

Effect of Rival Males on the Courtship of Paedomorphic and Metamorphic *Triturus alpestris* (Amphibia: Salamandridae)

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Abstract

Current theories on the alternative mating tactics suppose that individuals may opt for particular behavioral patterns depending of their morphological status. Facultative paedomorphosis in newts and salamanders is a suitable process to explore this question because it implies the coexistence of two different morphological morphs differing by the presence of gills and epigamic traits. The aim of this study was to find out whether paedomorphs and metamorphs use similar tactics to attract mates in the presence of a rival and whether there are differences in sexual activity and success between alternative morphs. Sexual interactions in triadic encounters were staged and analyzed in a standardized experimental design. The two kinds of males did not differ in terms of sexual activity, spermatophore deposition or female responsiveness. Both rival paedomorphic and metamorphic males exhibited sexual interference, but in most encounters, intruders just disturbed the courting pair. Sperm transfer success was lower in triadic encounters than in dyadic encounters. These results illustrate that intermorph breeding also occurs in the presence of competitors but that the success rate of the newts is considerably decreased in such competitive situations. Moreover, newts do not use alternative reproductive tactics depending on their status (i.e., paedomorph or metamorph).

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Introduction

In many populations, there are differences in mating behavior and morphology among males (Dunbar, 1982; Andersson, 1994; Taborsky, 1994). The tactics used often depend on the status of the individuals employing them (Gross, 1996; Taborsky, 2001). Size (Gross, 1985; Emlen, 1997), age (de Fraipont et al., 1993), and dominance status (Eason and Sherman, 1995) are factors affecting the choice of alternative reproductive tactics. Behavioral tactics are often associated with morphological specializations, such as between jack and hooknose salmon (Gross, 1985), hornless and horned scarab beetles (Moczek and Emlen, 2000), and heteromorphic (thickened third pair of legs terminated by a claw) and homomorphic (identical pairs of legs) acarid mites (Radwan et al., 2000).

Facultative paedomorphosis in newts and salamanders is an obvious example of polymorphism because it involves a major change of structure in association with metamorphosis (Whiteman, 1994; Schlichting and Pigliucci, 1998). Paedomorphs retain larval traits (e.g., gills and gill slits) in the adult stage while metamorphs are fully metamorphosed (Semlitsch and Wilbur, 1989). This heterochronic process is adaptive in allowing, for instance, resource partitioning between syntopic morphs (Denoël and Joly, 2001), earlier reproduction in terms of age and season in paedomorphs (Krenz and Sever, 1995; Ryan and Semlitsch, 1998; Denoël and Joly, 2000), and differences in breeding frequency between the two morphs (Whiteman, 1997).

In addition to differences in the respiratory and feeding systems, the two alternative heterochronic morphs differ considerably in the degree of development of the secondary sexual traits (2001a for the Alpine newt, see Denoël et al.). Although paedomorphs present juvenile morphological traits, they are mature and able to mate (Krenz and Sever, 1995; Whiteman et al., 1999; Denoël et al., 2001a). Consequently, on the basis of status-dependent selection (Gross, 1996), it could be expected that depending on their status (i.e., metamorph or paedomorph), each morph would adopt a particular alternative mating tactic. Yet in dyadic encounters in the Alpine newt the two morphs display the same behavioral pattern at similar frequencies (Denoël, 2002) and are fully compatible (Denoël et al., 2001a), but nothing is known about the effect of competitors on the sexual tactics exhibited by the alternative morphs and on the choice of females when confronted at the same time with the two kinds of males. Exploring this question in paedomorphic newts is important because previous studies on metamorphic newts suggest that competitive situations may imply alternative mating tactics (e.g., Arnold, 1976; Verrell, 1989).

The aim of the present study is then to examine the sexual interactions of trios consisting of female Alpine newts and two males, one metamorphic and one paedomorphic. Specifically the objective was to determine the success rates of paedomorphic and metamorphic males, the sexual tactics used by males to inseminate females, and the reaction of the courting male to a potential rival male.

Materials and methods

Subjects.—The sexual behavior of Alpine newts (*Triturus alpestris*) takes place in ponds and lakes after the winter period (Denoël, 1996). In Alpine lakes, such events usually occur after the thawing of the lake (Denoël, 1998). During dyadic encounters, the male tries to place himself in front of the female and follows her if she moves away (orientation phase). Once in front of the female, he exhibits several caudal displays in a static posture, mainly the fan which consists in a fast beating of the tail against the flank (display phase), before initiating the sperm transfer phase. During the latter phase, he deposits a spermatophore on the substratum, in front of the female (Denoël et al., 2001b; Denoël, 2002). Other males can interfere with the courting pair by displaying and by inseminating the female (Verrell, 1988).

Newts were caught with a landing net from La Cabane Lake (Alpes-de-Haute-Provence, Southern France, 44°24'N, 6°24'E, 1950 m elevation), the week after the lake thawed, that is, in May 2000. This population belongs to the subspecies *alpestris* but is considered to have been introgressed by the subspecies *apuianus* (Breuil, 1986). Sampling at that period allowed me to capture reproductive and receptive adults just before breeding starts. I collected 30 paedomorphic males, 30 paedomorphic females, 30 metamorphic males, and 30 metamorphic females. An individual was considered to be a paedomorph if the gill slits were open and a metamorph if they were closed. Sex was established using the presence of epigamic characters. In the sample used in these experiments, paedomorphs were the same snout-vent length as metamorphs (t test: $t_{58} = 0.572$, $P = 0.62$) but had a greater body mass (ANCOVA with snout-vent length as covariate: $F_{1,57} = 14.286$, $P < 0.001$), greater tail depth (ANCOVA: $F_{1,57} = 55.764$, $P < 0.001$), lower number of contrasted dots on the flank (ANCOVA: $F_{1,57} = 63.916$, $P < 0.001$), and smaller cloaca width (ANCOVA: $F_{1,57} = 7.375$, $P < 0.01$). Metamorphs and paedomorphs from the studied population do not differ in mean age (Denoël and Joly, 2000).

Housing.—I kept the newts in refrigerated boxes to transport them to the laboratory. Sexes and morphs were then kept separately in seven aquaria (four of 250 X 40 X 40 cm, two of 100 X 100 X 40 cm, and one of 200 X 100 X 40 cm). Newts were fed every two days with *Chironomus* larvae. The substratum of the aquaria was composed of gravel. Water was oxygenated; temperature ranged between 12.5 and 13.5 C and photoperiod was 14 h light/8 h dark. These laboratory conditions are within the range met by newts in the field. All newts were released in good health in their native lake after completion of the experiment.

Procedure.—In each experiment, a female (a metamorph or a paedomorph, depending on the experiment) and two males (a metamorph and a paedomorph), all randomly chosen, were placed together in an aquarium (60 X 30 X 30 cm) floored with gravel. Light intensity was 5000 lux (white light) and temperature 13 C, that is, conditions that newts may meet in natural lakes. Sixty encounters were planned with 30 metamorphic males, 30 paedomorphic males, 30 metamorphic females, and 30 paedomorphic females. Each male was used twice: first with a female of one morph and second with a female of the other morph. Each female was used once. To avoid any order effect with a specific type of female, males were split into two groups. Groups 1 and 2 each consisted of 15 paedomorphic and metamorphic males. These two groups were put into two dif-

ferent aquaria. Males of group 1 were used in experiments with paedomorphic females, and those of group 2 in experiments with metamorphic females. After each experiment, these males were stored in two other aquaria. At the end of these 30 experiments, observations were continued with the same set of males, but with a female of another morph than that used in the first session. Consequently, males of group 1 were used with metamorphic females and those of group 2 with paedomorphic females. Encounters were made alternatively with individuals of the groups 1 and 2. All encounters involved different combinations of males. Four encounters were organized each day between 0730 and 1330. The experiment lasted 18 days. Sexual interactions were recorded with a digital video camera (Sony TRV-510). Each experiment was stopped after the end of a sexual encounter involving spermatophore deposition or after 60 min.

Analysis.—The success of each kind of male (metamorph and paedomorph) with paedomorphic and metamorphic females was then determined. The following behavioral patterns were taken into account: exhibition of sexual display toward the female, the morph that exhibited sexual behavior first, the number of spermatophores deposited and picked-up, the responsiveness of the female, and the kind of interaction. Two main patterns of interaction are here identified: “disturbance” when the rival male only moves close to the courting pair (a behavior that often causes the end of the sexual encounter) and “sexual interference” when the rival male courts the female that is being courted by the courter. The courting male is defined as the male that first exhibits a courtship display to the female. The rival male is the male that interfere with a courting pair. All comparisons were made using chi-square tests in contingency tables between observed and expected values. Some dependence exists between first and second encounters because the same males were used in both of them. However, it is reduced by the large number of individual used in the study. To test for differences in duration of sexual interactions and number of spermatophore deposited, Mann-Whitney U -tests were applied.

Results

There were no significant differences in the behavioral pattern of males in front of paedomorphic and metamorphic females ($P > 0.05$ for all comparisons, χ^2 -test for binary data, Mann-Whitney U -test for time data). Data from encounters involving the two kinds of females have then been pooled in the subsequent analyses.

Of the 60 triadic encounters, 44 included courtship behavior, 18 of these were initiated by paedomorphic males and 26 by metamorphic males ($\chi^2 = 1.46$, 1 df, $P = 0.22$). Males that did not initially show sexual activity sometimes exhibited sexual behaviors later during the experiment. Indeed, several bouts of sexual activity occurred during the 60 min observation period. That means that in the 44 trials with sexual interactions, courtship behaviors were exhibited by metamorphic males in 32 trials and by paedomorphic males in 22 trials. No significant differences were outlined in the sexual activity of males (Table 1). The duration of sexual display sequences is significantly similar in the two male morphs (metamorphs: mean \pm SE = 499.5 ± 83.0 sec; paedomorphs: 340.7 ± 70.4 sec; $U = 188$, $Z = 1.495$, $n_1 = 26$, $n_2 = 20$, $P = 0.11$). Sexual interference was a rare behavioral pattern in which the rival male manifested courtship behavior toward the female. The intruder

first approached the female, sniffed her, and placed himself either between the courting male and the female or to one side of the courting male and in front of the female. The rival male then exhibited the fan, a rapid tail vibration movement, toward the female. In one case, the rival male started to display to the female just after the courting male had crept ahead of the female to start the spermatophore transfer phase. Sexual interference was initiated similarly by the two kinds of males (Table 1). More often, at the same time as the courting male exhibited sexual displays to the female, the rival male approached the pair, moved alongside them, and placed himself between the sexual partners or sniffed them, but did not show any kind of sexual display. Such a sequence involving the interaction of a rival male is called a disturbance. Rival paedomorphs exhibited such approaches of a courting pair as often as the rival metamorphs did (Table 1).

There was no significant difference between paedomorphic (16 encounters) and metamorphic (10 encounters) males in the number of encounters in which females responded positively (approach to the male; $\chi^2 = 1.39$, 1 df, $P = 0.24$).

The three kinds of sexual interactions are not exhibited at the same frequencies ($\chi^2 = 19.86$, 2 df, $P < 0.001$). Disturbance was the most usual behavioral pattern in triadic encounters ($n = 28$, vs dyadic display, $n = 9$: $\chi^2 = 9.76$, 1 df, $P < 0.05$; vs sexual interference, $n = 6$: $\chi^2 = 14.24$, 1 df, $P < 0.001$). Dyadic display encounters (situation similar to that in pure dyadic encounters) and sexual interference encounters did not differ in frequency ($\chi^2 = 0.60$, df = 1, $P = 0.43$).

The rival male, although he did not show sexual activity, modified the sexual sequence of the courting pair in 26 experiments. The arrival of the rival male in 20 experiments did not stop the sexual sequence of the courting pair. These two events do not differ significantly in frequency ($\chi^2 = 0.78$, 1 df, $P = 0.38$). Because of the arrival of another male, the courting male displayed three kinds of behaviors that significantly differ ($\chi^2 = 6.44$, 2 df, $P < 0.05$): he approached, sniffed, or displayed to the rival male ($n = 22$), moved away ($n = 8$), or continued to court the female ($n = 16$). The first response was significantly more frequent than the second ($\chi^2 = 6.53$, 1 df, $P = 0.01$) but not more frequent than the third ($\chi^2 = 2.83$, 1 df, $P = 0.09$). The second and the third responses did not differ significantly neither ($\chi^2 = 2.66$, 1 df, $P = 0.10$).

There was no significant difference in the number of spermatophores deposited per encounter by metamorphic and paedomorphic males (metamorphs: mean \pm SE = 2.1 ± 0.3 ; paedomorphs: 2.3 ± 0.5 ; $U = 120.5$, $Z = -0.206$, $n_1 = 12$, $n_2 = 21$, $P = 0.84$). Sperm transfer rates were low in triadic encounters with only two successful encounters (i.e., 3.3%). In one encounter, the metamorph inseminated the female, whereas in the other, the paedomorph did.

Discussion

This study shows that paedomorphic and metamorphic males are both able to court females in a competitive situation and that paedomorphic and metamorphic females are responsive to both kinds of male. Denoël et al. (2001a) found similar results in a dyadic situation. Males of the two morphs are thus able to attract mates in the absence and presence of rivals of the other morph, but the success rates of the encounters were very low. These two kinds of males did not differ significantly in the fre-

Table 1. Behavioral pattern of paedomorphic and metamorphic Alpine newt males during triadic encounters ($\chi^2 = 3.225$, 3 df, $P = 0.07$).

Behavior	Paedomorph	Metamorph	χ^2 (1 df)	P
Courtship	22	32	1.85	0.17
Interference	3	3	0	1
Disturbance	16	14	1.995	0.16
Nothing	37	28	1.25	0.26

quencies of encounters including sexual activity or in the number of spermatophores deposited. However, consistent with results from dyadic encounters (Denoël et al., 2001a), fewer paedomorphic males were involved in sexual interactions than metamorphic males, but the difference was not significant in the present study. Although largely different in the degree of development of their secondary sexual traits, the two morphs are not sexually isolated: the homotypic (i.e., within-morph) and heterotypic (i.e., between morphs) encounters have similar success rates in terms of female responsiveness. Gene flow is thus possible between heteromorphic morphs.

In the presence of male competitors, males can use alternative mating tactics, that is, behavioral patterns that improve their success (Andersson, 1994; Taborsky, 1994). Males of newt and salamander species often use such tactics to inseminate females (Arnold, 1976; Verrell, 1989; Denoël, 1999). In the experiments presented here, metamorphic and paedomorphic males used alternative reproductive tactics but did not differ in the frequency with which they exhibited them. Thus, in competitive situations, I found no evidence that Alpine newt males use particular reproductive tactics depending on their status (i.e., metamorph or paedomorph), contrary to other animal groups studied (Gross, 1996; Emlen, 1997; Radwan et al., 2000). In the present study, when a female is already being courted by a male, the other male, paedomorph or metamorph, approaches the pair, may sniff the female, and start to court the female by fanning his tail. These results are consistent with the observations of Verrell (1988) on metamorphic Alpine newts. They differ from results of experiments with species (e.g., *Ambystoma tigrinum* and *Triturus vulgaris*), in which the rival directly started a sperm transfer and used female mimicry, that is, a tail touch, a behavior eliciting sperm deposition of the courting male (Arnold, 1976; Verrell, 1984a).

Although sexual interference was a rare tactic in the studied population, rival males often interacted with the courting pair by moving close to the pair or sniffing the courting male or the female. These behavioral patterns disturb courtship. Indeed, half of sexual sequences between the courting male and the female stopped when the other male approached the pair. At the approach of an intruder, the courting male often left the female and moved toward him. Such response may come from the static behavior of the female compared with another newt that is moving. It may thus correspond to a misinterpretation: the moving male becoming a stimulus causing this approach of the courting male. But after sniffing the rival or displaying for a short time toward him, the courting male usually moves away from him.

Only 3% of the triadic encounters were successful in terms of sperm transfer. This means that less than 2% of the males managed to transfer their sperm to the female in a competitive situation. Thus, triadic

encounters have a lower success than dyadic ones, for which the proportion of successful encounters was 16% and in which 11% of spermatophores were transferred to the female (Denoël et al., 2001a), a characteristic found by Sparreboom (1996) and Verrell (1984a; 1988) for metamorphic individuals of newts. These large differences are explained by the disturbing effect of the other male in the vicinity of a courting pair. Such disturbance may act at several levels. The direct disturbance, as mentioned above, often causes the end of an encounter because the courting male moves away or approaches the rival. The courtship display sequences between a male and a female in presence of a rival male are shorter than in dyadic encounters (on average, 430 sec in triadic vs 1085 sec in dyadic). Courting males also deposited on average one spermatophore less per encounter than in dyadic situations (pers. obs.), reducing their chance to inseminate the female but also the risk of producing a large amount of sperm in the presence of other males. These results agree with those of Verrell and Krenz (1998) on *Ambystoma talpoideum* but not with those obtained on two other ambystomatid species, *A. maculatum* (Arnold, 1976) and *A. texanum* (McWilliams, 1992). As Verrell and Krenz (1998) note, these interspecific differences might be related to the very short period of reproduction of *A. maculatum* and *A. texanum*. The longer reproductive period of Alpine newts and mole salamanders may offer them the opportunity to meet other isolated females later. The low probability of transfer of the spermatophores deposited may signify that females avoid breeding in the presence of more than one male. Such aversive behavioral patterns of females have been previously recorded by Verrell who showed that *Triturus vulgaris* females preferred to mate with isolated males (Verrell, 1984b).

In conclusion, all of the ethological data on reproductive success suggest the potential for a large intermorph gene flow in heterochronic Alpine newts (Denoël et al., 2001a; Denoël, 2002; this study). The absence of sexual isolation is thus not in favor of sympatric speciation hypotheses in this species. The maintenance of the polymorphism may be then supported by strong selection on resource use (Denoël and Joly, 2001) which makes valuable the two ontogenetic alternatives (Denoël et al., 2002). Complementary studies on progenetic populations (Denoël and Joly, 2000) will help our understanding of the evolutionary process when morphs differ largely by size.

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References

ANDERSSON, M. 1994. Sexual selection, Princeton, NJ.
 ARNOLD, S. J. 1976. Sexual behavior, sexual interference and sexual defense in the salamanders *Ambystoma maculatum*, *Ambystoma tigrinum* and *Plethodon jordani*. *Z. Tierpsychol.* 42:247–300.
 BREUIL, M. 1986. Biologie et différenciation génétique des populations du triton alpestre (*Triturus alpestris*) (Amphibia Caudata)

dans le sud-est de la France et en Italie. Unpubl. Ph.D. Thesis, Paris-Sud Univ., Paris.
 DE FRAIPONT, M., G. J. FITZGERALD, AND H. GUDERLEY. 1993. Age-related differences in reproductive tactics in the three-spined stickleback, *Gasterocephalus aculeatus*. *Anim. Behav.* 46:961–968.
 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.
 ———. 1998. The modulation of movement as a behavioral adaptation to extreme environments in the newt *Triturus alpestris cyreni*. *J. Herpetol.* 32:623–625.
 ———. 1999. Le comportement social des urodèles. *Cah. Ethol.* 19:221–258.
 ———. 2002. Paedomorphosis in the Alpine newt (*Triturus alpestris*): decoupling behavioural and morphological change. *Behav. Ecol. Soc.* 52:394–399.
 ———, AND P. JOLY. 2000. Neoteny and progenesis as two heterochronic processes involved in paedomorphosis in *Triturus alpestris* (Amphibia: Caudata). *Proc. R. Soc. Lond. B Biol. Sci.* 267:1481–1485.
 ———, AND ———. 2001. Adaptive significance of facultative paedomorphosis in *Triturus alpestris* (Amphibia, Caudata): resource partitioning in an alpine lake. *Freshw. Biol.* 46:1387–1396.
 ———, P. PONCIN, AND J. C. RUWET. 2001a. Sexual compatibility between two heterochronic morphs in the Alpine newt, *Triturus alpestris*. *Anim. Behav.* 62:559–566.
 ———, ———, AND ———. 2001b. Alternative mating tactics in the alpine newt *Triturus alpestris alpestris*. *J. Herpetol.* 35:62–67.
 ———, F. HERVANT, R. SCHABETSBERGER, AND P. JOLY. 2002. Short- and long-term advantages of an alternative ontogenetic pathway. *Biol. J. Linn. Soc.* 77: 105–112.
 DUNBAR, R. I. M. 1982. Intraspecific variations in mating strategy, p. 385–431. In: *Perspectives in Ethology*. Vol. 5. P. P. G. Bateson and P. H. Klopfer (eds.). Plenum Press, New York.
 EASON, P. K., AND P. T. SHERMAN. 1995. Dominance status, mating strategies and copulation success in cooperatively polyandrous white-winged trumpeters, *Psophia leucoptera* (Aves: Psophiidae). *Anim. Behav.* 49:725–736.
 EMLEN, D. J. 1997. Alternative reproductive tactics and male dimorphism in the horned beetle *Ontophagus acuminatus* (Coleoptera: Scarabaeidae). *Behav. Ecol. Soc.* 41:335–341.
 GROSS, M. R. 1985. Disruptive selection for alternative life histories in salmon. *Nature* 313:47–48.
 ———. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol. Evol.* 11: 92–98.
 KRENZ, J. D., AND D. M. SEVER. 1995. Mating and oviposition in paedomorphic *Ambystoma talpoideum* precedes the arrival of terrestrial males. *Herpetologica* 51:387–393.
 MCWILLIAMS, S. R. 1992. Courtship behavior of the small-mouthed salamander (*Ambystoma texanum*). The effects of conspecific males on male mating tactics. *Behaviour* 121:1–19.
 MOCZEK, A., AND D. J. EMLEN. 2000. Male horn dimorphism in the scarab beetle, *Ontophagus taurus*: do alternative reproductive tactics favour alternative phenotypes? *Anim. Behav.* 59:459–466.
 RADWAN, J., M. CZYZ, M. KONIOR, AND M. KOŁODZI-EJCZYK. 2000. Aggressiveness in two male morphs of the bulb mite *Rhizoglyphus robini*. *Ethology* 106:53–62.
 RYAN, T. J., AND R. D. SEMLITSCH. 1998. Intraspecific heterochrony and life history evolution: decoupling somatic and sexual development in a facultatively paedomorphic salamander. *Proc. Natl. Acad. Sci. USA* 95:5643–5648.
 SCHLICHTING, C. D., AND M. PIGLIUCCI. 1998. Phenotypic evolution. A reaction norm perspective. Sinauer Assoc., Sunderland, MA.
 SEMLITSCH, R. D., AND H. M. WILBUR. 1989. Artificial selection for paedomorphosis in the salamander *Ambystoma talpoideum*. *Evolution* 43:105–112.
 SPARREBOOM, M. 1996. Sexual interference in the sword-tailed newt, *Cynops ensicauda popei* (Amphibia: Salamandridae). *Ethology* 102:672–685.
 TABORSKY, M. 1994. Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. *Adv. Study Behav.* 23:1–100.
 ———. 2001. The evolution of bourgeois, parasitic, and cooperative behaviors in fishes. *J. Hered.* 92: 100–110.
 VERRELL, P. A. 1984a. Sexual interference and sexual defense in the smooth newt, *Triturus vulgaris* (Amphibia, Urodela, Salamandridae). *Z. Tierpsychol.* 66:242–254.

- . 1984b. Responses to different densities of males in the smooth newt, *Triturus vulgaris*. "One at a time, please." J. Herpetol. 18:482–484.
- . 1988. Sexual Interference in the Alpine newt, *Triturus alpestris* (Amphibia, Urodela, Salamandridae). Zool. Sci. 5:159–164.
- . 1989. The sexual strategies of natural populations of newts and salamanders. Herpetologica 45:265–282.
- , AND J. D. KRENZ. 1998. Competition for mates in the mole salamander, *Ambystoma talpoideum*: tactics that may maximize male mating success. Behaviour 135:121–138.
- WHITEMAN, H. H. 1994. Evolution of facultative paedomorphosis in salamanders. Q. Rev. Biol. 69:205–221.
- . 1997. Maintenance of polymorphism promoted by sex-specific fitness payoffs. Evolution 51: 2039–2044.
- , J. J. GUTRICH, AND R. S. MOORMAN. 1999. Courtship behavior in a polymorphic population of the tiger salamander, *Ambystoma tigrinum nebulosum*. J. Herpetol. 33:348–351.

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