

Alternative Mating Tactics in the Alpine Newt *Triturus alpestris alpestris*

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ABSTRACT.—Sexual behaviors in dyadic encounters in the alpine newt, *Triturus alpestris alpestris*, is described to test whether male behavior is influenced by external cues, that is, female responsiveness. Depending on this factor, a male exhibits one of the two following tactics during the sperm transfer phase. The male either waits for a positive response from the female before initiating sperm transfer (“waiting” tactic), or creeps and deposits a spermatophore in front of a nonresponsive female (“luring” tactic). The sperm transfer success rates of these tactics are 31% and 6%, respectively, and encounter success rates, 64% and 8%, respectively. The success of the second tactic is linked to behaviors that lure the female, notably quiver and distal lure. The same individual can exhibit both tactics, and neither body size nor condition appears to influence the tactic a male exhibits. These tactics can be interpreted as the result of a conditional strategy, that is, a strategy that allows an individual to incorporate information about its ability to obtain fitness through alternative tactics and then express the tactic that maximizes its fitness. More particularly, these tactics are examples of a side-payment strategy, that is, a strategy that allows individuals to achieve small gains by capitalizing on passing opportunities.

Diversity in sexual tactics among same-sex individuals may be more the rule rather than the

exception in animals (Henson and Warner, 1997). Alternative mating tactics have been observed in different groups including fish (Gross, 1984), amphibians (Verrell, 1989; Halliday and Tejedo, 1995), birds (Hugie and Lank, 1997),

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mammals (Stockley et al., 1996), and insects (Convey, 1989). Most of these tactics can be categorized within a conditional strategy, that is, a strategy that allows an individual to incorporate information about his ability to obtain fitness through alternative tactics and express the tactic that maximizes fitness (Gross, 1996). For example, in some species small individuals sneak to gain access to mates (Gross, 1985), whereas in others, they fight (Convey, 1989). These tactics may be fixed, or facultative (Verrell, 1989; Gross, 1984; Henson and Warner, 1997). Switches between facultative alternatives may be determined by external factors such as mating opportunities (Verrell, 1983; Goldschmidt et al., 1992), light intensity (Reynolds et al., 1993), and predation risk (Magurran and Seghers, 1990).

In Salamandrids, one can observe what is called sexual interference, an obvious and well-documented alternative mating tactic exhibited by males. Here, rival males insert themselves between the courting male and the female (Verrell, 1984; Zuiderwijk and Sparreboom, 1986; Giacomini and Crusco, 1987; Verrell, 1988; Massey, 1988; Faria, 1995; Sparreboom, 1996).

Different male tactics also occur with respect to female receptivity. In the laboratory, in response to unresponsive females, male *Notophthalmus viridescens* clasp their partners (Verrell, 1982), whereas male *Triturus vulgaris* exhibit behavioral transitions in different ways during orientation and display phases (Halliday, 1975). Female behavior may also influence the transition between display and sperm transfer phases of courtship, particularly in *T. vulgaris* because the male requires a positive female feedback to initiate sperm transfer (Halliday, 1990). Rafinski and Pecio (1992) described "luring" behaviors toward females, such as the flamenco and distal lure, which involve movements of the tip of the male's tail. Their proposed function is to simulate prey movements in an attempt to attract the female's attention. But it is unknown how such luring behaviors affect the success of sperm transfer with an initially unresponsive female or whether such behavior depends on female receptivity.

The aim of our paper is to (1) determine how female behavior influences behavior patterns exhibited by the alpine newt (*T. a. alpestris*) male during the sperm transfer phase, (2) define alternative tactics adopted by males during spermatophore deposition stage, (3) determine whether these tactics can be categorized as conditional, (4) quantify success rates of alternative tactics, and (5) determine whether the tactic exhibited by a male depends on his body size and condition.

MATERIALS AND METHODS

Experimental Protocol.—Adult alpine newts *Triturus alpestris alpestris* ($N = 45$ males and 44 females), were collected from several ponds and during migration to these ponds in Liege Province, Belgium, at the start of the reproductive period (March and April). To facilitate identification of individuals, we toe clipped newts with a code similar to that of Twitty (1966). At least two days were allowed after toe clipping before behavior patterns were observed. Males and females were kept separately in seven aquaria (3 m² total water volume) and were fed 4–5 times a week with *Chironomus* larvae, *Tubifex*, and *Daphnia*. Newts were kept in captivity for a period of one week to one month and were then released after completion of the experiments.

In each experiment, a male and a female were placed together in an aquarium (45 × 30 × 25 cm) and sexual interactions were recorded with a Sony Hi8 camcorder at 25 frames/sec. Because temperature can influence newt courtship (Denoël, 1998), water temperature was maintained between 14 and 16 C. Viewing the tapes enabled us to time the succession of male behavior and female response patterns on a computer. We also recorded the success of both tactics we observed (described below). We analyzed 100 encounters between 45 males and 44 females. Mean use of newts ± SD was 2.2 ± 1.2 in males and 2.2 ± 1.5 in females. We studied in-depth behavior patterns of 29 males, recording only special events, such as success for the others (the last individuals studied).

Behavior Exhibited by Males and Females Alpine Newts.—In this study, we only considered two categories of female behavior: unresponsive (remaining stationary or moving away from the male) and responsive (moving toward the male or turning her head toward his tail or head). We noted the female behavior exhibited with respect to each male action. The sexual sequence begins with an orientation phase, during which the male either approaches the female or contacts her by chance, sniffs her and may follow her if she moves away. After that, the male may exhibit several courtship behaviors (display phase); then he may initiate spermatophore transfer (Halliday, 1977; Andreone, 1990; Denoël, 1996). Behaviors exhibited during this phase are described in Table 1.

Statistical Analyses.—We compared behavior patterns from each male when paired with either responsive or unresponsive females. Male tactics with responsive and unresponsive females are called "waiting" and "luring," respectively. To compare the frequencies of male behavior patterns in these two situations, we used a Wilcoxon Matched Pairs test. However,

TABLE 1. Description of male behaviors exhibited during sperm transfer phase in *Triturus a. alpestris*. Behavior patterns were previously described by ¹ Halliday (1977), ² Andreone (1990), and ³ Denoël (1996). ⁴ We followed Denoël's (1996) nomenclature for the caudal movements occurring during the braking posture. Sparreboom and Arntzen (1987), and Giacoma and Sparreboom (1987) called a movement of the tip of tail "distal lure," whereas Arntzen and Sparreboom (1989) and Rafinski and Pecio (1992) called it "wobble-tail-bent." Andreone (1990) described wobble-tail-bent as different from distal lure. We consider our distal lure as homologous to the movement described by Sparreboom and Arntzen (1987) and our wobble-tail-bent to that one described by Andreone (1990). But we coined the term "trembling tail" to characterize an undescribed behavior and the term "lateral-tail," which corresponds to the braking stage as described by Halliday (1977), to differentiate the caudal movement from body posture.

Behavior	Description
Creep ¹	The male turns away and walks ahead of the female
Quiver ¹	The creeping male quivers his tail in the same axis as his body
Tail-fold ¹	The male folds up his tail concertina-fashion
Deposition ¹	The male deposits a spermatophore while raising his tail above his back
Creep-on and brake ^{1,4}	After spermatophore deposition, the male creeps about one body length and pivots on one foreleg, turning 90° so as to stand perpendicular to the female's body. In this braking position, the male may exhibit four caudal movements (trembling-tail, distal lure, lateral-tail, and wobble-tail-bent)
Trembling-tail ³	A slow undulation travels through the tail from the base to the tip. The tail is held parallel but distant from the body, which is bent
Distal lure ^{2,4}	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
Lateral-tail ^{3,4}	The male holds his tail against his side, with the tip pointing up. The tail can be static, but a slight wave usually travels through the tail from base to tip
Wobble-tail-bent ^{2,4}	This behavior is similar to lateral tail, but only the tip of the tail moves between right and left
Pushback ¹	As the male stands in the braking posture, the female may push hard with her snout against his tail. In reaction, the male bends his body toward the female and flexes his tail away from his flank, so that the female is pushed back

before computing the statistical test, we divided the count of each behavior that a male exhibited by the total number of behaviors he exhibited to standardize our results (more acts were observed toward responsive females). The problem of repeated measurements (pseudoreplication) was eliminated by using mean values for each individual male during encounters with several females. We used a Mann-Whitney test to compare the size (snout-vent length, with a precision of 1 mm) and the condition (1000 body mass in g/SVL³ in mm, with a mass precision of 0.1 g) of newts creeping ahead of responsive and unresponsive females. To compare the success of both tactics, we used a chi-square test. For this, we took into account two levels of analysis: spermatophore transfer success and encounter success (that is, encounters where at least one spermatophore is picked up by the female). A chi-square test was also used to test whether distal lure influences female responsiveness (Siegel and Castellan, 1988). All tests were conducted with Statistica software (Statsoft, 1996).

RESULTS

Two alternative mating tactics were observed during encounters that resulted in spermatophore

deposition. Both tactics were identified in the first part of the sperm transfer phase. They corresponded to initiation of sperm transfer in front of responsive females (waiting tactic) and nonresponsive females (luring tactic). There was no significant difference in the frequency with which males crept and then tail-folded (the two first male behaviors of the sperm transfer phase) with responsive ($\bar{x} = 1.64$, range: 0–6) and unresponsive ($\bar{x} = 1.36$, range: 0–5) females (Wilcoxon matched pairs test; $Z = 0.867$, $P = 0.39$, $N = 34$). Following tail-fold, the female only showed her presence and responsiveness with a tail-touch. There was no significant difference in the frequency with which males deposited spermatophores ($\bar{x} = 1.15$, range 0–3.5) or resumed display behaviors ($\bar{x} = 1.12$, range 0–3.5) without this female stimulus (Wilcoxon matched pairs test; $Z = 0.189$, $P = 0.85$, $N = 26$).

Males exhibiting the waiting and the luring tactic did not significantly differ in body size ($\bar{x} = 36$ mm, range 29–41, $N = 13$ vs. $\bar{x} = 35$ mm, range 31–41, $N = 10$, respectively; Mann-Whitney $U = 60$, $P = 0.76$) nor in condition ($\bar{x} = 0.084$, range 0.055–0.124, $N = 10$; $\bar{x} = 0.079$, range 0.048–0.120, $N = 10$, respectively; Mann-Whitney $U = 60$, $P = 0.76$).

TABLE 2. Frequencies of male behaviors during courtship with either responsive or unresponsive females in *Triturus a. alpestris*. Frequencies were analyzed with a Wilcoxon matched pairs test ($N = 29$).

Male behavior	Responsive female mean (range)	Unresponsive female mean (range)	Z	P
Creep	1.81 (0-8)	2.49 (0-11)	2.822	0.004
Quiver	0	0.85 (0-5.5)	3.408	<0.001
Tail-fold	1.72 (0-8)	1.68 (0-5.5)	2.692	0.007
Deposition	1.35 (0-4)	0.76 (0-3)	0.270	0.787
Creep-on	1.31 (0-4)	0.76 (0-3)	0.054	0.957
Distal lure	0.19 (0-2)	1.09 (0-4.5)	2.971	0.002
Trembling-tail	1.02 (0-4)	0.38 (0-2)	1.442	0.149
Wiggle-tail-bent	0.83 (0-5)	0.66 (0-5)	0.544	0.586
Lateral-tail	3.57 (0-12)	0.17 (0-2)	3.980	<0.001
Pushback	1.95 (0-9.5)	0.04 (0-1)	3.408	<0.001

Nine courting males were used more than once. Among them, three did not react the same way in all encounters. They either deposited spermatophores in front of unresponsive females or waited for a positive response. Four other males only deposited sperm in front of unresponsive females, and two only in front of responsive females.

In each of the tactics, males displayed some particular behavioral patterns (Table 2). For example, males never exhibited quiver to a responsive female but did in rare cases exhibit distal lure (Table 2). Distal lure was significantly longer in duration in front of nonresponsive females than responsive ones ($\bar{x} = 85$ sec, range 5-248, $N = 17$ vs. 14 sec, range 4-39, $N = 10$; Mann-Whitney $U = 13$, $P < 0.001$). During distal lure, the female sometimes bit the male's tail, to which the male did not generally react. If the female pushed against the male's tail, he usually responded with a pushback, but this occurred only once, toward a nonresponsive female (Table 2). In one case, a spermatophore which was missed during the first approach of the female, was picked up after the pushback. Lateral-tail was shown significantly more frequently after the female responded (Table 2), but wiggle-tail-bent and trembling-tail were performed equally to unresponsive and responsive females (Table 2).

There was no significant difference in the frequency with which females responded positively ($N = 18$) or negatively ($N = 12$) to males exhibiting distal lure ($\chi^2 = 1.2$, $df = 1$, $P = 0.27$). There were significant differences in the rate at which females picked up sperm from males exhibiting the waiting tactic (30%, $N = 45$) and luring tactic (6%, $N = 33$; $\chi^2 = 7.33$, $df = 1$, $P < 0.01$). The insemination success rate measured per encounter when males exhibited the waiting tactic (64%, $N = 22$) was significantly different from that when males exhibited the

luring tactic (8%, $N = 25$; $\chi^2 = 16.13$, $df = 1$, $P < 0.001$).

DISCUSSION

We demonstrated that the exhibition and performance of several male behavior patterns during sperm transfer phase in *Triturus alpestris alpestris* depends heavily on the female's response. Even if the female is unresponsive during the display phase, the male may initiate sperm transfer by creeping. The male may then deposit a spermatophore without the female touching his tail. The male smooth newt, in contrast, usually does not initiate sperm transfer unless he receives a positive response from the female during the display phase, and he very often requires a female's tail-touch to deposit a spermatophore (Halliday, 1975, 1990). The degree of synchronization between male and female smooth newts is not seen in the alpine newt.

Male alpine newts depositing a spermatophore in front of a nonresponsive female may execute wormlike movements: "quiver" and distal lure. The quiver has been described as a behavior facilitating female orientation (Halliday, 1974). This may be one of its functions, but because it was only observed with unresponsive females, we think it is a luring behavior, at least in the alpine newt. In *T. vulgaris*, it also occurs with responsive females (Halliday, 1990). Therefore, a behavior shared between several species does not necessarily have the same function in all species. We cannot determine which function was ancestral because the phylogenetic position of *T. alpestris* is uncertain within the genus *Triturus* (Arano, 1988; Arntzen and Sparreboom, 1989). Males can also exhibit distal lure, which strongly attracts females. We interpret this movement as a lure because of the bites that the female inflicts on the male's tail. Luring is a common tactic in animals where it is used to catch prey and also to attract a sexual partner

(Wickler, 1968). In Salamandrids, several so-called luring behaviors have been described, such as flamenco and distal lure (Wambreuse and Bels, 1984; Pecio and Rafinski, 1985; Giacoma and Sparreboom, 1987; Arntzen and Sparreboom, 1989; Rafinski and Pecio, 1992), the former being associated with an unresponsive female and poor sperm transfer success in *T. boscai* (Rafinski and Pecio, 1992). Our results for the alpine newt indicate that the luring tactic (i.e., depositing a spermatophore in front of an unresponsive female and executing prey-mimicking movements) is also less successful in terms of sperm transfer than the waiting tactic (i.e., waiting for a female to respond). Nevertheless, the luring tactic attracts a nonresponsive female in 60% of cases. It appeared to be more successful than the sexual interference tactic exhibited by male alpine newts (7.5%; Verrell, 1988). Thus, male *T. alpestris* have two additional methods of obtaining mates: interfering with the courtship of a courting pair and sneakily inseminating the female without going through the time- and energy-consuming display phase himself or using prey-mimicking movements to lure an initially unresponsive female toward him and lead her over the spermatophore.

In contrast to male alpine newts, male *Notophthalmus viridescens* in the laboratory react to an unresponsive female by adopting an alternative courtship tactic (an amplexus) before sperm transfer. In the laboratory, such a tactic is more successful (71% success) than the alpine newt luring tactic, but it most likely costs the male more energy (Verrell, 1982). As amplexus does not exist in *T. alpestris*, this species has solved the same problem with a different solution.

In the wild, not all male newts exhibit the same degree of development of secondary sexual characters (e.g., crest height), so the chance of attracting a female may not be equal for all individuals (Hedlund, 1990; Gabor and Halliday, 1997). A body-size effect on the tactic exhibited by males has been shown in fish (Gross, 1985) and insects (Convey, 1989). Nevertheless, the flexibility of mating behavior and the lack of difference in snout-vent length and condition between the two groups of male alpine newts (i.e., creeping ahead of unresponsive and responsive females) suggest that males do not adopt an alternative tactic with respect to their body size or condition.

We suspect that individuals may exhibit both tactics with different frequencies depending on the availability of sperm and responsive females. Indeed, in other Salamandrid species, sperm is limited (Halliday, 1976; Verrell, 1987) and the operational sex ratio (OSR) influences sexual interference (Waights, 1996), amplexus

(Verrell, 1983), and mate choice (Gabor and Halliday, 1997). Long-term and highly manipulative studies are needed to confirm the modification of tactics with OSR and female receptivity. Moreover, experiments manipulating food supply given to females would make it possible to determine whether hunger influences female response to luring movements.

In conclusion, because the same alpine newt individual can switch between alternatives, these tactics can be considered as the result of behavioral plasticity (Henson and Warner, 1997). Because switching appears to depend on circumstances, the tactics may result from a conditional strategy (Gross, 1996) and more particularly a side-payment strategy (Dunbar, 1982) that allows male alpine newts to get small gains by capitalizing on passing opportunities.

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