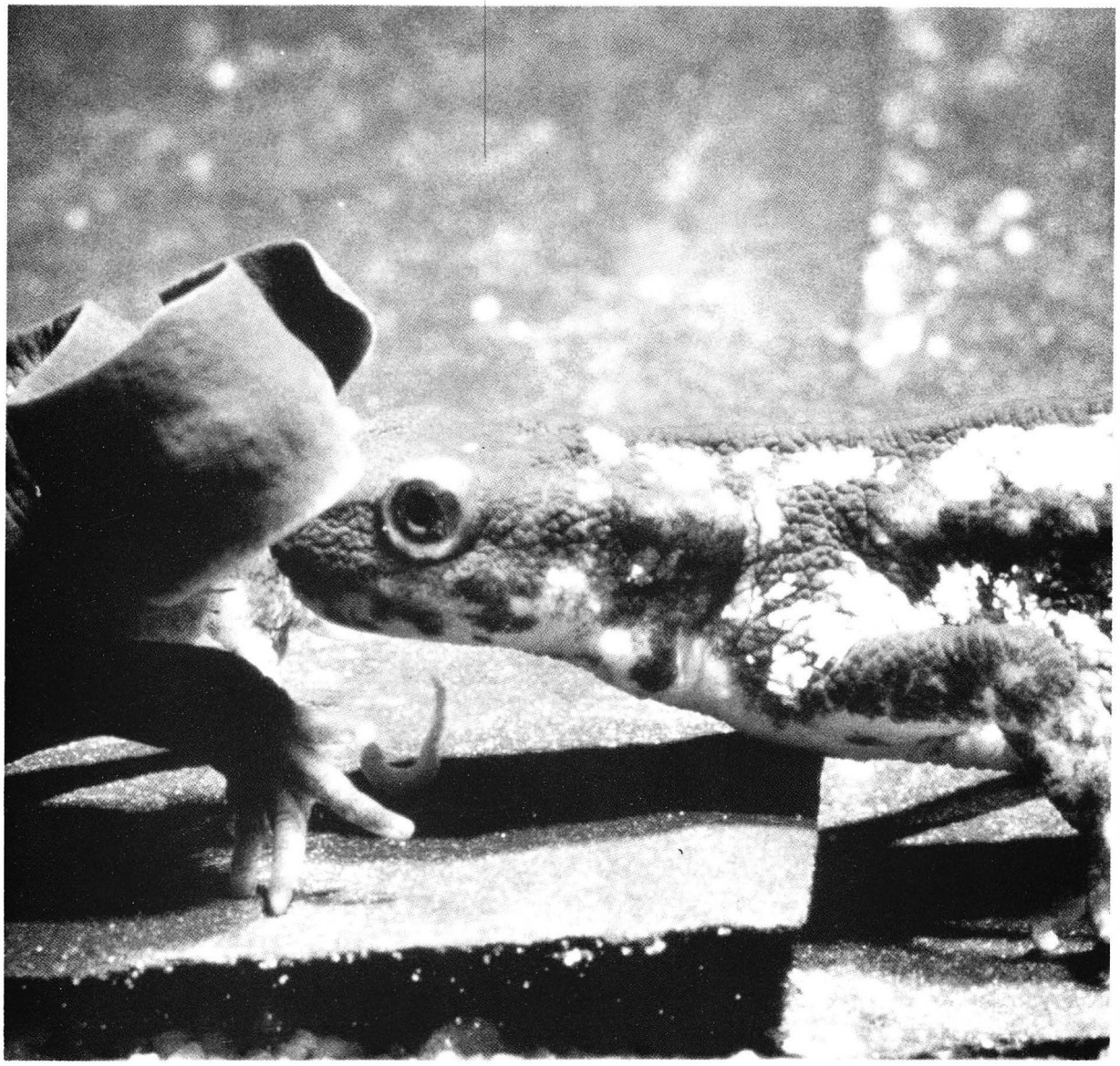
Volume 5, Number 4

October 1995
ISSN 0268-0130

THE HERPETOLOGICAL JOURNAL



Published by
THE BRITISH HERPETOLOGICAL SOCIETY

Indexed in
Current Contents

HERPETOLOGICAL JOURNAL, Vol. 5, pp. 310-315 (1995)

NOTES ON THE LIFE-HISTORY AND REPRODUCTIVE BEHAVIOUR OF *CYNOPS ENSICAUDA POPEI* (AMPHIBIA: SALAMANDRIDAE)

MAX SPARREBOOM[1] AND HIDETOSHI OTA[2]

[1]*Van Neckstraat 99, 2597 SC Den Haag, The Netherlands*

[2]*Tropical Biosphere Research Centre and Dept of Biology, University of the Ryukyus, 1 Senbaru, Nishihara-cho, Okinawa, 903-01 Japan*

Field observations of the sword-tailed newt, *Cynops ensicauda popei* (Inger 1947), have yielded preliminary data on life-history traits and reproductive behaviour. In April 1993 the animals were abundant in the breeding ponds and on land. Compared to European species of *Triturus*, this species has an extended breeding season. Few of the observed courtship encounters progressed to the spermatophore transfer phase. Competitive encounters were frequent. The sexual behaviour of *Cynops ensicauda popei* is characterised by a short duration of display behaviour and a small repertoire of courtship behaviour patterns. The reproductive behaviour is compared to that of related salamandrids.

INTRODUCTION

Although Japanese newts of the genus *Cynops* are common within their range, their life history has not been the subject of detailed study. Aspects of the reproductive biology of the Japanese fire-bellied newt, *Cynops pyrrhogaster*, have been studied by Tsutsui (1931), Kawamura & Sawada (1959), Sawada (1963*a,b*) and Arnold (1972). Much less is known of *Cynops ensicauda*, a closely related species (Hayashi & Matsui, 1988), consisting of two subspecies *C. e. ensicauda* and *C. e. popei*, both occurring at tropical latitudes on the southern islands of Japan (Stejneger, 1907; Inger, 1947; Thorn, 1968).

Observations of the sexual behaviour under experimental conditions suggest that this species may have a long breeding period, during which the animals can mate several times. In encounters with several males present there may be strong competition, with males scrambling for females and, in the process, reducing one another's mating success by interrupting on-going courtship sequences in various different manners (Sparreboom, 1994). These observations suggest that the patterns of courtship behaviour and reproductive strategy of this species may differ from the better-known species of the sister genus *Triturus*.

To obtain complementary data on the reproductive behaviour of the species and to gather data on its life-history, the newts were studied in their natural habitat.

METHODS

The present observations were made on *C. e. popei* on Zamami-jima, from 3 to 14 April 1993. This island is located some 40 km W of Okinawa-jima. From among the many water bodies where the newts occurred, six different habitats were selected for regular inspection: (1) a 90 m stretch of roadside ditch 1 m wide with concrete walls, functioning as a drain and containing water of 5-10 cm depth, covered with debris and algae; (2) a hole in a marshy meadow, measuring 200 x 100 cm and some 40 cm deep, dug out mechanically and serving as a cattle drinking place; (3) a puddle in the same meadow, measuring 400 x 250 cm and 20 cm deep, overgrown with reeds, grasses and algae; (4) a series of cattle waterholes with submerged vegetation and cow dung, varying from 100 to 300 cm in diameter, in the marshes 2 km west of Zamami port; (5) two puddles filled with water spilt over from three large water containers on top of the hill about 1 km west of Zamami port (see below) and (6) a recently dug cattle drinking place in the meadow bordering the dam, 200 x 200 cm and some 40 cm deep, about 2 km north of Zamami port.

Sexes could be distinguished by the tail, which is longer in the female, and also by the shape and size of the cloaca, which is larger in the male and swollen in breeding individuals (Inger, 1947). Males with swollen cloacae were regarded as sexually mature adults. Sexual maturity of females was more difficult to determine since they did not all have distended abdomens. Females found in water were considered adult. Terrestrial animals of similar size were also considered adult. In animals ranging from 90 to 95 mm total length, sex could already be distinguished on the basis of relative tail-length. Females of that size were found exclusively on land and considered sub-adult.

Estimates of the sex-ratio were made by intensive dip-netting in the various water bodies of site 4 and by capturing specimens found walking in the open in different habitats, in particular the forest edge. For the study of reproductive behaviour, the sites with better visibility were monitored twice daily. In the evenings the animals could be watched under torch-light. A total of 29 hrs were spent on observation of courtship behaviour, of which 12 hrs by day and 17 hrs in the evening between 19 and 22 hrs.

The best place for observations of sexual behaviour was the tank-spill pond (site 5). This waterbody measured 100 x 200 cm and was 10 to 25 cm deep. There

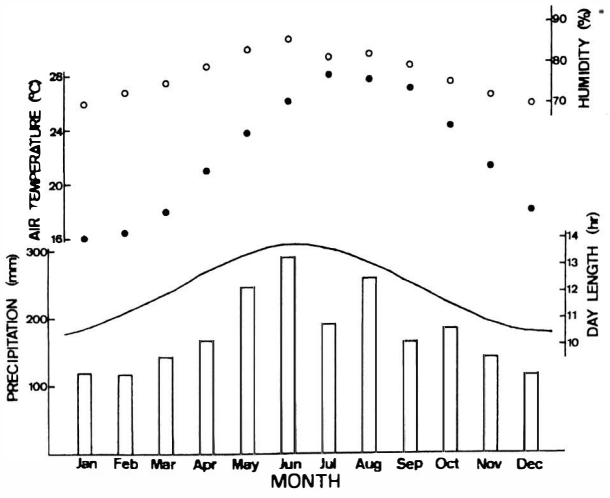


FIG. 1. Climatological data for Naha, Okinawa-jima (ca 40 km E of Zamami-jima), taken from JMAOB (1989). Open bars represent monthly precipitation; solid line day length; closed circles monthly average air temperature; open circles monthly average humidity. All values represent averages from 1951 to 1980.

were some reeds, algae and submerged grasses on one side; the floor consisted of a light coloured sandy clay and the water was mostly clear, allowing observation at very close range, close enough to recognise the newts individually by the pattern of spots on the dorsum. Newts were also wandering on land around the pond and could be seen entering and leaving the water. Other good observation sites were open spots in drainage channels, under bridges where there was less growth of weeds and algae and where the newts were also active during the day.

Fig. 1 summarises the annual climatological data for Naha, Okinawa-jima, some 40 km E of Zamami-jima, which can reasonably be expected to be similar to those for Zamami-jima. Precipitation is relatively high all year round, humidity hardly falls below 70%. During the study period there were mostly overcast skies, some rain and temperatures from 15 to 23° C.

The rains brought out the newts in great numbers. Breeding reportedly takes place from March to June or July, with the peak in April (Tago in Inger, 1947; Thorn, 1968).

LIFE-HISTORY

ADULTS

Adult newts were found in great abundance in the water bodies. They were even more numerous on land, where they were found at night roaming about. Some were seen eating. They were also active during daytime, particularly during and after rainfall. The size of adult females ranged from about 110 to about 140 mm, of males 93 to about 120 mm total length, which is broadly in agreement with existing data (Inger, 1947).

Colour patterns were extremely varied. Some animals were uniformly dark-brown to black on the dorsum. Other individuals were spotted with brown, yellow or greenish-white patches, which were scattered irregularly over the body, occasionally tending to form broad longitudinal bands over body and tail. Some animals also showed two, more or less distinct, reddish-brown dorso-lateral stripes. The ventral colour varied from a pale yellow to shades of orange and bright red, with irregular black spots or stripes. In some animals the belly showed no black markings at all, whereas in others the black parts obliterated most of the bright belly colour, leaving only a narrow coloured stripe on throat and vent. Most animals showed irregular black spots on an orange coloured vent. No sexual dimorphism was evident in the colour patterns. Two females were found which showed abnormal colouration, with mottled orange and greenish-white patches covering the entire back. Animals in the water normally had a smooth skin surface, whereas the majority of animals found on land had a more granular skin. But this was not consistent, both skin states being found amongst aquatic and terrestrial newts.

EGGS

Eggs were found mainly inside submerged and decaying grass-stalks, or between the stalks and leaves of grasses at the waters edge and between thin plant roots sticking out from the bottom and edges of ponds. Most eggs were well-hidden, and the more exposed ones were actively being preyed upon by the adult newts. This was observed on at least four occasions. Females laid their eggs singly and could be observed ovipositing both by day and at night. The females did not wrap the leaves of grasses and plants around the eggs in the well-known *Triturus* fashion, but simply pressed the leaves or twigs against the egg with their hind-feet. Eggs may also be deposited between dead leaves (Ikehara, Yonashiro, Miyagi & Toyama, 1984), or occasionally on land near the water.

LARVAE

Larvae were found in all waterbodies described above. They were most numerous in the cattle drinking holes containing vegetation (site 4). They could be spotted on the bottom of the observation ponds, contrasting with the sand-coloured floor. They were also found amongst vegetation pulled up during dip-netting. Larvae of all sizes were found in the same pond, ranging from 13 mm with remains of yolk still present, up to 47 mm, nearing metamorphosis.

JUVENILES

Juvenile newts, measuring from 50 to 89 mm total length, were found mainly during and after rain. They were found in and along the gutters, bordering a gravel road leading out of the marshes, to the west of Zamami port. These marshes probably form the main centre of dispersal of the newly metamorphosed animals. Table 1 shows the body size distribution. This finding suggests that most of the juveniles that were captured had recently completed metamorphosis. No juveniles were

TABLE 1. Body size distribution of juvenile *Cynops ensicauda popei* ($n = 75$), collected on Zamami-jima in April 1993.

Class of total length	Number	Ratio to total number
50-54 mm	10	(13 %)
55-59 mm	18	(24 %)
60-64 mm	19	(25 %)
65-69 mm	17	(23 %)
70-74 mm	5	(7 %)
75-79 mm	2	(3 %)
80-84 mm	2	(3 %)
85-89 mm	2	(3 %)

found in the water. The smallest animal found in the water was a male of 93 mm total length, with a swollen cloaca.

ADULT SEX-RATIO

The sex-ratio of newts captured in the ponds was skewed toward an excess of males, with 85% males and 15% females ($n = 222$; $\chi^2 = 109.6$; $P<0.001$), whereas the ratio of animals caught on land was almost even, with 51% males and 49% females ($n = 838$; $\chi^2 = 0.31$; $P> 0.05$). Interpreting these estimates is problematic due to possible differential 'catchability' of the sexes. The sex-ratio found in the aquatic habitat, where the animals breed, may be closer to the operational sex-ratio than that found on land.

FOOD

Newts were observed foraging both on land and in water. They were seen hunting very small animals, which could not be identified, in the clay on the bottom of the ponds. They were seen snapping at water striders (Gerridae) and could be seen eating their own species' eggs. On one occasion an adult newt was seen devouring a small, dead fish. In one of the gutter pits, an adult was observed with part of the half-decayed body of a juvenile sticking out of his mouth. Freshly captured newts, kept in a small plastic box, egested tiny snail-shells of the genus *Paludinella*, a taxon living at the water edge. On land, the newts were seen swallowing big earthworms and trying to devour snails, the shell sticking out of their mouths.

PREDATION AND MORTALITY

Adult newts appear to have few natural enemies. Cattle egrets (*Bubulcus ibis*) and white herons (*Egretta garzetta*) which were present in the marshes might incidentally prey on *Cynops*, but the newt's toxic skin secretion probably makes the animal unpalatable to many potential predators, including the birds. Even crows, which can normally be seen eating corpses on the street, did not touch the dead newts which could be found in great quantity on and along the roads. The natricine snake *Amphiesma pryeri* has been reported as preying occasionally on *Cynops* (Takara, 1962; Tanaka, 1986) and its larvae (Imaizumi, 1953). There is also an observation on record that the bullfrog, *Rana catesbeiana*, a species introduced in Okinawa-jima, preys on newts (Otani, 1987).

Many newts were found trapped in roadside gutters. These gutters are made of polished cement with 30 cm deep vertical sides, making it impossible for most animals, once fallen in, to escape. After every period of rain, the gutters were full of newts, many of which would die within a day if exposed to the sun. (Over a distance of 280 m, a gutter along a new road from the marshes eastward contained 347 recently dead adults and juveniles).

OTHER AMPHIBIANS

Rana limnocharis and *Microhyla ornata* and its larvae were found in the breeding ponds. Freshwater crabs and shrimps were found in several newt breeding localities, particularly in the sewage drains in the village and in the marshes.

SEXUAL BEHAVIOUR

BEHAVIOUR PATTERNS

The following patterns of sexual behaviour were distinguished in staged encounters of this species (Sparreboom, 1994; *in prep.*) and were also observed in the natural habitat. The terminology follows Halliday (1977) in as far as the behaviour patterns are similar to *Triturus*.

- Pursuit of the female (PURSUIT);
- Tail-fanning display (DISPLAY);
- Creeping ahead of the female (CREEP);
- SPERMATOPHORE DEPOSITION;
- SPERMATOPHORE PICK-UP;
- COMPETITION by one or more other males during fanning display;
- SEXUAL INTERFERENCE during the creeping stage.

Pursuit of the female is part of the orientation of the male towards the female: the male may swim or walk after the female with slow movements, nudge and sniff at her. He may also dash at her and try frantically to move in front of her if the female moves away from the male or ignores him.

The display consists of tail-fanning, a rapid vibration of the distal part of the tail, which is folded against the male's body on the side facing the female. Tail-fanning is performed in short bouts, alternated with pauses during which the tail is held stationary. During this display the male is more or less positioned perpendicular toward the female's longitudinal axis. Fanning may be performed after a direct approach if the female remains stationary, or after a period of pursuit. Pursuit and display may be rapidly alternating and cannot easily be separated as different stages.

Creeping is the term for a type of behaviour of the male, usually performed after some tail-fanning bouts. He turns away from the female, one or two air bubbles escape from his mouth ('guffing'), and he slowly

creeps ahead of the female, while she is following him and nudging his undulating tail.

Spermatophore deposition follows after the male has crept forward for a while and received tail-touches from the female. He pauses and raises his tail slightly, extruding a spermatophore in front of the female. When the female continues to follow the creeping male, her cloaca moves over the spermatophore. If all goes well, the sperm-cap sticks to her cloaca. The male continues creeping ahead without turning back to the female (Sparreboom, 1994).

Competition is here used to denote an attempt by two or more males to court the female simultaneously. A common form of competition consists of several males swimming after a female, trying to take up a position in front of her and attempting to fan at her. A male may also squeeze himself between a female and a fanning male and thus interrupt the courtship.

The term 'sexual interference' refers to a male's attempt to take over a female engaged in an on-going courtship encounter with another male during the creeping stage (see Arnold, 1976): the rival male puts himself between the female and the tail of the creeping male, occasionally inducing him into a fruitless spermatophore deposition by touching his tail. Subsequently the intruder displays to the female himself, or may move to creep straight away and deposit his own spermatophore (Sparreboom, *in prep.*).

Observed Patterns of Sexual Behaviour

During daytime four to ten animals were visible in the observation pond, whereas at dusk, from 10 to 18 animals could be counted. Usually the males outnumbered the females. There were four to six females in the pond; the observed number differed due to poor visibility of females during oviposition and a come and go of animals. In the course of the evening more animals would become visible or appear from outside the pond. Usually at least two or three females were laying eggs among the grasses in one corner. The others were immobile or foraging. They were only occasionally approached by males, who were usually more or less spaced out over the bottom of the pond. Occasionally the same males could be found at the same spot during several consecutive evenings, but they were not seen defending the site in any way against intruders. Their activity consisted of sitting still, foraging and slowly swimming short distances. Occasionally they would approach, sniff, nudge and briefly fan at a female.

Although females regularly attracted some attention from the males if they moved out of the reeds to the floor of the pond, there was a noticeable increase in male activity within a circle of about 40 cm, if a new and probably unmated female entered the pond. Such a female could be recognised by a silvery hue on her body, due to many tiny air bubbles on the dry skin. This appearance could last for a full day, after which her skin would become indistinguishable from that of the others. She would enter the pond and walk forward slowly, stopping from time to time, her buccal movements suggesting that she was perceiving odours from the water.

One or more males would approach the female, sniff at her and start fanning display. During this display the male would touch the female's body from time to time with his neck or snout or he would actually squeeze his snout between her and objects in the pond, when she moved away. If a displaying male was not disturbed by other approaching males, he would continue fanning, occasionally for three minutes. As a reaction to little movements of the female, the male would adjust his fanning position by moving back and forth a few steps, and in this way directing the water current more precisely to the female's snout. The female would either swim away or stay completely still for a short while and then turn her head towards the male. On this signal the male would turn round and start creeping ahead of her. If she followed him and touched his tail several times, he would deposit a spermatophore. If the female kept following the male's tail, she would eventually be led over the spermatophore which then might become attached to her cloaca. In the two observed sequences which resulted in sperm pick-up, one female was inseminated one hour after her entering the pond, another within ten minutes after arrival.

Quantification of Behaviour Patterns

A total of 100 courtship encounters were observed, 65 of which were in the tank-spill pond, the main ob-

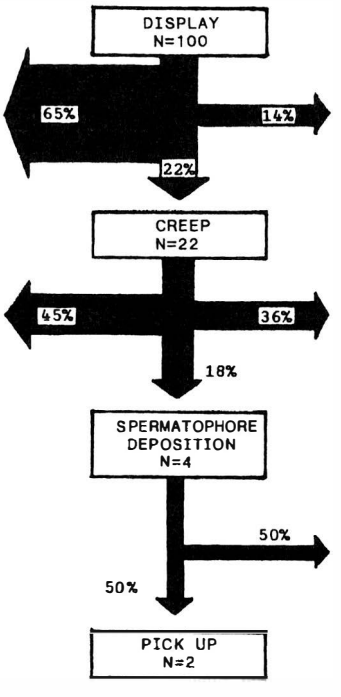


FIG. 2. Transitions between stages of courtship for sexual encounters between male and female *Cynops ensicauda popei*. Arrows that exit to the left indicate interruption of the courtship by the female moving away, arrows exiting to the right indicate that the sequence was broken off by the male, due to competition by one or several intruders.

servation site. 28% of the encounters were observed in daytime, 72% in the evening in darkness. Of the 22 courtships that progressed to the creep stage, 9 (41%) were observed by day and 13 (59%) in the evening.

Fig. 2 depicts the transitions from display behaviour onward. All courtship encounters were observed until the end of the encounter. Out of 100 courtship encounters only four progressed to the deposition of one or two spermatophores (6 in total). Of these four instances, one creep was interrupted by sexual interference without prior pick-up of the spermatophore cap, one other was also interrupted, but sperm pick-up could not be verified. In the two remaining sequences the first spermatophore was picked up successfully, but it did not progress to further spermatophore pick-ups due to interference (so the success rate was: 33% of 6 spermatophore depositions, 9% of courtships that progressed to the creep stage and 2% of the total number of observed courtship sequences).

Competitive Encounters

As there were invariably more sexually active males than females in the pond at the same time, a new female usually attracted the attention of more than one male at a time. A female might be followed persistently by two or more males and males might compete for a position to fan at the female.

Sexual interference, the form of competition taking place during the creeping stage, was observed particularly when a courting male had just turned round to creep: at this moment, neighbouring males who had not paid attention to the courting couple until that time, would suddenly approach the couple with rapid and agitated movements and attempt to move between the tail of the creeping male and the snout of the female. Alternatively, they could simply touch the female's tail, possibly depending on the position from where they started their assault on the on-going courtship sequence. Occasionally, such an approach was of a more determined nature, with the interfering male nudging forcefully or gently biting and thereby displacing the female as she was following the first creeping male. Usually, the female would react negatively to such behaviour and swim away, leaving the males behind, frantically swimming over and under and around one another, but losing the female from sight.

No instance was recorded where an interfering male succeeded in taking over the courtship and inseminating the female himself. The most successful cases of interference were those where creep and spermatophore transfer were interrupted and the first courting male was prevented from completing his courtship.

Quantification of Competitive Behaviour

Among the 100 observed courtship encounters, 25 instances of some form of competition were recorded: On 14 occasions this was an interruption in the display phase, during fanning. On eight occasions sexual interference took place during creep and on three occasions after a spermatophore deposition when the couple was creeping on (see Fig. 2). In 18 of the 25 competitive encounters two males were involved, in five encounters three males and in two encounters five different males were present at the same time.

DISCUSSION

Behaviour patterns and reproductive strategies may vary according to the progression of the breeding season, the availability of mates (operational sex-ratio) and other factors such as density of individuals at the breeding site (Verrell, 1989; Verrell & McCabe, 1988). The present observations are limited to a short period of what appears to be a peak in a prolonged breeding season and may therefore not give a fully representative picture of the mating system. However, they suggest a considerable flexibility of this species: the animals easily alternate between water and land and do not appear to be very selective in their choice of breeding habitat. Courtship takes place in deep (about 100 cm) as well as very shallow water (about 2 cm). Eggs can be laid in water and also on land. Not all adult animals simultaneously take part in reproduction. The simultaneous presence of adults in and out of breeding condition, of eggs and larvae in all stages of development, and of recently metamorphosed juveniles points to an extended reproductive season (potentially from October to June or July: Ota, *pers. observ.* in 1987 and 1990). With winter temperatures generally not falling much below 15 °C (see Fig. 1), there is no necessity for a winter break or hibernation. Precipitation and air humidity are generally high all year round (Fig. 1) and create the damp conditions under which the animals could in principle remain active a major part of the year. On the nearby island of Akajima many adult newts were found in slowly flowing and shallow waters of 28 °C. This suggests that the animals can tolerate relatively high water temperatures, so the species is able to exploit not only a variety of habitats but also a great part of the year for breeding activity. This and the scarcity of natural enemies may be an explanation for this species' abundance.

Related salamandrids such as species of *Triturus* have mating strategies that seem to be more adapted to dealing with specific ecological constraints and have more clearly synchronised periods of sexual activity (Verrell & McCabe, 1988; Verrell, 1989). Compared with such 'specialists', *Cynops ensicauda* is a 'generalist'.

The behavioural interactions observed in this study are qualitatively similar to descriptions of courtship and sexual interference in the laboratory (Sparreboom, 1994 and *in prep.*). This concurs with results obtained in similar but more extensive work on *Triturus vulgaris* (Verrell, 1984; Verrell & McCabe, 1988). The successful transfer of a spermatophore was rarely observed in the field (in 2 out of 100 encounters). This also parallels field observations of other species

(Giacoma & Crusco, 1987; Massey, 1988; Verrell & McCabe, 1988; Hedlund, 1990; Zuiderwijk, 1990; Pavignano, Sacchetto & Giacoma, 1993; Faria, in press). It may not be coincidental that the successful spermatophore pick-ups were observed on occasions where fresh and possibly unmated females entered the pond. Once inseminated, females may be unresponsive for some time. This could however not be verified at the observation site. What emerges from this study and the others cited is that successful insemination may be a relatively rare event in nature.

The observations on sexual interference suggest that a creeping male produces a substance (possible a courtship pheromone) that not only attracts the following female but also alerts other males. This may be worth testing experimentally.

Clearly the data reported in this paper are fragmentary and of a preliminary nature. Given the relatively good observability of this species as compared with others, a more extensive study of several populations and in different months of the breeding season may well be rewarding.

ACKNOWLEDGEMENTS

We thank Pim Arntzen and Manuel Faria for valuable comments on an earlier draft of this paper. We are grateful to the reviewers for helpful critical remarks.

REFERENCES

Arnold, S. J. (1972). *The evolution of courtship behavior in salamanders*. PhD thesis, University of Michigan.

Arnold, S. J. (1976). Sexual behavior, sexual interference and sexual defense in the salamanders *Ambystoma maculatum, Ambystoma tigrinum and Plethodon jordani*. *Zeit. Tierpsychol.* **42**, 247-300.

Faria, M. M. (1995). A field study of reproductive interactions in Bosca's newt, *Triturus boscai* (Amphibia: Salamandridae). *Amphibia-Reptilia. (in press).*

Giacoma, C. & Crusco, N. (1987). Courtship and male interference in the Italian newt: a field study. *Monit. zool. ital.* **21**, 190-191.

Halliday, T. R. (1977). The courtship of European newts: an evolutionary perspective. In *The reproductive biology of amphibians*, 185-232. Taylor, D. H. & Guttman, S. I. (Eds). New York: Plenum Press.

Hayashi, T. & Matsui, M. (1988). Biochemical differentiation in Japanese newts, genus *Cynops* (Salamandridae). *Zool. Sci.* **5**, 1121-1136.

Hedlund, L. (1990). Courtship display in a natural population of crested newts, *Triturus cristatus*. In Hedlund, L. *Reproductive ecology of crested newts, Triturus cristatus (Laur.)*. PhD thesis Uppsala, Report 16, Swedish University of Agricultural Sciences.

Ikehara, S., Yonashiro, Y., Miyagi, K. & Toyama, M. (1984). *Guide to the animals of the Ryukyus. Vol. 1: Terrestrial Vertebrates*. Naha: Shinsei-tosho. (in Japanese)

Imaizumi, Y. (1953). Harmful snakes and useful snakes. *Prevention of Epidemics to Plants* **7**, 27-29.

Inger, R. F. (1947). Preliminary survey of the amphibians of the Riukiu Islands. *Fieldiana (Zool.)* **32**, 297-352.

Japan Meteorological Association, Okinawa Branch (JMAOB) (1989). Meteorological Tables of Okinawa. Naha: JMAOB, 98 pp. (in Japanese)

Kawamura, T. & Sawada, S. (1959). On the sexual isolation among different species and local races of Japanese newts. *J. Sci. Hiroshima University, ser. B, div. 1 (Zoology)* **18**, 17-30.

Massey, A. (1988). Sexual interactions in red-spotted newt populations. *Anim. Behav.* **36**, 205-210.

Otani, T. (1987). Predation of *Cynops ensicauda* by *Rana catesbeiana*. *Akamata* **4**, 23-24. (in Japanese)

Pavignano, I., Sacchetto, C. & Giacoma, C. (1993). Field observations of the sexual behaviour of the smooth newt, *Triturus vulgaris*. *Ethology, Ecology & Evolution* **5**, 406-407.

Sawada, S. (1963*a*). Studies on the local races of the Japanese newt, *Triturus pyrrhogaster* Boie. I. Morphological characters. *J. Sci. Hiroshima University, ser. B, div. 1 (Zoology)* **21**, 135-165.

Sawada, S. (1963*b*). Studies on the local races of the Japanese newt, *Triturus pyrrhogaster* Boie. II. Sexual isolation mechanisms. *J. Sci. Hiroshima University, ser. B, div. 1 (Zoology)* **21**, 167-180.

Sparreboom, M. (1994). On the sexual behaviour of the sword-tailed newt, *Cynops ensicauda* (Hallowell, 1860). *Abh. Ber. Naturk. Magdeburg* **17**, 151-161.

Sparreboom, M. Sexual interference in the sword-tailed newt, *Cynops ensicauda popei* (Amphibia: Salamandridae). (*in prep.*)

Stejneger, L. (1907). Herpetology of Japan and adjacent territory. *Smiths. Inst. U.S. natn. Mus. Bull., Washington* **58**, 1-577.

Takara, T. (1962). Studies on the terrestrial snakes in the Ryukyu Archipelago. *Sci. Bull. Agr. & Home Econ. Div. Univ. Ryukyus* **9**, 1-202. (Japanese with English summary)

Tanaka, S. (1986). New observations on the stomach contents of *Amphiesma pryeri pryeri*. *Akamata* **3**, 5-7. (in Japanese)

Thorn, R. (1968). *Les salamandres d'Europe, d'Asie et d'Afrique du Nord*. Paris: Lechevalier.

Tsutsui, Y. (1931). Notes on the behaviour of the common Japanese newt, *Diemyctylus pyrrhogaster* Boie. I. Breeding habit. *Mem. Coll. Sci. Kyoto Univ. Series B*, vol. vii, **4**, 159-178.

Verrell, P. A. (1984). Sexual interference and sexual defense in the smooth newt, *Triturus vulgaris* (Amphibia, Urodela, Salamandridae). *Zeit. Tierpsychol.* **66**, 242-254.

Verrell, P. A. (1989). The sexual strategies of natural populations of newts and salamanders. *Herpetologica* **45**, 265-282.

Verrell, P. A. & McCabe, N. (1988). Field observations of the sexual behaviour of the smooth newt, *Triturus vulgaris vulgaris* (Amphibia: Salamandridae). *J. Zool., Lond.*, A, **214**, 533-545.

Zuiderwijk, A. (1990). Sexual strategies in the newts *Triturus cristatus* and *Triturus marmoratus*. *Bijdr. Dierk.* **60**, 51-64.

Accepted: 1.5.95