Sexual Interference in the Sword-tailed Newt, *Cynops ensicauda popei* (Amphibia: Salamandridae)

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Abstract

This paper describes competitive interaction between males of the salamandrid *Cynops ensicauda popei*. The sexual behaviour of the male is influenced by the presence of a second, rival, male. Competition for access to the female and other male interactions continuously interrupt ongoing courtships. Spermatophore pick-up success is lower than in encounters involving single pairs. During triad encounters, fewer spermatophores were deposited than in dyad encounters, due to interference during the creep stage of courtship.

Two basic forms of male sexual interference were distinguished: 'lure away' during the creeping stage, from a position that is different from the direction of creep; and 'female mimicry', during which the male presses his snout alternately against the courting male's tail and the female's snout. In both forms, a rival male may shove one of the courting individuals away.

The repertoire of sexual behaviour patterns of *Cynops ensicauda popei* appears to be less complex and varied than that of most *Triturus* species. The courtship of *Cynops* places less emphasis on display behaviour with tail and body, and a stronger emphasis on the creeping stage, where the male carefully leads the responsive female over a series of spermatophores, but during which rival males may interfere in a variety of ways.

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Introduction

Intermale competition is a widespread phenomenon in animals and a clear prediction of sexual selection theory, especially where females are a limiting resource for males (EMLEN & ORING 1977). Competition over mates can take several forms and favour a wide range of attributes. Mechanisms of such competition may consist of scrambles, endurance rivalry, contests, mate choice and sperm competition (ANDERSSON 1994). When individuals of the same sex can increase their fitness by competing for more or higher quality mates, intrasexual selection occurs (DARWIN 1871; ANDERSSON 1994). A number of species deal with the problem of direct competition by adopting more than one method of obtaining mates. Among anuran amphibians, for

instance, some species, known as explosive breeders, show at least three forms of alternative mating behaviour. A number of males attract females to a spawn-site by assembling there and calling in choruses. Some of the larger males may attempt to dislodge paired males from females which have come to the pond to spawn. Small, satellite, males may search for females at the edges of a spawn-site, where they attempt to sneak an arriving female without incurring the full cost of attracting and stimulating a mate (ARAK 1983). In many animals, one of several strategies may be chosen depending on available space, time of the breeding season or 'social context'. The fact that an animal has a number of choices available to it in terms of reproductive strategy raises the possibility that one strategy may be better than the others, or alternatively, that sets of strategies may be equally advantageous (DUNBAR 1983).

Salamanders show a variety of often very complex patterns of mating behaviour. There is a high degree of stereotypy in the later stages of courtship, notably in spermatophore transfer patterns. But many species are able to modify their courtship display according to circumstances (ARNOLD 1976; HALLIDAY 1976).

Competition between male salamanders for mates is common. Such competitive interactions may include spermatophore covering, wrestling and attempted displacement during amplectic courtship, overt fighting, spatial exclusion or territoriality and sexual interference through female mimicry (VERRELL 1989). Competition in which males interfere with one another's attempts to court and inseminate females is known as sexual interference (ARNOLD 1976). The indirect mode of sperm transfer found in the majority of salamanders is not foolproof and may make these animals especially vulnerable to this kind of reproductive competition. The nature and effect of sexual interference varies across species.

Competition by sexual interference has been studied under experimental and natural conditions in various salamandrid species (HALLIDAY 1974, 1976; VERRELL 1984a, b, 1988; ZUIDERWIJK & SPARREBOOM 1986; GIACOMA & CRUSCO 1987; MASSEY 1988; VERRELL & McCABE 1988; HEDLUND 1990; ZUIDERWIJK 1990; PAVIGNANO et al. 1993; FARIA 1995; HALLIDAY & TEJEDO 1995). In a breeding pond, usually a number of individuals are assembled at the same time, interacting and influencing one another's behaviour in different ways. Male interference in ongoing courtship encounters is one of the most commonly observed interactions. Experiments involving a female and several males have shown that newts may modify such behaviour patterns as are shown during single-pair encounters or may show behaviour not exhibited during single-pair encounters (HALLIDAY 1976; VERRELL 1984b).

Aspects of the sexual behaviour of *Cynops ensicauda* have been studied under controlled conditions (SPARREBOOM 1994). The behaviour of *Cynops pyrrhogaster*, which is closely related to *C. ensicauda* (HAYASHI & MATSUI 1988), has also been studied in the laboratory (TSUTSUI 1931; KAWAMURA & SAWADA 1959; SAWADA 1963; ARNOLD 1972). Nonetheless, data on sexual behaviour and reproductive strategies of *Cynops* are scarce. Newts of the two Japanese species of *Cynops* are common locally in Japan, and may occur in high densities in ponds during the breeding season (KREFFT 1905; SPARREBOOM & OTA 1995). Where many individuals are clustered at a breeding site, some form of competition is likely to occur.

The aim of this study was to investigate experimentally the forms reproductive competition in the sword-tailed newt, *Cynops ensicauda popei*, may take and to make comparisons with reproductive competition in *Cynops* and in other salamandrids.

Materials and Methods

Newts were purchased and identified as *Cynops ensicauda popei* from the Okinawa island group (INGER 1947). Five males and five females were kept separately in aquaria with a water temperature ranging from 18 °C to 25 °C. Food consisted of earthworms, chironomid larvae, maggots, *Daphnia*, *Cyclops* and *Mysis*. A photoperiod of 12 h L: 12 h D was maintained. Experiments were conducted in an aquarium measuring 60 × 30 × 30 cm, floored with flat stones and no leafy aquatic vegetation. Because the number of newts available at the time was limited, the animals used were the same as those used previously in courtship encounters involving single pairs (SPARREBOOM 1994). Only four out of five males were in breeding condition. Control experiments, including dyadic and triadic encounters, were conducted with 26 animals, caught fresh on various islands of the Ryukyu Archipelago, to check that behaviour observed in the captive animals was typical. Quantitative results for these control experiments are not reported here.

Two males of similar size were placed in the experimental aquarium and allowed a day to settle. An unmated female was then placed with them and interactions between the three individuals were recorded on videotape with a Hitachi VM 500 E VHS movie camera–recorder. Twenty such triadic trials, involving two males and one female, were conducted, each lasting 30 min. During each trial, forms of interaction were observed. These triads consisted of different combinations of individuals drawn from the pool of four males and five females.

In the comparison of triad and dyad encounters, the number of spermatophores deposited during triads is compared with those deposited during dyad encounters described in an earlier paper (SPARREBOOM 1994). A subset of three males was used in both experiments. To avoid possible pseudoreplication, the comparison was made with a two-way ANOVA, controlling for the effect of the twice-used males.

The behaviour patterns recorded during the observations were cast into a flow diagram, showing the frequencies at which transitions between behaviour patterns occurred.

The illustrations are based upon photographs, slides and videotapes made during the experiments, but are not exact copies of the photographic material. In this sense, the illustrations, however close to reality, reflect an interpretation of the observed behaviour patterns.

Behaviour Patterns Observed during a Dyad Encounter

The behaviour patterns typically observed during a dyad encounter are referred to here in summary form, as a more detailed description is given in an earlier paper (SPARREBOOM 1994).

The following actions are performed by the male.
1. *Sniff.* The male contacts the female by sniffing her lateral body or cloaca.
2. *Pursuit.* The male rapidly follows the female and attempts to move in front of her.
3. *Fan.* The male bends his tail to the side facing the female and makes rapid vibrating movements with the tail-tip, creating a current toward the female's snout. Fanning rapidly alternates with pursuit. In the analysis below, sniff, pursuit and fan are combined as 'courtship.'
4. *Creep.* This behaviour represents a distinct phase in the courtship sequence. The male turns away from the female and creeps ahead of her at a slow pace. In response to tail-nudging by the female, the male may deposit a spermatophore.
5. *Spermatophore deposition.* A spermatophore is deposited during creep behaviour. The male is stationary with the vent resting on the substrate and the body slightly arched. The cloaca is opened widely and a spermatophore is extruded. If the male keeps on creeping, and the female follows and repeats the tail-nudging, a male may deposit several spermatophores in succession, without turning back to the female.
6. *Bite.* The male gently bites another individual on the side of its head, body or tail.

The female performs the following actions.
1. *Move away.* The female swims or walks away from a courting male.
2. *Stand still.* The female remains motionless upon a male's approach.

3. *Turn towards male*. The female reacts to the male's courtship by turning her head towards him and making a few steps in his direction.
4. *Follow*. The female follows the male, which has turned round and creeps ahead of her. She closely follows his undulating tail and touches his tail with her snout.
5. *Bite*. While following the creeping male, the female gently bites or 'nibbles' at his tail-base or cloacal region.
6. *Sperm pick-up*. The female moves over the place where the spermatophore has been deposited and picks up the sperm-filled cap in her cloaca.

Results

Twenty staged encounters, each of 30 min duration and involving two males and one female, were observed completely. The behaviour patterns shown during these triadic encounters are similar to those seen in dyadic encounters (nos 1 to 6 above). This holds true for the actions performed by the males, as well as for all female behaviour patterns. The behaviour observed during the control trials, both in dyad and triad encounters, was not markedly different from that shown by the captive animals used for the experiments. The following additional behaviour patterns were shown by the males during triad encounters.

Scramble. Two males follow the female simultaneously and attempt to court her. They swim on either side or on the same side of the female, both trying to move to the front and fan to her. In the course of this pursuit, one male may push the other away by pressing his snout against the courting male's body and moving forward. By so doing, he shoves the courting male away from the female. A male may also push the female away in the same manner. By moving between the female and the first courting male, he hides him from her view and assumes a prime position from which to court her. Males alternate in doing this and compete for the best fanning position in front of the female. The female normally flees from such situations. A chase ensues, with both males swimming relentlessly after her while making agitated movements with their legs and tails.

Male interaction. Male interaction alternates with scramble and often occurs after the female has moved away from the two males. Several different behaviour patterns fall under this category: the males move quickly around, or over and under one another. They turn round in circles, sniffing and pushing each other. Occasionally they may fan briefly. These are rapid interactions consisting of irregular and agitated movements, but mostly without biting or other signs of overt aggression.

Interference. Although, in a way, both scramble and male interaction can be considered acts of interference by competing males, the term sexual interference is here used in a more restricted sense (ARNOLD 1976, 1977), namely as the behaviour by which a male attempts to disrupt the ongoing courtship sequence of a courting male by intervening during the creep stage. In 14 of the 20 triadic encounters, some form of sexual interference was seen. Two different forms of this behaviour can be distinguished in *Cynops ensicauda*: (a) lure away; and (b) female mimicry.

In *lure away*, the interfering male approaches the couple at the creep stage from a position that is different from the direction of creep. He nudges the lateral body or cloaca of the female and pushes her with his snout (Fig. 1a). He may also crawl under her and lift her up with his body and snout (Fig. 1b). This action may distract the female and interrupt her progress toward the creeping male. While the female is diverted in this manner, the first creeping male will stand still for a while and wait in vain for further tail-
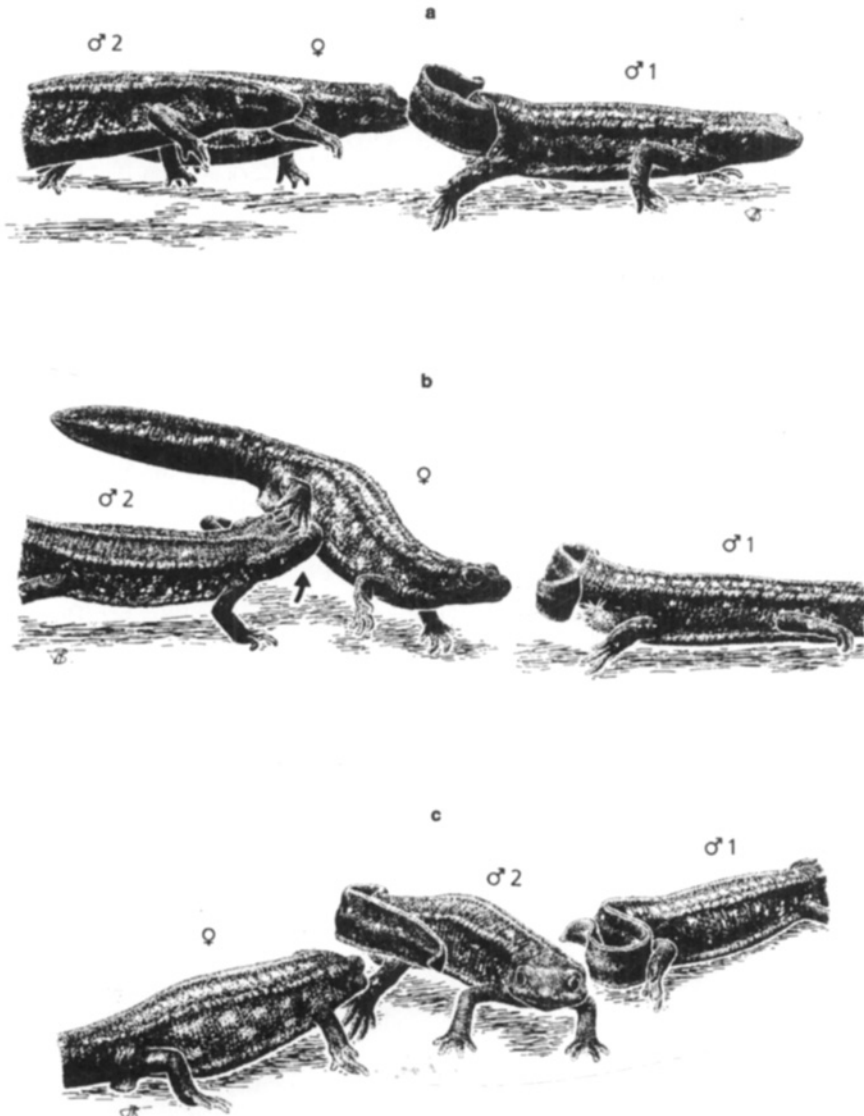
Fig. 1:   Interference of the 'lure away' type. (a) While the courting male (1) is creeping and being followed by the female, the interfering male (2) approaches alongside the female. (b) Interfering male (2) forcefully nudges the belly and cloaca of the female while she is following the courting male (1) in creep. (c) The result of a successful 'lure away' interference: the courting male (1) remains standing in creep position while the interfering male (2), in the middle, now fans to the female

touches. In the meantime the interfering male courts the diverted female (Fig. 1c) and will creep himself if she is still responsive.

In *female mimicry*, the interfering male rapidly approaches a courting pair during the creep stage, moving between the two animals (Fig. 2a). He thrusts his snout between

the tail of the creeping male and the snout of the female. He rapidly swings his head on a horizontal level and, by doing this, presses his snout alternately against the female's head and the tail of the male (Fig. 2b). The interfering male then turns to the creeping male and may give several tail-touches, inducing him to deposit a spermatophore ('female mimicry', sensu ARNOLD 1976). He quickly turns back to the female, courts her if she is still there and turns to creep (Fig. 2c). Often the female moves away at this stage (Fig. 2d). If the female is still 'on course', the interfering male turns to creep and deposits a spermatophore himself. He may do this in a position away from the first male, but may also do so while positioned alongside or right behind him (Fig. 2e). The courting male, which was led to deposit a spermatophore through deceit, slowly raises his tail slightly, extrudes the spermatophore, creeps forward a few cm and waits until he receives a further tail-touch. This reaction is an entirely stereotyped behaviour sequence. While the courting male is 'manoeuvred away' in this creep position and facing away from the female, the interferer has the opportunity to take over the courtship.

Normally one or both males notice the female within minutes of the start of the experiment. The female reacts to the initial approaches with receptive behaviour, including standing still, turning towards the male and following him during creep. However, shortly after the first occurrences of interference the female became unresponsive. The female regained interest after some time, if a male succeeded in courting her without disturbance. On the two occasions where spermatophore pick-up was achieved, this took place at the beginning of the encounter, when one of the two males was incidentally out of sight of the place where the courtship sequence occurred.

If interference occurs, the female may react in three different ways: she keeps orientated to the first creeping male in spite of the interfering rival (as in Fig. 1a,b); or she changes over to the rival male (Fig. 2c); or she moves away from both males and is no longer responsive for some time (Fig. 2d). The predominant behaviour of the female consisted of moving away from competitive situations.

From all recorded instances of interference behaviour (n = 75), 39 % were stages of lure away and 61 % of the category described as female mimicry. Of the episodes of female mimicry, 48 % led to the fruitless deposition of a spermatophore by the first courting male. Occurrences of both types of interference were mostly clustered: if a female stayed responsive for a couple of minutes, the males might interfere with one another's courtship in turn up to six times during a single series of successive creeps. Both types of interference were exhibited by the same male, and all courting males were capable of interference.

Biting

During the 20 triadic encounters, biting was observed on 36 occasions. The action consisted of pushing or shoving another animal away with open mouth, rather than more forceful snapping. Males were seen biting other males on five occasions, three times during scramble or male interaction and twice during interference. Males bit females on 12 occasions, once during creep and spermatophore transfer and 11 times during scramble or interference. This biting resulted in a temporary displacement of the
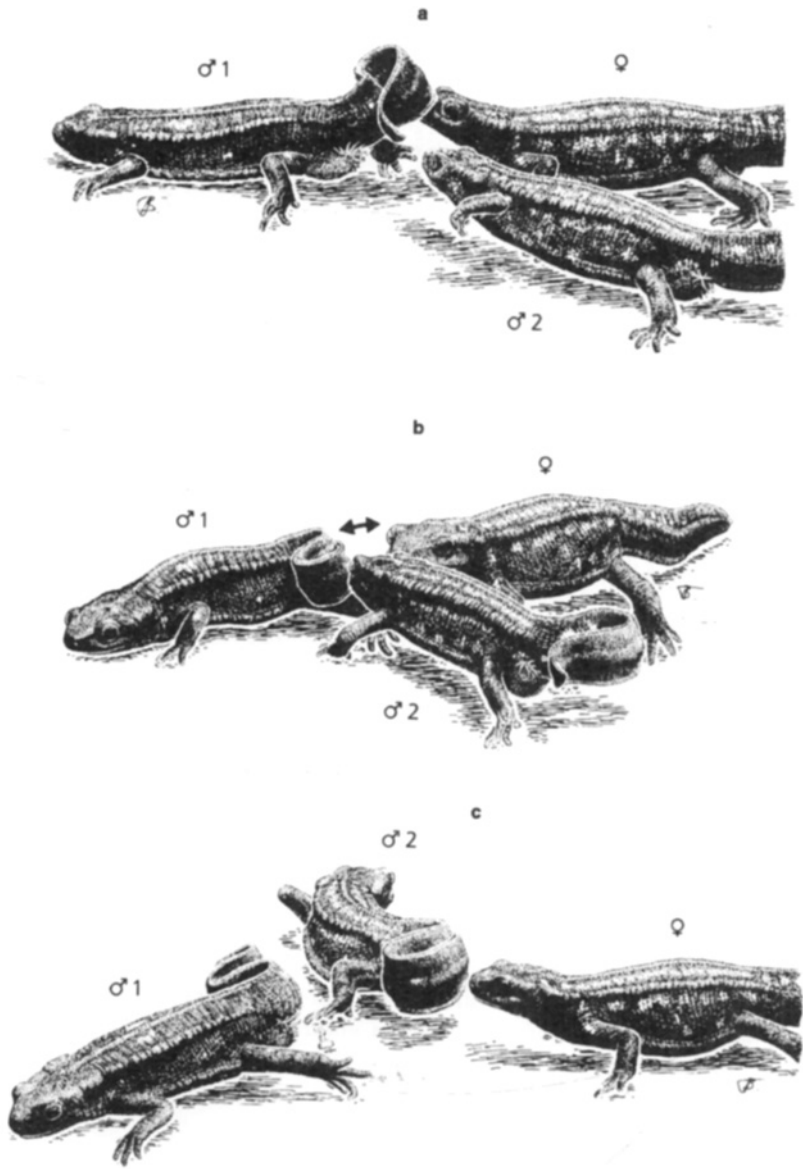
Fig 2: Continues opposite.

other animal over a short distance. The biting was normally gentle and did not appear to intimidate the bitten animal. It could, however, actually displace an individual: occasionally the biting male would keep the bitten female or male in his jaws and walk away some 10 cm, then release him or her and engage in courtship behaviour.
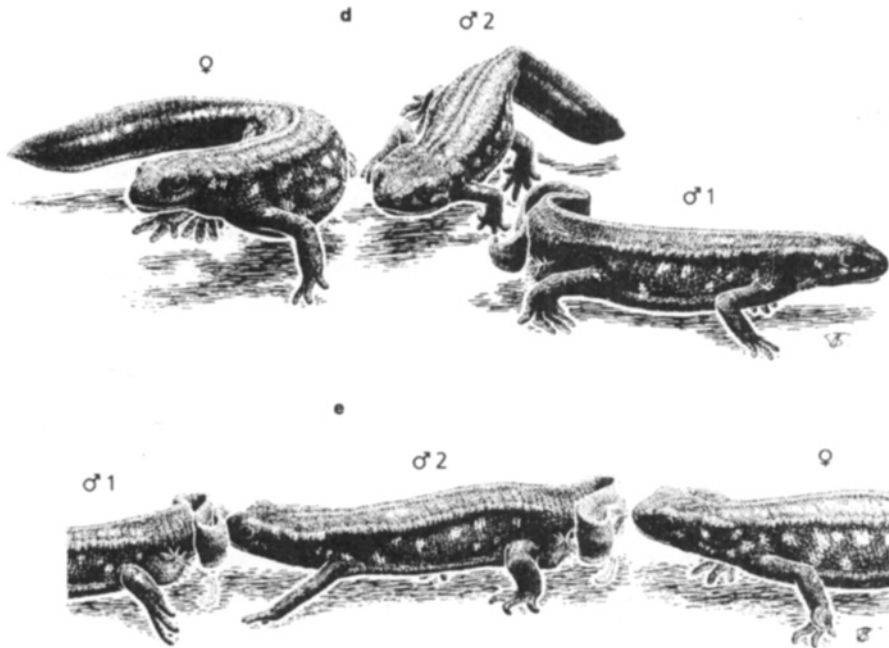
Fig. 2: Interference of the 'female mimicry' type. (a) While the female closely follows the creeping male (1), an interfering male (2) interrupts the ongoing courtship. (b) Seconds after the situation depicted in (a): the interfering male (2) moves between the tail of the creeping male (1) and the snout of the female. He rapidly swings his head on a horizontal level, touching the male's tail and shoving the female away. (c) The result of 'female mimicry' interference: courting male (1) has been led to deposit a spermatophore by the tail-touches of interfering male (2) and the interfering male (2) turns to creep behaviour himself, while the female remains responsive. (d) The female loses interest and moves away after interruption by interfering male (2) in an ongoing courtship. (e) After inducing spermatophore deposition in the creeping male (1) by 'female mimicry' interference, the interfering male (2) deposits a spermatophore himself. In this instance he is still standing with his snout against the first male's tail

Females were seen biting or 'nibbling' at the male's cloaca during creep 19 times. This biting did not seem to trigger a specific response from the male. Some individuals showed more inclination to bite than others.

Comparison of Triad with Dyad Encounters

Comparison with dyad encounters suggests that spermatophore pick-up is negatively influenced by the presence of more than one male. Of 140 spermatophores deposited by males during dyad encounters (in observations made over 3 yr, SPARREBOOM 1994), 43 were picked up by females (23.5 %), whereas of 89 spermatophores deposited by two males during triad encounters, only three were picked up successfully (3.4 %). This difference is statistically significant ($\chi^2 = 23.67$; df = 1; p < 0.0001).

The presence of a constantly interfering rival male influenced the duration of the creeping stage considerably. In dyads, continuous creeping behaviour could last from 4 to 7 min (SPARREBOOM 1994). In triads, the longest uninterrupted creeping episode lasted 2.5 min. The three spermatophores that were picked up during the triads were deposited during uninterrupted creeping episodes of 2–2.5 min.

The number of spermatophores deposited by a male during dyad encounters was higher than in triads; comparison of the number of spermatophores deposited by three males exposed to both types of encounter shows that the difference is statistically significant (two-way ANOVA: F $(1, 60) = 35.93$; $p < 0.0001$). The average number of spermatophores deposited by these three males per sequence was 3.8 in dyadic ($n = 21$) and 1.6 in triadic encounters ($n = 45$).

Temporal Relations

In dyad encounters, the transitions between behaviour patterns are largely predictable (SPARREBOOM 1994). In triadic encounters, the interaction is more complex and many encounters do not end in spermatophore deposition and pick-up. To illustrate the events, all transitions between the observed behaviour patterns were recorded and cast into a flow diagram (Fig. 3). Fig. 3(a) indicates the frequency of transitions in the early stages of a courtship sequence. Fig. 3(b) shows the events in the final part of the courtship sequence. The diagram does not distinguish between 'courter' and 'rival' or between the different types of interference.

Discussion

Male *Cynops ensicauda* employ a number of different behaviour patterns to interfere in ongoing courtship sequences. Scramble and male interaction cause a disturbance of the regular courtship sequence in a more general way. Sexual interference sensu stricto (ARNOLD 1976) is a more sophisticated strategy to increase an individual male's reproductive success by reducing the competitor's success. The two forms of interference differ in their immediate effect: lure away leads to a disturbance of the responsive female, but does not dispose immediately of the first courting male, which may attempt to resume courtship a few seconds later. During female mimicry, the interferer disposes of the first courting male in a more complex manner: he touches the courter's tail, mimicking a responsive female. As a result, the first male may be duped into an unsuccessful spermatophore deposition and become locked into the stereotyped behaviour pattern that follows.

Males appear to have an abundant supply of spermatophores, at least in the short term. Up to 11 can be deposited per evening (SPARREBOOM 1994). The loss of one or two may therefore not significantly depress a male's mating success. My data suggest that loss of time or opportunity to mate, for instance when a deceived male is engaged in the stereotyped spermatophore-deposition behaviour, or when a female temporarily loses interest due to intermale competition, may be more disadvantageous.

As no spermatophores were picked up immediately after interference, it is not possible to say which mode of interference is more effective. Also, it was not possible to
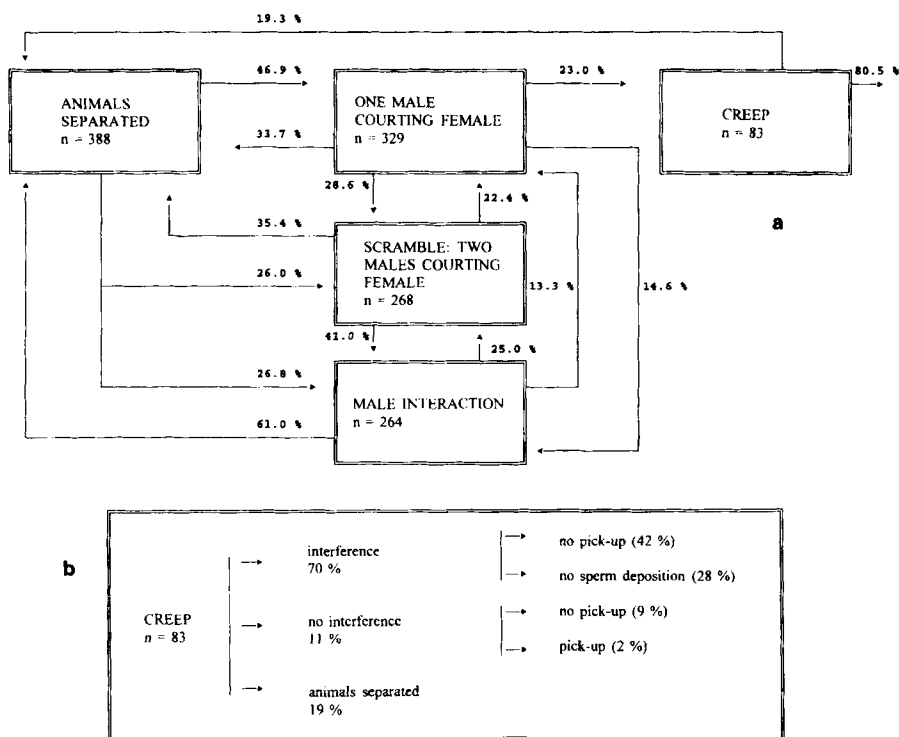
Fig. 3: (a) Frequency of transitions of behaviour patterns of *Cynops ensicauda popei* during triadic encounters. Percentages are of the total number of times that a transition occurred from one particular behaviour pattern to another. Transitions occurring at less than 2 % frequency are omitted. (b) Frequency of transitions of behaviour patterns during the spermatophore-deposition phase of a courtship sequence. Percentages are of the total number of times that a transition occurred from creep to another behaviour pattern

establish what factors determined the chosen mode of interference. The choice may be influenced by the stage of the courtship sequence that has been reached by the courting pair when the rival male attempts to interfere. Rival males in a 'waiting' position near a courting couple, as observed in *Triturus boscai* (FARIA 1995), have not been observed in *Cynops ensicauda*.

In the light of earlier work on other species, one might expect that males would modify certain behaviour patterns to defend their courtship against the attempts at interference (VERRELL 1983, 1984a). In the presence of competitors, species such as *Ambystoma texanum* were found to increase the frequency of spermatophore deposition within a sequence or produce more spermatophores in total (MCWILLIAMS 1992). In *A. laterale*, males were found to be inhibited by the presence of rival males, producing fewer spermatophores on average than solitary males (UZZELL 1969). By such a strategy, a male may save spermatophores for mating opportunities with less interference and

more chance of successful sperm transfer. The latter seems to be the tactic adopted by *A. talpoideum* (VERRELL & KRENZ unpubl. data). In *C. ensicauda*, there was no indication that spermatophores were deposited with shorter or longer intervals during triad encounters than during dyad encounters. Longer and continuous episodes of creep behaviour resulted in the deposition of more spermatophores (SPARREBOOM 1994). Fewer spermatophores were produced if creep sequences were interrupted by an interfering male.

Biting behaviour may be explained as an aggressive way of chasing another animal away. However, a male bites not only a rival male, but also the female. This kind of biting may therefore serve to monopolize the courtship by manoeuvring the female into a position where the courtship can be performed undisturbed, or by displacing the competing male for some time. Prolonged biting of the female after deposition of the first spermatophore, as has been observed for instance in *Cynops orientalis* (pers. observ.) and *Triturus marmoratus* (SPARREBOOM & TEUNIS 1990), was not seen in *C. ensicauda*, but further study of the timing of biting behaviour may reveal that, in *C. ensicauda* too, this behaviour is shown more frequently after the deposition of a spermatophore and may have different functions at different stages of the courtship. The biting did not take on a more aggressive form such as is occasionally seen during feeding, or such as is seen in *Triturus vittatus*, where biting forms part of a kind of territorial behaviour (RAXWORTHY 1989).

After an initial period of responsiveness to the courtship of a courting male, the female would mostly swim away when two males scrambled for access or when sexual interference occurred. This observation parallels observations on *T. vulgaris*, in which females prefer one partner at a time (VERRELL 1984b; compare also *T. alpestris*, VERRELL 1988).

If male courtship behaviour has evolved, at least in part, as a response to the selective pressure of sexual interference and sexual defence mechanisms (MASSEY 1988; VERRELL 1989; HALLIDAY 1990), one should expect to find cues to the origins of certain courtship behaviour patterns in the varied repertoire of interference behaviours. In *Triturus cristatus* and *T. marmoratus*, for instance, intermale display actions were found to take place more frequently than male–female display, and it has been suggested that courtship behaviour in these species was modelled on the common site defence display among males in a type of lek aggregation (ZUIDERWIJK & SPARREBOOM 1986; HEDLUND 1990; HEDLUND & ROBERTSON 1990). The particular type of interference described under the category of lure away, when a male approaches a pair in creep from behind and carries the female away from the first courting male (Fig. 1b), may well be regarded as a precursor to a courtship behaviour such as the ventral clasping mode of courtship that is found in some other salamandrids (*Salamandra, Chioglossa, Pleurodeles, Mertensiella, Tylototriton*). The question of whether clasping behaviour in salamandrids is derived remains for future discussion in a phylogenetic context.

A conspicuous difference between the behaviour on the one hand of the salamandrid genera *Cynops* and *Paramesotriton* (SPARREBOOM 1983, 1984, 1991), and on the other hand, *Triturus* and *Neurergus* (ARNOLD 1972; ARNTZEN & SPARREBOOM 1989; SCHMIDTLER 1994; STEINFARTZ pers. comm.), is that in the former two genera, the males remain in the same position in front of the female after each spermatophore

deposition. In the latter two genera, the male swings through an arc of 90° after each spermatophore deposition (a behaviour termed brake by HALLIDAY 1974). Several explanations have been suggested for this behaviour, such as a way by which males increase the likelihood that a particular spermatophore will be picked up by a female (HALLIDAY 1977, 1990). *Triturus* and *Neurergus* seem to invest more specific and stereotypic behaviour in each individual spermatophore than *Cynops* and *Paramesotriton*. The latter two genera seem to exhibit another strategy for increasing the likelihood of pick-up, namely an extended phase of careful creeping and spermatophore deposition and of frequent tail-nudging by the female (SPARREBOOM 1994), signalling to the male that the female is still there and is responsive.

The display behaviour patterns of *Cynops* appear to be less diversified than those in *Triturus*. The *Triturus* species the behaviour of which is generally considered to be the most 'primitive' (in terms of absence of apomorphic traits) is *Triturus alpestris* (HALLIDAY 1977; ARNTZEN & SPARREBOOM 1989). Indeed, the courtship repertoire of *Cynops ensicauda* is more similar to that of *T. alpestris* than to that of any other species of *Triturus*. *C. ensicauda* appears to possess a wider array of behaviour patterns related to sexual interference than has been observed in other species thus far (including *T. alpestris* VERRELL 1988).

The observations reported here suggest that the mating strategy of *Cynops ensicauda* differs from that of *Triturus* species: the courtship behaviour of *C. ensicauda* consists of a brief and simple display act which consists of short fanning bouts, inserted at intervals during the pursuit of the female. The long creeping phase — which calls to mind the tail-straddling walk of plethodontids and the tail-nudging walk in ambystomatids (ARNOLD 1972, 1976, 1977) — takes up the major part of the sexual interaction. *Cynops ensicauda* has a relatively large number of spermatophores available and invests less in each single spermatophore than *Triturus* in terms of display behaviour executed with the tail. Instead of an elaborate display, which may enable the male to persuade the female to mate with him or to keep her away from rival males, this species shows a wide variety of interference behaviour patterns, which may effectively depress the mating success of competing males. The observations reported here suggest that further comparative study of interference behaviour in *Cynops*, *Triturus* and other genera may contribute to our understanding of the evolution of different reproductive strategies in salamanders.

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