i.e. trials) involving courtship;
– The occurrence of sperm deposition;
– The success of the encounters (an encounter is successful when at least one spermatophore was transferred from the male to the female during a trial);
– The female response index (i.e. the proportion of time during which the female was responsive to the male during a sexual interaction: a female response was considered positive when the female approached the male or moved her head in his direction);
– The female responsive index to display (i.e. the proportion of time during which the female was responsive to the male during the male's courtship displays, excluding orientation behaviors of the male between courtship displays).

Statistical procedures

The effect of temperature on the absolute frequencies of behaviors was tested using a multivariate analysis of variance (MANOVA). In addition, continuous variables were introduced as covariates in MANCOVA analyses. Multiple regressions were computed in the MANCOVA to determine the significance of the relation between continuous variables. To achieve normality, proportions were normalized

Table 2 Absolute frequencies (mean±SE) of the main courtship displays exhibited by *Triturus alpestris* males at two different temperatures (low, $n=38$: mean=7.4°C, high, $n=36$: mean=12.7°C)

Behavior	Temperature		$F_{1,72}$	P
	Low	High		
Fan	29.13±6.49	27.81±4.93	0.006	0.94
Cat-buckle/lean-in	0.36±0.22	1.31±0.40	4.828	<0.05
Quiver	0.26±0.11	0.44±0.19	0.67	0.42
Sperm deposition	1.47±0.20	2.11±0.19	5.870	<0.05
Distal lure	0.40±0.12	0.55±0.12	1.364	0.25
Push-back	1.74±0.51	3.47±0.57	7.314	<0.01

by arcsine transformations, other continuous data were normalized by log transformation, and counts were normalized by square-root transformation before calculating the parametric significance test. Chi-square tests were computed to compare proportions of events in two×two contingency tables (Sokal and Rohlf 1995). We applied a maximum error risk of 0.05 for all tests.

Results

There were no significant differences in the number of encounters (i.e. trials) involving courtship behavior at low and high temperatures ($\chi^2=0.72$, 1 *df*, $P=0.40$). Courtship occurred in 38 out of 40 encounters at low temperatures (95%) and in 36 out of 40 encounters at high temperature (90%). Similarly, there were no significant differences in the number of encounters involving sperm deposition ($\chi^2=1.73$, 1 *df*, $P=0.19$). At low temperatures, males deposited at least 1 spermatophore in 28 out of 40 encounters (70%). At high temperatures, spermatophore deposition occurred in 33 out of 40 encounters (82.5%).

The absolute frequencies of courtship displays differed significantly at low and high temperatures (MANOVA: $\lambda=0.771$, $F_{6,67}=3.312$, $P<0.01$; Table 2). At low temperatures, males used the cat-buckle with lean-in ($P<0.05$) and the push-back ($P<0.01$) movements on significantly fewer occasions than at high temperatures. Males also deposited significantly fewer spermatophores per encounter ($P<0.05$) at low temperatures. However, no significant difference was found for the most-used courtship behavior of the exhibition phase, the fan, or for the quiver and distal

lure, two behavioral patterns of the sperm-transfer phase ($P>0.05$; Table 2).

The mean fanning bout duration and the tail-beating rate during this fanning movement differed significantly at low and high temperatures (MANOVA: $\lambda=0.288$, $F_{2,41}=50.836$, $P<0.001$; Fig. 1). Males exhibited significantly longer fanning bouts ($F_{1,42}=5.33$, $P<0.05$), but beat their tail at a significantly slower rate ($F_{1,42}=103.52$, $P<0.001$) at low versus high temperature (Fig. 1). The mean fanning duration was negatively correlated with the tail-beating rate at high temperatures ($r=-0.49$, $F_{1,19}=5.912$, $P<0.05$), but not at low temperatures ($r=-0.11$, $F_{1,21}=0.237$, $P=0.63$).

The two indexes of female responsiveness were highly correlated ($r=0.98$, $F_{1,72}=1386.71$, $P<0.001$). Consequently, only the female response index was used in the other analyses. Female responsiveness to male courtship was significantly affected by temperature and male display index (ANCOVA: $F_{1,71}=6.728$, $P<0.05$ and $F_{1,71}=8$, $P<0.01$, respectively). At low temperatures, females were less responsive to males (mean±SE=20±4%) than they were at high temperatures (35±4%). Male sexual display was not affected by temperature (low temperature: 84±3%, high temperature: 89±2%; $F_{1,72}=1.797$, $P=0.18$).

The female positive response index significantly affected the frequencies of male displays (MANCOVA: $\lambda=0.559$, $F_{6,66}=8.669$, $P<0.001$). Although the effect of temperature remained significant ($\lambda=0.824$, $F_{6,66}=2.358$, $P<0.05$), only one male courtship behavior (in terms of number of acts per encounter) was directly affected by temperature to a significant degree (cat-buckle: $F_{1,71}=5.229$, $P<0.05$). The number of fan (multiple regression in MANCOVA: $\beta=-0.35±0.12$, $F_{2,71}=4.451$, $P<0.05$), sperm deposition ($\beta=0.42±0.11$, $F_{2,71}=10.832$, $P<0.001$), distal lure ($\beta=-0.29±0.12$, $F_{2,71}=3.675$, $P<0.05$) and push-back ($\beta=0.45±0.11$, $F_{2,71}=13.438$, $P<0.001$) behaviors were significantly dependent on the female positive response index. More spermatophores were deposited and more push-back movements were performed with highly responsive females, but males performed distal lure and fan less often in such conditions. In contrast, mean durations of fanning and beating rates were directly affected to a significant degree only by temperature (MANCOVA: $\lambda=0.256$, $F_{2,38}=55.366$, $P<0.001$) and not by female positive response index ($\lambda=0.929$, $F_{2,38}=0.244$, $P=0.25$).

Fig. 1 Tail-beating rates (**a**) and mean duration (**b**) of fanning movements exhibited by *Triturus alpestris* males at two different temperatures (low, $n=23$: mean=7.4°C, high, $n=21$: mean=12.7°C). Points: means, whiskers: SE, *$P<0.05$, ***$P<0.001$.
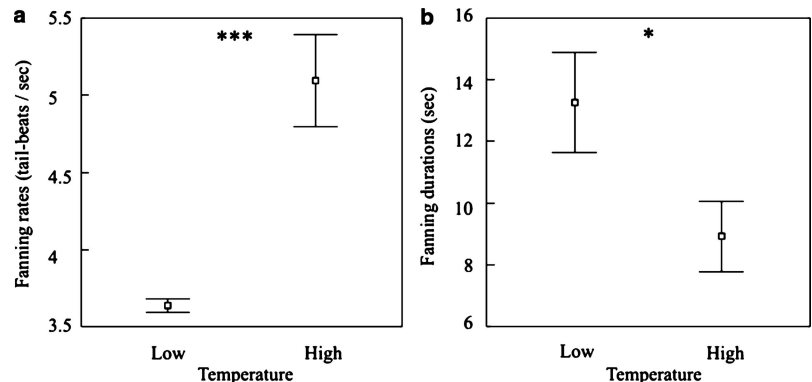
Twice the number of encounters included successful sperm transfer between the male and the female at high (12 out of 40) temperatures than at low ones (6 out of 40 encounters), but no significant differences were found (χ^2=2.58, 1 df, P=0.11). Similarly, there were no significant differences in the number of encounters during which females responded positively to males during sperm transfer at high (27 out of 40) and low (20 out of 40) temperatures (χ^2=2.53, 1 df, P=0.11).

Regardless of the temperature (ANCOVA: $F_{1,70}$=8.044, $P<0.01$), male body length and mass ($F_{1,70}$=0.284, P=0.60 and $F_{1,70}$=0.171, P=0.68 respectively) had no significant effect on female responsive index. Regardless of temperature (ANCOVA: $F_{1,70}$=2.002, P=0.16), female body length and mass ($F_{1,70}$=1.246, P=0.27 and $F_{1,70}$=0.126, P=0.72 respectively) had no effect on male display index. Female responsive index was not influenced by the body length and mass of females (ANCOVA: $F_{1,71}$=0.049, P=0.82 and $F_{1,71}$=0.032, P=0.86 respectively).

Discussion

Our results demonstrate that temperature has a major effect on the behavioral patterns of both males and females of the Alpine newt. At low temperatures (around 7°C), males exhibit several types of courtship displays at different frequencies than at a higher temperature (around 13°C). Females are also affected by temperature: at low temperatures, females respond less positively to male sexual displays. Most previous studies on the effect of temperature on courtship in animals focused on acoustic communication in both insects (Walker 2000; Gerhardt and Huber 2002; Sueur and Sanborn 2003) and anurans (Vasara et al. 1991; Sullivan and Malmos 1994; Wells et al. 1996; Howard and Young 1998; Navas and Bevier 2001; Gerhardt and Huber 2002; Wong et al. 2004). Our data extend these findings in showing that behavioral patterns other than acoustic communication are temperature-dependent, as previously shown for competition in fish (Kvarnemo 1996, 1998). With the exception of a preliminary observation on the effect of temperature on courtship (Denoël 1998), this is the first study to show that the courtship pattern of urodeles is affected by ambient temperature. Temperature-dependence has profound consequences for our understanding of the proximate mechanisms behind plasticity of courtship and of the evolution of mating tactics. Future studies should control ambient-temperature effects to avoid biased results. This is particularly important when behavior is taken as a trait in comparative studies (Halliday 1977; Arntzen and Sparreboom 1989).

The display phase of *Triturus* newts includes several courtship behaviors that may help persuade the female to follow the male during the ultimate courtship phase, the sperm-transfer phase (Teyssedre and Halliday 1986). The standard courtship behavior of the male Alpine newt is the tail-fanning movement. This behavior consists of tail vibrations that produce a water current. The current carries pheromones in the direction of the female's snout, providing her with visual, chemical and mechanical mating cues (Cogalniceanu 1994; Kikuyama et al. 1995; Denoël 1996). Although the absolute frequency of this act is not affected by temperature, its mean duration and the rate of tail beats during a given fanning bout are strongly influenced by temperature. At low temperatures, the tail beats at a slower rate, but for a longer time than at high temperatures. This corroborates preliminary observations on Iberian Alpine newts, which also beat their tails at a slower rate at low temperatures, though no other variables were examined (Denoël 1998). Similarly, in anurans (Vasara et al. 1991; Howard and Young 1998) and fish (Connaughton et al. 2002), call rate is positively related to temperature, while pulse duration is negatively related to temperature. There is thus a trade-off between calling at high pulse rates and during a long period of time, the two variables being negatively correlated (this study). The two behavioral changes have opposite effects: the low pulse rate during fanning in newts and during calling in anurans and fish should provide less stimulation to the female than higher rates, but the higher bout duration might compensate for this defect. However, quantitative data on stimulation levels are needed to test this hypothesis.

Temperature can have an indirect effect on sexual interactions in ectotherms and may modulate our results. For example, temperature has an indirect effect on sexual interactions in fish (Ahnesjo 1994; Kvarnemo 1994, 1996). The reproductive rates of male fish vary with temperature, causing shifts in the operational sex ratio which, in turn, affect sexual selection (Ahnesjo 1994; Kvarnemo 1994, 1996). Because the behavioral pattern of males is strongly dependent on the responsiveness of females in our study species (Denoël 1996, 2002; Denoël et al. 2001b), an indirect effect may be expected. Indeed, some male behaviors, notably sperm deposition and push-back, appear to be due to female response and not directly to temperature. Luring movement (distal lure) is also dependent on female behavior, as shown in previous studies (Denoël et al. 2001b; Denoël 2002). Female behavior did not affect fanning parameters—tail-beating rates and mean fanning bout durations—indicating that these behaviors are directly affected by temperature (this study).

Starting reproductive interactions in low temperatures is adaptive in newts. Indeed, if eggs were laid later in the season, the progeny of the newts would be at risk of dying if they did not reach the minimum body size for metamorphosis before the ponds dry up (Rafinska 1991; Newman 1992) or freeze (Schabetsberger 1993). Although overwintering of larvae has been documented at some places (Denoël and Joly 2001a), a pond's shallowness and anoxic conditions can eliminate all individuals that do not leave the pond early (Schabetsberger 1993). Finally, larvae that hatch early may have an adaptive advantage over those that hatch later because older larvae are less gape-limited for feeding and less vulnerable to predation than young larvae are (Denoël and Joly 2001b; Denoël and Andreone 2003; Ryan and Plague 2004).

The absence of size-based mate choice in the present study corroborates the results of previous experiments on *T. alpestris*, in which females did not select males based on morphological traits (Denoël et al. 2001a; Garner and Schmidt 2003). And although low temperatures decreased female responsiveness in the Alpine newt, our experiment showed that low temperatures did not affect their mating criteria, as also observed with sand gobies (Kvarnemo 1998). However, males did not select females on their body mass or length. This is quite surprising because larger females are more fecund, a factor of mate choice in other newt species (Verrell 1986).

During their reproductive period, fertilized females breed with more than one male, and multiple paternity has been found among a female's offspring (Rafinski and Osikowski 2002; Garner and Schmidt 2003). In turn, male Alpine newts can produce dozens of spermatophores and mate with several females (Denoël 1996). Risking sperm loss while reproducing in cold waters is thus not necessarily too costly as long as males accrue sufficient benefits. The observed successful transfer at cold temperature shows that this tactic is valuable even if males lose more spermatophores at low than at high temperatures. Following Dunbar's terminology (1982), Alpine newts exhibit a side-payment strategy to maximize their success on passing opportunities. Such a trait seems typical of Alpine newts, which display several behavioral patterns at low success rates (e.g., luring an unresponsive female: Denoël et al. 2001a, or starting sexual interactions in the presence of rivals: Verrell 1988; Denoël 2003). Long-term studies in natural conditions are needed to model the variation in mating success of newts due to environmental factors. Particularly, it would be interesting to record newt courtship behavior and space use in function of the diurnal and daily variation of water temperature. However, our study demonstrates how an abiotic factor, temperature, can have a major impact on courtship patterns in an ectotherm.

References

Ahnesjo I (1994) Temperature affects male and female potential reproductive rates differently in the sex-role reversed pipefish, *Syngnathus typhle*. Behav Ecol 6:229–233

Arntzen JW, Sparreboom M (1989) A phylogeny for the old world newts, genus *Triturus*: biochemical and behavioral data. J Zool Lond 219:645–664

Cogalniceanu D (1994) The relative importance of vision and olfaction in mate recognition in male newts (Genus *Triturus*). Herpetologica 50:344–349

Connaughton MA, Fine ML, Taylor MH (2002) Weakfish sonic muscle: influence of size, temperature and season. J Exp Biol 205:2183–2188

Davenport J (1992) Animal life at low temperature. Chapman & Hall, London

Denoël M (1996) Etude comparée du comportement de cour de *Triturus alpestris alpestris* (Laurenti, 1768) et *Triturus alpestris cyreni* (Wolterstorff, 1932) (Amphibia, Caudata) : approche évolutive. Cah Ethol 16:133–258

Denoël M (1998) The modulation of movement as a behavioral adaptation to extreme environments in the newt *Triturus alpestris cyreni*. J Herpetol 32:623–625

Denoël M (1999) Le comportement social des urodèles. Cah Ethol 19:221–258

Denoël M (2002) Paedomorphosis 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, Andreone F (2003) Trophic habits and aquatic microhabitat use in gilled immature, paedomorphic and metamorphic Alpine newts (*Triturus alpestris apuanus*) in a pond in central Italy. Belg J Zool 133:95–102

Denoël M, Joly P (2001a) Adaptive significance of facultative paedomorphosis in *Triturus alpestris* (Amphibia, Caudata): resource partitioning in an alpine lake. Freshwater Biol 46:1387–1396

Denoël M, Joly P (2001b) Size-related predation reduces intramorph competition in paedomorphic Alpine newts. Can J Zool 79:943–948

Denoël M, Poncin P, Ruwet JC (2001a) Sexual compatibility between two heterochronic morphs in the Alpine newt, *Triturus alpestris*. Anim Behav 62:559–566

Denoël M, Poncin P, Ruwet JC (2001b) Alternative mating tactics in the Alpine newt *Triturus alpestris alpestris*. J Herpetol 35:62–67

Dunbar RIM (1982) Intraspecific variations in mating strategy. In: Bateson PPG, Klopfer PH (eds) Perspectives in ethology, vol 5. Plenum, New York, pp 385–431

Endler JA (1995) Multiple-trait coevolution and environmental gradients in guppies. Trends Ecol Evol 10:22–29

Garner TWJ, Schmidt BR (2003) Relatedness, body size and paternity in the alpine newt, *Triturus alpestris*. Proc R Soc Lond Ser B Biol Sci 270:619–624

Gerhardt HC, Huber F (2002) Acoustic communication in insects and anurans. The University of Chicago Press, Chicago

Gross MR (1996) Alternative reproductive strategies and tactics: diversity within sexes. Trends Ecol Evol 11:92–98

Halliday TR (1977) The courtship of European newts: an evolutionary perspective. In: Taylor DH, Guttman SI (eds) The reproductive biology of amphibians. Plenum, New York, pp 185–232

Hirano M, Rome LC (1984) Jumping performance of frogs (*Rana pipiens*) as a function of muscle temperature. J Exp Biol 108:429–439

Houck LD, Arnold SJ (2003) Courtship and mating behavior. In: Sever DM (ed) Reproductive biology and phylogeny of Urodela. Science, Enfield, N.H., pp 383–424

Howard RD, Young JR (1998) Individual variation in male vocal traits and female mating preferences in *Bufo americanus*. Anim Behav 55:1165–1179

Hutchinson VH, Dupré RK (1992) Thermoregulation. In: Feder ME, Burggren WW (eds) Environmental physiology of the Amphibians. The University of Chicago Press, Chicago, pp 206–249

John-Alder HB, Barnhart MC, Bennett AF (1989) Thermal sensitivity of swimming performance and muscle contraction in northern and southern populations of tree frogs (*Hyla crucifer*). J Exp Biol 142:357–372

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

Kissner KJ, Forbes MR (1997) Rattling behavior of prairie rattlesnakes (*Crotalus viridis viridis*, Viperidae) in relation to sex, reproductive status, body size, and body temperature. Ethology 103:1042–1050

Kvarnemo C (1994) Temperature differentially affects male and female reproductive rates in the sand goby: consequences for operational sex ratio. Proc R Soc Lond B 256:151–156

Kvarnemo C (1996) Temperature affects operational sex ratio and intensity of male-male competition: an experimental study of sand gobies, *Pomatoschistus minutus*. Behav Ecol 7:208–212

Kvarnemo C (1998) Temperature modulates competitive behaviour: why sand goby males fight more in warmer water. Ethol Ecol Evol 10:105–114

Kvarnemo C, Ahnesjö I (1996) The dynamics of operational sex ratios and competition for mates. Trends Ecol Evol 11:404–408

Lass S, Spaak P (2003) Temperature effects on chemical signalling in a predator-prey system. Freshwater Biol 48:669–677

Mori A, Burghardt GM (2001) Temperature effects on anti-predator behaviour in *Rhabdophis tigrinus*, a snake with toxic nuchal glands. Ethology 107:795–811

Navas CA, Bevier CR (2001) Thermal dependency of calling performance in the eurythermic frog *Colostethus subpunctatus*. Herpetologica 57:384–395

Newman RA (1992) Adaptive plasticity in amphibian metamorphosis. Bioscience 42:671–678

Noldus (2002) The observer. Reference manual version 4.1. Noldus Information Technology, Wageningen

Rafinska A (1991) Reproductive biology of the fire-bellied toads, *Bombina bombina* and *B. variegata* (Anura: Discoglossidae): egg size, clutch size and larval period length differences. Biol J Linn Soc 43:197–210

Rafinski J, Osikowski A (2002) Sperm mixing in the Alpine newt (*Triturus alpestris*). Can J Zool 80:1293–1298

Rome LC, Stevens ED, John-Adler HB (1992) The influence of temperature and thermal acclimation on physiological function. In: Feder ME, Burggren WW (eds) Environmental physiology of the Amphibians. The University of Chicago Press, Chicago, pp 183–205

Ruano F, Tinaut A, Soler JJ (1999) High surface temperatures select for individual foraging in ants. Behav Ecol 11:396–404

Ryan TJ, Plague GR (2004) Hatching asynchrony, survival, and the fitness of alternative adult morphs in *Ambystoma talpoideum*. Oecologia 140:46–51

Schabetsberger R (1993) Der Bergmolch (*Triturus alpestris*, Laurenti) als Endkonsument in einem alpinen Karstsee (Dreibrüdersee, 1643 m, Totes Gebirge). PhD Thesis, University of Salzburg

Shine R, Olsson MM, Lemadter MP, Moore IT, Mason RT (2000) Effects of sex, body size, temperature, and location on the antipredator tactics of free-ranging gartersnakes (*Thamnophis sirtalis*, Colubridae). Behav Ecol 11:239–245

Sokal RR, Rohlf FJ (1995) Biometry. Freeman, New York

Sueur J, Sanborn AF (2003) Ambient temperature and sound power of cicada calling songs (Hemiptera: Cicadae: *Tibicina*). Physiol Entomol 28:340–343

Sullivan BK, Malmos KB (1994) Call variation in the Colorado river toad (*Bufo alvarius*): behavioral and phylogenetic implications. Herpetologica 50:146–156

Teyssedre C, Halliday T (1986) Cumulative effect of male's displays in the sexual behaviour of the smooth newt *Triturus vulgaris* (Urodela, Salamandridae). Ethology 71:89–102

Vasara E, Sofianidou TS, Schneider H (1991) Bioaccoustic analysis of the yellow-bellied toad in Northern Greece (*Bombina variegata scabra* L., Anura, Discoglossidae). Zool Anz 226:220–236

Verrell PA (1986) Male discrimination of larger, more fecund females in the smooth newt, *Triturus vulgaris*. J Herpetol 20:416–422

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

Walker TJ (2000) Pulse rates in the songs of trilling field crickets (Orthoptera: Gryllidae: Gryllus). Ann Entomol Soc Am 93:565–572

Ward JV, Stanford JA (1982) Thermal responses in the evolutionary ecology of aquatic insects. Annu Rev Ecol Syst 27:97–117

Wells KD, Taigen TL, O'Brien JA (1996) The effect of temperature on calling energetics of the spring peeper (*Pseudacris crucifer*). Amphib Reptil 17:149–158

Whitehead PJ, Puckridge JT, Leigh CM, Seymour RS (1989) Effect of temperature on jump performance of the frog *Limnodynastes tasmaniensis*. Physiol Zool 62:937–949

Wong BBM, Cowling ANN, Cunningham RB, Donnelly CF, Cooper PD (2004) Do temperature and social environment interact to affect call rate in frogs (*Crinia signifera*)? Aust Ecol 29:209–214