A STUDY OF THE BEHAVIOUR OF NEWTS

'Being an investigation of the Sexual Behaviour of some species of the European genus Triturus.

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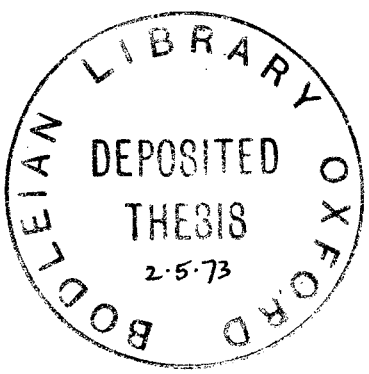

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VOLUME 1

"Only a strong effort of the imagination, after a careful, first hand study of the behaviour of newts, can conjure up in our minds a comparatively truthful picture of the dreary monotony and automatism of the life of the Newt as a whole."

B. F. Cummings (1910).

This Thesis is dedicated to the memory of Bruce F. Cummings (1889 - 1919).

ABSTRACT

Many ethologists have found the sexual behaviour of animals to be a fruitful field of study. This thesis reports an investigation of the sexual behaviour of the Newt, an animal that has hitherto received little attention from ethologists. The study includes a number of species of the European genus Triturus (Urodela, Salamandridae).

The Introductory Chapter presents information concerning the biological background to newt sexual behaviour, including life-history, general behaviour and sensory capacities, together with an account of the observational and experimental procedures used in the study.

The sexual behaviour of the Smooth Newt, Triturus vulgaris, is described. The behaviour consists of a complex sequence of actions which lead to the transfer of a spermatophore from male to female. This sequence may be repeated a number of times in the course of a sexual encounter.

By a form of sequence analysis a number of correlations are established between male and female behaviours. For some behaviours, temporal correlations are established also. The hypothesis that these correlations are indicative of causal relationships is tested by a number of experiments in which the behaviour of the female is manipulated.

Much of the sexual behaviour sequence can be understood in terms of male responses to the female's general movements and, at certain points in the later part of the sequence, to specific stimuli provided by the female. Not all transitions between male behaviours can be explained in these terms; some parts of his behaviour are stereotyped patterns which are unaffected by the female's behaviour.

The sexual behaviour of T. vulgaris is compared with that of the Palmate Newt, T. helveticus and the Alpine Newt, T. alpestris, using data obtained during this study, and with that of the Crested Newt, T.

cristatus, using the account given by J.B. Nelson (1959). Differences in the details and in the overall pattern of sexual behaviour in these species are discussed.

Some pilot experiments to investigate reproductive isolation between T. vulgaris and T. helveticus are described. These suggest an ethological isolating mechanism based on female selective responsiveness to the male's display.

Newt sexual behaviour is discussed as a functional system and is compared with the sexual behaviour of some other animals. Some factors that affect courtship success (i.e. successful spermatophore transfer) are discussed.

The evolution of sexual behaviour within the genus Triturus is discussed. Evolutionary aspects are considered also in relation to the sexual behaviour of other Urodeles.

Motivational aspects of sexual behaviour are discussed, with particular reference to the concepts of behavioural conflicts and thwarting. It is argued that the newt courtship sequence is better understood in terms of stimulus-response relationships than through the use of motivational models.

NOTE TO THE READER

This Thesis is divided into two volumes, the first containing text and references, and the second illustrations, tables and appendices to the text. It is intended that this arrangement will make it more convenient for the reader to cross-refer between text and figures.

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CONTENTS

VOLUME 1

	Page
Abstract	i
Note to the Reader	iii
Acknowledgments	iii
CHAPTER 1. INTRODUCTION	1
The European Newts	1
A Review of the Literature	2
The Life of Newts	4
The Sensory Capacities of Newts	14
General Approach to the Study	15
The Species used in this Study	16
The Smooth or Common Newt, Triturus vulgaris	16
The Palmate Newt, Triturus helveticus	17
The Alpine Newt, Triturus alpestris	18
The Crested or Warty Newt, Triturus cristatus	19
The Marbled Newt, Triturus marmoratus	20
Methods	20
Keeping of Animals	20
Observational Procedures	21
Recording Procedures	22
Experimental Methods	24
Interference with a "free" female	25
The Newt Model	25
The Strait Jacket	26

Page

CHAPTER 2. A DESCRIPTION OF THE COURTSHIP BEHAVIOUR OF THE SMOOTH NEWT, Triturus vulgaris 29

Aberrant Behaviour shown by Females . . . 40

Glossary of Terms used in the Description of Courtship Behaviour 42

CHAPTER 3. ANALYSIS OF THE CAUSAL RELATIONSHIPS BETWEEN MALE AND FEMALE BEHAVIOURS 45

The Male's Initial Behaviour 47

The Male's Approach 47

The Approach Experiment 48

The Male's Sniffing of the Female . . . 51

Orientation and Display Behaviour 52

Analysis of Behaviour Sequences 54

Analysis of Transitions between Male Acts . . 56

Analysis of the Time Intervals between Consecutive Male Acts 58

Uninterrupted Male Transitions 60

Other Factors affecting Uninterrupted Male Transitions 63

The Relationship between Transition Interval and Female Interruption 65

Male Transitions in relation to both Time and the Female's Behaviour 66

The Effect of the Female on the Timing of the Male's Behaviour 67

Interruptions During Fanning Bouts . . 67

How the Male's Behaviour Influences that of the Female 68

Page

Summary of the Analysis of Orientation and Display Behaviour 70

Experiments on Display and Orientation Behaviour . 70

The Negative/Static Experiment . . . 72

The Static/Positive Experiments . . . 73

Other Orientation/Display Experiments . . 75

Orientation and Display Behaviour - A Summary based on Observational and Experimental Data . 76

The Deposition Phase 77

What Initiates the Male's Creep? . . . 77

Sequential Analysis of Deposition Phase . . 78

The Tail-Touch Experiment. 79

The Post-Spermatophore Experiment . . . 81

Summary of Deposition Phase Analysis . . . 82

Conclusion 82

CHAPTER 4. COMPARATIVE ASPECTS OF SEXUAL BEHAVIOUR IN THE GENUS *Triturus* 85

Sexual Behaviour of other *Triturus* Species. . . 85

The Palmate Newt, *Triturus helveticus*. . . 85

The Alpine Newt, *Triturus alpestris* . . . 87

The Crested Newt, *Triturus cristatus* . . . 89

The Marbled Newt, *Triturus marmoratus* . . 91

Other *Triturus* Species 92

Sexual Behaviour of *Triturus* Species: A Summary . 92

Reproductive Isolation among *Triturus* Species . . 93

Cross-mating Experiments between *T. vulgaris* and *T. helveticus* 94

Newt Courtship as a Functional System . . . 98

Synchronisation of Newt Sexual Behaviour . . 105

Page

The Success of Newt Courtship and Factors that Affect it 107

Evolution of Sexual Behaviour within the Genus Triturus . 110

The Form of the Display Movements . . . 110

The Overall Pattern of Display Behaviour . . 115

Fanning and its Anatomical Correlates . . . 116

Comparison of Triturus Sexual Behaviour with that of other Urodeles 118

Some Wider Comparisons 125

The Motivation of Sexual Displays 126

REFERENCES 129

VOLUME 2

ILLUSTRATIONS AND TABLES 1

APPENDICES 95

CHAPTER 1

CHAPTER 1

INTRODUCTION

This thesis reports a study of the sexual behaviour of a number of species of European newts, genus Triturus. In common with the majority of tailed amphibia fertilisation is internal but there is no copulation. During sexual behaviour, which takes place in water, the sperm is transferred from male to female in a capsule, or spermatophore. Earlier workers (see literature review below) have described much of the elaborate behaviour that attends this process. The aim of this study was to augment and clarify this descriptive work and, further, to analyse some of the biological processes involved.

The European Newts

The genus Triturus is distributed across Europe, parts of Scandinavia and eastwards into Asia. There are eight generally recognised species in the genus which can be classified into three groups (Lantz 1947). The largest group, of five species, is grouped around T. vulgaris, the Smooth Newt, which is the most widely distributed species. Other members of this group are T. helveticus, the Palmate Newt; T. boscai, Bosca's Newt; T. montandoni, the Carpathian Newt; and T. vittatus, the Banded Newt. These are all relatively small forms, generally under 10 cm in length. Two larger species, T. cristatus, the Crested Newt, and T. marmoratus, the Marbled Newt, form a second group. The third group consists of one species, T. alpestris, the Alpine Newt, which is intermediate in size between the other two groups. Spurway (1953) groups T. boscai with T. alpestris on the basis that these two species readily hybridise in captivity. Authorities vary as to whether the Italian newt is a separate species, T. italicus (Lantz 1947, Smith 1951, Spurway 1953),

or a subspecies, T. vulgaris italicus (Steward 1969). The distribution of these species is shown on page 2/1. (These maps are based on those of Steward 1969.) Only three species, T. vulgaris, T. helveticus and T. cristatus are native to Britain.

A Review of the Literature

The earliest known account of newt sexual behaviour seems to be that of Spallanzani (1780), who established that fertilisation is internal and performed experiments involving artificial insemination. Rusconi (1821), working with Crested and Palmate Newts, gave the first account of egg-laying and established that fertilisation is achieved without bodily contact. He also described a tail movement that "excites" the female - a rapid "vibration" in the Palmate Newt, a less vigorous movement in the larger species. T. Bell (1839) described two tail movements, the rapid tail vibration and "a motion similar to that of smacking a whip". These early naturalists were principally interested in the development of the egg and tadpole and a number of meticulous studies of this process were made (Rusconi 1821, T. Bell 1839, Higginbottom 1853). Gasco (1880) suspended glass containers from the ceiling of his laboratory and observed the deposition and pick-up of the spermatophore from below - a technique essentially similar to that used in part of this study. Boulenger (1892) and Gadow (1901) drew attention to the fact that European newts differ from most other Urodeles (tailed amphibia) in that no amplexus is involved in their sexual behaviour, and they related this to the marked sexual dimorphism shown by these newts.

B.F. Cummings carried out much experimental work on British newts, in particular on their homing abilities (1912) and their learning capacities (1910). He attributed the rapid tail movements of the male to a functionless elimination of "a surplus of nervous energy" (1911).

Finkler (1923) described the sexual behaviour of the Alpine Newt and coined "Finkler's rule" which states that the displaying male "always bends his tail towards the side on which he sees the eyes of the female". He found that these tail movements could be elicited in solitary males by adding common salt to their water. He also showed that the male's "love-play" is a necessary pre-requisite for the successful pick-up of the spermatophore by the female.

The work of Matthes, though not directly concerned with sexual behaviour, is of great importance. He investigated the olfactory capacities of newts when they were aquatic (1924a) and when they were in their terrestrial phase (1924b), and he also described the changes that take place in their olfaction when they changed from one medium to another (1927).

Tinbergen and Ter Pelkwijk (1938) described feeding and sexual behaviour of the Smooth Newt and carried out experiments that showed that vision, smell and sensitivity to water currents are all important in these two activities. They also described how the rapid tail vibration - "Fanning" - creates a water current that carries the male's smell towards the female. Zippelius (1948) found that males kept alone for a long time will show "tail-wagging" to a cotton wool ball impregnated with female scent, but not to an odourless ball.

Marquenie (1950) gave a more complete account of the sexual behaviour of the Smooth Newt than previous authors. He described three distinct display movements - fanning, the violent tail lash, and a "showing off" movement. He also described how the behaviour of the male after he's deposited the spermatophore ensures that the female is reasonably likely to pick up the spermatophore.

Prechtl (1951) gave less complete descriptions of sexual behaviour in a number of Triturus species, and he interpreted the behaviour as a sequence of Innate Releasing Mechanisms. Hellmich (1956) suggested that

Fanning wafts sperm towards the female, a myth that had been dispelled nearly 200 years earlier by Spallanzani. J.B. Nelson (1959), studying the courtship behaviour of Triturus cristatus, graded the various male behaviours and suggested that this gradation provides a measure of the male's internal motivation. He also analysed the role of the female and showed how her responsiveness influences the male's behaviour.

Gauss (1961), unlike most earlier authors, studied newts in their natural habitat and concentrated on those behaviours that precede the sexual behaviour as described by Zippelius and Prechtl. He found that males of three species, T. cristatus, T. alpestris and T. vulgaris, have undefended "territories" in which they mark solid objects with cloacal secretions. Wandering females, on encountering these scent marks, writhe about in a way that attracts the attention of the resident male. The significance of these findings and of those of other recent authors will be discussed more fully in subsequent chapters.

The Life of Newts

"Everybody's making love or else
expecting rain." (Bob Dylan)

The natural history of newts, as far as it is known, is described by Smith (1951) and Steward (1969). The life cycle of the Smooth Newt is shown schematically on page 2/2. In common with many amphibians, newts lead a double life. They are as characteristic a feature of the fauna of ponds as the familiar Stickleback, but the time they spend in water represents a very small proportion of their life cycle. For eight or nine months of the year the newt leads a terrestrial existence of which virtually nothing is known. They are very difficult to find when they are in their terrestrial phase; one's best hope is to turn over logs and stones near their known breeding ponds, but this usually only yields the occasional immature animal. In their terrestrial state they are dull and

dark in colouration and generally very thin, in marked contrast to their splendour in the breeding season.

In the course of this study a number of animals have been kept in terraria after the breeding season, and one may tentatively suppose that the behaviour of these animals is indicative of their natural behaviour in the wild. They spend most of their time hidden under logs and stones, often in tangled groups, though this is probably due to their unnaturally crowded conditions. They can be lured out into the open by putting a live food item near their hiding place. At night they come out and walk about the terrarium and they will climb up plants. These excursions are not wholly confined to the night; during the day one or two animals can usually be seen out in the open. These newts have been fed on maggots, chopped worms and Drosophila, and they use very different techniques to catch different sorts of prey. Maggots and worms are stalked with great deliberation and stealth, and, in a final lunge with the head, the food item is grasped in the mouth. A fruit fly is stalked in the same way but in this situation the newt stops about $\frac{1}{2}$ cm short of the fly and then spits out a blunt protrusible tongue on which the fly is stuck and carried immediately into the mouth. It is noticeable that newts seem to respond primarily to movement when stalking these prey, the writhings of a maggot or worm and the wing flicks of a fruit fly being apparently essential to initiate an approach. Inanimate food items such as chopped meat are ignored unless they are moved about near a newt.

During the winter months newts are said to hibernate (Smith 1951, Steward 1969). The animals that I have kept in the laboratory have remained very active throughout the winter, but they have been kept under abnormally clement conditions. In the wild a period of terrestrial winter inactivity is not an invariable rule; there are a number of records of newts being found in ponds during the winter (Smith 1952, Steward 1966, 1969, G. Bell 1970). My captive animals have shown a level of activity

roughly proportional to the prevailing temperature. Whether the period of terrestrial "hibernation" is simply a period of torpidity induced by cold conditions, or whether it involves internal mechanisms like those found in mammals, is not known.

According to Smith (1951) and Steward (1969) newts enter their breeding ponds in mid-March to April. In the course of this study and that of G.A.C. Bell, who is studying the ecology of newts, it has been clear that a number of newts are present in the ponds as early as January. There is a mass migration to the breeding ponds coinciding with mild, damp weather in March or April (Bell 1970, and work in progress). Even the earliest newts to be caught show some development of their epigamic characters - colouration and crests - and it seems that these have begun to develop by the time newts migrate to their ponds. Once in their ponds these features, characteristic of newts in their aquatic phase, are quickly developed in full.

Metamorphosis from the larval to the adult state is a characteristic feature of Amphibia in general. In many forms, newts among them, this metamorphosis also involves a transition from aquatic to terrestrial life. In the process the animal must become adapted to its new medium, losing certain features adapted to aquatic life and acquiring new terrestrial adaptations. In newts, and other Amphibia who return to water for a protracted period, this process must be reversed. There is thus a partial "reverse metamorphosis", by which the newt, on returning to the water to breed, reacquires many of the characters it possessed as a larva. The principle changes that take place in the transition from land to water are:

1. Modification of the tail and limbs for aquatic locomotion. The tail loses its thin, thread-like appearance and becomes a ventrodorsally broad, flat structure which can provide powerful thrust for swimming. Newts swim comparatively rarely; most of the time they crawl about through weeds and along the pond bottom. For this they retain their limbs in their

terrestrial form but with two striking exceptions. The male of both the Smooth Newt, T. vulgaris, and the Palmate Newt, T. helveticus, shows aquatic adaptation of the hind limbs. In the Smooth Newt this is in the form of fringes of skin along both sides of the toes, while in the Palmate Newt there is complete webbing between the toes, the feature that gives this species its common name. These features would clearly seem to be adaptations for aquatic locomotion. The most likely explanation for this sexual dimorphism in a locomotory character is probably that proposed by Darwin (1871). He suggested that the webbed hind foot of the Palmate Newt "aids the male in his eager search and pursuit of the female". As will be seen later the male's role in courtship is a very active one, involving much chasing of initially unresponsive females. These two species are generally more active in their courtship behaviour than other species studied, in which courtship is a largely static affair. For sustained swimming newts do not use their legs, tucking them back against their sides and using only their tails to propel them (see page 2/3, fig A).

2. Changes in the skin for aquatic respiration. The skin of terrestrial newts is dry, rough and velvety in appearance, that of aquatic newts is smooth and slippery. The skin serves as an auxillary respiratory surface, the lungs also being important. Aquatic newts make regular trips up to the surface to take in atmospheric oxygen, and the frequency of these trips can be experimentally reduced by increasing the oxygen content of the water (Spurway and Haldane 1953).

3. Modification of the mouth for aquatic feeding. In water newts maintain their carnivorous habits, in contrast to the common Frog, Rana temporaria, which does not feed in the breeding season (Ashby 1969). The protrusible tongue is not used to catch aquatic prey, only the lunge and snap method being retained from the terrestrial phase. The snapping method of feeding presents problems in an aquatic medium. In particular, a rapid closure of the jaw creates a blast of water that tends to push a food item away. It

has been suggested by Tinbergen and Ter Pelkwijk (1938) that a feature shown by aquatic newts is a feeding adaptation. This is a flap of skin that projects downwards from the upper lip and overhangs the lower lip at the side (see page 2/4). It is suggested that when the jaws are snapped shut water is expelled laterally under this flap and not forwards. This feature is more developed in females than in males, a fact which Tinbergen and Ter Pelkwijk correlate with the female's extra food requirements to make eggs.

4. Development of lateral line organs. These receptors, which are sensitive to vibrations in the water, are found in all but the most terrestrial amphibia and are a relic of their fish ancestry. In fish, lateral line organs are generally arranged in longitudinal canals and are important in the detection and location of moving animals, including prey, enemies and social partners (Dijkgraaf 1963, 1967). In amphibians they are arranged in small clusters over the body with a concentration around the head. In newts each organ consists of a cluster of sensory cells in a slight pit (page 2/5, fig A) and they are scattered over the dorsal surface, particularly around the head (page 2/5, fig B). They are present during the terrestrial phase but are partially atrophied and covered over by the thickened epidermis (Smith 1952).

5. Modification of other sense organs. Newts are largely dependent on vision for finding food both in water and on land, and their eyes must presumably be modified on the return to water to compensate for the change in the refractive index of the medium, but the mechanism by which this is achieved has not been analysed. It is known that in the metamorphosis of frog tadpoles the cornea becomes more sharply curved and the lens flatter (Walls 1963), and it may be that a reverse process occurs in newts when they return to water. In a closely related genus, Notopthalmus, from North America, it has been shown that at larval metamorphosis the visual pigment in the retina changes from a system typical of freshwater vertebrates to

one typical of terrestrial vertebrates, and that this process is reversed on the return to water (Wald 1946). Smell is also used in both media in feeding and this also requires changes if it is to be effective in both situations. In air the nasal passages are filled with a mucus plug in which odours become dissolved. In water this is not necessary and the mucus plug is lost (Matthes 1927). Matthes showed that the changes required for aquatic life are completed by the time newts enter the water, but that, at the end of the breeding season, they are unable to smell effectively for some time after leaving the water.

6. Development of secondary sexual characters. All the changes listed above adapt the newt to life in an aquatic environment. Newts return to water to mate and lay their eggs and so in addition to the changes demanded by the different environment there are modifications required for breeding. All the Triturus species show sexual dimorphism and all the additional adornments are shown by the male. These are illustrated in the pictures of individual spp (pp. 2/9 - 2/13) and are as follows:

a. The development of a dorsal crest which begins just behind the head and continues posteriorly as a vertical extension of the tail (see page 2/6). There is considerable variation between species in the height and shape of this crest. In some species the dorsal edge is deeply denticulated (Crested Newt, Banded Newt), in others it is gently waving (Marbled Newt) and in others it is smooth (Palmate Newt, Alpine Newt). In the Smooth Newt, T. vulgaris, the form of the crest is highly variable, being denticulated in the most widespread subspecies, vulgaris vulgaris, but smooth in other subspecies, such as vulgaris meridionalis and vulgaris graecus. The crest is an extension of the dorsal skin and is devoid of muscular tissue.

b. The development of extensions of the toes of the hind limb

in the Smooth Newt and webbing of the hind foot in the Palmate Newt (see 1 above).

c. The development of conspicuous colour patterns. These will be described in detail later. In general male epigamic colouration consists of dark spots, either evenly dispersed over the body or grouped into patterns and contrasting with a paler ground colour. Most species have a vivid yellow or orange colouration on the belly and some have stripes on the tail. The belly colouration is apparent throughout the year but becomes more extensive in the breeding season. Lantz (1953) showed that the extent of black colouration on the belly of T. cristatus is affected by the colour of the substrate during early development. Newts raised from larvae on pale backgrounds developed less black pigment, relative to the yellow ground colour, than newts raised on dark backgrounds. The resultant colour pattern of the mature animal was found not to be subject to adaptive colour changes.

d. The development of hedonic skin glands. The skin of aquatic newts is highly glandular (see page 2/7). Little is known of the secretions produced by these glands, but there is circumstantial evidence, which will be detailed later, that suggests that there are important olfactory stimuli produced by the skins of both sexes in courtship behaviour.

While on the subject of skin secretions mention should be made of those not apparently associated with sexual behaviour. In some species, notably the Crested Newt, Marbled Newt and Alpine Newt, a creamy-white slime is produced from the skin when the animal is handled. This slime has a musty odour and is highly irritating if it gets

into the eyes and is very distasteful in the mouth. Smith (1951) recounts a highly colourful account of the effects of licking a newt and these effects may be the basis for the extraordinarily evil reputation that newts had in ancient folklore (e.g. Kinahan 1854, Wood 1863). In the course of this research it has been found that handling Alpine Newts produces prolonged bouts of uncontrollable sneezing. Little is known of the natural predators of newts, if there are any, but it seems likely that this slime is an anti-predator device, and that the bright colouration on the belly, which in most species is shown by both sexes in all seasons, has an aposematic function.

e. Enlargement of the cloaca. This becomes a large globular structure, dark in colour on the outside and with contrasting pale colouration visible within when the cloaca is open.

f. Development of dorso-lateral ridges. According to Smith (1951) these are formed by a glandular pad that develops dorsally and extends laterally to form a slight ridge running along each side of the body. Careful examination of whole sections through the thorax shows that this block of tissue is muscular and not glandular in composition (see page 2/80). This feature used only to be associated with the Palmate Newt in which species it is particularly marked (Smith 1951). However, Steward (1969) describes it in several subspecies of the Smooth Newt, namely T. vulgaris ampelensis, dalmaticus, graecus and meridionalis. As will be described later, under certain circumstances it is apparent in the subspecies used in this study, T. vulgaris vulgaris, though it is

never as conspicuous as it is in T. helveticus. No function has previously been ascribed to this structure but it will be suggested (see Chapter 4) that it has an important function in sexual display.

With all these changes complete, the newt has successfully reversed many of the changes it underwent in its metamorphosis from tadpole to adult and it is well adapted to lead an aquatic life throughout its breeding season. Although it has reacquired many of the characteristics of its fish ancestors it does not possess the fish's ability to maintain neutral buoyancy. Sexual displays in fishes such as Sticklebacks can take place in three dimensions; newts must confine their sexual activities to the two dimensions afforded by the bottom of a pond or aquarium.

Between three and ten days after courtship, description and analysis of which forms the bulk of this thesis, the female begins to lay her fertilised eggs. These are laid singly and each egg is wrapped carefully in the curled leaf of a water plant. In an aquarium this behaviour is readily observed. The female moves about among the plants, nosing the leaves. In this behaviour she looks as though she is examining and testing leaves but it is not at all clear to what factors she might be responding. Having found a leaf that she presumably considers suitable, she grasps it between her hind feet and wraps it around her cloaca which at this stage is somewhat protruded (see page 2/8). A single egg is then extruded into the cavity she has created within the folded leaf, the female making small body movements which can best be described as pelvic thrusts. When the egg is in position she maintains her position for some minutes, in which time the egg becomes firmly stuck to its encircling leaf. The female then releases the leaf and moves off to another leaf to repeat the process. One egg takes between 3 and 5 minutes to lay and, as the female lays up to 200 eggs (Smith 1951), she takes several days to lay all her eggs.

The development of the egg and larva was meticulously described by Rusconi in 1821 and more recent authorities (e.g. Smith 1951) have added little to his account. Once the eggs are laid neither parent shows any interest in them. After mating and egg-laying the adults begin to leave the ponds around late May or early June, and return to their mysterious terrestrial habits for the next nine months. After about 21 days the eggs develop into tiny tadpoles which, for the first day of their life, hang motionless from weeds and other objects. They then become very active, swimming about at great speed. At first they have large external gills. They develop forelimbs and then hindlimbs. Throughout their development they are carnivorous, unlike frog (Rana temporaria) tadpoles which go through a period of herbivorous feeding habits. At metamorphosis the gills are absorbed and the baby newts leave the water as miniature versions of their parents. Newly metamorphosed Smooth Newts are about 2 cm long, Crested Newts 4 to 5 cm long. The majority of larval newts metamorphose and leave the ponds in the summer in which they are laid but in certain ponds (e.g. Kidlington, near Oxford) it is quite common to find gilled larvae throughout the winter still in the water. These larvae metamorphose and leave the water in their second year. As with their parents, little is known about the life of young newts on land but it is believed that they spend 3 to 4 years in the terrestrial phase before they reach full adult size and return to ponds to breed (Smith 1951, Steward 1969).

As already mentioned, newts are occasionally found in ponds during the winter. These animals are not the remnants of the spring breeding population but are the result of an autumn migration. They usually show partly developed secondary sexual characters which become fully developed the following spring (Steward 1966, G. Bell (in progress)). It has been shown that Common Toads (Bufo bufo) are hormonally ready to breed in the autumn, but breeding is delayed by the persistence of adverse climatic conditions (Eibl-Eibesfeldt 1950).

The Sensory Capacities of Newts

In any discussion of display behaviour, a knowledge of the sensory capacities of the species concerned is important. In newts, these can be assessed by observation of their feeding behaviour. It has been shown that aquatic newts use vision, olfaction and sensitivity to water currents in the location and detection of food items (Matthes 1924a, Tinbergen and Ter Pelkwijk 1938). Vision is the primary sense used in the location of food, particularly from a distance, and movement of a prey object is essential if it is to be seen. Newts generally sniff prey objects when they have reached them and introducing food extracts into their tanks has the effect of generally exciting them. Stationary food items, which smell the same as moving ones, are taken only rarely. A small jet of water from a pipette, which provides neither visual nor olfactory stimuli, evokes a response in a newt. It will turn towards such a stimulus and must have perceived it by means of its lateral line organs. Blind newts are able to catch frog tadpoles and probably detect them by means of their lateral line organs (Cooke and Fulford 1971). There is good reason to suppose that these three senses, sight, smell and perception of water currents, are used in newt sexual behaviour.

In view of the vivid colouration shown by newts in breeding condition, it is relevant to consider to what extent newts possess colour vision. The retina of Triturus is known to contain cones, suggesting an ability to discriminate colours (Walls 1963). J.B. Nelson (1959) carried out a number of behavioural tests for colour vision in T. cristatus, which were not conclusive but which suggested that colour discrimination is absent. He showed that newts are sensitive to red, orange and green light, but this does not necessarily mean that they are appreciated as colours. Much of the vivid colouration is shown by both sexes, in particular the belly colour in T. alpestris and T. cristatus, which suggests that the primary selection pressure for this colouration may not be sexual but for its

warning properties, in association with newts' distasteful secretions. Those colour patterns that are sexually dimorphic are probably as likely to be effective as visual stimuli by virtue of their properties of contrast as of their colour; for example the dark spots of T. vulgaris males and the white tail stripe of T. cristatus males.

General Approach to the Study

The first aim of the research was to build up a thorough and detailed description of newt sexual behaviour. Earlier authors (Tinbergen and Ter Pelkwijk 1938, Marquenie 1950, Prechtl 1951) have described many of the behaviours that occur, but only J.B. Nelson (1959) has systematically investigated their sequential organisation and the relationships between the behaviours of the two sexes. By watching a number of courtship encounters a "catalogue" of the behaviour patterns that occur was built up, which included some behaviours not previously described (Chapter 2). This descriptive approach concentrated on Triturus vulgaris but also included other species (Chapter 4).

Having established a clear picture of the sexual behaviour repertoire, the next stage was to collect precise descriptive data for the purpose of analysis. This analysis aimed to investigate certain interesting questions raised by newt sexual behaviour:

1. The behaviour consists of a complex chain of behavioural events, some male, some female. Prechtl (1951) and Marquenie (1950) suggested that this chain could be understood in terms of stimulus-response relationships between male and female behaviours, similar to that found in the Sticklebacks (Tinbergen 1942, Morris 1958). J.B. Nelson (1959) approached the courtship of T. cristatus in a different way, explaining the sequence of male acts largely in terms of increasing sexual motivation, though stimuli provided by the female are also important. In this study the question of

to what extent the behaviour sequence is explicable, either in terms of mutual interaction between the sexes, or in terms of internal factors, is approached primarily by detailed analysis of observational data and secondarily by experiments (Chapter 3).

2. Vertebrate courtship behaviour is usually associated with conflict between the incompatible motivations or tendencies to flee, to attack and to mate (Morris 1956, Hinde 1970). In newts, whose behaviour repertoire does not include agonistic behaviour, this model does not seem to apply. This problem is discussed in Chapter 4.

3. All sexual behaviour has a definite function - to achieve fertilisation. In newts the successful transfer of the spermatophore is essential for this and the way in which male and female sexual behaviour are integrated will be crucial. The "functional design" of newt sexual behaviour, and the extent to which it is successful, is discussed in Chapter 4.

4. The evolution of newt sexual behaviour is of interest at two taxonomic levels: (a) Within the genus Triturus. Chapter 4 presents comparative data for a number of species and proposes a scheme for the evolution of sexual behaviour within the genus. (b) In a wider context. Triturus differs from all other Urodeles that reproduce by spermatophore exchange in that no amplexus is involved. The relationship of Triturus sexual behaviour to that of other Urodeles must be considered in the light of the fact that not all Urodeles, and none of the other Amphibian orders, employ a spermatophore. These aspects are discussed in Chapter 4.

The Species used in this Study

The Smooth or Common Newt, Triturus vulgaris

This species shows very marked sexual dimorphism (see page 2/9). The male has a very well developed, denticulated crest, and the whole body,

crest and tail are covered with large, conspicuous black spots of irregular shape and size. The head has seven irregular black stripes which converge on the tip of the nose, the belly is orange, marked with black spots, the cloaca is dark and the base of the tail bears parallel stripes of blue and red. The females are very variable in appearance, but are always much less conspicuously marked than males. The upper parts are greenish brown, the belly pale straw in colour. The variation between females is principally in the extent and patterning of darker spots on the back, flanks and belly.

The Smooth Newt is the most common species in and around Oxford and a number of substantial populations were located in the course of the study. Most of the newts used were caught in ponds at Kidlington and Water Eaton. Small numbers were also collected from Hinksey Stream in Oxford, and from Thornhill Pond in Savernake Forest near Marlborough in Wiltshire. Regular visits were made to these ponds throughout the breeding season and newts could be caught, used in observations or experiments and returned to the same pond, all within a few days.

As this species was so easily obtained in large numbers, and as it readily showed courtship behaviour in the laboratory, much more data was obtained from it than from other species. All the data from observations and from experiments used in the analysis of causal relationships (Chapter 3) were obtained from this species.

The Palmate Newt, Triturus helveticus

In many respects this species is somewhat similar to the Smooth Newt and in fact it was not recognised as a separate species in Britain until 1843 (Baker 1848), though it had been earlier described in Europe (Razoumowsky 1788). The females of the two species are very easily confused but the males are quite distinct. The male has only a very low, even-edged crest and is generally less dramatically coloured and

patterned (see page 2/10). The ground colour is variable, ranging from greenish to brown, and the spots, smaller than in the Smooth Newt are black, brown or reddish. The belly is pale but subdued in colour. The distinctive features of the Palmate male are the black, webbed hind foot and the shape of the tail with its smooth outline, truncated tip and characteristic terminal filament. The main difference between the female Palmate and the female Smooth Newts is that the former usually has very few dark spots and frequently none at all. However, since quite a few Smooth Newt females are also quite spotless, this is not a reliable character. An experienced newt collector can differentiate the two on the basis of the shape of the head. In the Palmate female the width of the jaw is greater, viewed from above, than in the Smooth Newt, relative to the distance between the eyes.

The Palmate Newt is not found around Oxford and so specimens were obtained from elsewhere and maintained in laboratory populations. The majority of Palmate Newts used in this study were very kindly provided by Professor H.G. Callan and were collected by him around St. Andrews, Fife. A small number were also purchased from Garrard and Haig Ltd., Newdigate, Surrey, who collected them from local populations.

The Alpine Newt, Triturus alpestris

This species could not be confused with any other on account of its spectacular colouration (page 2/11). There is sexual dimorphism, but it is less marked than in other Triturus species. Both sexes are blue, mottled with black, on the upper surface and flanks, and brilliant orange on the belly. Both sexes have a lateral band of black spots, but in the male these are larger and are ringed with white. The male has a very low crest of alternating black and creamy white stripes and he also has large irregular dark spots on the tail. There is no sexual dimorphism of the hind-limb and the male does not possess dorso-lateral ridges.

This species is not native to Britain but is readily available from most biological suppliers. Those used in this study came from Garrard and Haig Ltd. who maintain their own population. They proved to be very easy to keep and readily showed courtship behaviour in the laboratory. They do not show the strong tendency to leave the water at the end of the breeding season that British species show, but can be kept in aquaria all the year round. Some individuals have shown courtship behaviour in successive breeding seasons.

The Crested or Warty Newt, Triturus cristatus

This species, the largest of the three species native to Britain, has a most spectacular sexual dimorphism (page 2/12). The male has a very high, deeply denticulated crest which is not continuous with the very deep tail. In the breeding season the general skin colour, which is black in terrestrial animals, pales to a brownish or blueish grey, bringing into prominence large, irregular black patches. The belly is vivid orange, patterned with black markings. The lower flanks are spotted with white dots which in this area coincide with the raised "warts" that give this species one of its common names. On the tail there is a very striking white band which tapers towards the tail-tip. The female is much less spectacular than the male, lacking crest, white markings and many of the black spots.

Crested Newts are reasonably common around Oxford, being found in many of the ponds where Smooth Newts occur. It is a considerably larger animal and this may be connected with the fact that it did not take kindly to being kept in captivity. Males very quickly lost their crests and both sexes showed a strong tendency to leave their tanks. It was not easy to get this species to court in the laboratory and only a few sequences, using freshly caught animals, were recorded.

The Marbled Newt, Triturus marmoratus

This is another continental species and is similar in size to the Crested Newt (page 2/13). The ground colour of both sexes is green, and there is great variation in time and between individuals in the exact shade of green, ranging from a pale, vivid lime-green to a dark, brownish olive. The body and tail is heavily mottled with black and the belly is greyish brown, also marbled with black. The male has a very well developed crest of alternating black and yellowish stripes and a similar pattern on the dorsal tail edge. The tail also carries a white stripe similar to that seen in the Crested Newt. The female has no tail stripe or crest. Instead there is a shallow mid-dorsal groove which may be coloured red or brown.

This species was also obtained from biological suppliers. A number were bought from W. de Rover Ltd. of Holland. Like the Crested Newt, this is a large species but it lived well in tanks, the males keeping their crests for some weeks. The males showed interest in females but no female was ever responsive and so only fragmentary data was obtained for this species.

Method

Keeping of Animals

All newts were kept in aquaria 52 cm x 30 cm x 30 cm deep; males and females were kept separate, with up to 20 animals per aquarium. These aquaria were floored with soil overlaid with gravel, planted with a variety of waterweeds and aerated. (Aeration is not necessary for the newts, which breathe air from the surface, but for their live food and for snails which keep the aquarium walls free of algae.) When available, live food such as Daphnia and insect larvae was provided. Otherwise live maggots or chopped worms were used, and occasionally Tubifex. Males and females

of each species were kept in separate tanks, though in some cases males of different species were kept together. The keeping tanks were kept on a light schedule of 16 hours light, 8 hours dark; temperature was not controlled, and ranged from 9° to 22°C.

To aid identification of individuals, some of which could be recognised by their markings, all newts were toe clipped, using a code similar to that used by Twitty (1966) (see page 2/3, fig B). This is not permanent, but lasts for the duration of a breeding season.

Every attempt was made to use as many animals as possible for observations of courtship and to use particular individuals as few times as possible. However, this consideration had to be balanced against the need to build up a mass of data and so, as the breeding season is short and not all newts tried would show sexual behaviour, one frequently had to resort to "known courters". Appendix 1 contains information about how many individuals were used and how often.

Observational Procedures.

All observations and experiments were carried out in an aquarium 52 cm x 20 cm x 30 cm deep, floored with gravel and without plants. The front of the tank was marked at 10 cm intervals as an aid in assessing distances. This observation tank was subject to the same lighting and temperature conditions as the keeping tanks.

For a courtship observation the female was put into the observation tank first and left for 15 minutes before the male was put in. Usually a food item - a maggot or worm - was provided and this generally helped to calm the female. A few females would not settle down in the tank but swam frantically about. These were removed and replaced.

Males rarely reacted adversely to the strange tank and would immediately begin to walk slowly around it. Actual recording of behaviour was begun either when the animals came close to each other -

about 10 cm apart - or when either animal made a deliberate approach towards the other. Recording continued until the newts lost contact with each other, which might or might not have been after a complete courtship. When contact was lost the newts were either removed from the observation tank or left until contact was re-established. The decision as to when to end an observation and remove a pair depended on a subjective assessment of the probability that courtship behaviour would occur or continue. An important factor here was the patience of the observer. The willingness of animals to court was highly variable, changing from day to day and over the breeding season. Since the research concerned what happened during courtship and not what factors affect it in a general sense, no attempt was made to control for or to investigate such variations. In general courtship was more likely to occur early in the season than late, in the early morning than later in the day, between recently-caught animals than long-kept animals, and, on days when nothing went right, courtship could sometimes be elicited by adding warm water to the observation tank. In about a third of the pairings tried, the male showed no interest in the female nor she in him and no data was collected from such pairings. All pairings where the male did show interest were recorded and of these, approximately half involved females who also responded positively. As positive female behaviour is a prerequisite for a complete courtship sequence, only about half the courtship encounters recorded included the full behaviour repertoire. As a result more data was obtained for the early parts of the courtship sequence than for later parts.

Recording Procedures

The behaviour was recorded as a spoken commentary using a tape recorder. This commentary was subsequently transcribed twice. The first transcription was a written one, using specially prepared data sheets. The second transcription employed the "Organ" event recorder system

(Dawkins 1971) (see page 2/14). This consists of an electronic keyboard which produces pure musical tones, each event button being represented by its own particular note. These notes were played directly into a PDP 8 computer which printed out a record, on paper and on tape, with a code for each behavioural event and the time at which the corresponding button was pressed (see page 2/15).

This double transcription is obviously a very time-consuming procedure and it would have been far quicker to have used the organ as the primary method of recording the behaviour and thereby eliminated all the transcription. There are a number of reasons why this was not done:

1. The Newt-Organ has 29 buttons and there is a high risk of pressing the wrong button when one is trying to watch the behaviour. Transcribing the data from a verbal commentary to the organ virtually eliminated all such errors. Also recording the initial commentary into a tape-recorder makes it possible for the observer to devote all his attention to watching the behaviour.

2. The Organ system will only print out what it has been programmed to print out, and therefore unusual events which may occur cannot be recorded. The written record was very useful in this respect and also some parts of the data were more conveniently retrieved from the written record than from the Organ record.

3. All the experiments carried out during the study required the use of the observer's hands to manipulate the newts or models of newts. This clearly ruled out direct use of the Organ and the double transcription procedure was obligatory for recording the experiments. While this restriction did not apply to the purely observational work, using the same procedures for both observations and experiments had the advantage that all the data was collected and treated in the same way throughout the study, eliminating possible variations due to the use of different recording procedures.

The primary function of the Organ record was to provide data about the timing of the behaviour. Clearly this method of double-transcribing in which the organ is one stage removed from the behaviour as it happens will tend to introduce errors of timing. Although the organ gives times accurate to one tenth of a second, such a high degree of accuracy has not been assumed in the analysis of the data. On balance, it is felt that errors of timing would generally be of little significance and would be preferable to the errors in the recording of what events occurred which would have been likely had the organ been used as the primary recording method. The accuracy of the recording system was checked by making records from 16 mm motion-picture film of courtship encounters, and comparing the resultant Organ record with timing assessed by counting film frames.

Experimental Methods

The data produced by the Organ system provides information about what acts occur and when in the courtship sequence. From this one can obtain correlationsbetween acts in sequence and in time. From these correlations one can form hypotheses about which acts by one animal are causally linked with particular acts performed by the other. These can only be hypotheses. No matter how strong or suggestive the correlation one is always open to the "two church clocks" fallacy (Cullen 1972). To answer this objection one must manipulate the behaviour of one or both of the animals so as to "generate" behaviour according to objective criteria formulated by the experimenter.

In the description of courtship behaviour emphasis will be put on the difference in complexity of the male and female roles. The male's behaviour is very elaborate and involves many different behaviours, whereas the female's is very simple and consists of simple locomotor changes. Clearly the experimenter is much more likely to be able to

manipulate or imitate the female's behaviour than he is the male's. In the experiments in this study the female's behaviour has been manipulated or imitated in three ways:

Interference with a "free" female

The pair are allowed to behave normally until a certain point at which the female is restrained or removed, without directly disturbing the male, so that she cannot stimulate the male. This method has the advantage that it interferes least with the natural situation, but it has only limited applicability and has been used in only one experiment.

The Newt Model

The aim of making a model or dummy is to create a sufficiently good mimic of the female that the male is fooled into showing sexual behaviour toward it. In ethological studies models have been successfully used to investigate many aspects of stimulus situations. They have been used to show not only what visual features of a stimulus are relevant (Tinbergen 1951, Lack 1943, Heiligenberg et al. 1972), but also the relevance of orientation (Simpson 1968) and of postures (Hunsacker 1962, Stout and Brass 1969). In this study a model has been used to investigate the significance of the female's overall movements, moving away from or towards the male, or staying still.

Page 2/16 shows a variety of objects that male Smooth Newts have been observed to court in their living tanks during the course of this study. It includes other males, of their own and of other species, fishes, snails and stones. Clearly, some males do not seem to be very selective in what they will court which suggests that a fairly crude model should be sufficient to effectively mimic the female. For a few males such is the case. The model consists of a suitably sized piece of perspex rod, rounded at each end and mounted on a transparent perspex tube. The model itself is painted olive green above and straw yellow below (page 2/18, fig A). As observations suggested that the male responds to olfactory

stimuli provided by the female, the model incorporated a simple syphoning system which brings water carrying female scent down the perspex tube and out of the model's "cloaca" (page 2/18, fig B). It was found that, though most males showed an interest in the female smell emanating from the model, only a small proportion would actually court it. Those few males that would court it generally did so regardless of whether female smell was being piped through it or not.

There are certain limitations in the use of such a model. Males will court a model that approaches them - that is, is apparently responding positively to the male - but if the model stays still or moves away most do not seem to be deceived by it and will not court it or follow it. The model is therefore only of use in experiments involving those parts of courtship behaviour in which the female is positively responsive. A more general limitation is that, as mentioned above, only a small proportion of males will court models at all. Some initially unresponsive males could be induced to respond to models if they were first "primed" by being allowed to court a real female for a few minutes, after which the model was quickly substituted for the real female, but still not all males would court the model. Thus model data could be collected only from a limited sample of males who may be unrepresentative of the species as a whole. There is no evidence in any of the data obtained from model experiments that the behaviour of males who court models is aberrant, but the possibility exists. On the practical level, the use of models leads to the waste of a considerable amount of time trying to induce males to court models.

The Strait Jacket

This device is really a combination of the other two. A real female is used but is so restrained that she is effectively a morphologically and olfactorily perfect model. The Strait Jacket consists of a length of 8 mm (internal diameter) polythene tubing 2 cm long. This is mounted from

above on perspex tubing and is cut longitudinally along the lower side. The tubing can be opened up, the female put in and the natural elasticity of the polythene closes the tubing around her belly (see page 2/19). Thus the female can be moved about wherever the experimenter wishes and she is giving out all the stimuli, visual and olfactory, that a free female would.

This device does not have any of the limitations of the simple model and would have been used in all the experiments had it been invented at an earlier stage in the study. All males who will respond to free females will court a Strait Jacket female and will do so even if it is moving away from them (see page 2/20). Thus it can be used for experiments on the early stages of courtship behaviour where the simple model could not.

To be of any use a model or Strait Jacket female must do more than look and smell like a female; it must behave like a female. The experimenter must move it about in such a way that the male accepts it as a real female. To do this effectively the experimenter must be thoroughly familiar with the natural behaviour.

A thorough knowledge of the natural behaviour is important also in the design of experiments. The details of experimental procedures are described in Chapter 3 but in general all experiments were suggested by observations of variations in the behaviour, including "natural experiments" (Tinbergen 1953, Cullen 1972). These are the occasional unexpected events that occur from time to time in the observations of the behaviour, and are exceptions to the usual course of events. They frequently provide important clues about the causation of behaviour. Experiments based on these natural variations in the behaviour have the advantage that they do not represent too extreme a departure from the normal course of events and they are, therefore, likely to work and provide biologically meaningful results.

One final, important, note must be made in this introductory chapter. All the data presented in this thesis was obtained from observations in the laboratory. Every attempt was made to keep newts under as natural conditions as possible, and to disturb them as little as possible, but the possibility exists that the behaviour observed was not typical of animals in their natural habitat. The nature of newts' home ponds which are generally murky, weed-filled and cluttered with refuse, does not lend itself to accurate systematic observations, although some aspects, such as movements and distribution, have been successfully studied in the field (Gauss 1961). If a suitable site could be found for observations of newt sexual behaviour in the wild, the observations reported in this thesis could be seen in their proper perspective.

CHAPTER 2

CHAPTER 2

A DESCRIPTION OF THE COURTSHIP BEHAVIOUR OF THE SMOOTH NEWT, Triturus vulgaris

> "The more one contemplates this extraordinary proceeding the more one marvels at the evolution of a departure from the normal sexual relations so inconceivably strange." (W.P. Pycraft 1913.)

In this chapter the acts that occur in the courtship behaviour of the Smooth Newt, Triturus vulgaris vulgaris, will be described in detail. In addition, the general outlines of the sequential organisation of these acts will be described. A quantitative analysis of the sequence and timing of courtship acts is presented in the next chapter. This descriptive account is based on a total of 135 observations of free pairs of newts, involving 58 different males and 52 different females.

Before any sexual behaviour can occur, the male and female must come together. This happens in two ways. Very often the male and female, as they walk around the observation tank, literally bump into each other. Alternatively, the male may make a directed approach towards the female. In recording the behaviour a distinction has been made between incidental movements that the animals may make towards each other in the course of their wanderings and the directed APPROACH. There are two criteria for recognising a directed Approach. Firstly, it is generally preceded by some movement on the part of the female as she moves about, feeds or goes up for air, that is followed by him turning his head towards her and starting to approach. One sees the same kind of "purposeful" movement made towards a food item. Secondly, the attitude of the male in the directed Approach is different from his attitude when he is walking about in a non-sexual situation. His body

is raised at the front and his movements are rapid; indeed, in some instances he will swim rather than walk towards the female. The distance from which an Approach is made is clearly correlated with the distance between the animals when the male first sights the female. This is generally around 10 to 15 cm but the experimental situation clearly does not reach the limits of the newts' vision since males have on occasion been observed to approach a female from across the full length of the observation tank - 52 cm.

The characteristic head-up posture shown by an approaching male may, in certain circumstances, be shown by stationary males. A male who has been in recent close contact with a female who has moved away from him may adopt this ALERT POSTURE (see page 2/21). Prechtl (1951) described how males showed this posture when put into a tank that had recently contained females.

In the majority of sexual encounters the first meeting between male and female is the result of a chance contact, not of a directed Approach. However, if the animals lose contact with each other in the course of an encounter, as they quite frequently do, contact is usually restored by a male Approach. It would seem that the male is more receptive to a distant female if he has previously had some contact with her.

In a very few sexual encounters first contact is made by a directed Approach on the part of the female. In these instances her behaviour resembles that of the male described above and her approach usually serves to attract the attention of the male towards her.

Once male and female have come together the male begins to SNIFF the female. His head is lowered and his snout pressed against the female's tail, cloaca, body or head, and frequently the tip of his tail begins to twitch. That the male is sniffing the female is suggested by the fact that the movements of the floor of his mouth become more rapid (Matthes 1924a). The female's reaction to this is generally to move away, often

so vigorously that contact is lost. The male will almost invariably follow her and, if he catches up with her, will resume his sniffing or attempt to take up his display position in front of her. Most encounters begin with a prolonged period of this pursuit of the female by the male, with the male taking advantage of the female's passive moments to sniff her.

One of the most striking movements in sexual behaviour is that with which the male takes up his display position. This I have called MOVE TO THE FRONT. As its name implies, it is primarily an orientation movement but the fact that it is very conspicuous and stereotyped in form suggests that it may also have signal function. The male, from his position behind or to the side of the female, swims round one side of her with his body inclined inwards towards her and his head turned towards her. As he passes her head he cuts in sharply across her snout and comes sharply to a halt in front of her, using a powerful lash of his tail to brake his movement (see page 2/21). In most cases the female swims away when this first happens, in which case the male resumes his chase and tries again to take up his position in front of the female. In many sexual encounters this chasing continues for some time. If the female's movements away from the male become more and more vigorous then she is considered to be unresponsive and is removed. A responsive female becomes less likely to swim away when the male Moves to the Front so that he is able to begin his display and a full courtship sequence generally follows.

The male's DISPLAY consists of movements of his deep, highly decorated tail. Throughout his Display the male maintains his position in front of the female with his head pointed at hers. His body is generally within an arc of 45° on each side of the female's midline axis (see page 2/22), but he may be forced to one side by an obstruction such as the wall of the observation tank. Three tail movements have been

differentiated, the WHIP, the FAN and the WAVE. Discriminating between these three tail movements brings the observer to an important theoretical consideration. At this early stage of a study one is attempting to describe behaviour without interpreting it. However, in saying that one action is distinct from another similar action the observer is making interpretative assessments of the behaviour by treating it as a series of discrete, discontinuous units. In many instances actions are so strikingly different that this problem does not arise. Such is the case with the Whip and the Fan. Each is a highly stereotyped and conspicuous action and they differ strikingly in a number of ways. In contrast, the term Wave refers not to a distinct act, but to a broad category of acts, all of them distinct from Whip and Fan but not from one another, at least with the recording method used. It is probable that, if the behaviour was analysed on film or video this category could be further subdivided, but in the confusion of a courtship encounter it is not possible to make the necessary precise distinctions.

The tail movements performed by the male in his Display are illustrated on pages 2/23 to 2/25. The Whip is a vigorous lash of the tail, essentially the same movement as that which ends the Move to the Front. The body is held rigid, and the tail, from a position out to one side of the body, is suddenly whipped back against the male's flank. This creates a powerful blast of water towards the female's head, often so violent that she is pushed backwards. This movement is virtually always incorporated into the Move to the Front movement, but is also frequently performed independently.

The Fan is a complete contrast to the Whip. Whereas the Whip is a sudden, violent, single action, the Fan is a gentle, sustained movement. The body is rigid and the tail is flexed in the middle so that its distal portion lies parallel and close to the body. Very rapid waves pass along this distal portion of the tail towards its tip so that the tail tip

vibrates. Fanning produces a steady stream of water that is usually directed, because of the male's orientation, towards the female's snout. Its path can be readily seen by the movement of small detritus particles that are caught up and carried along by the current. Fanning is a continuous movement and Fanning bouts can last for several seconds.

The Wave category includes all other conspicuous tail movements made by the male during his display, which can be very variable in form. In experiments carried out in the later stages of the research, this early part of courtship behaviour has been experimentally prolonged by manipulation of the female's behaviour. This makes it possible to observe more courtship actions than normally occur in encounters between free animals. In the course of these experiments a particular type of movement has been noted which should perhaps be differentiated from other Wave movements. In this movement the tail is held out to one side so that it makes an obtuse angle with the side of the body nearest the female, the body is inclined slightly inwards towards the female and frequently the male bobs gently up and down. Since this is the only courtship action of the male in which his highly developed epigamic characters are effectively displayed to the female, it is an attractive hypothesis that this type of Wave is a visual display movement. This movement is similar to that which immediately precedes the Whip, but the tail is held out instead of being whipped back. Since there are no good criteria to quickly differentiate between these "Showing Off" Waves and other less dramatic movements, no attempt has been made to do so in recording the behaviour. For the purposes of analysis, therefore, the term Wave includes the Showing Off movement and some other, less dramatic movements. This is not a very satisfactory situation, but, without making too many interpretative assessments at the descriptive stage, unavoidable.

The male's display consists of a series of these three tail movements, Whip, Fan and Wave. The precise sequence in which these acts are

performed is dealt with in a later chapter. During the male's display the female may do one of three things; she may move away, stay still, or move towards the male. If she moves away the male reverts to his earlier behaviour, pursuing her and trying to Move to the Front to resume his Display. When she stays still the male keeps displaying to her and, after a time, the female may begin to show signs of interest in the male. She turns her head towards him and the sniffing movements of the floor of her mouth can sometimes be seen to increase in rate. These signs of interest precede her movement towards the male. This is a crucial point in the courtship sequence, being the first indication that the female is responding to the male's behaviour. It is followed by a change in the male's behaviour.

As the female approaches the male, he begins to retreat in front of her, all the time maintaining his orientation relative to her, his head pointed at her head. As he retreats before her he continues his display of Whips, Fanning bouts (now less frequent and of shorter duration) and Waves. When the male displays to a stationary female he must brace himself against the backwards propulsive force generated by his powerful Whips. In his retreating display he no longer does so, so that his Whips help to push him backwards. He may also make RETREAT movements in which no tail movement is incorporated or he may Fan as he retreats. As the male retreats and displays before her, the female follows him. Once she has begun to approach the male the female will usually continue to do so with great persistence. Occasionally, however, she may revert either to negative behaviour, moving away from the male, or to static behaviour, stopping in her tracks. In each case the male adjusts his behaviour appropriately, either following her and resuming his display position, or reverting to his stationary display behaviour.

As she begins to approach the male, the female's cloaca can be seen to extend slightly downwards so that it projects about 2 mm from her

body. The significance of this will be seen in a later part of the courtship behaviour.

Throughout his Display, both static and retreating, the male maintains his orientation relative to the female, two to five centimetres in front of her, and facing her. When he is Fanning the male faces directly towards the female's head; during the Whip and Wave movements his body is usually rather more side-on to her. Thus the female is presented with a partial or complete view of one side of the displaying male. There is no constancy as to which side the male presents to the female and, in the course of his display, a male quite often changes the side that the female sees by a movement called TURN ABOUT. In this movement he jumps up slightly from the substrate and turns his body so that he lands with his opposite side presented to the female.

The later stage of the male's display, with the male retreating before the oncoming female, continues for some time until a second crucial point in the sequence is reached. This is when the male turns away from the female and begins to CREEP. In this movement the male faces away from the female for the first time in the courtship sequence. He moves along the line of his previous Retreat movement with his body held low, his tail straight and rigid, with slow, jerky steps. The female follows him. By this stage in the courtship sequence she behaves as if mesmerised. She follows the male closely and if a glass screen is put into her path, she does not show any alarm, but continues to try and press on after the male. When the male has Crept for 10 to 20 cm he stops and shows another movement, the QUIVER. In this movement the body remains rigid and is held low. The tail is held straight and slow waves pass along it from base to tip. The female is still moving steadily towards the male, and so she simply bumps into his quivering tail-tip. This is called the TAIL-TOUCH and when it occurs the male folds up his tail concertina-fashion and at the same time lifts the whole tail up. As the

tail lifts the cloaca opens fully and the spermatophore is extruded onto the substrate in front of the female's nose. The spermatophore is clearly visible as a tapering white object, about 5 mm long. In fact this is the sperm core which is contained in a large gelatinous structure which can only be seen under particular lighting conditions. As the spermatophore appears the cloacal lips are open wide, revealing two parallel white bands, one on each side of the cloacal opening, which contrast strongly with the black colouration of the outside of the cloaca.

As soon as the spermatophore has been deposited the male moves away from it in a movement called CREEP-ON. In this movement the male moves away from the spermatophore with his body held low and his movements slow and jerky. As he moves away he turns to one side so that he moves through an arc, until his body has passed through about 90°, at which point he stops with his body across the path of the female, who has followed the male's movement. In this position, which is called BRAKING, his tail, still folded, is on the side facing the female. She, following him, maintains close contact with his folded tail so that when he stops in the Braking position her nose is pressed against his tail. The sequence of behaviours from Creep to Braking is illustrated on pages 2/26 to 2/29.

This is the crucial part of the courtship sequence, the part that involves the free spermatophore. Following spermatophore deposition, the male moves forwards and sideways in such a way that his body takes up a position perpendicular to his original direction of movement, and approximately one body's length from the point where the spermatophore was put down. At the same time the female, following the male closely, has moved from the point where she touched his tail prior to deposition to the point where she presses her nose against his tail in the Braking position. Thus her snout, and therefore her cloaca, has moved through a distance roughly equal to that moved by the male, i.e. one body's length. Thus her cloaca will, at the Braking stage, be approximately above the

point on the substrate where the spermatophore was deposited. If cloaca and spermatophore come together the tip of the spermatophore attaches to the female's cloaca. The female shows no interest in the spermatophore at this or at any other stage in the courtship sequence. Her attention seems to be directed at the male's tail from the point when he turns away to Creep until he Brakes and she presses her nose against it. The female clearly pushes quite hard against the male's tail, as he can be seen to be resisting her pressure. This resistance frequently manifests itself as a movement called PUSH-BACK (see page 2/30). In this the male bends his body towards the female and at the same time flexes his tail away from the body. The effect of this is to push the female backwards along the path of her previous movement. Having pushed her back in this way the male resumes his Braking position and the female again moves towards his tail and resumes her position with her nose pressed against his tail. Push Back does not invariably occur in a courtship sequence, whereas all the other actions described do. If it does occur it may or may not be repeated several times.

The process by which the spermatophore becomes attached to the female's cloaca is not understood in detail. As mentioned earlier, the female's cloaca becomes extended when she first starts to move towards the male. What seems to happen is that this extension is achieved by turning the distal part of the cloaca inside out. When the female follows the male after spermatophore deposition, her belly, swollen with eggs, often brushes against the spermatophore but it rarely becomes attached to the belly. In contrast, if the cloaca brushes the spermatophore it invariably becomes attached, which suggests that there is some special affinity between the spermatophore and the female cloaca. The spermatophore remains trailing from the female's cloaca for some time and is still trailing after sexual behaviour has finished and male and female have gone their separate ways. Gradually the sperm disappears into the

body of the female. It seems that this is achieved by the cloaca becoming restored to its original state - the reverse of the process by which the cloaca is extended. When the white sperm has disappeared the gelatinous capsule remains attached to the female's cloaca and, after courtship has finished, the female can be observed moving about the tank rubbing her cloaca against stones to remove the capsule.

Push Back ends the courtship sequence. Following it one of two things may happen. Either animal may move away, most commonly up to the surface to breathe. Alternatively the male will back a little away from the female, turn his head towards her, and he is back in his earlier Display position. He then begins his Display of Whips, Fan bouts and Waves. The female is usually still responsive and so the animals are back in the retreating display situation and from this point the whole process already described is repeated.

In a sexual encounter between a pair of animals the whole courtship sequence may be performed once, twice, three times or, very rarely, four times in succession. Thus in any one encounter between a male and a female up to four spermatophores may be produced. In no instance has an encounter continued beyond four spermatophores; usually the animals break off after two or three spermatophores, when one animal loses interest or goes up to the surface for air.

At this point it is necessary to clarify a point of terminology. The term courtship ENCOUNTER refers to any courtship interaction between a male and a female. The term courtship SEQUENCE is applied to that behaviour that leads up to and involves the deposition and possible pick-up of one spermatophore. Thus an encounter may include one or more complete courtship sequences, or none at all.

Page 2/31 shows a schematic representation of the courtship sequence of T. vulgaris. The sequence is divided into four separate phases. The

first of these, the ORIENTATION PHASE, includes all those actions leading up to the male's adopting his Display orientation in front of the female, from his initial approach, his sniffing of her, trying to Move to the Front and following her when she moves away. If she stays still the courtship sequence moves into its second phase, STATIC DISPLAY, in which the animals remain in the same place with the male displaying to the female. It is rare that these early phases are as clearly defined as this diagram suggests. Frequently the female swims away during Static Display so that the animals revert to the Orientation Phase. To keep the diagram simple, all possible transitions have not been included. The female's approach towards the displaying male signifies the transition from Static Display to the next phase, RETREAT DISPLAY. Again the diagram could include reverse arrows to indicate those occasions when the female stops still or swims away and the animals revert to the appropriate earlier phase. The start of the final phase, the DEPOSITION PHASE, is when the male turns away to Creep and this phase includes all those behaviours associated with the deposition and picking-up of the spermatophore. Finally, following Braking or Push Back, the sequence re-cycles with a return to the Retreat Display Phase.

These phases have been named according to the male's behaviour. The first three phases of the courtship sequence could also be labelled on the basis of the female's behaviour. In the Orientation phase she is typically moving away from the male, in the Static Display Phase she is stationary and in the Retreat Display Phase she is moving towards the male. It should be stressed that this diagram represents a greatly simplified and "idealised" summary of the courtship sequence.

The summary diagram is built up from many observations of courtship behaviour. There is so much variation at all points in the sequence that no two sequences are exactly the same. There is, however, much more variation in the earlier parts of the sequence, chiefly because females

generally oscillate between moving away from the male, staying still and moving towards him. In contrast, the later stages, particularly the Deposition Phase, are much more predictable.

There is a marked contrast between the roles of the two sexes in the courtship sequence. Whereas the male's behaviour involves a variety of complex movements and postures, the female's behaviour can be simplified into three simple locomotory states, moving away, staying still and moving towards the male.

Another important point is that at no stage does either animal seem to respond to the spermatophore as such. The behaviour sequence proceeds as if the spermatophore were quite incidental to the whole process. This is well illustrated by the observations of W.C. Grant (pers. comm.) who induced courtship behaviour by means of injection with the hormone Prolactin. This treatment stimulated males to show the entire repertoire of courtship behaviours though no spermatophores were produced. They even performed a pseudo-deposition movement. In the course of this study four such pseudo-depositions have been recorded in sequences involving untreated animals. The tail is lifted in the usual way and the cloaca is opened but no spermatophore appears. Despite the absence of a spermatophore, post-deposition behaviour proceeds as usual. Unusual variations from the normal behaviour sequence such as this provide the "natural experiments" mentioned earlier. These are described fully in Chapter 3 in the context of the experiments which are based on them.

Aberrant Behaviour shown by Females

The most remarkable variation from normal sexual behaviour, which is seen only rarely, is pseudomale behaviour. Females have been observed to show behaviours that are typical of the male's normal repertoire. Very occasionally a female has been observed displaying to a male in the course of an encounter, but more often pseudo-male behaviour is shown by one

female to another in their home tank. The acts concerned include Whip, Wave and Fan and in one case a female showed a recognisable Creep to a male. This behaviour is associated with what can loosely be called "frustration" of the female. All the females concerned were very fat with eggs and had been kept for some days with only other females for company.

Sexual frustration is suggested as the causal factor leading to the pseudo-male behaviour which is shown on very rare occasions by female Sticklebacks (Morris 1952). In a discussion of pseudofemale and pseudo-male behaviour Morris (1955) lists a number of causal factors which, singly or in combination, may lead to such aberrant behaviour. In many cases sexual inversion can be related to the aggressive or hierarchical context in which the behaviour occurs. Thus a subordinate or submissive male may show pseudofemale behaviour, or a dominant female pseudomale behaviour. In newts, which show neither fighting nor a social heirarchy, this relationship cannot be made. Another of the factors in Morris' list, sexual thwarting or frustration, does seem to be relevant, as suggested above. Hinde (1970) discusses sexual inversion in relation to conflict situations in which sexual behaviour is thwarted. He suggests that sexual arousal in either sex involves an increased tendency to perform both male and female behaviour, though male behaviour is normally of higher priority in males, and vice versa. If the appropriate behaviour is thwarted, that of the other sex may be shown.

A rather more common occurrence that seems also to be associated with females deprived of sexual contact is unusually strong approach towards the male. Mention has already been made of the fact that in a few encounters first contact is brought about by a female approach. This is unusual in itself and these females often approach the displaying male much more vigorously than is usual. This has the effect that the female moves towards the male faster than he can retreat before her and so he is forced to move sideways rather than backwards. The pair thus move round

in a tight circle and the male's display becomes disjointed and erratic. In some cases males faced with such females turn and swim away, but usually the male will Creep. The round and round behaviour seen with these highly active females is called WALTZING.

Glossary of Terms used in the Description of Courtship Behaviour

Where abbreviations are used in subsequent parts of this thesis these are given after the name of the behaviour.

ALERT POSTURE. A posture shown by the male in which he stands only on his hind feet, with his head and forelimbs lifted off the substrate.

APPROACH (A). A directed movement by one animal towards the other. Movements rapid, body usually slightly raised. Usually a male act, occasionally female.

BRAKING (Br). A position taken up by the male after spermatophore deposition. Body perpendicular across the female's path, tail folded on side facing her.

CREEP (C). A male act following display and preceding spermatophore deposition. Male moves away from female, body low, tail straight, steps slow and jerky.

CREEP-ON (CO). Male act immediately following spermatophore deposition. Male moves forwards and to one side with slow jerky steps.

DEPOSITION PHASE. That part of courtship behaviour involving deposition and picking-up of the spermatophore.

DISPLAY. All that behaviour shown by the male positioned in front of and facing the female. Consists principally of tail movements. Subdivided into Static and Retreat Display.

ENCOUNTER. A unit of behaviour including all that occurs between the male and the female from the time they are put into a tank to the time one or both is removed.

FAN (N). A male display act. Tail held curved against rigid body and distal part vibrated rapidly. Sets up water current towards female. Of variable duration.

FOLLOW (F). A male orientation movement, seen when female moves away from him.

MOVE TO THE FRONT (M). A male orientation movement. Male, from behind or to one side of female, swims past her flank, body inclined towards her, head turned towards her, and then cuts sharply across her snout to take up his Display orientation.

ORIENTATION PHASE. All behaviour leading to the male taking up Display orientation in front of female.

PUSH BACK (PB). A male act following Braking. Body moved towards female, tail flexed away from body. Female is pushed away from the male.

QUIVER (Q). A male act following Creep. Body stationary, slow waves pass down tail from base to tip.

RETREAT (R). A male act associated with Display. Male moves backwards in front of female and remains facing towards her head.

RETREAT DISPLAY. All male display behaviour performed while retreating in front of the approaching female.

RETREAT & WHIP (RW). The Whip movement performed at the same moment as the male's body is moved backwards.

SEQUENCE. A unit of behaviour including all that occurs between male and

female prior to, and immediately involved with the deposition of one spermatophore.

SNIFF (SN). One animal presses its snout against the other. Olfactory movements of the mouth-floor increase in frequency. Usually a male act, occasionally performed by females.

STATIC DISPLAY. All behaviour shown by the male while he is in his Display Orientation and the female is not moving.

TAIL-TOUCH (TT). A female action shown twice in the courtship sequence. The first occasion is after the male's Quiver and before spermatophore deposition, the second occasion follows Braking.

TURN-ABOUT. A male act performed during Display. Male jumps up and resumes his display orientation but with his other side presented to the female.

WALTZING. Display behaviour in which the female approaches the male abnormally vigorously. As a result the animals move around in circles.

WAVE (WA). A male display act. A loosely defined category of acts including the conspicuous SHOWING-OFF WAVE and less distinctive tail movements.

WHIP (W). A male Display act. Tail is flexed away from the body, then brought back rapidly against the flank. Creates a blast of water towards the female.

A comparison of the terminology for newt behaviours used in this thesis with that of earlier authors is presented in Appendix 2a.

Appendix 2b consists of a courtship record of a sample Encounter.

CHAPTER 3

CHAPTER 3

ANALYSIS OF THE CAUSAL RELATIONSHIPS BETWEEN MALE AND FEMALE BEHAVIOURS

The aim of this chapter is to establish as far as is possible the causal links between the behaviour of the male and that of the female in the courtship sequence. Put another way, the aim is to determine to what extent a given act A by one animal is the immediate stimulus that causes the other animal to perform a particular act B. The evidence from which such causal relationships are inferred is twofold:

1. The records of courtship encounters obtained by means of the Organ event recorder system. This data is from animals that were not interfered with in any way by the observer and is hereafter referred to as Observational Data. This data has been analysed to establish sequential relationships between courtship actions, and in many instances the time information contained in the Organ output has been analysed to establish the temporal pattern of transitions between actions.
2. Experiments in which the behaviour of one animal - in all cases the female - has been manipulated in some way. The nature of these experiments varies according to the part of the courtship sequence concerned, but the basic principle of them all is to change the female's behaviour according to some predetermined scheme and to record the male's behaviour.

The data presented in this chapter has all been obtained from T. vulgaris and has been collected over three years, 1970 to 1972. The Organ system was used in 1971 and 1972 only and the bulk of the data used in this analysis is from these years. However, in some instances where only sequential information is required, 1970 data has also been included.

There are reasons why one might expect differences in the data from

different years. Firstly, there is the general point that one would expect accuracy of observation to improve with increasing familiarity with the behaviour. For this reason the rarer behaviours might at first be missed but be more reliably recorded in later observations. In the course of the first year of observation, 1970, this was certainly the case, but there is no evidence of any such variation between 1971 and 1972 data. A further possible reason for year to year variation is that in 1970 and 1971 all observations were made in a hut whose insulation was poor and there was considerable variation in temperature from day to day and from hour to hour. After the 1971 season there was a move to a new building which had a generally stable temperature of 18 - 22°C, which is somewhat higher than the average temperature recorded in the hut. It was not expected that temperature variations would have a very dramatic effect on sexual behaviour, since the variations in the laboratory would be much less extreme than those prevailing in the natural situation, but it is possible that the discrepancy in mean laboratory temperature between years might introduce slight behavioural variations. For this reason the data from different years has been analysed, and is presented, separately. In fact, with a very few exceptions, the data from different years is very uniform.

This chapter deals with the various parts of the courtship sequence in the general order in which they occur, as shown in the summary diagram on page 2/31. The pattern of the behaviour changes from stage to stage, not only in the behaviours shown, but in the degree of variation of behaviour shown by the two sexes. For this reason the courtship sequence is not analysed as a whole but is considered in three sections, with a different method of analysis applied to each section. The first section deals with the male's initial behaviours, Approach and Sniff, the second section deals with Orientation and Display behaviour and the third section is concerned with the Deposition Phase.

The Male's Initial Behaviour

At the start of a courtship sequence, the male is generally the active animal, Approaching the female and Sniffing her, before taking up his Display position in front of her. The question to be answered is: by what cues does the male recognise the female for what she is?

The Male's Approach

Most male Approaches are from fairly short distances, after the two animals, in their independent movements around the observation tank, have come close together. However, some Approaches begin when the male is some distance from the female. It seems that the Approach is generally a response to some movement by the female. In recording the behaviour the distance from which the male began to approach was estimated by reference to the 10 cm markings on the front of the observation tank. The distance measured was from the male's head to the part of the female nearest to him. Analysis of this data (see page 2/32) shows that 61% of all male approaches (top histogram) are from 5 cm or less, 20% from 5 to 10 cm, and only 19% are from distances greater than 10 cm. These data can be split according to whether an approach was the first made by a male in a courtship encounter (middle histogram) or a subsequent approach following a loss of contact (bottom histogram). When split in this way it is clear that there is still a preponderance of approaches from a short distance in both first and subsequent approaches, but, overall, subsequent approaches are from further than first approaches. The mean value for first approaches is 5·1 cm, that for subsequent approaches is 7·7 cm. The difference between these two distributions is statistically significant - $0{\cdot}01 < p < 0{\cdot}05$ (Kolmogorov - Smirnov Test). (Data from only one year, 1972, was used in this analysis because greater care was taken in the measurement of distance in that year.)

These results support the conclusion that courtship encounters usually begin with a chance meeting and not with a long-distance directed approach. They also suggest that once the animals have met, and the male has had close contact with the female, he is thereafter, for a short time at least, more responsive to her.

The Approach Experiment

The aim of this experiment was to assess which stimuli, given out by the female, are important in eliciting the male's approach towards her. From general familiarity with newts I expected the stimuli most likely to be important to be visual, olfactory or vibrational. The experiment was conducted in a tank 45 cm x 25 cm x 25 cm deep which contained no gravel and no plants. The floor of the tank was glass and was marked with concentric circular lines, 5 cm apart, radiating from the centre, which were used for assessing distances. Observation was through both the front of the tank and the bottom, using a mirror positioned at 45° to the tank floor (see page 2/33). Each experiment consisted of four trials and in each trial a different test object was placed in the centre of the tank:

Trial A: A live female in a conical glass flask with its own opening to the air. This would enable the male to see the female but not to receive any olfactory stimuli from her, or to perceive water currents generated by her.

The female's movements, which, on observational grounds, I think attract the male's attention to a female, were not controlled in this set-up. In practice, females generally moved about all the time when so confined and so were providing more-or-less continual movement stimuli.

Trial B: A live female in a conical glass flask with 5 mm diametre holes bored at 1 cm intervals around its base. In this situation the male would potentially be able to receive all three sorts of stimuli from the female, though water currents would be much distorted.

Trial C: A glass tube with 6 arms radiating from it, through which was piped water which had previously passed through a flask containing a live female. This arrangement would present the male with olfactory and turbulence cues but no visual cues.

Trial D: The same glass device through which was piped water from the test tank which was not passed over a female. This arrangement would provide turbulence cues only.

Ten different T. vulgaris males were tested, each male being presented with the four test objects in a different order. The water in the test tank was changed between trials to eliminate residual odours, and a full 24 hours was allowed to elapse between trials to minimise any effects due to experience of one trial being carried over to the next trial. In each trial the male was put into the test tank 15 minutes before the test object was put into position, and this was done when the male had moved into one of the corners of the test tank. Thus all males began the trials the same distance from the test objects. The male was left to move around the tank until he had spent a total of 60 seconds within the 10 cm circle, i.e. within roughly 5 cm of the test object. A number of measures were recorded: total time in the tank, the number of lines crossed (a crude measure of general activity), the distance at which the male showed a response to the test object, and the water temperature. Responses were classified as strong or weak. A strong response was an approach towards a test object that was maintained from the time the male first started to move towards the test object to the time he reached it. A weak response was either an approach which was not maintained for the full distance, or a mere turn of the head towards the female. The number of Approach responses shown to each type of test object, and the distances from which these responses were made, are shown on page 2/34.

These results show:

1. That visual cues alone can effectively elicit a male Approach at the

start of a courtship encounter. There are significantly more responses (strong and weak combined) in both conditions A and B than there are in either condition C - $p = 0{\cdot}01$ - or in condition D - $p = 0{\cdot}0004$ (Fisher Exact test).

2. That the addition of olfactory cues does not increase the probability of approach. In fact in this experiment the addition of olfactory cues apparently decreased the probability of approach. This is possibly due to the fact that the holes bored in the glass flask for condition B have the effect of distorting the glass and thereby interfering with the male's view of her. Approaches towards the purely visual test object are from further than those to the more complex object, but this difference is not statistically significant.

3. There is the slightest suggestion that olfactory and turbulence stimuli together can elicit approach but there is no evidence that turbulence stimuli alone can.

This was not a very satisfactory experiment, principally because there was no way of knowing whether the olfactory and vibrational cues received by the male were of a type and intensity present in the natural situation. More exhaustive experiments would be needed before one could say for sure that such cues are or are not used by the male in the location of the female. There is evidence that female odour elicits the male's Alert Posture (see Chapter 2), and it is probable that, in this posture, the male is more responsive to visual stimuli.

This experiment took a great deal of time, principally because a full day was allowed between trials. As it was somewhat peripheral to the main aim of the study, which was to investigate causal relationships within courtship, and not those leading up to courtship, it was not pursued further. The one positive result that it did provide is that visual cues are operative in the Approach by the male towards the female.

The Male's Sniffing of the Female

The male may Sniff at any part of the female's body, but he is more likely to Sniff at some parts than at others. The proportions of Sniffing bouts directed at different parts of the female's body are shown on page 2/35. There are marked differences in the data from different years; a 3 x 4 chi-square test shows that the data from the three years is heterogeneous - $p<0{\cdot}001$. On inspection, the proportion of bouts directed at the female's head and trunk do not vary appreciably from year to year, but the proportions directed at her tail and her cloaca do. This variation is in a consistent direction, with apparently an overall tendency by the male to sniff less at the female's cloaca and more at her tail. It is not easy to explain this trend. It is most improbable that these year-to-year variations reflect any real change in the natural behaviour of newts over the period. These variations may be an artefact due to some variation in the laboratory conditions, or, more likely, they reflect a more accurate differentiation by the observer between sniffs directed at the cloaca and sniffs directed at the most anterior portion of the female's tail.

Data on the distribution of male Sniffing bouts are presented by Marquenie (1950) (see page 2/35). His data differ from all those obtained in this study in that he recorded a smaller proportion of Sniffing bouts directed at the female's trunk.

It is difficult to make firm conclusions from these data, because of the variation from year to year. Marquenie's data show that the male's attentions are directed principally at or around the female's cloaca, suggesting that he is responding to sexual odours. The data from this study do not unequivocally support this.

There is considerable anecdotal evidence concerning the function of the male's Sniffing behaviour. Some males will court inappropriate objects that have been in recent contact with females such as cotton-wool balls (Zippelius 1948) and stones (personal observation), and they will court

other males when water from a tank containing females is introduced into their tank (Tinbergen and Ter Pelkwijk 1938). Many males show an intense interest in the "cloaca" of a newt model through which female-tainted water is being passed. These observations suggest that female smell has the effect of sexually arousing the male; though the fact that males do not invariably Sniff females before displaying to them suggests that female smell is not always a necessary stimulus for further courtship behaviour.

Apart from serving to excite the male, female odours may be a means by which the male can recognise a female. This recognition could be important in two contexts: in chosing females of the same species and in chosing females who are sexually "ripe". I have never observed a male "reject" a female after Sniffing her - that is, do anything but begin to court her. However, in the laboratory males may, as suggested by their responses to crude models, be less selective than in the natural situation, possibly as the result of being confined without contact with females.

Orientation and Display Behaviour

The idea that the early parts of the courtship sequence can be divided into three distinct phases has been introduced into the description of the behaviour to emphasise and to clarify the important changes that take place. To say that three distinct phases are apparent in all courtship sequences would be misleading. As mentioned before, the behaviour in the early parts of the sequence is highly variable. One of the objects of the analysis that follows and of the experiments carried out on the Display phase is to provide evidence for the hypothesis that the male alters both his orientation behaviour and his display behaviour according to the nature of the female's behaviour. However, in the analysis that follows the assumption that the male shows two types of

Display behaviour is not made. Instead, all the males' behaviours are considered in the same way as discrete and independent actions. In most courtship sequences Display behaviour and Orientation behaviour are intermixed. Consequently it is not realistic to treat the two types of behaviour in total isolation. In this analysis the links between Display and Orientation behaviour are examined as well as those between one Display behaviour and another.

The male acts included under the heading Display are: Move to the Front, Whip, Fan, Wave, Retreat, Retreat and Whip. This grouping separates them on the one hand from Orientation movements - Approach, Follow and Sniff, and on the other hand from Deposition Phase Actions - Creep, etc. A number of points should be made about this classification of acts:

1. Move-to-the-Front. The name of this action suggests that it should more properly be considered as an Orientation movement. It is included as a Display act partly because I have suggested that it has signal properties, but primarily because it is so closely associated with Display behaviour, particularly with the Whip movement. It is perhaps best regarded as a linking act between Orientation behaviour and Display.

2. Retreat. The name of this act also suggests orientation. It is treated as a Display act because it is so closely associated with the male's tail movements and because it is concerned with maintaining the male's Display orientation and not with initiating it.

3. Whip and Retreat-and-Whip. These could be considered together as one action, as the tail-movement involved is the same in each action. However, as they occur in different circumstances, for the purposes of analysis they are considered as separate acts.

4. Fan. This is the only action whose duration is both variable and conveniently measurable, and that was therefore recorded in such a way that its duration was recorded. In recording the behaviour the start and end of Fanning bouts were recorded as separate events. All other actions are

assumed to have negligible duration. This is clearly a simplification but it is imposed on one's consideration of the data by the limitations of the recording technique which was not suitable for recording behaviours of very short duration.

Only two female behaviours have been differentiated in the recording of the behaviour - moving away from the male and moving towards the male; otherwise it is assumed that she did nothing.

To save space in the figures and tables the abbreviations given in the glossary at the end of Chapter 2 (page 1/42) are used. Female behaviours are abbreviated to -ve (moving away from the male) and +ve (moving towards the male).

The aim of the analysis that follows is to establish as far as is possible the causal relationships between the male and female behaviours involved in Orientation and Display. A causal mechanism can be inferred if there is good evidence that the behaviour of one animal in some way influences the behaviour of the other. Such evidence is that provided by correlations between behaviours. Thus the analysis that follows aims to answer the question: how is the male's behaviour correlated with that of the female, and vice versa? The data available contains information about what behaviours occurred and about when they occurred. Thus from this data it should be possible to determine to what extent the behaviour of one animal is correlated with that of the other not only sequentially, but also in time. These correlations are established by a form of Sequence Analysis.

Analysis of Behaviour Sequences

The integration of behaviours into a functional sequence will depend on a variety of factors. These have been summarised by Hinde and Stevenson (1969) as: (1) common causal factors, (2) consummatory stimuli,

(3) stimulus-response chains, and (4) effects consequent upon performance and not demonstrably related to changes in the stimulus situation. Hinde and Stevenson stress that one would not expect, nor does one find, that a given behaviour sequence is explicable in terms of any one of these processes alone.

In the analysis of sequences the ethologist formulates models which, to a greater or lesser extent, fit the sequences that he observes. In sexual behaviour two animals are interacting, and for a number of species the stimulus-response chain has been found to be a good model for courtship sequences. Such a model fits the courtship behaviour of Sticklebacks in a general sense (Tinbergen 1951) though, at a more detailed level, the situation is more complex (Morris 1958, Wilz 1967). A similar contrast between the idealised stimulus-response chain and the overlapping relationship between stimuli and responses that actually occurs is seen in the Teleost fish Badis badis (Barlow 1962).

In some sexual behaviour sequences the female's behaviours are few and far between relative to the male's. In such situations a more constructive approach has been to analyse the sequence of male behaviours in isolation, explaining links between behaviours in terms of internal processes (Hinde's and Stevenson's category 4). Such an approach has been applied to Drosophila (Bastock and Manning 1955) and to various fish species (Baerends et al. 1955, K. Nelson 1964), although in none of these examples can sexual behaviour be understood entirely in terms of processes internal to the male. In Drosophila courtship, for example, it has been shown that the female's behaviour does influence that of the male (Brown 1964).

In newt sexual behaviour the male shows many, varied behaviours, and, though the female shows only two behaviours, she performs these frequently. Thus it is not realistic to consider the male's behaviour in isolation. On the other hand, since there are many more types of male behaviours than

there are of female behaviours, one would not expect the idealised stimulus-response chain to be a good model for newt sexual behaviour. In the analysis that follows the behaviour of the two sexes is considered together. The male's behaviour is considered as a sequence of discrete behaviours and, at each link of the chain, the behaviour of the female is considered also.

Analysis of Transitions between Male Acts

The male's behaviour consists of a sequence of discrete actions. In the time interval between any two consecutive male acts there may occur a female act, in which case the male act to male act transition is said to have been INTERRUPTED. The female's interruption may be either negative (move away from the male) or positive (move towards the male). Since the male act Fanning has duration this may similarly be interrupted by a female act.

The male's behaviour is treated as a series of single order transitions: 1st Act - 2nd Act, 2nd Act - 3rd Act, etc. Each transition may be interrupted, positively or negatively, or uninterrupted. All such transitions between male display acts are extracted from all the data obtained from courtship observations and are accumulated in three separate transition matrices, one matrix for each possible interrupt situation (see pages 2/36 and 2/37).

Included in these transition matrices are not only transitions between Display acts, but also transitions from Display acts to Orientation acts (OR.) and to Creep (C). In each matrix the row for Fan (N) has been subdivided into three so that transitions from uninterrupted (U); negatively interrupted (-) and positively interrupted (+) Fan bouts are presented separately.

Transition matrices have been used extensively in the analysis of behaviour sequences (e.g. Blurton-Jones 1968, Delius 1969). Recently this

method of analysis has been criticised, in particular in relation to the statistical methods used to calculate expected frequencies (Slater and Ollanson, in press). In the present transition analysis no comparison is made with expected transition frequencies. These matrices are intended simply as a convenient way to summarise and present a large amount of sequential data and to give a very general picture of how the male's behaviour is correlated with that of the female. Two general conclusions can be made from them:

1. That there are very marked differences between the matrices for the three interrupt situations. The important difference between the three matrices is not that the row and column totals are different, but that the relative frequencies of transitions from one male behaviour to other male behaviours is different. For example, the majority of transitions that begin with Whip (W) lead to Fan (N) in the uninterrupted matrix, to Orientation (OR) in the negative interrupt matrix, and to Retreat-and-Whip (RW) in the positive interrupt matrix.
2. That the data for 1971 (page 2/36) and for 1972 (page 2/37) are similar, and show the same variation between matrices.

The differences between these matrices are best shown when the data are plotted as a series of "flow diagrams" (see page 2/38). These diagrams use the conventions used by Baerends et al. (1955), and are based on the combined 1971 and 1972 data. Each flow diagram shows the transitions between the six male Display acts which are arranged in the centre, and also transitions from these acts to Orientation acts (far left) and to Creep (far right). The transitions from Fan bouts are only those from bouts with the appropriate interrupt situation. Thus only transitions from uninterrupted Fan bouts are presented in the uninterrupted transitions diagram.

The pattern presented by such diagrams depends largely on the order from left to right in which the acts are represented. In this case the

arrangement is not arbitrary but reflects the general order in which the acts occur, with Static Display acts on the left and Retreat Display acts on the right. Clearly any arrangement will bias the picture in some way but this arrangement is presented as a biologically meaningful one.

Like the transition matrices, these diagrams contain a lot of information and are not intended to show details of the behaviour but to illustrate more general effects. There are dramatic differences between the three flow diagrams. The majority of uninterrupted transitions are in the central area, being from one Display act to another, in particular from one Static act to another. The overall trend of negatively interrupted transitions is leftwards, towards Orientation behaviours, and that of positively interrupted transitions is to the right, towards Retreat Display acts and towards Creep.

The following conclusions can be drawn from this analysis of the transitions between consecutive male acts:

1. The male's behaviour is correlated with what the female has just done.
2. It gives an overall impression of how the male's behaviour is influenced by what the female does. If the male receives no interruption from the female he continues to Display to her, either repeating the action he has just performed or else performing another from his Display repertoire. If she moves away from him he generally switches from Display behaviour and reverts to Orientation behaviour. In other words, he acts so as to restore his Display orientation. If the female approaches him, the male reacts either by continuing to Display and, in addition, retreating before her, or else turning from her and beginning to Creep.

Analysis of the Time Intervals between Consecutive Male Acts

In this analysis the time information contained in the Organ data has been used to calculate the time intervals between consecutive acts. These time intervals are plotted as frequency distributions with frequency of

transition against time. To allow comparison between frequency distributions for different transitions, the frequency distributions are expressed as probability plots, observed frequencies being converted to probabilities by the formula P = F ÷ N (where P is probability, F the observed frequency and N the total number of observations of the transition concerned). Thus a probability plot for a transition between two acts, A and B, shows the observed probability with which that transition was completed when a given time interval had elapsed after the performance of A. It must be stressed that these plots do not represent absolute probabilities; they are not relative to all possible transitions from A, but to the total frequency of occurrence of the transition A - B.

The probability plots for transitions from one male act to another (uninterrupted transitions) are shown on page 2/39, those for transitions from male acts to female acts on page 2/40, and those for female acts to male acts on page 2/41. Each graph shows probability (ordinate) against time (abscissa). Time is expressed in half-second intervals. On each graph data for 1971 and 1972 is plotted separately. Only those transitions for which there are 25 or more observations in the data from the two years combined are presented. (N.B. the abbreviation Ns = Start of Fan bout; Ne = End of Fan bout.)

On most of these plots there is a good fit between the plots for data from different years. A statistical comparison of the data for each transition from different years is given in Appendix 3e. Where there is a poor fit, for example in the W - W plot, it is associated with a small total number of observations. The important point is that the variation between data for the same transition from different years is much less than the variation in the data for different transitions.

Some of these probability plots show a marked peak, others do not. For example, the transition M - W shows a very marked peak in the first half-second, WA - W shows a peak in the second half-second, and RW - N

shows a peak in the fifth half-second interval. The importance of this variation in the time-intervals between successive acts is seen when the probability plots for male-male and male-female transitions are compared. This comparison is made in the next section.

Uninterrupted Male Transitions

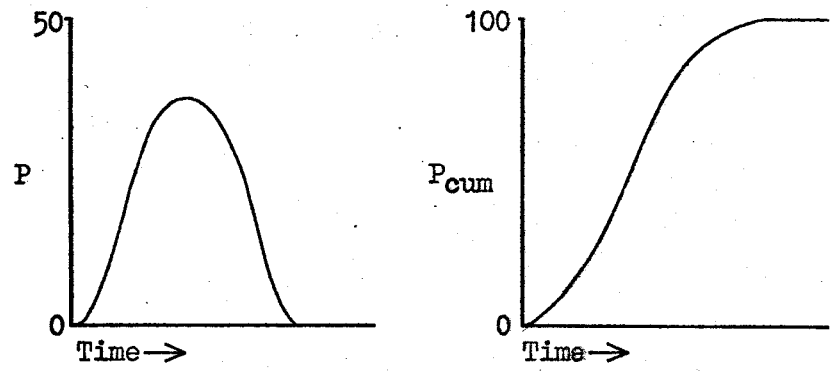
The fact that a transition between two consecutive male acts is not interrupted by a female act may be the result of two different conditions:

(1) That the two male acts are so close together in time that there is no time available for the female to do anything.

(2) That there is sufficient time for the female to act but she does not do so.

It is possible to see which of these two conditions is the more likely in a particular uninterrupted male act - male act transition by comparing the probability plot for that transition with the probability plots for transitions between the first male act and female acts. In condition 1 the probability plot for the male act to male act transition will have an earlier peak than the probability plot for the corresponding male act to female act transition. In condition 2 the reverse will be true; the male act to female act transition will have the earlier peak (see page 2/42, fig A).

Comparison of one probability plot with another is made clearer if the probability plots are converted to cumulative probability plots. In this conversion the cumulative frequency with which transitions are completed with respect to time is expressed as a probability: $P_{cum} = F_{cum} \div N$ (where P_{cum} is cumulative probability, F_{cum} is cumulative frequency and N is the total number of observations of the transition concerned). Below is shown a hypothetical probability plot and its corresponding cumulative probability plot:



Any given point on the cumulative probability curve gives the probability that, at a given time, the transition concerned will have occurred.

The picture provided by comparing cumulative probability plots for male act to male act and male act to female act transitions will vary, depending on whether condition 1 or condition 2 is operative. Page 2/42, fig B shows the sorts of plots one would expect from the two conditions. In condition 1 the probability plots show that the male act to male act transition peaks at an earlier time than the male act to female act transition. The corresponding male act to male act cumulative probability plot is to the left of that for the male act to female act transition. In other words, the probability that the male will have completed his transition is, at a given time, greater than the probability that the female will have acted. In condition 2 the reverse is true - whenever the male completes his transition the probability is greater that the female will have acted.

The next step in the analysis is to compare the cumulative probability plots for each male act to male act transition and to compare them with the similar plots for the appropriate male act to female act transitions, and to see for each transition which of these two hypothetical plots is the better model. These comparisons are presented on pages 2/43 to 2/54, and the results are summarised on page 2/55. (Statistical comparison of male and female cumulative probability plots is presented in Appendix 3f.)

From this analysis of the uninterrupted transitions between male acts

the following conclusions can be drawn:

1. Some transitions between male acts are completed so quickly that the female does not have an opportunity to interrupt them, e.g. M - W, W - N, N - RW. In other words, these transitions are not correlated with what the female does but are consequent upon the performance of the first male act.

2. Some transitions between male acts are completed after a time interval which is long enough to allow the female an opportunity to interrupt the transition, e.g. W - WA, WA - WA, RW - N, RW - WA. These transitions can be interpreted on two alternative hypotheses:

   a. Like the short-interval transitions they are consequent upon the performance of the first male act but, due to what may be called "internal programming" within the male, are characterised by a long transition interval.

   b. The second act of the transition is not consequent upon the first act but is a response to the fact that the female has done nothing.

Further analysis is required to test these two hypotheses. This follows in a later section.

3. Some transitions between male acts are intermediate between categories 1 and 2, e.g. W - W, N - WA. It is more reasonable to interpret these transitions in terms of hypothesis (a) than hypothesis (b).

It must be made clear that this analysis does not assume that a female act that interrupts a transition between two male acts is a response to the first male act alone. For the purposes of this analysis it does not matter if the female is responding only to the male act that immediately precedes her act, to an earlier male act or to a combination of earlier male acts. This analysis compares the observed temporal patterning of male acts with that of female acts and makes no assumptions about the causation of those acts.

Other Factors affecting Uninterrupted Male Transitions

The previous section compared uninterrupted male transitions with the appropriate male act - female act transitions. There are also interesting comparisons to be made between different uninterrupted male transitions.

Some male Display acts are very highly correlated with other particular male acts. For example, 95% of all the uninterrupted transitions that begin with Move-to-the-Front (M) end with Whip (W). Other male acts are not highly correlated with other acts; the transition Fan (N) to Wave (WA) is the commonest uninterrupted transition from Fan, but it represents only 33% of all the observed uninterrupted transitions from Fan. Another way to express this is to say that what happens after a Move-to-the-Front is highly predictable; what happens after a Fan is not. Page 2/56 shows two measures of this predictability of the uninterrupted transitions from the male's Display acts, the percentage of all the transitions from a given act that are accounted for by the commonest transition, and a value H which is a measure of the level of "uncertainty" with which the outcome of transitions from each act can be predicted (Shannon and Weaver 1949, Dawkins and Dawkins, in press). Clearly, there is considerable variation in the extent to which male Display acts are correlated with other male Display acts.

Comparisons can also be made between the different transitions from the same act. For example, there are three possible transitions from Whip: to another Whip, to Fan, and to Wave, and each of these shows a different time distribution (see page 2/57). Immediately after a Whip there is a high probability that Fan will occur. As this declines, there is an increasing probability that Wave will occur. The data for Whip - Whip is too small to discern any peak in the time distribution. The transition Whip - Fan approaches condition 1; Whip - Wave fits condition 2. This variation suggests an internal "programming" mechanism within the male controlling his behaviour in such a way that each transition has its

own preferred time interval.

A similar effect is shown by the two uninterrupted male transitions that follow a Fan bout: Fan to Retreat-and-Whip and Fan to Wave (see page 2/58). A Fan bout is likely to be followed immediately by Retreat-and-Whip or, after a pause, by Wave. In this case there is a biological explanation for this variation. Referring back to the transition matrices for uninterrupted male transitions (page 2/36 and 2/37), it can be seen that the transitions from Fan to Retreat-and-Whip are predominantly from positively interrupted bouts, whereas those from Fan to Wave are from uninterrupted bouts. On the general hypothesis that the male's behaviour is adjusted in response to that of the female this makes good sense. At the end of a positively interrupted Fan bout the male has received comparatively recent indication of the female's behaviour. He therefore performs a new act, Retreat-and-Whip, without waiting to assess the female's behaviour. Conversely, at the end of an uninterrupted Fan bout, he has not had recent indication of her behaviour, and so waits for a time to assess her behaviour before performing his next act, a Wave.

This comparison shows up a limitation of the method of analysis that has been used. In treating the Display behaviour as a succession of single order transitions one cannot make the assumption that each single order transition is independent of earlier ones. In the case of transitions after a Fan bout, this is clearly not so. However, despite this limitation, this method of analysis has served to provide the evidence that it was intended to provide: that what the male does is correlated with what the female does. In addition, it has shown that the male's behaviour is timed in such a way that there are some transitions that allow time for the female to act, and some transitions which are too short to allow her time to act.

The Relationship between Transition Interval and Female Interruption

The previous analysis has established that some male acts characteristically follow other male acts after a long time interval, others after a short interval. If the male's behaviour was independent of the female's one would expect to find a simple linear relationship between the time interval of a transition and the proportion of that transition interrupted by the female; that is, the longer the transition interval, the more likely is it that the female will interrupt it. Page 2/59 shows the actual relationship between mean transition interval and the percentage of each transition that was interrupted. For this analysis the data from 1971 and 1972 has been pooled and only those transitions which occurred with a frequency of 50 or more have been plotted.

This plot does not show a simple linear relationship, but a considerable spread between points. This is not surprising since the first stage of the analysis showed that the assumption that the male's behaviour is independent of the female's is invalid. However, this plot does show an important effect not shown by the earlier analysis. Long-interval transitions depart from a theoretical linear relationship in two directions:

1. The cluster of points at the top represent long-interval transitions, of which a very high proportion were interrupted. The second act of these transitions can be interpreted as a response to the female's interruption.
2. Of more interest are the points towards the bottom right-hand corner of the plot, which represent long-interval transitions, of which very few were interrupted. In an earlier section (see page 1/62) two hypotheses were proposed for the causation of long-interval uninterrupted transitions. This analysis provides evidence for hypothesis (b); the acts that end these transitions are responses to the female's having done nothing, just as those at the opposite extreme of the plot are responses to her observed behaviours. It is noticeable that three of these transitions end with the

behaviour Wave, which suggests that this act is a response to female non-behaviour.

Male Transitions in relation to both Time and the Female's Behaviour

Another approach to the analysis of the transitions from male Display acts is shown in the diagrams on pages 2/60 to 2/63. In these the transitions from the four most common male Display acts, Whip, Wave, Retreat-and-Whip and Fan, are plotted against time (horizontal axis) and against female interruption (vertical axis). These diagrams are based on 1971 and 1972 data combined (see Appendix 3i). They all show an essentially similar picture and illustrate two different effects:

1. The striking differences between the three horizontal levels indicate the strong correlation between the female's behaviour and the outcome of the male's transitions.

2. The change with time (from left to right) in the relative frequencies of the acts performed indicates the changes that take place in the male's "internal programming".

In all four diagrams it is apparent that there is an increasing probability with time that, in the uninterrupted situation, the act Wave will be performed. This, as suggested above, indicates that Wave is performed in response to female immobility.

In the diagram for transitions from Fan there is a less marked discontinuity in the transitions shown in the three interrupt situations. This can be interpreted by assuming that, in those instances when the female interrupts a Fanning bout, the male's behaviour immediately after the Fanning bout is in response to that interruption.

The analysis so far has established that the sequential patterning of the male's behaviour is correlated with what the female does, and it has also examined temporal relationships between the different male behaviours. The next step in the analysis is to examine the relationship

between the female's behaviour and the temporal pattern of the male's behaviour.

The Effect of the Female on the Timing of the Male's Behaviour

There is suggestive evidence that the female influences not only what the male does, but also when he does it. It has been shown that many of the male act to male act transitions show late timing peaks and that some show no marked peak (see page 2/39). In contrast, all of the female act to male act transitions show more or less marked early peaks (see page 2/41). This suggests that the male generally acts more quickly when the female has shown a response than he does when she shows none.

Interruptions During Fanning Bouts

Much better evidence that the female influences the timing of the male's behaviour is obtained from an analysis of the effect of female interruptions during Fanning bouts. In this situation the male act to male act transition must necessarily be always the same, regardless of what the female does; having started to Fan, the male's next act must be to stop. Thus one can compare the same male transition under each of the three female interrupt conditions. For most other male transition the outcome varies according to the female's behaviour and so such a comparison would not be strictly valid.

Figure A on page 2/64 shows the cumulative probability plot for uninterrupted Fan bouts. It shows, in other words, for any given time after a Fan bout has begun, the probability that it will have ended at that time, provided that the female has not interrupted it. Figure B on the same page shows the cumulative probability plot for positively interrupted Fan bouts, from the time that they were interrupted, and figure C shows a similar plot for negatively interrupted Fan bouts. It is clear that the slope of these post-interrupt curves is much steeper than that of the uninterrupted bouts

curve - in other words the rate at which Fan bouts stop after they have been interrupted is greater than the rate at which, on average, they stop when they are not interrupted.

The two post-interrupt plots represent an accumulation of data from all female interrupts, regardless of when in a Fan bout the interrupts occurred. One can separate out this data and plot separately the cumulative probability plots for bouts interrupted in the first half-second, bouts interrupted in the second half-second, and so on. In practice the total figures for each sub-plot are too small for meaningful analysis. However this can be done by using Fan data from T. helveticus. (As will be shown in a later chapter T. helveticus shows relatively more Fan bouts than T. vulgaris.) This data is plotted on page 2/65 and it shows that the data from Fan bouts interrupted in different half-second intervals all show the same pattern.

Clearly, the length of a Fan bout is strongly influenced by what the female does during the bout. If the female shows any behaviour during a bout, the male is very likely to stop Fanning immediately - more likely than if she had not interrupted him. This is strong evidence that, at least in the case of Fanning, the female's behaviour influences the timing of the male's behaviour.

How the Male's Behaviour Influences that of the Female

From observations it is known that the female usually moves away from the male at the start of an encounter, and that as he displays to her, her behaviour becomes passive and then she starts to move towards him. This change in her behaviour can be confirmed by appropriate analysis of the Organ data. The data was scanned for male display acts. The transition from each male display act to the next male act was scored as to whether it was interrupted by the female or not. If it was it was scored positive or negative, depending on the nature of the female's behaviour; if not

it was scored as a female "non-response" if the time interval of the transition exceeded an arbitrary criterion value. This value is different for each male Display act and is defined as that time interval after the male act by which 75% of all observed female responses to that act had occurred. This criterion value can be easily read off from the cumulative probability plots for male act - female act transitions. If uninterrupted transition intervals fell below the appropriate criterion value no inference was made about the female's response state.

The results of this analysis are presented on page 2/66. The three graphs show the percentage of each of the three possible female acts observed in the transitions immediately following the 20 male Display acts that precede the first Creep in a courtship encounter. There is a dramatic increase in the number of positive female behaviours and a less dramatic decrease in the number of negative behaviours and of "non-responses". These figures are expressed as percentages of the total number of transitions, many of which were uninterrupted transitions of too short duration to qualify as non-responses. This analysis supports my subjective impression that, in the course of the male's Orientation and Display behaviour, the female's behaviour undergoes a change from moving away from the male, to moving towards him. Sometimes females will remain static for several seconds while the male displays to them. Thus, at any one moment in time, the female can be said to be in one of three "behaviour states": positive, negative or static.

Not all females show this overall behavioural change. Many females initially move away from the male and persist in doing so, and neither become passive nor start to move towards him. On the other hand, as described in Chapter 2, some females will approach a male before he has begun to display to them.

Summary of the Analysis of Orientation and Display Behaviour

1. The male's behaviour has been treated as a sequence of discrete acts, many of which are movements performed with the tail. Two female behaviours have been differentiated - move towards and move away from the male.

2. Much of the male's behaviour is sequentially correlated with the female's behaviour. If she moves away he performs mostly Orientation movements; if she moves towards him he performs mostly Retreat Display acts.

3. The sequential pattern of the male's behaviour cannot be explained entirely in terms of correlations with the female's behaviour. Some male acts are highly correlated with each other (e.g. Move-to-the-Front and Whip; Whip and Fan) and the time interval between them is so short that the female has no opportunity to behave.

4. There is evidence that male acts that occur after long, uninterrupted intervals (e.g. Wave) are responses to female immobility.

5. A female interruption during a Fanning bout has the effect of causing the male to stop Fanning quicker than he otherwise would.

6. The female's behaviour generally undergoes a change during the course of the male's Orientation and Display behaviour. Initially she moves away from him but gradually she begins to move towards him.

This analysis has examined the data obtained by observations of free pairs of newts. The next stage of the research was to test some of the conclusions and hypotheses concerning the causation of the male's behaviour that arise from this analysis. This involved the experimental manipulation of the female's behaviour.

Experiments on Display and Orientation Behaviour

The principle of these experiments was to move the female, who was held in a Strait Jacket, in a predetermined pattern, changing her from one

behaviour state to another, and to record the male's behaviour. These experiments were based on "natural experiments" in the sense that the way the female's behaviour was manipulated was consistent with the variation that is seen in the behaviour of free females. The aims of these experiments were:

1. By changing the female's behaviour, to show that the male responds by making immediate changes in his behaviour.
2. By maintaining the female for specified periods of time in each behaviour state - positive, negative and static - to show that the male's behaviour is different in each case. In other words, these experiments were intended to confirm that the early part of the courtship sequence can be divided into three distinct "phases".

Ten of each type of experiment were carried out and a different male was used for each individual experiment. The male was put into the test tank and left for 15 minutes to settle down. Then the female in her strait-jacket was put into the tank and moved near the male so as to attract his attention to her. If the male approached her and began to court, the test could proceed. In those rare cases where he failed to court a female the male was rejected as a test subject. Once it was clear that the male would court the female a stop-clock was started and, at the same time, the female was switched into one of the three possible behaviour states, moving away, staying still, or moving towards the male. This situation was maintained for a specified period of time at the end of which the female's behaviour was changed and she was maintained in a different behaviour state for a further specified period. At the end of this second period the female was switched back to her original behaviour. Thus in each experiment a male was presented with a female whose behaviour consisted of alternating bouts of two of the three states. Three types of experiment were carried out, one in which static behaviour and negative behaviour were alternated, and two in which static and positive behaviour

were alternated. Care was taken to keep the female's behaviour as uniform as possible during each timed period, so that when she moved away from or towards the male she moved as evenly as possible.

In each experiment the female's behaviour was changed twelve times so that each male received six bouts of each type of female behaviour. In the ideal experiment all twelve bouts followed each other without a break, but sometimes contact was lost, for example when the male went up for air. In this event, the timed period in which the loss of contact occurred was immediately terminated, contact was reestablished by moving the female towards the male and the experiment was continued from the start of the next timed period. Thus the timed periods of female behaviour lasted for their pre-determined times unless the male's behaviour ruled otherwise. The time intervals used varied in the three experiments. For the purposes of these experiments the actual time intervals chosen are not important. What is important is that the female's behaviour was controlled according to pre-determined criteria.

The behaviour during these experiments was recorded in the same way as observational data - verbal commentary transcribed via the Organ.

The Negative/Static Experiment

In this experiment the female was alternated between negative and static behaviour. The female was held stationary in front of the male for 20 seconds, and then moved away from him at a steady rate for 10 seconds. Thus in each trial the male was, potentially, exposed for a total of 120 seconds to a static female and for 60 seconds to a negative female. In this experiment contact was occasionally lost when the male failed to follow a female moving away from him. If this happened the test was stopped and restarted as described above.

The results of this experiment are presented on page 2/67. In this presentation the results from the ten tests are added together. The upper

table shows the frequency of occurrence of male acts that immediately follow the switches in the female's behaviour. There is clear evidence that the male responds to changes in the female's behaviour, following her as soon as she starts to move away, and performing a static Display act, Wave (WA) or Fan (N), as soon as she stops still.

The histograms show the relative frequency of occurrence of male acts during the timed periods of female behaviour. The upper histogram is based on a total of 295 male acts, the combined efforts of ten different males, and representing an overall total of approximately 600 seconds of male behaviour. There is a clear preponderance of Follows (F), Moves-to-the-Front (M) - both orientation movements - and Whips (W), which analysis has shown are closely associated, sequentially and in time, with Moves-to-the-Front. The lower histogram is based on a total of 316 acts, performed by the same ten males, and representing a total of 1200 seconds of male behaviour towards static females. There are virtually no orientation movements, the majority of male actions being Static Display actions, particularly Waves (WA).

(It will be noted that a very similar number of male actions were recorded in the two situations - 295 acts in negative bouts, 316 in static bouts. This is why the 10 second - 20 second schedule was chosen from other schedules tried in pilot tests.)

The Static/Positive Experiments

In these experiments the female was alternated between static and positive behaviour, being kept static in front of the male for a period, and then moved steadily towards him. Two sets of these experiments were carried out, each using ten different males. In the first experiment bouts of static and positive female behaviour were both of 20 seconds duration; in the second, static behaviour was maintained for 30 seconds and positive behaviour for 10 seconds.

It was found in the course of the first experiment that the male, presented with a persistently approaching female, frequently turned away and began to Creep before the end of the 20 second period. This happened in 49 out of the 60 positive bouts. By reducing the positive bouts to 10 seconds in the second experiment, the probability of this occurring was reduced so that it occurred in only 22 of the 60 positive bouts. I will return to this effect in a later part of the analysis. When the male turned away to Creep the positive bout was stopped, reducing its length to less than the intended 20 seconds. The female was stopped and, when the male reverted to his display position the female was moved towards him very briefly and then stopped so that the experiment continued from the start of the next scheduled static bout.

The results of these experiments are presented together on page 2/68. Despite the fact that the two sets of data are based on different time units, they are very similar. The upper table shows male acts immediately after switches from one female state to another. As in the previous experiment, the male makes the responses one would expect from the analysis of the behaviour of free animals, showing Static behaviours, Fans or Waves, when she stops still, and a Retreat behaviour, usually Retreat and Whip, when she starts to approach him.

There is a clear difference in the relative frequencies of the various male acts in the periods of static and positive behaviour, as shown by the histograms. This is good evidence that there are two Phases of male Display behaviour - Static Display with many Waves, some Fan bouts, and few Whips, and Retreat Display with mostly Retreats and Whip, some Retreats, few Fans and fewer Waves.

In the Static bouts in both the negative/static and the static/positive experiments much the most common act performed by the male was Wave (over 55% in both experiments). This is further evidence for the

hypothesis formulated from the analysis of observational data - that Wave is performed as a response to female immobility.

Other Orientation/Display Experiments

A number of pilot experiments were conducted in which both the Negative/Static experiment and the Static/Positive experiment were carried out on different time schedules to those described above. These pilot experiments, as expected, produced results similar to those presented here. It was found in these pilot experiments that males would continue to display to a static female for a very long time. Periods of continuous static display lasting 123, 133 and 242 seconds were observed.

In addition, pilot tests were conducted for a third experiment, the Negative/Positive experiment, in which the female was alternated between moving away from the male and moving towards him, without any appreciable pause between the two. The male showed the behaviour that was expected on the basis of the other experiments. When an approaching female suddenly turned and started to move away from him, he would stop displaying to her and immediately followed her. When she then turned back and started to approach him again, he resumed his Retreat Display behaviour.

Unfortunately all these experiments were performed at the end of the 1972 season which was shorter than in previous years because of a very mild March, and this seemed to encourage newts in the wild to breed rather early. Consequently all the intended experiments could not be carried out.

These experimental results are summarised in the diagram on page 2/69. Results based only on pilot experiments are indicated by broken lines. Male actions are classified into three types - Orientation movements, Static Display acts and Retreat Display acts. After each act the female may show one of her three behaviours - positive (+), static (0), or negative (-). Negative female acts, regardless of the male behaviour that preceded them, are followed by male Orientation movements (green arrows),

static female acts are likewise followed by male Static Display acts (blue arrows), and positive female behaviours are followed by male Retreat Display acts (red arrows). The only variation in this pattern is that positive female responses to male Retreat Display acts may lead either to further Retreat Display acts or to Creep.

Orientation and Display Behaviour - A Summary based on Observational and Experimental Data

1. The male's behaviour prior to Creep consists of:
   a. Orientation movements - Approach, Follow, Move-to-the-Front. (Sniffing is associated with these behaviours.)
   b. Tail movements performed while standing still - Wave, Whip and Fan.
   c. Tail movements performed while retreating before an advancing female - Retreat-and-Whip, Fan, and Wave (rarely).
2. The female's behaviour is highly variable but shows a general trend; from initially moving away from the male, she then begins to stay still and finally she starts to move towards the male.
3. Changes in the female's behaviour elicit immediate changes in the male's behaviour. If she moves away, he moves so as to resume his display orientation; if she stops still he performs Static Display acts; if she moves towards him he shows Retreat Display acts. However some of the changes in the male's behaviour cannot be explained as responses to female behaviours, but are due to effects internal to the male.
4. If the female maintains any of her behaviours for a period of time the male continues to show behaviour appropriate to that behaviour. Thus the early part of the courtship sequence can be divided into three phases on the basis of both the male's and the female's behaviour:

PHASE:	1	2	3
♀ Behaviour:	Moves away	Stays still	Approaches
♂ Behaviour:	Orientation movements	Static Display	Retreat Display

The Deposition Phase

The Deposition Phase is defined as all that behaviour that follows the male's Creep and which involves the deposition and pick-up of the spermatophore. Throughout the Deposition Phase the male's orientation with respect to the female is different from his orientation in the earlier phases. He is either facing away from the female or is side-on to her; at no point does he face her.

What Initiates the Male's Creep?

From observational data it is seen that Creep invariably follows a period of Retreat Display behaviour. The male never Creeps unless the female has been persistently approaching him. No particular action or change of behaviour on the part of the female seems to provide an immediate stimulus that causes the male to Creep. The hypothesis based on observations is that the male does not Creep in response to any particular female action. Rather, he Creeps in response to continued female approach, and the exact moment at which he Creeps is determined by internal factors within the male.

The results of the two Static/Approach experiments provide support for this hypothesis. Throughout the Approach periods of these experiments the female's behaviour was kept as uniform as possible, but, despite the fact that the female's behaviour is constant, the male, in many tests, turned away to Creep. In the 60 tests in which female approach behaviour was maintained for 20 seconds, the male turned to Creep in 49 of them. In the

second experiment, in which approach behaviour was maintained for only 10 seconds, the male only Crept in 22 of them.

The onset of the male's Creep does not mark an irreversible discontinuity between Display behaviour and the Deposition Phase. In certain circumstances, which will be described, the male turns back in the course of Deposition behaviour and reverts to his Display behaviour.

Sequential Analysis of Deposition Phase

The behaviour of the male is treated as a series of single-order transitions, which are accumulated in a transition matrix (page 2/70). At this stage of the courtship sequence the female persistently follows the male and so for the purposes of this analysis her behaviour is ignored except for the two occasions when she touches the male's tail - after the male's Quiver movement and when he is in his Braking position. This transition matrix is presented visually as a flow diagram (page 2/71).

The most striking feature shown by this flow diagram is the small degree of variation that is seen in Deposition phase behaviour; the behaviour is highly predictable. This is in marked contrast to the earlier parts of the courtship sequence which are anything but predictable. The majority of variation that does occur comes after the spermatophore has been depositied.

This analysis shows that about 20% of male Creeps do not lead to Quiver but to a return to Retreat Display. It is not clear why the male does this.

The sequential analysis of Deposition behaviour suggests that the two female Tail-Touches may be causally related with male behaviours, the first with spermatophore deposition, the second with Push Back. Experiments were carried out at these two points in the Deposition Phase to determine whether the male's behaviour is indeed causally related to that of the female.

The Tail-Touch Experiment

The single-order transition analysis shows that there is a 100% correlation between the female's Tail-Touch and deposition of the spermatophore by the male (page 2/70). It is therefore a reasonable hypothesis that the Tail-Touch is the immediate stimulus that causes the male to deposit the spermatophore. The flow diagram shows what happened on those rare occasions (4 of them) when the female did not touch the male's tail (see page 2/71). On one such occasion the male deposited a spermatophore, but on the other three occasions he turned back and reverted to Display behaviour. These abnormal sequences are good "natural experiments", suggesting that if the male does not receive the female's Tail-Touch he will usually not deposit a spermatophore.

In the Tail-Touch experiment the male was induced to court a Model and, when he turned away from the model, Crept and Quivered, he was presented with one of two alternative situations. In the experimental situation the model was kept still as soon as he Quivered; in the control situation it followed him and gave him a Tail-Touch. A total of twelve different males were used, and each male was induced to produce three spermatophores in the course of his trial, with a different test situation for each spermatophore:

Situation A: Tail-Touch given after first Creep and Quiver.

Situation B: Tail-Touch withheld after the first Creep and Quiver, but given after the second.

Situation C: Tail-Touch withheld after the first two Creeps and Quiver, but given after the third.

Thus each male received the experimental situation (Tail-Touch withheld) three times and the control situation three times, provided, of course, that he performed according to expectation and did not deposit a spermatophore in the experimental situation. The order in which each male received situations A, B and C was systematically varied so that all

possible combinations were used.

The results, presented on page 2/72, clearly support the hypothesis that the female's Tail-Touch is usually a necessary stimulus for spermatophore deposition. In only four out of the 36 control situations did the male deposit a spermatophore.

In the natural situation the female's failure to touch the male's tail may be because he does not give her sufficient time to do so before reverting to Display behaviour. In the experimental situation, when the Tail-Touch is withheld, the male continues to Quiver for some seconds, sometimes continuously, sometimes in bouts of tail movement. Then he turns back towards the model which is stopped still a little way from him and he generally begins to display to it. The fact that he turns back after several seconds of Quivering suggests that the male's behaviour is timed so as to give the female adequate opportunity to touch his tail. Figure A on page 2/73 shows the frequency distribution with time of Tail-Touches after Quiver, based on observational data. Figure B on the same page shows the frequency distribution for the male's return to Display behaviour after Quiver in the experimental situation. Figure C shows the cumulative probability plots for the two types of transition. It is clear that the male turns back to Display behaviour only after a time interval which, in normal circumstances, would have given the female plenty of opportunity to Touch his Tail.

In some unsystematic pilot experiments the male was given a Late Tail-Touch by a Strait-Jacket female. The aim of these experiments was to show that throughout the "waiting-period" between the male's Quiver and his return to Display he is responsive to the female's Tail-Touch in the usual way. A total of 18 such experiments were carried out, with Quiver to Tail-Touch intervals ranging between 3·5 seconds and 15·5 seconds. (In sequences involving free animals 95% of all Tail-Touches occur within 3·5 seconds of Quiver.) In 15 of these experiments the male

deposited a spermatophore after being touched. Clearly the male will deposit a spermatophore even when he is touched later than is usual.

The Post-Spermatophore Experiment

The sequence analysis of the Deposition Phase (page 2/70 & 2/71) shows that there is a virtually unvarying sequence of behaviours immediately after spermatophore deposition - Sperm down ... Creep-On ... Brake. The aim of this experiment was to establish whether or not this behaviour sequence is influenced by what the female does.

There were two test conditions, the experimental and the control. In both a male and a free female were put into the observation tank and allowed to begin courtship behaviour. In the experimental situation a glass plate was placed in front of the female as soon as the spermatophore appeared so that the female was unable to follow the male. In the control situation the female was left alone. Ten different pairs were used, each pair performing two trials which occurred on consecutive days. In each trial the male produced two spermatophores; in trial A the experimental condition was imposed after the first spermatophore, in trial B after the second. Half the pairs performed trial A on the first test day, the other half trial B. Thus each male produced a total of four spermatophores, of which two were followed by the experimental condition, and two by the control condition. The results are presented as separate transition matrices on page 2/74 and as flow diagrams on page 2/75.

It is clear that, up till the point where she touches the tail of the Braking male, the female has no influence on his behaviour. The sequence of male behaviours from deposition to Brake is performed regardless of whether she is following him or not.

In contrast, the male's behaviour after Braking is dependent on what the female does. If he does not receive the female's Tail-Touch he invariably turns back and resumes his Display. If, however, the female

does touch his tail, as in the control condition, he may revert to Display behaviour but he is more likely to show the Push Back behaviour. Clearly the female's Tail-Touch is a necessary stimulus for the Push Back behaviour, although the male does not invariably show this behaviour when his tail is touched.

Summary of Deposition Phase Analysis

1. The behaviour is highly predictable, showing very little variation.
2. The female follows the male persistently and at two points in the deposition sequence touches his tail.
3. The first Tail-Touch is usually a necessary stimulus for spermatophore deposition. If this stimulus is withheld, the male reverts to Display behaviour.
4. After deposition of the spermatophore, the male's behaviour is independent of the female's until the Brake stage, when her second Tail-Touch may stimulate the male to show the Push Back behaviour.

Conclusion

To sum up the results of this analysis of the newt courtship sequence it is instructive to consider again the categories of factors that affect the integration of behaviour sequences as listed by Hinde and Stevenson (1969):

Stimulus-Response Relationships. The relationship between the female's Tail-Touch and spermatophore deposition represents a simple Stimulus-Response situation in which a particular female act has a specific causal link with a particular male act. Other female actions have less specific causal relationships with male actions. Thus, when the female approaches or moves away from the male, or stays still, he responds with one of a variety of actions, some actions being statistically more common

than others. Each female behaviour state is causally linked with a group of male actions. So, when she approaches him, he performs one of a number of Retreat Display actions - Retreat-and-Whip, Retreat, Fan or Wave. These actions are not all exclusively linked with particular female behaviours; for example, Fan and Wave are more commonly performed in response to female passive behaviour.

Changes in the female's behaviour cannot be causally related to specific male actions. There is an overall change in her behaviour from moving away from the male to moving towards him which seems to be due to the cumulative effect of his Display.

Effects consequent upon performance. A number of male actions are strongly correlated with each other and transitions between them are not correlated with the female's behaviour. One example is the transition Move-to-the-Front to Whip, another is the sequence of behaviours that follows spermatophore deposition - Creep-On and Brake. The switch from Display behaviour to Creep seems to be a response to persistent female approach but its precise timing is determined by factors internal to the male.

Consummatory Stimuli. (These are not to be confused with the drive-reducing consummatory acts of classical drive theory.) It is notable that the fact that a spermatophore has been picked up does not affect subsequent behaviour; the courtship sequence is repeated regardless of whether the spermatophore was picked up or not. Thus the picking-up of the spermatophore does not act as a consummatory stimulus terminating sexual behaviour.

Common Causal Factors. Newt sexual behaviour has been elicited by the hormone Prolactin, which also causes terrestrial newts to become aquatic (Grant 1966). Prolactin treatment may even have the effect of eliciting male sexual behaviour in the absence of females.

Males kept apart from females will display to a variety of inappropriate objects, and females who have been kept apart from males may,

when paired with a male, start to approach him before he has begun to display to her. These results suggest that deprivation of contact with the opposite sex has, like hormones, a general causative effect on sexual behaviour.

CHAPTER 4

CHAPTER 4

COMPARATIVE ASPECTS OF SEXUAL BEHAVIOUR IN THE GENUS *Triturus*

So far I have only considered the sexual behaviour of *T. vulgaris*. In this chapter the description of sexual behaviour is extended to other *Triturus* species. *Triturus* sexual behaviour is considered as a functional system and its evolution within the genus is discussed. The evolutionary aspect is discussed further in a comparison of *Triturus* sexual behaviour with that of other Urodeles.

Sexual Behaviour of other *Triturus* Species

The Palmate Newt, *Triturus helveticus*

Descriptions in the literature of sexual behaviour in this species are fragmentary. A very rapid Fanning movement has been described by Rusconi (1821) and Cummings (1911), otherwise sexual behaviour is described as being identical to that of *T. vulgaris* (Smith 1951, Steward 1969).

Palmate Newts, particularly the males, are generally smaller than Smooth Newts. In their general movements they are rather more active and can be seen making frequent very rapid swimming movements around their home tanks. A total of 52 courtship encounters were observed for this species, involving 20 males and 19 females. In all a total of 47 spermatophore depositions were observed and recorded (see Appendix 1).

In all general aspects the courtship behaviour of *T. helveticus* is the same as that of *T. vulgaris*, with the same overall pattern of four courtship phases (page 2/31). At first acquaintance the courtship of the two species seems to be identical in every respect, but, as more observations are made a number of differences of detail become apparent.

These differences are all in the earlier, Display phases. The Deposition phase is identical in the two species (see pages 2/81a and 81b).

The male's Display incorporates the same three tail movements as in T. vulgaris: Wave, Whip and Fan. Waves are generally less conspicuous than they are in T. vulgaris; the "Showing-off" movement in which the tail is held still for a moment is very rarely seen. The Whip is not as violent a movement as it is in T. vulgaris. Whereas T. vulgaris uses the full length of the tail to generate a violent blast in the water, in T. helveticus only the distal portion of the tail is used and the turbulence generated is much less dramatic. A Whip very frequently precedes a Fanning bout and, in this context, looks more like an exaggerated first Fanning beat than a separate action. However, Whips do occur independently of Fanning bouts and a Whip may precede another Whip.

There are distinct differences between T. helveticus and T. vulgaris in the manner in which they Fan (see page 2/76). In T. helveticus the Fanning movement of the tail is much more rapid and only the distal portion of the tail - approximately the last centimetre - is used. In T. vulgaris the Fanning movement is sufficiently vigorous to cause the whole body to move slightly as if the animal is under strain. (In observations of T. vulgaris males in glass-bottomed tanks fanning males are unable to maintain their position and are pushed gently backwards by the reverse thrust they are creating.) In T. helveticus the body is kept completely steady; only the vibrating tail tip can be seen moving. In his Display to a static female Fanning bouts may last for several seconds (Fan bouts lasting up to 23 seconds have been recorded), and in general uninterrupted Fanning bouts are longer than they are in T. vulgaris (see page 2/77).

There is a statistically significant overall difference in the relative frequencies of the various Display acts shown by the male in the two species (see page 2/78). Fan bouts are relatively more common in helveticus; this effect being particularly marked in the Retreat Display

phase. In T. vulgaris Retreat Display consists almost entirely of Retreat-and-Whips with only occasional Fanning bouts. In T. helveticus Whips and Fans are roughly equally common and more or less alternate with one another.

It is in the Fanning of the Palmate Newt that the probable functional significance of the dorso-lateral ridge is apparent. The effect of this ridge is to create below it a broad, shallow groove which is bounded along its ventral margin by the swell of the male's belly (see pages 2/79 and 2/80). During Fanning the male holds his body in such a way that this groove becomes much more pronounced on the side on which he is Fanning (see page 2/76). This effect was first described by Cummings (1911). The vibrating tail tip is positioned in the posterior end of this groove and it seems that the groove has the effect of channelling the water current generated by the tail along the side of the male's body towards the female's nose. Carmine particles introduced near to a Fanning male are carried along this groove. This hypothesis for the functional significance of the lateral ridge is discussed more fully in a later section on the evolution of the Fanning movement.

In observations of T. helveticus courtship encounters it was found that the courtship sequence was rarely repeated more than once. Thus there were rarely more than two Sequences (and, therefore, two spermatophores) in an Encounter.

The Alpine Newt, Triturus alpestris

Some elements of the sexual behaviour of this species have been described by Finkler (1923) and Prechtl (1951).

The Alpine Newt is more sluggish than the Smooth Newt and the Palmate Newt, both in its general activities and in courtship behaviour. In their living tanks they spend most of their time stationary among the weeds or occasionally walking slowly about on the bottom of the tank. A total of 36 encounters were observed and recorded, involving 13 males and 12 females,

and a total of 44 spermatophore depositions were observed (see Appendix 1).

In its overall pattern the courtship sequence in T. alpestris differs markedly from that of the two smaller species (see page 2/82). Orientation behaviour is similar and this is followed by Static Display, but this is much more prolonged than in the other two species, and there is no Retreat Display. Instead, the male Creeps from his Static Display position. He simply stops his display and begins to Creep away from the female. Generally she follows him and Deposition behaviour is in essence the same as in the other species. The male's Quiver movement is slightly different in this species; instead of slow, lateral waves the male makes spasmodic vertical jerks with his tail. On average there are rather more Push Back movements per sequence in this species.

The male's Display differs from that of the other species in that only one tail movement is used. This most closely resembles the Fanning movement in form (see page 2/83). The male takes up his Display position in front of the female with a Move to the Front movement which is much less dramatic than that of T. vulgaris or T. helveticus. He simply walks quickly round the front of her head, without any distinctive orientation of his body, and without the terminal Whip shown by the other species. He then begins to Fan at the female with a long series of Fan bouts, most of them of short duration, with a short break of half a second to a second between bouts. Durations of T. alpestris Fanning bouts are presented on page 2/77. When he has been doing this for some time a new behaviour is added to his display - the LEAN-IN. In between bouts of Fanning he raises his body by extending his legs and tilts it over towards the female so that his flank or tail touches her snout. The incorporation of this behaviour into his Display, which does not always occur, is indicative that the male is about to turn away from the female and start to Creep.

The Fanning movement of T. alpestris is different in form from the similar movement in T. vulgaris and T. helveticus. The distal half of the

tail is used and the individual tail beats are at a much slower frequency than those of either the other two species. They are also cruder in their execution, with the tail apparently much less flexible. The orientation of the Fanning male relative to the female is the same as in the other two species, but there is no sign of a dorso-lateral ridge or lateral groove (see page 2/83).

The name Fan has been used to describe a courtship action in three different species and attention has been drawn to the differences in the form of this movement between species. I will argue later in this chapter that the Fanning movements of the different species are homologous in the evolutionary sense, but it should be stressed that the use of the same term for three different actions came about as a matter of convenience of description and should not be taken at this stage to imply any relationship other than similarity of appearance.

A striking difference between the sexual behaviour of T. alpestris and that of other species is that following the completion of the first sequence, i.e. at the Brake or Push Back stage, the male does not revert to Display behaviour but turns away to Creep, thus starting another sequence at the Deposition Phase. This may happen two or three times. If the female moves away immediately after one sequence then the male will follow her and revert to Display behaviour.

The Crested Newt, Triturus cristatus

Sexual behaviour in the Crested Newt has been described in varying degrees of detail by Rusconi (1821), Prechtl (1951) and J.B. Nelson (1959).

In the course of this study only a few fragmentary observations have been made because, although this species is common around Oxford, sexual behaviour was rarely observed in the laboratory as the animals very quickly went out of condition. The account that follows is principally based on the description given by Nelson.

Orientation behaviour is essentially the same as that of the other species. The male is the more active partner, approaching the female, sniffing her and making "eager rushes" round to the front of her head. His Display is very different from anything shown by the other species so far described, in particular the male's very distinctive Display Posture (see page 2/84). The male lifts his hind legs and body off the substrate and stands on his fore-limbs. His throat is parallel to the ground and his body is sharply kinked in the middle so that his thorax is vertical while the rest of his trunk and his tail are parallel to the substrate, and angled over slightly towards the female. The male's display consists of slow, generous beats of the tail. In each beat the tail is flexed towards the female's head, and then back to a more-or-less straight position, each beat incorporating a slight flick of the tail-tip at its furthest extension towards the female. At first these tail beats are irregular in performance and in frequency but they quickly settle into a steady rhythm of uniform movements, between one and two beats per second. The tail beats are performed in bouts of between three and eight beats per bout with a brief pause between bouts. The tail beats are so powerful that the whole rear part of the male's body is swung from side to side and the very high crest is waved in a conspicuous way. As he displays the male makes small body movements which apparently offset the tendency of his tail beats to topple him over. As Display progresses the male incorporates a Lean-In movement similar to that seen in T. alpestris. These appear at first in the pauses between bouts of tail beats but become more and more frequent until they approximately alternate with individual tail beats. The Lean-Over movement gets progressively more exaggerated until the male's tail begins to touch the female's head. At this stage the tail beats become Lashes, the male's tail being lashed against the female's head. The incorporation of Lashing into the male's display signifies that the male is about to Creep. At no time during the male's display does the female move; as in T. alpestris

there is no Retreat Display.

The Deposition Phase is very like that of the other species described. Nelson describes a Tail-Touch action by the female but from his account it appears that Tail-Touch is not as invariable a precursor to spermatophore deposition as it is in the other species. Sometimes the female does not start to follow the male until after he has turned side on to her. The male's movement after deposition is the same as in the other species except that the male does not stop rigidly in the Brake position but moves sideways away from the female in a crab-like fashion. There is no mention in any account of the Push-Back movement. Following the completion of the courtship sequence, the male reverts to his display and the sequence is repeated.

Nelson classifies female behaviour into three states - uncooperative, receptive and intense. Uncooperative females move away from the male, receptive females remain passive, and intense females approach the male. Nelson describes a very responsive female who moved towards a displaying male so eagerly that she knocked him over and prevented him displaying to her. He also describes instances of pseudo-male behaviour by females, namely taking up the display posture, regular tail beats and lashes. These effects are very similar to those that I have described for T. vulgaris under the heading "Aberrant Female Behaviour" in Chapter 2.

The Marbled Newt, Triturus marmoratus

Of the few specimens of this species obtained during this study, only the males showed any sexual behaviour. Steward (1969) states that sexual behaviour is the same as in T. cristatus, and from the few observations that I have made this seems to be so. Certainly the display posture is the same with the deeply kinked body and hand-stand position. The same regular tail beats have also been observed.

Other Triturus Species

There is very little information in the literature concerning sexual behaviour in other Triturus species. Steward (1969) gives a brief account which is said to cover all species.

The male of the smallest species, T. boscai, has no crest but shows sexual dimorphism in other respects (Steward 1969). Prechtl (1951) gives a brief description of sexual behaviour in this species. The male has a "tail-wagging" display similar to that of the other species, but the Display orientation is different. Male and female are side by side and head to tail in such a way that the male's tail is wagged just in front of the female's nose. Bouts of tail-movement are very long, lasting about a minute, and display continues for several hours before a spermatophore is deposited.

The male Banded Newt, T. vittatus, has the most highly developed crest of all the species (see page 2/6) and has a conspicuous white stripe along the lower flank. The courtship Display of this species is said to incorporate a vertical head-bobbing movement (Steward 1969).

Of the sexual behaviour of the Carpathian Newt, T. montandoni, which is closely related to the Smooth and Palmate Newts (Lantz 1947, Steward 1969), nothing seems to be known. Males have virtually no crest, but dorso-lateral ridges and a terminal tail filament, both reminiscent of T. helveticus, are present.

Sexual Behaviour of Triturus Species: A Summary

1. In all species the male takes up a position such that his Display is directed at the female's head. There is a period of Display of variable duration, after which the male turns away from the female to begin the Deposition Phase which is similar in all species.

2. In some species Display is divided into a Static Phase when both animals stay in the same place and a Retreat Phase in which the displaying

male retreats in front of the advancing female - e.g. T. vulgaris and T. helveticus. In other species there is only Static Display, e.g. T. alpestris and T. cristatus.

3. In all species the male's Display consists of tail movements. There is considerable variation between species in the number of different tail movements, the form of the tail movements and in their relative frequency.

Reproductive Isolation among Triturus Species

When two or more species inhabit the same area, their continued independent existence depends on the maintenance of some degree of reproductive isolation between them. The agents which prevent or reduce interbreeding between species are varied and are grouped under the general heading "isolating mechanisms" (Dobzhansky 1951, Hinde 1959, Mayr 1963, Liley 1966). The genus Triturus presents a particularly interesting situation in this respect since it includes a number of forms, of both specific and sub-specific status, which are extensively sympatric.

Since the start of this century a considerable amount of work has been done on the genetic affinities of Triturus species and sub-species, and many hybrid forms have been studied. The most intensively studied hybridisation situation is that between T. cristatus and T. marmoratus whose hybrid form, T. blasii, though rare, is well known in the wild (de l'Isle 1862, 1872, Spurway 1953), and has been repeatedly created in the laboratory (Wolterstorff 1908, Lantz 1947, Spurway 1953). This work, and that on many other crosses, has been reviewed by Lantz (1934, 1947). In the context of reproductive isolation I shall consider two species, T. vulgaris and T. helveticus.

Isolating mechanisms can be classified under two general headings, pre-mating and post-mating mechanisms (Mayr 1963). In his study of reproductive isolation in Poeciliid fishes, Liley (1966) lists as

pre-mating factors: geographical barriers, habitat and seasonal differences, mechanical barriers, and ethological mechanisms. As the distribution maps indicate (see page 2/1) the general geographical ranges of T. vulgaris and T. helveticus overlap considerably (Steward 1969), and geographical overlap exists also at the local level (Taylor 1948, Smith 1951, Spurway 1953, Steward 1969). There is no precise knowledge about the habitat preferences of the two species, but in general T. vulgaris is found in lowland areas and on alkaline soils whereas T. helveticus is found in upland areas and on acid soils, though the two species frequently inhabit the same ponds (Smith 1951, Steward 1969, Bell 1970). The breeding seasons of the two species is the same, allowing for geographical variations, and pairs of both species have been observed courting in the same pond on the same day (Smith 1951). In view of the spermatophore method of sperm exchange and of the similarity in size and morphology of the two species, mechanical barriers can be discounted.

Post-mating mechanisms include such factors as gamete and zygote mortality, and hybrid inviability and sterility. Experimental crosses between T. vulgaris and T. helveticus have produced hybrids which are at least viable (Wolterstorff 1925). However, hybrids between the two species have not been recorded in the wild (Lantz 1947), which argues for a highly effective isolating mechanism between the two species which, by elimination, is probably ethological.

Cross-mating Experiments between T. vulgaris and T. helveticus

I have carried out a number of pilot experiments to investigate the possible role of sexual behaviour as an ethological isolating mechanism between these two species. In all these experiments a female of one of the two species was put into the test tank and was paired with males of her own and of the other species. The female was used as the constant factor in all these experiments because females were found to be more disturbed

than males by being transferred from one tank to another.

In the first four experiments a female was paired first with a heterospecific male and then with a conspecific male, both pairings being on the same day. Two T. vulgaris and two T. helveticus females were tested in this way. In all four experiments, which included a total of eight different pairings, the males pursued and displayed to heterospecific and conspecific females with equal vigour and with no apparent variation in their behaviour. In contrast, no female showed any positive behaviour, or even passive behaviour, when displayed to by a heterospecific male. When paired with males of their own species, two females, one T. vulgaris and one T. helveticus, showed positive behaviour towards conspecific males after failing to do so to heterospecific males; the other two females did not.

In the next four experiments females were paired first with conspecific males, and then with heterospecific males only if they had shown positive behaviour towards the males of their own species. Then, if they were unresponsive to heterospecific males, they were again paired with conspecific males. Two females from each species were tested in this way. As in the previous experiments, all the males courted conspecific and heterospecific females in the same way. However, neither T. vulgaris female, though responsive to a conspecific male both before and after, showed any positive or passive behaviour when displayed to by a T. helveticus male. In contrast, both T. helveticus females did respond when courted by T. vulgaris males, and spermatophores were deposited and picked up in both experiments. The behaviour of these two females was markedly different from the normal behaviour of responsive females. Instead of moving towards the male in a steady way, they moved in sudden jerks. It must be stressed that in these experiments the heterospecific pairing was conducted within minutes of the first conspecific pairing.

These results suggest that the males of both species are indiscriminate

when courting females. This is not surprising in view of the catholic selection of objects that T. vulgaris males have been observed to court (see page 2/16). However, one cannot discount the possibility that, in the natural situation, males exercise some degree of discrimination, as male Guppies have been shown to do (Liley 1966). One would expect that such discrimination would be on the basis of the female's smell, perceived during the Sniff behaviour. It is possible that males kept in the laboratory apart from females, as the males used in these tests were, become unselective.

Some of the results suggest that females will respond positively only to the display of conspecific males. In the two instances when females responded to heterospecific males, the females had, just minutes before, become responsive to males of their own species. There is no evidence that males can elicit positive behaviour from initially unresponsive females of the wrong species.

An ethological isolating mechanism based on female discrimination has been demonstrated for three-and ten-spined Sticklebacks (Wilz 1970); males of both species are unselective. Liley (1966) has shown that female selectivity is an important isolating mechanism in guppies, though males are selective to a certain extent, depending on their previous experience.

The hypothesis that reproductive isolation between T. vulgaris and T. helveticus is the result of female selectiveness is consistent with other facts:

1. There are marked differences between the epigamic characters of the males of the two species, whereas the females are very similar. (This refers to visual features; one does not know if there are differences in olfactory characters.)

2. The sexual behaviour of the two species, though similar in overall plan, differs in many details. These differences are in the Display behaviour, the later parts of the courtship sequence being similar in the

two species. It has been found in a number of species that, where behaviour is important in species isolation, it is behaviour that occurs early in the sexual process that differs most markedly between sympatric species. Examples include the pair-formation behaviour of cardueline finches (Hinde 1959), the orientation songs of Chorthippus spp. (Perdeck 1958), and the mating calls of various frog species (Blair 1964, Ball and Jameson 1966).

One cannot base very firm conclusions on these few results. However, these pilot tests do provide very suggestive evidence about reproductive isolation between these two species, and they do point the way to a line of future research. As outlined at the beginning of this section, much work has been done on hybridisation between Triturus species, but, as this work was carried out by workers interested primarily in genetics and taxonomy, very little information of the sort that the ethologist needs has been reported.

There is a very interesting gradation in the morphology of the subspecies of T. vulgaris from the typical form T. vulgaris vulgaris in north-west Europe to the more south-eastern subspecies, such as T. v. lantzi, T. v. dalmaticus, T. v. italicus and T. v. graecus. This consists of a reduction of the dorsal crest and the development of dorso-lateral ridges and a tail filament, so that the most southerly subspecies closely resemble T. helveticus. It is reported that these southern subspecies readily mate with T. helveticus, whereas the typical form, which is sympatric with T. helveticus, will not (Lantz 1947).

On the basis of this evidence, and on that from the cross-species experiments, I suggest that an important selection pressure in the evolution of Triturus sexual behaviour, especially of the male's display, has been for reproductive isolation on the basis of female choice, and that this selection may have been operative since the species became sympatric. The process by which isolating mechanisms are evolved in sympatry though

selection against hybrids has been called "Reinforcement" (Dobzhansky 1940, 1951, Liley 1966) and the mating calls of frogs provide evidence that such a process has occurred (Blair 1964).

Newt Courtship as a Functional System

All sexual behaviour has a definite function - to achieve successful fertilisation. The ethologist believes that the sexual behaviour that he observes in animals has evolved as a result of natural selection favouring behaviour that increases the probability that this function will be achieved. It is instructive to consider the sexual behaviour of newts as a functional system and to ask to what extent the "design" of the behaviour is suited to functional requirements. Other studies of sexual behaviour have emphasised certain functional aspects of sexual behaviour which fall within the scope of the general function of achieving fertilisation (Bastock 1967). These functions have been summarised by Tinbergen (1953b) as Synchronisation, Persuasion, Orientation and Reproductive Isolation.

Before any sexual behaviour can occur, male and female must come together. This is one aspect of the Orientation function of sexual behaviour and some species have methods of attracting mates over a considerable distance. The sexual odours of silkworm moths (Schneider 1969), the stridulations of Grasshoppers (Perdeck 1958), and the mating calls of frogs (Blair 1955, Bogert 1960, Capranica 1968) all have this function. The laboratory approach to newt courtship excludes the possibility of analysing long-range orientation in newts, if it occurs. In this context the observations of Gauss (1961) are of particular interest. He studied Triturus cristatus in ponds and obtained evidence that the males have restricted home ranges within which they mark sticks and stones by rubbing their cloacas against them. The marking behaviour that Gauss described seems to be essentially similar to the movements by which

defecating newts remove waste matter from their cloacas. Wandering females are said to sniff these marking sites and to show a behaviour called "Sprawling" which attracts the attention of the resident male who is nearby. Gauss's study was not very extensive but it is the only real field study of newt behaviour, and only by studies like this would it be possible to analyse behaviours leading to the first contact of male and female.

Once the male and female newts have established contact another aspect of Orientation becomes apparent as the male takes up his display position in front of the female. How does the male know which end of the female is the front? There are two possibilities - that the male responds to the head end, as opposed to the tail end of the female, or that he responds to the end that leads as the female moves. In the great majority of courtship encounters the female is on the move in the early stages so it is not possible to distinguish between these two hypotheses, but on just three occasions males have been observed to make the Move to the Front movement to the tail end of a stationary female. The newt model has identical ends and in model experiments the male always moved to the end that was leading. If a strait-jacket female is moved backwards away from a male he will swim round and take up position in front of the female's tail. These few observations suggest that the male responds to cues provided by the female's movement and not to specific cues associated with her anterior end, but more systematic experiments are required before this can be verified.

In many animals the male is initially more sexually active than the female, and she is generally unresponsive to his first sexual advances. In such species the male's courtship behaviour has the function of making the initially unresponsive female responsive. In the system of spermatophore transfer shown by newts it is essential that the female should follow the male closely. The function of the male's display behaviour seems to be to arouse the female so that she will follow the male when he

turns away to deposit the spermatophore. Thus the male's display fulfils the Persuasion function of courtship behaviour. The analysis of the female's behaviour during the Display phase showed that, as the male displayed to her, there was an increase in the number of approach movements shown by the female and a corresponding decrease in the number of her movements away from the male.

While it is clear that the male's display behaviour, considered as a whole, has the effect of making the female responsive, it is not possible to attribute to each particular type of male display act, Wave, Whip or Fan, a particular effect or function. A similar situation is seen in the complex displays of Eider Ducks and McKinney (1961) suggests that it is not realistic to suppose that each of the drake's movements carries a special message to the female, but that it is the overall pattern of the male's display that influences her. It has been suggested in earlier chapters that the different male display acts are perceived by different sensory modalities, with vision, olfaction and perception of vibrations all possibly being involved. Thus the female is bombarded with a variety of stimuli, the overall effect of which is to make her responsive to the male.

At the end of the previous section evidence was presented in support of the hypothesis that the male's display acts as a reproductive isolating mechanism in that females respond positively only to the display of males of their own species. Thus the male's display may serve not only to "persuade" a female to respond to the male but also, through the selectivity of the female's response, ensure that it is the right female that is persuaded.

In many species, particularly those that are territorial, males spend much of their time showing aggressive behaviour towards conspecifics, sometimes of both sexes. In such species it is suggested that the persuasion element in courtship behaviour involves the additional factor

that the male's behaviour must not only stimulate the female to approach him but must also reduce any tendency to flee from him (Tinbergen 1953b, Morris 1956). In some species the female shows behaviour in the sexual situation that has been interpreted as having Appeasement function; that is to say that it causes the male to be less aggressive towards the female. Examples are the Herring Gull (Tinbergen 1953a) and the Jewel Fish (Baerends & Baerends-van Roon 1950). These hypotheses about the function of sexual displays in relation to agonistic behaviour are essentially speculative, for, while it is possible to observe what the animals do, there is no direct evidence about the nature of the internal state that causes them to do it.

The important point to be made about the relationship between sexual and aggressive behaviour with regard to newts is that newts, with perhaps one exception, have not been observed to show intraspecific fighting. Several authors have described a behaviour that looks like fighting in feeding frenzies, in which animals of both sexes sometimes snap at each other's limbs (Tinbergen & Ter Pelkwijk 1938, Smith 1951). These authors agree that this behaviour is not fighting behaviour but is a feeding response to moving objects when the newts are excited by the scent of food. It is a common occurrence among groups of newts who are given food after some days of food deprivation. Gauss (1961) has described site attachment shown by males of T. cristatus but he does not consider this to be territorial behaviour in the accepted sense as no fighting is involved. Mendelssohn (pers. comm.) has extensively studied several Triturus species but only in T. vittatus has he observed serious fighting between males. Spurway (1953) states that laboratory stocks of T. cristatus establish "peck-orders" in which the dominant animal gets most of the food provided. Her account of this phenomenon is not detailed, and she presents little evidence for it. I have never observed any sort of heirarchical system in any of my laboratory stocks.

In T. vulgaris and T. helveticus, the male's display stimulates the female to start to approach the male, a condition vital for the success of spermatophore transfer. The male does not turn away to deposit his spermatophore as soon as the female starts to approach him; instead he continues to Display to her while retreating before her. The experiments on the Display phase showed that the male does not Creep unless the female has shown persistent approach for some seconds. They also showed that if the female reverts to negative or static behaviour, the male likewise reverts to an earlier stage in his behaviour. Thus the adaptive significance of the Retreat Display behaviour seems to be that it provides an opportunity for the male to receive repeated stimuli from a persistently responsive female. Putting it anthropomorphically, the female's first approach suggests to the male that she is responsive; by continuing his display he can confirm that she really is. The Display phase experiments also showed that the time for which the male maintains his Retreat Display before Creeping is very variable. This could suggest that the male does not turn away until he is ready to deposit the spermatophore, perhaps for internal reasons connected with the mechanism of spermatophore production. The Retreat Display phase provides a mechanism by which the male can keep the female in her responsive condition until he is ready to deposit.

Having argued the adaptive benefits of the Retreat Display phase one is faced with the fact that this phase is absent in T. alpestris and T. cristatus. In both species the male stops displaying, turns away to Creep, and the female usually follows him. The observer has no way of predicting whether or not the female will follow the male when he Creeps, and there is no apparent way by which the male could perceive this either. Possibly the male responds to stimuli not apparent to the human observer but in many sequences involving T. alpestris I have observed the male Creep, receive no Tail-Touch, and then turn back to resume his Display. The Retreat Display eliminates this element of uncertainty about the female's

responsiveness and would seem to be a more sophisticated system than the purely Static Display system. This variation in sexual behaviour could be correlated with ecological factors; possibly T. vulgaris and T. helveticus live in habitats where space is less restricted and where they can afford to move about over a wide area during courtship. Alternatively the presence of the Retreat Display behaviour may be correlated in some way with the generally higher level of activity shown by the smaller species. With a very active female there might be a higher probability of a "false positive" move towards the male. By evolving a system whereby the male Creeps only after repeated indications of the female's positive behaviour, the chance of his Creeping in response to some incidental movement towards him is reduced.

The male usually Creeps away from the female for five to ten cm, but occasionally he will Creep further than this. J.B. Nelson (1959) suggested that the male may select a suitably even substrate before depositing the spermatophore, as some scorpions do (Alexander 1959). Nelson tested newts on a choice of substrates of different textures but obtained no clear results. The substrate of the observation tank used in this study consisted of uniformly fine gravel, but on two or three occasions unusually long Creeps seemed to be associated with the avoidance of obstacles, in one instance a large snail, in another the corner of the tank. The Strait-Jacket technique makes it possible to control to a considerable extent where in the observation tank courtship behaviour takes place. It should therefore be possible to repeat experiments like Nelson's, comparing the male's Creep behaviour when he is creeping onto a smooth substrate as opposed to an uneven one.

Having turned away from the female to Creep, the male can no longer see the female, but he can still receive stimuli from the female following him in the form of the Tail-Touch. Only when he has received this stimulus will the male deposit his spermatophore. This stimulus-response

relationship thus ensures that the male will only deposit a spermatophore when there is a responsive female close behind him.

Once the spermatophore has been deposited, the function of subsequent behaviour is to ensure that it is successfully picked up by the female's cloaca. The way in which the male Creeps-On through a body's length before Braking and stopping the female's progress gives a reasonable chance that the female, provided she moves along the right line, will end up with her cloaca over the spermatophore. Clearly, this procedure cannot be expected to be anything but approximate. For one thing newts are very variable in length and it is difficult to conceive of a procedure by which the male could adapt his Creep-On movement to allow for this.

While the Creep-On procedure ensures that the female moves through approximately the right distance, the crucial factor for a successful pick-up is that the female should move along the correct line. Here one is concerned with another aspect of the Orientation function of courtship behaviour. From observations it is clear that the majority of missed spermatophores were missed because the female went to one side of them, and not because she stopped short of them. One cannot be sure what determines the line that the female takes but it seems likely that she follows the male's open cloaca (and perhaps also the coloured stripes at the base of the tail in T. vulgaris). The female shows no behaviour directed at the spermatophore itself so that her orientation relative to it seems to be entirely dependent on her orientation with respect to the male. Gauss (1961) suggests that the female follows a scent trail left by the male but he presents no evidence for this. There is no indication that this is so in any of the species that I have observed. The female does not show the characteristic sniffing posture, nor does she press her nose to the substrate as she follows the male.

The male maintains his Brake posture, with the female pressing against him, for an average of 25 seconds, though he may stay in this position for

up to a minute. This delay before continuing courtship behaviour could be seen as a device to allow time for the absorption of the spermatophore to begin. At first the spermatophore is but tenuously attached to the cloaca and if the female is moved immediately after the spermatophore is picked up it becomes dislodged.

In many, but not all sequences there then follows the curious Push-Back behaviour. It would seem that this behaviour creates a further opportunity for picking up the spermatophore if it was missed initially, by moving the female backwards and forwards over the area where it was deposited. This is not a very satisfactory hypothesis for the functional significance of this behaviour because, in all the many instances when the Push-Back behaviour has been observed, not once has a spermatophore that was missed at the first opportunity been picked up as a result.

At the completion of the courtship sequence, the male generally reverts to his display position and the sequence is repeated from the Retreat Display stage. Repeating the courtship sequence a number of times would clearly seem to increase the probability that at least one spermatophore will be picked up. This point will be referred to in a later section of this chapter.

Synchronisation of Newt Sexual Behaviour

In the sexual behaviour of most animals correct timing is an essential pre-requisite to successful fertilisation. In most species that copulate it is necessary that the female be receptive for copulation to be successful, and it is therefore essential that the female be receptive at the same moment that the male attempts copulation. In species that practice external fertilisation, for example the Stickleback and the Common Frog, accurate synchronisation of behaviour is equally vital. If there were to be any appreciable time lag between the release of the female's eggs and of the male's sperms there would be a high risk that the two would become dispersed,

with a consequent decrease in the probability of successful fertilisation. In newts, fertilisation is internal but, for a short time, the sperm is exposed to the outside world. The less time for which the spermatophore is exposed, the less likely is it that it will be lost in the process.

It has been shown for a number of fish species that sexual behaviour consists, at least in an ideal sense, of a chain of reciprocal stimuli and responses, for example the Three-spined Stickleback (Tinbergen 1951), the Ten-spined Stickleback (Morris 1966) and the Asian Teleost Badis badis (Barlow 1962). Such a chain ensures that, at the vital moment of sperm transfer, the behaviour of the two sexes will be appropriately synchronised. The courtship behaviour of the European Salamander Salamandra salamandra has been interpreted by Joly (1966) as a similar chain, but this is not based on experimental evidence. Similarly the stimulus-response chains presented by Marquenie (1950) and Prechtl (1951) in their descriptions of Triturus courtship behaviour are based only on observational evidence.

If the male's Orientation and Display behaviour is considered as three units, Orientation behaviour, Static Display and Retreat Display, and not in terms of a number of discrete actions, the sexual behaviour of T. vulgaris can be depicted as a Stimulus-Response chain (see page 2/85). Solid lines represent causal relationships that have been tested experimentally; broken lines are inferred from observations.

This presentation of newt courtship does not show the elegant interplay between male and female behaviours that is seen in the idealised examples quoted above. However, it does show that newt courtship fulfils the basic principle of such stimulus-response chains - that the behaviour of the male keeps pace with that of the female. The male does not proceed from one stage in his behaviour to the next until the female has shown the correct response to the first stage. This ensures that there is synchronisation of the moment at which the male releases his spermatophore and the point of high female responsiveness. Thus the female is following

the male closely when he deposits the spermatophore and it is exposed to the outside world for the minimum of time.

The Success of Newt Courtship and Factors that Affect It

The previous section discussed newt courtship as a functional system and suggested a number of ways in which the behaviour can be considered to be adapted to fulfil a specific function, the achievement of fertilisation. The next step is to examine to what extent the behaviour does in fact fulfil this function. Within a complex behaviour sequence there is considerable variation and one might expect that this variation would be the source of specific factors that could affect the success of courtship behaviour. In practice it is not easy to determine whether or not fertilisation has successfully been achieved, but it is easy to see whether or not the spermatophore has been successfully transferred. Thus success, as discussed in this section, relates to the transfer of spermatophores.

At this point it is important to differentiate between two levels at which one can consider the success of newt courtship. One can consider each courtship Sequence and consider the factors that influence the pick-up of the individual spermatophore concerned. Alternatively one can look at the courtship Encounter as the biological unit and consider factors that influence Encounter success. In this discussion an Encounter is said to be successful if at least one spermatophore is picked up during the encounter. To what extent this is biologically strictly true depends on whether or not one spermatophore contains sufficient sperms to fertilise all of one female's oocytes, something which is not at present known.

The overall success of Encounters and of Sequences for the three species studied is presented on page 2/86. The data for T. vulgaris and T. helveticus is from two years, 1970 and 1971, combined; that for T. alpestris is one year's data. For all three species the number of successful Sequences is approximately equal to the number of Encounters.

In other words, each species averages one successful Sequence per Encounter. These figures suggest that T. helveticus is more successful in both respects than the other two species but this difference is not significant.

On a simple chance basis, the more spermatophores that are put down, the greater is the probability that one will be picked up; and one would expect that the principle factor affecting the success of Encounters would be the number of spermatophores produced. If one assumes that all spermatophores are equally likely to be picked up one can predict the number of Encounters, of different numbers of Sequences, which will be successful. The comparison between these expected values and the observed values are presented on page 2/87. (Only the data for T. vulgaris is presented since the data for the other two species are too small for meaningful analysis.) This comparison shows that Encounters containing only one Sequence are less successful than expected, whereas those incorporating two and three Sequences show a very close fit.

When the success of Sequences is analysed on the basis of the order in which they occur within an Encounter (see page 2/88), it is found that first Sequences have a lower success rate than second Sequences, which are in turn less successful than third Sequences. The upper figure shows the plot for all Sequences, regardless of the length of Encounter they occurred in. The trend of this plot is significant when the data are tested with a modified chi-square test which tests for trends (Maxwell 1961) - chi-square = 7·267, $p < 0{\cdot}01$. The lower figure shows the plots for Encounters of different lengths. The trend of these plots is the same as that for the combined data, showing that this trend is consistent within Encounters incorporating different numbers of Sequences. J.B. Nelson (1959) found a similar effect with T. cristatus; the pick-up rate for first, second, third and fourth spermatophores was 15%, 30%, 36% and 67% respectively.

This leads to the question of why early Sequences are less likely to be successful than subsequent ones. The data were scanned for variations within Sequences which correlate with the order of the Sequence within an Encounter and with the success or failure of the Sequence. Only two such correlations were found, and these are shown on page 2/89. The time interval from spermatophore deposition until the end of a Sequence (defined as when the male turns back to his Display orientation) is significantly longer in second Sequences than it is in first Sequences. Much of this time is taken up with the Push-Back behaviour and these show a similar correlation, there being more Push-Backs in second Sequences than in first Sequences. However, there is no correlation between either post-deposition time or the number of Push-Backs and Sequence success.

The correlation between the order of a Sequence within an Encounter and the post-deposition time might suggest that a reason for pick-up failure is that the male reverts to display behaviour before the female has had time to pick up the spermatophore, although the non-correlation between post-deposition time and Sequence success does not support this hypothesis. This hypothesis is dispelled when the time at which the male reverts to display is related to the time at which the spermatophore is generally picked up. On average, spermatophores are picked up 10·7 seconds after they were deposited, and the average time at which the male turns back is 22·7 seconds in unsuccessful Sequences and 27·8 seconds in successful Sequences.

Likewise, observational evidence does not suggest any direct link between Push-Backs and spermatophore pick-up. As stated earlier, no spermatophore has ever been observed to be picked up as the direct result of a Push-Back. Thus it seems that neither of these correlations represents a causal relationship with spermatophore pick-up or non pick-up. Direct observational evidence shows that spermatophores are missed because the female passes to one side of them. Why this should happen more in first

than in subsequent Sequences is not known. It could be due to inaccuracy in the way the male creeps-on after deposition, or to inaccuracy in the way the female follows him, or to a combination of the two. It is possible that very precise analysis of the deposition phase using video or cine-film might resolve this problem.

Evolution of Sexual Behaviour within the Genus Triturus

The evolutionary history of behaviour is generally deduced by comparing the behaviour patterns of closely related animals (Tinbergen 1959, Cullen 1972), though it can also be inferred by analysis of the survival value of behaviour (Tinbergen 1965). The comparative approach has been applied to the behaviour of a number of animal groups including the Pheasant family (Schenkel 1956), the Cormorant family (van Tets 1963) and Salticid spiders (Crane 1949). An important factor in a comparative approach is that there should be available other criteria, such as morphology or genetic affinities, by which taxonomic relationships can be independently assessed. As described earlier, the genetic affinities of Triturus species have been the subject of much research.

In the most general terms, sexual behaviour is similar in all the Triturus species studied. The male first orients himself in front of the female, there follows a period of Display involving movements of the male's tail, which leads to the spermatophore deposition and pick-up procedure. Within this general pattern there is considerable variation between species, particularly in the overall organisation and in the finer details of Display behaviour.

The Form of the Display Movements

In all species the tail is the structure used in Display. In evolutionary terms the tail must have been primarily a locomotory structure.

The deep, laterally flattened shape demanded by its locomotory function makes the tail ideally preadapted for use as a display "flag" and increasing its height and decorating it with spots and coloured stripes make it an even better flag without impairing its locomotor function in any way. The manner in which the tail is used for display in the different species shows considerable variation.

There is great variety in the form of individual tail movements. There are slow, large amplitute movements of the whole tail - the Wave of T. vulgaris and the tail beats of T. cristatus. There are sudden, violent movements of the whole tail - the Whip of vulgaris and T. helveticus and the Lash of T. cristatus. Finally, there are smaller, high frequency movements of the distal portion of the tail - Fanning of T. vulgaris, T. helveticus and T. alpestris.

There is an important variation between the species in the number of distinct tail movements used in the display. In T. alpestris there is only one movement - the Fan - whereas in T. vulgaris and T. helveticus there are three - Wave, Whip and Fan. On the principle of economy of hypotheses, it is more likely that characters are acquired in evolution than that they are acquired and then secondarily lost. Thus the alpestris condition, with only one type of tail movement, would seem to be the more primitive.

The situation in T. cristatus is somewhat different. Separate tail movements have been described - irregular tail beats, regular tail beats and lashes, but according to Nelson these are not discrete acts but are a gradation of acts which he interprets as being indicative of successively higher states of arousal. This situation is quite unlike the display of T. vulgaris and T. helveticus, where the tail movements are quite distinct, do not grade into one another and do not follow each other in any rigid way. The display movements of the two smaller species differ from each other in the amount of tail used, the amplitude of the movement and the frequency of the movement. The tail movements of T. cristatus all use

the whole tail, their frequency varies little and only the amplitude of the movement changes. Thus T. cristatus seems to have retained the primitive, T. alpestris-like condition of employing basically one type of tail movement, but it shows an advance on this primitive condition by having the capacity to vary this movement according to the stage of display.

This comparison suggests that the display movements shown by Triturus species have evolved from one ancestral movement. The responsiveness of newts to any movement in their immediate environment is readily observed. It seems probable that the ancestral tail movement "exploited" this responsiveness and that, by becoming repetitive and rhythmic, it became increasingly effective in attracting the female's attention.

All Triturus species (with the possible exception of T. boscai - see Prechtl 1951) show the same Display orientation, with the male in front of the female. Since such an orientation would have been necessary for the ancestral tail movement to be perceived, it probably evolved at an early stage in the evolution of the behaviour.

From this hypothetical ancestral movement three lines of evolution seem to have occurred:

1. Modification into a single, stereotyped movement - Fanning in T. alpestris.
2. Modification into a single, variable movement, with the emphasis on slow, rhythmic movements - the tail beats of T. cristatus.
3. Multiplication into a number of discrete, contrasting movements - the Wave, Whip and Fan of T. vulgaris and T. helveticus.

An important factor to be considered is the nature of the stimuli provided by the male's display movements. Besides being a visual stimulus, the ancestral tail movement would set up water currents which could, potentially, be perceived by the female's lateral line organs and which would disperse any odour that was secreted by the male. (Hedonic glands are found in the majority of Urodeles (Noble 1931.) Thus this hypothetical

ancestral movement would provide good raw material from which the evolutionary process of Ritualisation could produce movements that provide visual, olfactory or vibrational stimuli. Unfortunately, there is at present no conclusive evidence about the exact nature of the relevant stimuli conveyed to the female by the various tail movements seen in the different species. All of them are visible, all must create water currents which, if appropriately orientated, would carry water currents and smell towards the female. However, the differences in the form of the various movements suggest that different movements are specialised to present particular types of stimuli.

In the Fanning movement of T. vulgaris, T. helveticus and T. alpestris the male presents little visual stimulation to the female. The water current that is created in Fanning seems ideally suited to carry odour towards the female and the fact that the male's cloaca, which is very rich in mucous glands, is open during fanning, supports the idea that fanning carries olfactory cues to the female. Mucous glands are also plentiful on the male's flanks (see page 2/7 and page 2/80), and any odour provided by these would also be carried by the Fanning stream to the female's nose. The female's head is well equipped with lateral line organs which would very likely be stimulated by the fanning current, so Fanning could be a vibrational stimulus as well as, or rather than, an olfactory one.

In contrast to Fanning, the Wave movement of vulgaris, and the tail beats of cristatus, expose the full length of the male's tail to the female's view and, therefore, seem to provide visual stimuli. It is in these species that conspicuous tail patterns are most highly developed in the male - spots and coloured stripes in T. vulgaris and the very conspicuous white tail stripe of T. cristatus. The idea that these provide visual cues is supported by the fact that these movements are rather slow, giving the female plenty of opportunity to see the tail. In the Wave movement of T. vulgaris the tail is often presented for a full half-second

to a second. It is important in this context to differentiate between those colour patterns that are sexually dimorphic and those that are not. Those that I have suggested are associated with visual display movements are shown only by males; others, such as orange belly colouration, are shown by both sexes. T. alpestris is one of the most brightly coloured species but is one of the least dimorphic (see page 2/11).

It is difficult to imagine that the Whip movement of T. vulgaris and T. helveticus is anything but a violent tactile stimulus. The female has virtually no opportunity to see the male's tail and the male's smell must be widely dispersed by it. Similarly the Lash movement of T. cristatus is most likely a tactile stimulus.

The process by which display movements have evolved is called Ritualisation (Huxley 1923, 1966). The kinds of alterations of movements that occur in their evolution have been listed by Hinde (1959) (see also Cullen 1972), and a number of these seem to have taken place in the evolution of the tail movements used in Triturus Display. The species differ in the relative frequency with which they perform different acts, and in the variety of acts used. The Fanning movements show rhythmic repetition and are associated with a specific orientation which is necessary for the effective functioning of the signal. Different species Fan at different speeds. Display in general is associated with conspicuous structures (crests) and colour patterns, and some individual tail movements seem to be associated with specific patterns, a typical feature of displays (Baerends 1950). Some of the tail movements have become stereotyped; the Fan movement of each species has evolved its own "typical intensity" (Morris 1957). In any discussion of Ritualisation one must consider the ancestral movements from which display movements may have evolved. In newt sexual behaviour the orientation of the male relative to the female is crucial and, as the tail is used extensively in movement, it is reasonable

to suppose that the various tail movements may have evolved from incipient orientation movements.

A number of different selection pressures are likely to contribute to the evolution of displays. Natural selection will favour displays that are more effective; for example those that attract the attention of females more effectively. I have earlier suggested another possible selection pressure - that for reproductive isolation on the basis of female discrimination of the male's display. For this an important evolutionary trend would be the reduction of ambiguity in the displays of different sympatric forms (Cullen 1966). Other aspects of the newts' life, such as habitat, will have an evolutionary hand in the shaping of displays. One might expect that those species that have more visual displays are to be found in more open, clearer waters. As so little is known of the ecology of newts at the present time, this can only be raised as a possibility.

The Overall Pattern of Display Behaviour

An important difference between the Display behaviours of the different species is that in two species, T. vulgaris and T. helveticus, Display is divided into Static and Retreat phases, whereas in the other species there is only Static Display. As Static Display is common to all species one may assume that it is an ancestral feature and that Retreat Display is a secondary feature. The adaptive significance of Retreat Display was discussed in the previous section, where it was suggested that Retreat Display represents a more sophisticated communication system.

By the same argument, the situation in T. alpestris, which follows one deposition phase immediately with another, seems to be more primitive than that seen in the other species, which revert to Display behaviour between successive depositions. This ensures that the male has the opportunity to receive stimuli from a responsive female before the deposition of each precious spermatophore.

The changes that appear to have taken place in the evolution of Display behaviour within the genus are summarised on page 2/90. The species whose sexual behaviour is known fall into three groups on the basis of their display behaviour, and this grouping corresponds with that based on anatomical characters and genetic affinities (Lantz 1947). Within only one of these groups is there sufficient information to make comparisons between species - between T. vulgaris and T. helveticus. The differences between these two species are small compared with those that exist between the three groups.

Comparison of the sexual behaviour of the different species shows that there is great variation between species in the early stages of the courtship sequence, whereas the later behaviour, involving the deposition and pick-up of the spermatophore, is essentially the same in all species. A comparative approach within the genus is, therefore, not likely to give any clue about the evolution of this part of the behaviour. This aspect is discussed in a later section in a comparison of Triturus sexual behaviour with that of other Salamandrid genera.

Fanning and its Anatomical Correlates

Attention has already been drawn to the lateral body groove, formed by the dorso-lateral ridge, that is seen in T. helveticus and, to a lesser extent, in T. vulgaris. I have suggested above that this groove has the effect of channelling the water current created by the movement of the tail into a compact stream. The lateral ridge above, and the swell of the belly below, would inhibit any flow of water dorsally and ventrally respectively. This hypothesis gains support from the fact that this groove becomes more pronounced during Fanning on the side of the male against which his tail is beating. How this is done is not clear, but it seems to be under muscular control. In T. helveticus males the groove is obvious at all times

(see pages 2/76 and 2/81). In T. vulgaris the groove is apparent during Fanning (see pages 2/20 and 2/24) but is less so at other times (see pages 2/3 and 2/6), a fact which may have led to the assertion that it is absent in the typical form of this species (Smith 1951).

Another anatomical feature of reproductive T. helveticus males that has so far defied any satisfactory functional explanation is the caudal tail filament. This structure, about 5 mm in length, appears at the end of the male's tail and is present only during the breeding season. It was suggested by Noble (1931) that this tail filament "... may serve to direct the secretion of the abdominal glands towards the female during courtship ...". Noble also drew attention to a similar structure in the male Japanese Newt, Cynops pyrrhogaster, which in his day was included in the genus Triturus. It is possible that the caudal filament, because of frictional forces which cause water to "stick" to solid surfaces, does indeed have the effect of directing the water current generated by the fanning tail in the direction of orientation of the tail filament.

These hypotheses for the functions of these two morphological characters relate to what are essentially hydrodynamic processes of which very little is known. It is probable that the mode of action of the male's tail during Fanning is similar to the tail movements used for swimming in anguilliform fishes. The hydrodynamics of these movements have been the subject of several studies (Gray 1936, 1957, Gero 1952, Rosen 1959). It proved impractical to build a model newt that could simulate the Fanning movement and to investigate the water currents around it, but hydrodynamic systems are so complex and are so radically altered by small variations in the physical situation that simple simulations are meaningless. What is required is a method for analysing the water currents around male newts as they Fan, as Rosen studied currents around swimming fishes.

If these two morphological characters, lateral groove and caudal filament, are adaptations associated with the Fanning movement, then it

follows that T. helveticus, which shows both features and has the more highly developed lateral ridge, is more highly adapted for Fanning than T. vulgaris. That this should be so makes sense since T. helveticus, as has been shown, employs the Fanning movement more than does T. vulgaris. However, this argument is not tenable when T. alpestris is also considered, since this species shows neither feature but shows only Fanning in its display.

An alternative hypothesis might be found from a comparison of the speed of Fanning of the three species. The fanning movement is slowest in T. alpestris - about 4 tail beats per second, is approximately twice as fast in T. vulgaris and is faster still in T. helveticus. Thus increased development of morphological features correlates with increased speed of fanning. It may be that increasing the frequency of the tail movements that generate the water current has the effect of increasing the dispersal of that current, so that modification of the body is necessary to keep the current compact. Again one can come to no sort of conclusion because of the absence of hydrodynamic evidence.

This discussion has been highly speculative because there is no direct evidence about either the hydrodynamics of the Fanning movement, or about the nature of the stimuli involved. One can say that the lateral groove and caudal filament of T. helveticus appear to be adaptations to channel a water current towards the female, but it is not clear why these features should be less developed or absent in other species that Fan.

Comparison of Triturus Sexual Behaviour with that of Other Urodeles

There have been few detailed studies of sexual behaviour in Urodeles. Most of the information that does exist in the literature, much of it anecdotal, has been reviewed by Salthe (1967), who relates Urodele

courtship behaviour to taxonomy and to habitat. In the discussion that follows the authors quoted are those who have described sexual behaviour in the relevant species; if no reference is given the source is Salthe (1967). (The reader may find it helpful to refer to the scheme of Urodele taxonomy presented in Appendix 4d.)

Salthe presents a basic courtship pattern to which all Urodele genera conform (see page 2/91). This divides sexual behaviour into five stages:

A. Preliminary stage. The male approaches and investigates the female.

B. The male EITHER captures and grasps the female and arouses her by rubbing her, OR blocks her path and displays to her.

C. (Shown by only a few groups.) The male moves away from the female and she follows him.

D. The spermatophore is deposited on the substrate.

E. The male moves away from the spermatophore. The female follows him over it or is pulled over it by the male.

The sexual behaviour of Triturus species incorporates all five of these stages.

The genera most closely related taxonomically to Triturus are Taricha from Western North America (Twitty 1966, Davis and Twitty 1964), Notopthalmus from Eastern North America (Jordan 1893, Hilton 1902, Shaffer pers. comm.), and Cynops from Japan (Prechtl 1951). Until recently these three were grouped with the European newts in a single genus, Triturus. The later parts of sexual behaviour are essentially the same in all four genera; the male deposits the spermatophore, creeps away in an arc, and the female follows and picks it up. There are, however, marked differences between these genera in the earlier parts of courtship behaviour (see page 2/92).

In Taricha the male mounts the female's back and clasps her pectoral region with his forelimbs which, in the breeding season, are equipped with horny pads. He rubs the female's head with the hedonic glands around his

head and, at the same time, strokes her cloaca with his hind-feet. After a time he dismounts and deposits the spermatophore.

In Notopthalmus the male similarly mounts the female dorsally, but grasps her with his hindlimbs which, like the forelimbs of Taricha, are equipped with horny pads. He rubs the female's head with his snout and, at the same time, shows a "fanning" movement with his tail which creates water currents around her head. After a time he dismounts and spermatophore deposition follows after a tail-touch.

In Cynops the male does not grasp the female in any stage of the behaviour. The male nudges the female along the length of her body and then swims round to block her path in the manner shown by Triturus. In his position in front of her the male rubs the female's head with his snout and performs a "fanning" movement with his tail. His behaviour is thus essentially similar to that of Notopthalmus, except that he does not grasp the female, although in some species the male restrains the female by putting one leg around her neck.

The fact that the later parts of the sexual behaviour sequence are essentially similar in these four genera suggests that this method of spermatophore transfer, in which there is only minimal contact between the sexes, evolved before these genera became separated. The success of this method of spermatophore transfer depends on the female following the male closely; that is, she must be responsive to him. The variation between the genera in the earlier parts of their behaviour suggests that each genus has evolved its own method of making the female responsive. In three of them the male uses a rhythmic tail movement; and in three genera the male rubs his hedonic glands against the female's nose. The males of two genera use amplexus to hold the female while they court her, one genus showing forelimb amplexus, the other hindlimb amplexus. Triturus differs from the other three genera in lacking either amplexus or rubbing behaviour in the early stages but, as shown in an earlier section, shows elaboration and

multiplication of the tail movements which are of crude form in Cynops and Notopthalmus. The Fanning movement of Triturus may be thought of as comparable to the rubbing of the other genera in that it is an alternative method by which male odour can be conveyed to the female.

An interesting feature of this comparison is that these four genera differ in the extent to which the female is free during sexual behaviour. In Triturus she is not restrained in any way by the male, but can move away from him at any time. In the other genera she is, to a greater or lesser extent, restrained by the male during the arousal stage. The Triturus system provides greater opportunity for the female to exercise discrimination between males, and it is arguable that, since female gametes are less expendable than male gametes, a sexual system based on female discrimination is evolutionarily more sophisticated than one based on male discrimination in which "rape" of a female of the wrong species is more possible. It is significant in this context that Triturus species generally show a more marked sexual dimorphism than any of the closely related genera.

Widening this comparison to more distant relatives of Triturus, it can be seen that Triturus and its three closest relatives form a distinct group within the family Salamandridae. Salthe (1967) divides the Salamandrids into three groups on the basis of their sexual behaviour, and of these groups the group described above is number three. Group one consists of only one genus, the European Mountain Salamanders Euproctus (de Bedriaga 1895, Ahrenfeldt 1960). These animals live in fast-flowing streams and the male is said to "ambush" females and then grasp her around her pelvic region with his prehensile tail, in such a way that the two cloacas are directly opposed (see page 2/93). Amplexus may last for several hours and females have been reported to die in the process.

Salthe's group two includes the European Pleurodeles (Gallien 1952, Steward 1969) and Salamandra (Joly 1966). The characteristic feature of

this group is that amplexus is maintained throughout the entire length of the courtship sequence, and that the male captures the female from below (see page 2/93). In Salamandra the female rubs the female's chin with his head. After a time he deposits a spermatophore and then flips his body to one side so that the female drops onto the spermatophore. In Pleurodeles this tactile courtship from below leads to the male moving ahead of the female, depositing a spermatophore, and then pulling the female over it.

In these animals the courtship behaviour - consisting of rubbing with the hedonic glands - cannot be said to serve the function of making the female responsive in the sense that it does in those species in which the female is free to follow or not to follow the male when he turns away from her to deposit the spermatophore. In Salamandra and Pleurodeles the function of the rubbing behaviour seems to be to stimulate the female in such a way that her cloaca becomes suitably receptive for taking up the spermatophore. The changes that occur in the female's cloaca during the Display phase in Triturus (see Chapter 2) suggest that this is an important function of Triturus display behaviour also.

The variation in sexual behaviour shown by the Salamandrids is related by Salthe to differences in habitat. All four genera in his group three live in lowland areas and in still or slow-moving water. It is difficult to conceive their method of spermatophore transfer being effective in anything but such conditions. The method of Euproctus seems to be an adaptation to life in swift-flowing water, and many of the Group 2 genera live in upland areas, though Salamandra mates on land.

Two other Urodele families, the Plethodontidae and the Ambystomatidae, show essentially the same courtship pattern as the Triturus group of Salamandrids, except that the tail is generally not used for making display movements. Most Ambystomatids mate in water, some of them in mass groups (Anderson 1961, Storez 1969, Spotila and Beumer 1970, Brandon 1970). The male captures the female dorsally, in some species with the hindlimbs, in

others with the forelimbs (c.f. Taricha and Notopthalmus). In one species, Ambystoma gracile, the male lashes the female with his tail while clasping her with his forelimbs, a behaviour reminiscent of that of Taricha (Licht 1969). In all genera the male rubs the female's head with his snout before dismounting and depositing the spermatophore, in many species in response to a nudge from the female. The male then leads her over the spermatophore and she picks it up in a manner similar to Triturus. Most Ambystomatids are lowland species, living in still or slow waters. The Plethodontids show an essentially similar pattern of sexual behaviour but generally mate on land (Organ 1968, Organ and Organ 1968, Salthe and Salthe 1964).

The single European representative of the Proteidae, the blind cave-dwelling Olm Proteus anguinus, has a sexual behaviour very similar to that of Triturus (Briegleb 1961, 1962). The male is territorial and courts any female who enters his territory. He takes up a position in front of her and performs a tail-wagging display. The female responds by nudging his tail and he retreats before her, still tail-wagging, before turning away to begin a spermatophore transfer sequence similar to that of Triturus. This similarity of behaviour leads Salthe to suggest that the Proteids are derived from the Triturus group.

In the most primitive Urodele families, the Hynobiidae and the Cryptobranchidae, fertilisation is external. The female extrudes eggs in sacs which are grasped by the male who fertilises them by covering them with sperm in the form of a milt. An interesting variation on this basic pattern is shown by the mountain stream-dwelling Hynobiid Ranodon in which the male deposits a spermatophore to which the female then attaches her egg sacs.

The spermatophore is shown by all but the most primitive Urodeles and is therefore seen by Salthe (1967) as being one of the first developments in the evolution of the order. Some of the selective pressures that led to the evolution of the spermatophore are possibly reflected in the

advantages that this method of sperm transfer provides. Firstly, it makes internal fertilisation possible, with a consequent reduction in the risk of producing unfertilised eggs. When the eggs are fertilised internally the female can exercise a greater degree of choice of laying site than would be possible if the male had to be present at egg-laying. Thus she can hide the eggs in crevices, attach them to the substrate or, as in Triturus, lay each egg in its own protected site. Another advantage of internal fertilisation is that fertilisation and egg-laying can be separated in time. Many Urodeles live around water whose existence is transitory and some species mate in one wet period and delay egg-laying until the next (McDiarmid and Worthington 1970).

A scheme for the evolution of Urodele courtship behaviours, largely based on that of Salthe, is presented on page 2/94. The first step in this scheme is the evolution of the spermatophore from the primitive milt condition. Salthe considers that the spermatophore evolved primarily as an adaptation for mating in running water, beginning with the external fertilisation such as that seen in Ranodon today. Consequently Salthe considers that ancestral salamanders lived in montane habitats. In view of the other advantages associated with the spermatophore system, one should not exclude the possibility that the spermatophore could have evolved in lowland habitats. From the primitive Ranodon-like situation fertilisation became internal and the spermatophore was transferred during an amplexus. This situation persists in Euproctus. The second Salamandrid group remained montane stream dwellers and employed amplexus from below. From the ancestral montane type Salthe traces three parallel lines of evolution represented by the Plethodontids, the Ambystomatids and the Triturus group of Salamandrids. The general trend in all these groups is towards decreased contact with the female. I have argued above that this trend may represent an evolutionary advance, in that opportunity for female selectivity is increased. In all these groups amplexus is absent at

the spermatophore transfer stage but is retained in most forms in the earlier stages. Triturus represents the extreme of this trend, having lost bodily contact altogether. In the Triturus group and in the Ambystomatids this trend is associated with occupation of lowland habitats and slow or still waters. The Plethodontids are montane dwellers but mate on land and are thought to be secondarily mountain-dwelling, having passed through a lowland stage.

This survey of the sexual behaviour of Urodeles suggests that the first evolutionary step was the adoption of the spermatophore method of sperm transfer. At first this was transferred in a close, prolonged amplexus, which gave way to situations in which the female is increasingly free during sexual behaviour. Triturus represents the extreme result of this evolutionary trend.

Some Wider Comparisons

Among Amphibians, only the Urodeles have evolved the Spermatophore system of sperm transfer. The Caecilians show internal fertilisation and possess intromittent organs; virtually nothing is known of their behaviour (E.H. Taylor 1968). In the Anura, the frogs and toads, fertilisation is external except in some exceptional genera such as Ascaphus (Wernz 1969). Anurans show little complex sexual behaviour; the sexes usually locate each other and signify sexual responsiveness by calls (Duellman 1967, Heusser 1970, van Gelder and Hoedemaekers 1971). Many frogs and toads show territorial and aggressive behaviour (Lescure 1968).

The Spermatophore is not a uniquely Urodele invention, but is present in many arthropods (Schaller 1964) and in some fish groups (Breder and Rosen 1966). The arthropod spermatophore-producers can be graded according to the extent to which there is bodily contact during sexual behaviour (Schaller 1964). In some collembolans the male deposits spermatophores for wandering females to pick up later; some pseudoscorpions show a similar

system (Weygoldt 1969). In the collembolan Podura the male deposits spermatophores and then pushes the female onto them (Schliwa and Schaller 1963). In some amblypigids the male lures the female over the spermatophore by waving his pedipalps (Alexander 1962) and very little bodily contact is involved. In contrast, male Buthid scorpions grasp the female, search for a suitable substrate on which to deposit the spermatophore, and then haul her over it (Alexander 1959). It seems that a number of animal groups have evolved the spermatophore system for sperm transfer, as a means for achieving internal fertilisation in the absence of an intromittent organ. Like the Urodeles, these groups vary in the extent to which bodily contact is involved in spermatophore transfer.

The Motivation of Sexual Displays

In many fishes, birds and mammals sexual behaviour is frequently associated with aggressive behaviour, and the motivation of sexual displays is commonly explained in terms of a conflict between tendencies to flee, to attack, and to mate (Morris 1956, Bastock 1967, Hinde 1970). The usefulness of the Conflict hypothesis has been questioned (Blurton-Jones 1968, Hinde 1970). For example, Andrew has argued that it is more instructive to talk in terms of conflicting behaviour patterns or responses (Andrew 1956), and also that the application of conflict theory to major behaviour systems is misleading, though it may be constructive when applied to small units of behaviour, such as individual postures (Andrew 1972).

Evidence that courtship displays are associated with motivational conflicts comes from the nature of the situation in which they occur, the behaviour that accompanies the display and that which precedes and follows the display, and the form of the display pattern itself (Tinbergen 1959, Hinde 1970).

There is no reason to suppose that newt sexual behaviour is associated

in any way with tendencies to attack or to flee. Aggressive behaviour is absent from the newts' behaviour repertoire, both in general terms and in the context of sexual interactions.

Newts are not unique in this respect; Drosophila also have an elaborate courtship display and are not aggressive. Bastock and Manning (1955) explain the switch from one male behaviour to another in terms of a threshold model which invokes a single internal variable or motivation. In Drosophila a male's sexual behaviour is thwarted if the female fails to respond or if she rejects him. Brown (1964, 1965) has analysed the situations in Drosophila courtship in which a particular wing posture occurs. It is seen most commonly when a persistent male is thwarted by female unresponsiveness.

The question of the motivation of sexual displays in non-aggressive animals has led Bastock (1967) to the broader statement that "courtship displays tend to occur when mating behaviour is simultaneously stimulated and opposed". The opposition may not necessarily take the form of conflicting behaviours such as fleeing or attack but may be any factor that blocks or thwarts further sexual behaviour (Bastock et al. 1953, Manning 1967).

Hypotheses or models relating to behaviour, such as the conflict and thwarting hypotheses, can be said to be useful if they help in the understanding of behaviour. They may be helpful, if used carefully, in describing the situations in which specific displays occur. A more useful application of these concepts is the formulation of testable predictions. Blurton-Jones (1968) tested the conflict theory for the motivation of threat displays in the Great Tit by systematically varying the stimuli that elicit attack and fleeing, and showed that "threat" postures are evoked in artificially created conflict situations. Certain of these postures, but not all of them, are also evoked when attack is thwarted by a physical barrier. Thus Great Tit threat postures are characteristic of situations

in which attack behaviour is thwarted, whether it be by a conflicting behaviour such as escaping or by a physical barrier.

In newt sexual behaviour there is no evidence of any major behaviour pattern conflicting with sexual behaviour, in the way that aggressive behaviour is intimately associated with the sexual behaviour of many fishes and birds. One could invoke a conflict such as approach-withdrawal, since the male is approaching and moving away from the female at different times during sexual behaviour, but this would have little descriptive or predictive value. One could hypothesise that the male's display is associated with thwarted sexual motivation. Those experiments in which a female was held still for prolonged periods could be said to create a thwarting situation. In such situations the male shows persistent display, and, in particular, performs the Wave movement. It could be said, therefore, that the Wave movement is the result of thwarted sexual motivation. In the analysis of newt Display behaviour I have argued that the Wave movement is a response to female immobility. This is a more economical expression of the behaviour in that it describes it in terms of external stimuli and does not invoke an intervening variable such as motivation, and it is, therefore, a more explicit description of the behaviour.

The integration of the behaviours that make up the newt sexual sequence can be understood largely in terms of causal relationships between male and female actions. For the purposes of the present analysis it is neither necessary nor helpful to invoke motivational models to account for the moment to moment changes in the male's behaviour. That motivational factors are important variables affecting the male's internal state is not in dispute; as mentioned at the end of Chapter 3, hormones and sexual deprivation affect sexual behaviour. However, to account for the sequence of behaviours described in this thesis there does not seem to be any good reason to invoke motivational models.

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"Why is it that a snake horrifies us, or even a newt? .... What is it, in our life or in our feeling, to which a newt corresponds? Is it that life has the two sides, of growth and of decay, symbolised most acutely in our bodies by the semen and the excreta? Is it that the newt, the reptile, belong to the putrescent activity of life; the bird, the fish to the growth activity? Is it that the newt and the reptile are suggested to us through those sensations connected with excretion?"

D. H. Lawrence (1914) "Study of Thomas Hardy"